Coral Reefs of the World 9

Covadonga Orejas
Carlos Jiménez *Editors*

Mediterranean Cold-Water Corals: Past, Present and Future

Understanding the Deep-Sea Realms of Coral

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Editors

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to Wolf Isbert for his continuous support in the gestation and completion of this volume.

to Helmut Zibrowius for mentoring and teaching the sorcerer's apprentice into the Mediterranean marine ecology.

Foreword

Spend any time working on cold-water corals and you will quickly find yourself, like the corals themselves, at the confluence of ocean physics, geology, chemistry and biology. This meeting of disciplines is beautifully explored in the diverse chapters of this book where Covadonga Orejas and Carlos Jiménez have carefully selected an impressive collection of contributions spanning the past, present and future of Mediterranean cold-water corals.

The very word Mediterranean derives from the Latin "in the middle of land", and this almost land-locked sea has long fascinated marine scientists. The relatively small volume and rapid overturning circulation patterns of its waters make the Mediterranean an intriguing location to follow the implications of global climatic change from ocean warming to acidification. Its present biodiversity and biogeography reflects the imprint of major climatic changes from the severity of the Messinian Salinity Crisis, when the entire basin was cut from the Atlantic, through to its recolonisation over subsequent millennia. Much later during the last glaciation, while northern latitudes were under ice and the Atlantic's overturning circulation slowed, it is highly likely that the Mediterranean provided refuge for some of the cold-water corals today most abundant in the Atlantic Ocean. Our understanding of this fascinating history is far from complete, but the revolution in our abilities to accurately date fossil coral remains and trace genetic lineages with next-generation sequencing approaches mean the pieces of this complicated jigsaw are gradually being assembled.

The Mediterranean also has a very special place in the history of cold-water coral research. In popular culture the word coral is often linked to the coral jewellery produced since antiquity from skeletons of the Mediterranean precious coral *Corallium rubrum*, a practice that has sadly had severe consequences for today's *Corallium* populations. Linnaeus described the scleractinian *Madrepora oculata* from samples taken from the central Mediterranean and Tyrrhenian Sea and some of the best-preserved fossil reef occurrences of the iconic Atlantic framework-former *Lophelia pertusa* are found on islands like Rhodes and Crete. Indeed, it was until relatively recently that it seemed the Mediterranean no longer supported substantial live cold-water coral reef habitats. At the turn of the twenty-first century I vividly remember the excitement when the Santa Maria di Leuca coral mounds were first discovered in the northern Ionian Sea – reversing the accepted wisdom that the Mediterranean had become a graveyard for living reefs of *Lophelia*, *Madrepora* and *Desmophyllum*.

Thus, the Mediterranean holds a special place for deep coral researchers, particularly those working in the Atlantic. We cannot understand the interconnectivity of today's Atlantic cold-water coral habitats if we do not understand their wider relationships to neighbouring sea basins, especially those that formed important glacial refugia. This book is being published half way through one of the most ambitious attempts to understand deep-water ecosystems, including cold-water corals, at the scale of the North Atlantic Ocean. The European Horizon 2020 ATLAS project (2016–2020) brings together over 120 researchers from Europe, Canada and the USA with the shared objective of producing a transatlantic assessment of deep-water ecosystems and developing integrated ecosystem-based spatial management plans for their long-term conservation and management. It is telling that the second dedicated ATLAS research cruise in 2016 was the MEDWAVES expedition that sailed from the Strait of Gibraltar to the Azores and back again to follow the influence of Mediterranean outflow water on the biodiversity and biogeography of cold-water corals and other key taxa on Atlantic seamounts and offshore banks.

As I write this it is simply fantastic to reflect upon how much has been achieved since the renaissance of cold-water coral research in the Mediterranean began, arguably kick-started with the discovery of the Santa Maria di Leuca coral mounds 18 years ago. We now know so much more about the diversity of Mediterranean cold-water coral habitats from these deep reef frameworks through to the habitats associated with dramatic canyons, mysterious mud volcanoes and beautiful coral gardens of delicate antipatharian and gorgonian corals. We know more about how important they are in the ecology of other species, notably fish, and are starting to really understand how these corals are intimately linked with surface productivity and tight coupling of that primary productivity to supply food via dynamic near-bed currents. We are beginning to reveal just how important the archives locked in the chemistry of coral skeletons will be in helping us to understand past environmental conditions, a resource we badly need to understand as we move further into the Anthropocene and truly unparalleled rates of environmental change.

Huge congratulations are due to everyone involved in this book, a book important not just for the Mediterranean but for cold-water coral researchers across the world.

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January, 2019

J. Murray Roberts

Acknowledgements

This book is an eclectic selection of topics that encompass the knowledge of the past, present and future of the Mediterranean cold-water corals. It draws on the help and time of many people. We are in debt to our families and friends for the many hours stolen from the "theoretical" free-time and weekends with them and for delaying and delaying once again visits and holidays. Thanks to you all for your understanding and continuous support, for your patience and for being there!

We also would like to express our gratitude to Springer for granting their trust in us for this adventure, in particular we would like to express our thanks to Alexandrine Cheronet and Judith Terpos who gave us excellent support and advice during the entire process. Thanks for your enthusiasm and also for being patient and accepting our proposal of the "drop" chapters, and for allowing us as well to introduce a new concept for the book's cover thanks to Autun Purser, who provided us with a stunning drawing. Our colleague Christine Ferrier-Pagès (Scientific Centre of Monaco) had a paramount role in this book concept and its inception, thanks Christine for your trust and support! Also special thanks to Marco Taviani (Instituto di Scienze Marine, Bologna). Marco was one of the main inspirational characters for this book, not only by participating in several chapters but also providing ideas and suggestions all very useful for Carlos and me.

A book of these characteristics cannot be constructed without the help of altruist, engaged, dedicated and very, very patient reviewers, from those we got more than 80 in this project, our biggest thanks go to: Agostina Vertino, Alessandro Cau, André Freiwald, Andrea Gori, Andrea Peirano, Andrés Rüggeberg, Aneleen Foubert, Antonieta Rosso, Branko Velimirov, Bruno Sabelli, Marina Carreiro-Silva, Cheryl Morrison, Claudia Pichler, Claudia Wienberg, Claudio Lo Iacono, Cristina Linares, David Johnson, Dierk Hebbeln, Di Tracey, Eleonora Martorelli, Eric Douville, Ester Serrao, Federica Constantini, Gemma Ercilla, Jarek Stolarski, Jordi Grinyó, José Templado, Juancho Movilla, Jürgen Titschack, Kathleen Roberts, Christina Kellog, Lehne Buhl-Mortensen, Luís Pinheiro, Marco Roveri, Marco Taviani, Marie Claire Fabri, Marín, Marina Carreiro-Silva, Mark Wilson, Marzia Bo, Nadia Santodomingo, Nadine Le Bris, Paolo Montagna, Patric Schembri, Rana Abu Alhaija, Ricardo Aguilar, Ronald Osinga, Sandra Brooke, Sebastian Hennige, Sergio Rossi, Simone Pietro Canese, Sophie Arnaud-Haond, Stephan Ekehaug, Stephanie Reynaud, Thierry Baussant and many more who decided to remain anonymous.

We feel really honoured having the collaboration of Prof. Murray Roberts in this book. Murray Roberts is one of the big names in the cold-water coral research world, a reference scientist in the field, and a very good friend. Many thanks, Murray, for your continuous support and interest in this volume and for being willing to write the foreword.

Frequently, the "helping hands in the shadow" are paramount to conclude a project (for us a big project) like this one. Among these hands, the two from Wolf Isbert were fundamental, especially in the last weeks before finishing the volume. Wolf many thanks for your vital help, support … thanks for being always there!

Finally, we are grateful that we can work in the topic which is also our passion: the sea and its creatures. Carlos and I are enthusiastic coral devotees, and it is a privilege to have the opportunity to explore, discover and investigate these fascinating creatures and habitats. The

privilege is double if the passion can be shared with friends as we have been able to do for this book.

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Contents

Introduction

Part I Past

Part II Present

Part III Future

Introduction

An Introduction to the Research on Mediterranean Cold-Water Corals

1

Covadonga Orejas and Carlos Jiménez

1.1 About this Introductory Chapter

The aim of this chapter is to introduce the history of the deep-sea and specifically living cold-water coral (CWC) research in the Mediterranean Sea, as well as additional topics that the 46 chapters included in this volume provide to the marine researchers interested in this field. The history of CWC research in the Mediterranean begun in the eighteenth century. Several names stand out in the discovery of the Mediterranean CWCs, but without doubt Jean-Marie Pérès has a special place in the tale of the Mediterranean deep living coral communities, being one of the pioneers of the Mediterranean CWC research. The contributions of Pérès and others are highlighted in this introductory chapter, as well as information about some of the most relevant and pioneering deep-sea scientific expeditions and marine laboratories. In addition, the main topics of each full and short ("drop") chapters are succinctly discussed while it is also pointed out that large gaps in the knowledge of Mediterranean CWCs still exist (e.g., reproduction, demography). A number of concepts and definitions identified throughout the process of the compilation of this volume were found to respond to multiple meanings potentially resulting in confusion within the CWC research community and thus warranting clarification. In the last part of this introductory chapter, a short reflection is included on aspects that we consider need further research efforts and discussion, such as the major concern on the future of the CWC habitats in the Mediterranean Sea as a result of previous, current and past anthropogenic activities.

Despite being separated in three sections (Past, Present and Future) the sections often contain elements of the other ones. The time-line perspective provides better ecological understanding of these deep-sea ecosystems.

1.2 Discovering the Mediterranean Deep-Sea Benthos

The image of the Mediterranean as a relatively shallow and warm-temperate sea still prevails in the collective mind. However, this picture does not reflect the reality. In the Mediterranean, deep submarine canyons incise the continental shelf, reaching depths in excess of 2000 m. Abyssal plains are also present in the central parts of the three main Mediterranean basins: western, central and eastern. As is the case for most oceans and seas all over the world, most research in the Mediterranean carried out in the past has also been focused on the shallow areas. Hence, the story of the research of the deep parts of the oceans is still young as the first deep-sea discoveries took place in the middle of the nineteenth century (Gage and Tyler 1992). Among the pioneer explorers of the life in the deep sea, names such as Michael Sars (1805–1869), Edward Forbes (1815–1854) or Sir Charles Wyville Thomson (1830–1882) stand out. The Royal Society of London set the foundations of the deep-sea research by supporting the first, truly deep-sea global expeditions on board the vessels "Lightning" (1868), the "Porcupine" (1869, 1870) and the legendary "Challenger" (1872–1876). At around the same time, Mediterranean researchers, such as Antoine Risso (1777–1845), described the crustacean and fish faunas at depths from 600 to 1000 m. These discoveries provided valuable information against the so-called "azoic hypothesis"[1] by Forbes (1843). However, at

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[1] The azoic hypothesis was proposed by Edward Forbes in 1843. It stated that the abundance and variety of marine life decreased with increasing depth. By extrapolation of his own measurements, Forbes calculated that marine life would cease to exist below 550 m.

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the time, these Mediterranean findings were unfortunately largely overshadowed by the discoveries from John Ross (1777–1856) and his nephew James Clark Ross (1800–1862) from the Antarctic expeditions on board the vessels “Erebus” and “Terror” (1839–1843). In 1861, Edward Milne-Edwards (1800–1885) officially rejected the “azoic hypothesis” after the recovery of a damaged submarine cable from >2000 m depth off Sardinia, which was colonised by dozens of live organisms, mostly molluscs and corals.

Subsequent to these initial discoveries, the Mediterranean deep-sea studies were followed by the expedition on board the vessel “Travailleur” (1880–1882), setting off from the Gulf of Biscay in the Atlantic and making its journey to the western Mediterranean. Later in 1890, the first truly Mediterranean expedition took place on board the vessel “Pola”, and was the first of a series of expeditions across the entire basin. The Prince of Monaco, Albert I, a renowned scientist, supported this expedition, which together with the creation of the Oceanographic Institute in Paris, as well as the Oceanographic Museum in Monaco, at the beginning of the twentieth century were significant milestones in the history of marine research in the Mediterranean. Additionally, the research vessels from the Oceanographic Museum in Monaco, “Hirondelle I” and “Hirondelle II”, as well as “Princess Alice I” and “Princess Alice II”, were fundamental for the development of the marine research in the Mediterranean. At the same time, Danish expeditions on board the RV “Thor” and “Dana”, had also the Mediterranean as a research target (Mavraki et al. 2016). In mid twentieth century, several international scientists played important roles in the Mediterranean basin research, including the deep-sea areas. Among them was Rupert Riedl (1925–2005), who published the most comprehensive guide of the Mediterranean flora and fauna (Riedl 1963). Jacques-Yves Cousteau (1910–1997) is famed for technical advances in the scuba diving, as well as notable scientific discoveries in the shallow and in the deep-sea Mediterranean by pioneering video recordings of the habitats and for the small submarine known as the “soucoupe plongeante” (diving saucer) that opened the gates of information to depths up to -400 m. For the first time, some of the earliest images of CWC inhabiting the deep parts of the Mediterranean Sea were shown to astonished eyes and amazed audiences. While a number of scientists largely contributed to increase the knowledge of the deep-sea benthic realm, four in particular are especially relevant: Jacques Picard (1922–2008), Jean-Marie Pérès (1915–1998), Daniel Desbruyérès and Daniel Reyss. These researchers explored tirelessly the shallows and depths of the Mediterranean. The benthic bionomy of the Mediterranean, by Pérès and Piccard (1964), is still the most comprehensive work closely followed by the one published by Desbruyérès and collaborators (1972–1973) for the French-Spanish continental shelf and by the work on the submarine canyons of the Gulf of Lions by Reyss (1972–73). To our best knowledge these studies were the first to document the presence of live CWCs in the Mediterranean, reports that came from Cap de Creus (Pérès and Piccard 1964) and Lacaze-Duthiers submarine canyons (Reyss 1964).

Corals are normally associated with shallow and warm waters and mostly to the tropical realm. However, CWCs have been described as early as in the eighteenth century; some of the first written records are notes by the Right Reverend Erich Pontoppidan, who was the bishop of Bergen in Norway (Pontoppidan 1755, in Roberts et al. 2009). For readers interested in the geology, biology, but also in the history of the discovery and research of CWCs, we highly recommend “Cold-water corals. The biology and geology of deep-sea coral habitats” by J. Murray Roberts, Andrew Wheeler and André Freiwald (2009).

After the pioneer studies, the CWC research in the Mediterranean proliferated during the 1970s and 1980s. The geological and palaeontological aspects were developed with remarkable contributions of Marco Taviani, Georgette Delibrias and Philippe Bouchet; the taxonomical research was enriched as a result of the comprehensive work by Helmut Zibrowius, and the first attempts to understand CWC biogeography. The 1990s marked the beginning of the biological studies. These were followed by an exponential increase of ecological and physiological studies on CWCs during the first decade of the twenty-first century, for the most part due to the rapid and important advances in technological developments and focus on the European deep-water ecosystems thanks to large European collaborative projects (e.g. ACES, HERMES, HERMIONE, CORALFISH). These advancements allowed the exploration of great depths in the oceans by means of remotely operated vehicles (ROVs), towed cameras, photographic sledges or manned submersibles.

In this volume, we present the current state of the art in Mediterranean CWC research as comprehensively as possible. The structure of the book (Past, Present, Future) provides a “road map” from the paleontological records of CWCs in the Mediterranean, continuing through the research that is currently done in the living CWC communities inhabiting the basin, culminating in the possible future scenarios awaiting this research. The volume contains two different types of contributions, full chapters that are devoted to comprehensive specific topics and reviews, and short chapters (“drops”) consisting of short informative essays on recent findings and focus on very specific topics. A total of 146 authors and approximately 80 reviewers contributed in producing the 46 chapters of the present volume. In the following paragraphs we present an overview of these chapters.

1.3 Mediterranean Cold-Water Corals: An Old and New Story

1.3.1 The Old Story

The information about the Mediterranean CWCs presented here does not refer only to the living communities, but also to their fossil counterparts. Several chapters highlight the important role of the fossil records for the understanding of the past but also of the current state of the Mediterranean CWCs. Marco Taviani and co-workers present a short review on Mediterranean CWC paleoecology, mostly focusing on the submerged locations but also considering land occurrences. Additionally, in his “drop chapter”, M. Taviani bridges the past and present through the elaboration of a research timeline of the Mediterranean CWCs. In the same context, Julian Evans and co-workers highlight in their “drop chapter” the first records of Mediterranean CWCs by Carl Linnaeus (1707–1778), who documented *Madrepora oculata.* Rare observations of living specimens led scientist to believe that the documented Mediterranean CWC assemblages were relics of the flourishing communities that thrived during the Pleistocene. As highlighted by M. Taviani, this view has indeed changed only recently with the exploration and discovery of several CWC sites in the western and central Mediterranean basins.

The CWC communities have inhabited the Mediterranean since at least the Miocene (26–5 million years ago), as discussed by Agostina Vertino and co-workers. Their review on the current state of knowledge on Mediterranean frame-building CWCs and solitary species through geological time is an excellent “sister chapter” of the ones by Giovanni Chimienti and co-workers and José Luis Rueda and co-workers. They describe, respectively, the current biogeographic distribution of the living CWC communities and present day Mediterranean CWCs fauna. Throughout their history, environmental fluctuations and catastrophic events took place affecting the occurrence and distribution of the CWC communities in the Mediterranean. André Freiwald revised in his “drop chapter” one of the fundamental events that occurred in the Mediterranean during the Late Miocene: the Messinian Salinity Crisis. The author gives a brief description of CWC communities before, during and after this major event. A. Vertino and Cesare Corselli highlight in their “drop chapter” the ability of CWC to store historically important climatic information and use fossil records of Mediterranean deep-sea corals to demonstrate the strength of the influence of climatic variations on the distribution and diversity of CWCs during the Quaternary (1.6–0.01 millions of years ago). The importance of fossil CWCs as climatic archives is comprehensively discussed by Paolo Montagna and M. Taviani. By storing information about the changing physico-chemical properties of the surrounding seawater within their aragonite skeleton, scleractinian CWCs can shed light on the past environmental conditions and climatic events. However, to obtain more accurate interpretations, coral skeleton data should be related to the current knowledge on coral physiology, including biomineralisation; this will contribute to a better understanding and interpretation of the geochemical proxies.

Life of any benthic organism is dependent on the currents surrounding its habitat, and this is also the case for CWCs. Michele Rebesco and M. Taviani bring together the climate paleo-archives provided by CWCs and the typical Mediterranean contourite drifts. The authors explore the effects of the bottom currents as well as the role of contourites in the presence of CWCs, highlighting the link between these geomorphological features and the Levantine Intermediate Water (LIW). The LIW seems to be, as it is discussed in other chapters (Nikolaos Skiris and Daniel Hayes and co-workers), a key element for the presence of CWCs in the Mediterranean basin.

For CWCs, the Levantine Basin is one of the regions of the Mediterranean where not enough research has been conducted. This is true for both fossil remains and living communities. Jürgen Titschack presents recent findings on the bathyal coral community in the Aegean Sea including live and fossil records of CWCs, and gives description of the topographic features and reconstruction of environmental conditions in which they were found. Two more Mediterranean case studies, located in the Alborán Sea are presented in the “drop chapters” by Claudia Wienberg and by Dierk Hebbeln. Wienberg’s “drop chapter” focus on the temporal occurrence of CWCs, particularly *Lophelia pertusa* and *M. oculata*. These two species formed coral mounds in the geological past, experiencing a boom since the last deglaciation until the Early Holocene (~10,000 years ago). During this period, a shift in coral species dominance took place with *M. oculata*-dominated CWC communities in the Mediterranean. The author hypothesised that the higher temperature tolerance of *M. oculata* for warmer waters was one of the most important factors for such shift in dominance. Hebbeln describe the impressive seafloor structures formed by CWCs from East Melilla CWC Mound Province with highly variable morphologies and dimensions, discussing the different drivers which might have interacted to generate these astonishing seascapes.

The history described through the chapters dealing with the “old” story is fundamental for the understanding of the past of CWCs, but also for the understanding of today’s state of the Mediterranean CWC communities.

1.3.2 The New Story

The study of the living CWCs of the Mediterranean is still in its infancy and many research fields are yet to be explored and developed. A basic and fundamental aspect when undertaking the study of any living organism is the taxonomy; without taxonomic knowledge the study of the biological and ecological characteristics of the species will be meaningless. In their comprehensive overview of the taxonomy of the Mediterranean CWCs, Álvaro Altuna and Angelo Poliseno include species of the six orders of the phylum Cnidaria (Antipatharia, Scleractinia, Zoantharia, Alcyonacea, Pennatulacea and Anthoathecata) totalling 82 species of deep-sea corals, 13 of which with habitat-building ability at depths of 200 m and below.

The reader might have realised that in the previous sentence the term "deep-sea corals" was used instead of "CWCs", which is the term most frequently used to refer to this group of organisms. This is something we would like to briefly address at this point of this introductory chapter. Through the process of compiling the contributions for this volume, it was recognised that certain concepts and topics were poorly defined or unclear, resulting thus in slightly, and on occasion strikingly, different interpretations between the various chapters. These emerging issues are not necessarily a problem, they can be considered as an interesting and stimulating part of the scientific discussion, flagging the need to revisit some concepts and definitions. This is the case for "CWC" or "deep-sea coral" concepts. Some authors considered both terms as synonyms. Others were, however, inclined to use "deep-sea corals" for the specific case of the Mediterranean Sea due to the fact that the temperatures of the Mediterranean deep-sea areas rarely decrease below 12–13 °C. Altuna and Poliseno dedicated a specific section in their chapter to this issue, presenting the different concepts according to different authors, when using the term CWC. Altuna and Poliseno's chapter was exclusively based on corals occurring below 50 m depth, regardless of whether they are habitat builders or not. In contrast, other authors (e.g. G. Chimienti and co-workers) used the concept of CWC only when dealing with framework-building species. The chapter by Chimienti and co-workers presents a comprehensive review of the current knowledge of the occurrence and biogeography of CWCs across the Mediterranean basin, in the context of oceanography, bottom topography, geographical areas of distribution, as well as the bathymetric ranges. The biogeographical approach of these authors is partially based in the "CWC- province" concept. The term "province" in the context of CWC studies was firstly used in publications from the Atlantic Ocean (e.g., Henriet et al. 1998) as "deep-water reef provinces" or "mound province", and later from the Mediterranean as "CWC province" by Taviani et al. (2011). The difference in interpretation of the "CWC province" concept that appears in the chapters of this volume gives foundation for further interesting and stimulating scientific discussions among researchers, which we believe deserve additional attention and perhaps also a re-formulation and redefinition of the concept. This might prevent subsequent misrepresentations of the real meaning of the word "province" in the biogeographical context. The term "province" was originally coined within the botanical science, and the definitions included in the Dictionary of Ecology, Evolution and Systematics by Lincoln et al. (1998) are: "…1. A major division of the biosphere; 2. A phytogeographical subdivision of a region characterised by dominant plant species of similar past history; 3. A biogeographical zone characterised by a 25–50 percent endemic flora or fauna." Pondering these original definitions, it is worthy to recall for some specifications when using the term "province" in the case of the CWCs. While the definition of "province" in the biogeographical context considers large spatial scales, currently studied areas with CWCs in the Mediterranean exhibit notably smaller spatial extension. Therefore, further discussions are needed when using the term "CWC province" which would take into consideration aspects like spatial scale, dimensions or even distribution patterns of CWCs, in order to distinguish this "province" to the original definition in the biogeographical context.

Generally, most studies on CWCs have been focused on scleractinian corals, remarkably the so-called "coral triad" (Pérès and Piccard 1964): *L. pertusa, M. oculata* and *Desmophyllum dianthus*. However, there are other groups, such as octocorals and antipatharians, which are also ecologically important, forming dense populations and dominating benthic communities. Two "drop chapters" are dedicated to the gorgonian and black coral assemblages found in the deep Mediterranean. Andrea Gori and co-workers present an overview on recent studies investigating the gorgonian and black coral communities inhabiting the deep coastal seafloor and continental shelves, mostly of the western and central Mediterranean, whereas Marzia Bo and Giorgio Bavestrello summarise some of the most recent findings, such as the fundamental role these coral gardens play as structuring communities. Advances in taxonomical knowledge and discoveries of new populations and communities also contribute to increasing information of the CWC biogeography, which is fundamental for generation and improvement of the mapping of habitats populated by these deep-sea communities. In the chapter by Claudio Lo Iacono and co-workers, two of the most researched CWC areas of the Mediterranean are revisited: the Chella Bank (also known as Seco de los Olivos) in the Alborán Sea, and the CWC province of Santa Maria di Leuca in the Ionian Sea. The authors present a comprehensive and integrated study of the environmental characteristics of the benthic habitats. To identify the geological and oceanographic processes, most likely responsible for the CWC distribution and associated benthic communities, habitat mapping is performed using supervised automated classifications, applying a combination of several methodological approaches.

Several of the submarine canyons explored in the Mediterranean are characterised by conditions suitable for settlement and development of CWCs. La Fonera and Blanes canyons are discussed in the chapter by Anna Aymà and co-workers; they describe CWC habitats in the canyons with different dominance of the species, including novel, deep records in the Mediterranean for *D. dianthus*, documented in La Fonera as deep as 1400 m. Further details about La Fonera are given by Galderic Lastras and co-workers in their "drop chapter". The authors describe the features of the communities dominated by *M. oculata*, as well as the results on predictive habitat modelling, showing the extent of the CWC habitats in this canyon. Cap de Creus canyon, located in the Gulf of Lions, is reviewed in the "drop chapter" by Pere Puig and Josep Maria Gili, complementing the information given in the other canyon-themed. The authors present a short overview of the northwestern Mediterranean canyons, where the first CWCs in the Mediterranean were reported.

Other topographic features in the Mediterranean Sea where CWC are known to exist are the fluid-venting submarine structures. Two "drop chapters" describe different aspects of the vents. Desirée Palomino and co-workers highlight the role of mud volcanoes and mud diapirs as habitats for CWCs. Additionally, they describe the typical fauna associated with these features in several Mediterranean locations and briefly summarise the formation processes of these features. Andres Rüggeberg and Anneleen Foubert focus on the origin and the past history of these features, including fossil records, describing the different records of these fluid venting submarine structures in the Mediterranean.

Although the Mediterranean deep-sea is still a largely unexplored realm, the increasing number of explorations owed to current technological developments, is notable. Some of the recently explored deep-sea areas reveal new CWC sites, which are described in several contributions. Leyla Knittweiss and co-workers present the recently discovered CWCs in Maltese waters and Covadonga Orejas and co-workers demonstrate the recent discovery of a *Dendrophyllia ramea* population off Cyprus at about 150 m depth.

The advances in the biological, physiological and ecological fields of Mediterranean CWC species, communities and habitats are presented in an updated and comprehensive manner in several of the chapters. Biology and physiology of scleractinian CWCs are reviewed by Stéphanie Reynaud and Christine Ferrier-Pagès. These authors compare the responses of CWCs to changes of environmental parameters; they consider feeding rates and preferences, respiration, and the role of these organisms in the organic matter fluxes. Knowledge on the biological traits and functionality of the species is fundamental for ecological studies, and to be able to develop and apply management and conservation measures. However, many basic aspects of the CWC biology in the Mediterranean are still unknown. This fact is also reflected in this book and the readers will realise that some fundamental aspects have not been included. This is the case of reproductive and larval biology and ecology. To the best of our knowledge, there is not a single publication dealing with this topic for Mediterranean CWCs. However, this important aspect is summarised by S. Reynaud and C. Ferrier-Pagès, who reviewed literature mostly available for the North Atlantic. Franck Lartaud and co-workers reviewed the studies on the most important aspects of coral growth processes: from skeleton microstructure and crystallography to the different methodologies applied to measure and study CWC growth. The growth process is also discussed at different scales, from colony to reef formation, where environmental factors and their influence on present and future growth scenarios were considered.

Closely related to reproduction processes and growth is the demography of CWC populations. To the best of our knowledge, only scarce literature on this subject is available (but see Gori et al. 2013) worldwide. Lorenzo Bramanti and co-workers provide an introduction to the science of demography, which originated long time ago for the purpose of tax collection and conscription orders. From these origins to animal demography, the review encompasses different methodologies, models and the results for one of the most well studied species in the Mediterranean, the precious red coral (*Corallium rubrum*). Although this gorgonian, considered as quasi-endemic from the Mediterranean, is not a CWC *sensu stricto*, the species reach very great depths and has been recorded down to 1016 m (Knittweis et al. 2016). The lack of demographic models for CWCs in the Mediterranean and elsewhere, is identified as one of the aspects (together with reproduction and larval studies) that needs to be urgently addressed in the incoming research.

Although the collection of contributions in this volume clearly reveal the important advances made in CWC research during recent decades, generally, and in the Mediterranean in particular, society is still unaware of the existence of these spectacular deep-sea communities. Efforts must be made from the scientific side, to transfer knowledge to the general public; reflective thoughts on this topic are presented by Sergio Rossi and Covadonga Orejas in a "drop chapter".

1.4 Cold-Water Coral Structure, Shelter, and Associated Diversity

Bioengineering species (*sensu* Jones et al. 1994), such as CWCs, modify the environment they inhabit, and those places are widely recognised and documented as biodiversity hotspots (e.g., Henry and Roberts 2016). The Mediterranean is not an exception; CWC ecosystems have been comprehensively studied and have a high diversity of associated species, from invertebrates to vertebrates (fish), many of which are of commercial interest. In the chapter by José Luis Rueda and co-workers, an historical background of studies dealing with CWC associated diversity is presented. It includes a comprehensive, up-to-date, and illustrated comparative (with the Atlantic Ocean) overview on the high diversity of associated species of different CWC communities across the Mediterranean Sea. The chapter is structured in subchapters according to different taxa: Porifera, Cnidaria, Annellida, Mollusc, Crustacea, Echinodermata, Bryozoa, Brachiopoda, Teleostea and Chondrichthya. The last two taxa are also discussed in the chapter by Gianfranco D'Onghia. The Mediterranean CWC communities' role as Essential Fish Habitat (EFH) is highlighted, as well as their fundamental function as shelter, feeding and life-history critical habitat for many fish species including several of commercial importance.

The biodiversity hotspot role played by CWC communities not only refers to metazoans but also to microorganisms. This is still an unexplored world; Markus Weinbauer and co-workers, review this research in the Mediterranean, and present the bacterial diversity and biogeography associated to *Lophelia pertusa* and *Madrepora oculata*. In another "drop chapter", Weinbauer and co-workers deal with a specific topic in the same context: the potential role of *Archaea* in the specific case of CWCs, as high abundance of *Archaea* in the abiotic and biotic environment of CWCs is detected.

1.5 Cold-Water Corals, Oceanographic and Geological Past, Present and Future

Life in the oceans cannot be understood without taking into account the oceanographic features, which embed pelagic ecosystems and surround the benthic ones. The CWC communities are not an exception; the understanding of the occurrence of these communities in specific locations is directly related to the water circulation regimes of these areas, which in turn, directly affect the transport and delivery of food to these organisms and their associated fauna. Daniel Hayes and co-workers describe the main features of the circulation and properties of the intermediate water masses of the Mediterranean. The authors review the paramount importance that the LIW seems to play for the presence of Mediterranean CWC communities, which is also discussed by M. Taviani and J. Evans and co-workers in two "drop chapters", among others. Two other contributions deal with specific aspects of the circulation patterns in the Mediterranean and their effects on the CWC habitats. One of the main characteristics of the Mediterranean is the connection to other water masses, notably the Atlantic Ocean, but also to the Black and the Red Seas. Rinus Wortel and Paul Meijer discuss the importance of these connections and the changes which are experienced due to the tectonic activity. The authors discuss the potential effects of those changes on the CWC habitats, as well as revisiting their past history and current evolution. Thus, this complements the discussions regarding the connectivity of water masses and their effects on CWC ecosystems given in other chapters, such as in the one by Joana Boavida and co-workers and in the "drop chapter" by Bella Galil.

Finally, the increasing evaporation in the Mediterranean Sea, together with the decrease of freshwater river discharge leading to a higher net evaporation in the Mediterranean, is discussed by Nikolaos Skliris reviewing the effects of such a strong evaporation on the salinity from the surface to the deep layers of the sea, influencing the LIW and consequently, the occurrence and distribution of CWC habitats.

1.6 Understanding Distribution Patterns and the Mediterranean – Atlantic Link: Studies on Connectivity

The geographical distribution of CWC species is linked to many factors; while some are environmental (e.g. suitability of the habitat, parameters of the water column), others are intrinsic to the biological characteristics of the species. An example of the latter is the dispersal capability of the coral larvae, which together with the oceanographic patterns of the area, will be crucial to allow the dispersion of coral propagules at short or large distances. The small size of planulae and the large dimensions of the oceans and seas make tracking of coral larva virtually impossible. Fortunately molecular analyses provide the means to estimate connectivity between populations at different spatial and/or temporal scales. Boavida and co-workers review the new insights and methodologies dealing with the genetic dispersion patterns of CWCs in the Mediterranean. They also review the present knowledge on this research field and highlight the studies dealing with the connectivity between the Atlantic Ocean and the Mediterranean Sea. Related to this review topic, Anna Maria Addamo presents a specific case study that focuses on *Desmophyllum dianthus*, summarising the most recent and novel information on the molecular ecology, systematics and evolution of this CWC species. There are still many pieces to gather of the complicated Mediterranean CWCs connectivity puzzle. Indeed, as previously mentioned, basic aspects such as reproductive traits have not being studied for Mediterranean CWC species. The environmental conditions are fundamental when tackling the study of species connectivity. The contribution of Matthew Johnston and Ann Larsson brings together both the oceanographic expertise and the knowledge on CWC dispersion; this chapter combines the current knowledge on Mediterranean oceanographic patterns and the existing knowledge on CWC planulae. This topic has been mostly developed in the NE Atlantic, at the large reefs built by *Lophelia pertusa* off the Norwegian margin.

1.7 Approaching the Study of the Mediterranean Cold-Water Corals at Different Scales

An important aspect included in this volume is the current state of methodological approaches developed to study Mediterranean CWC communities. Methodologies vary according to studies: from paleo research to models generated to predict future scenarios, as well as methodological approaches that deal with different physical and temporal scales included in the book. Lorenzo Angeletti and co-workers discuss the use of X-ray Computed Tomography as a useful, non-destructive technique to detect the presence, content and preservation of CWCs in sedimentary cores, facilitating taxonomic identification, recognition of the coral three-dimensional distribution as well as taphonomic aspects. Within the study of the occurrence and distribution of any CWC species mapping is a fundamental aspect – mentioned earlier when commenting the contribution of C. Lo Iacono and co-workers. Mapping is an important approach for any biogeographical and taxonomic study, especially for biological and ecological studies as species can display different adaptations/accommodations depending on the past and present distribution ranges. The chapter by L. Angeletti and co-workers is fully dedicated to the multiscale habitat mapping and the up-to-date technologies devoted to this aim, utilising Mediterranean examples of CWCs.

There is no doubt that image technologies are the most important recent contributions to approach the study of the deep-sea benthic ecosystems in a non-destructive way. The possibility to visualise, count and measure organisms, thanks to georeferenced video recording and the use of scaling elements (e.g. laser pointers), highly increases the possibilities of video footage to be considered among the essential elements in scientific research. Several chapters in this collective volume (e.g. A. Gori and co-workers, M. Bo and G. Bavestrello, L. Knittweiss and co-workers, among many others), present results obtained with underwater cameras. Maia Fourt and co-workers deals with the visual methodological approach and its application in some deep-sea areas in France, specifically the Mediterranean submarine canyons of the Gulf of Lions.

Besides the *in situ* and non-destructive approach of video and photographic cameras, there is a fundamental methodological issue when talking about developing experimental work at the organism level in deep-sea areas. In tropical and temperate shallow areas, *in situ* experimental work is usually feasible using SCUBA equipment which is not feasible in the deep sea. However, some experimental work, using ROVs has been done: stained corals were deployed to study *in situ* growth rates of the corals (see chapter by F. Lartaud and co-workers). The caveat of this type of experimental work on CWCs is that it often needs to take place *ex situ* in research centres, universities or aquaria with suitable facilities and systems. Several chapters discuss the results of experiments conducted in aquaria equipped with the proper infrastructure (e.g. S. Reynaud and C. Ferrier-Pagès, F. Lartaud and co-workers, among others). The contribution by Covadonga Orejas and co-workers aims to be a practical guide/handbook on CWC aquaria research, providing many examples from aquaria facilities working with Mediterranean and word wide CWCs.

1.8 Threats for Cold-Water Corals in the Mediterranean Sea, Conservation Actions and Perspectives

The fate of Mediterranean CWC communities is inexorably linked to environmental and biological factors, as well as to the anthropogenic activities conducted directly in the coral habitats and/or within their vicinity. The decrease of marine resources in shallow waters, due to overfishing, has led to an increased depth range in which the fisheries sector operates, reaching the deep benthic ecosystems where CWCs thrive. To identify and quantify the threats affecting Mediterranean CWCs is a key step to find solutions and develop strategies for proper conservation of these precious habitats, and for sustainable management of the deep-sea fisheries resources. It is important to remember that many Mediterranean CWC habitats have been identified as fundamental for the developmental stages of invertebrates and fish, acting as a nursery for species, many of which are of significant commercial interest. The CWC habitats also constitute feeding grounds or refuge for many species, a topic that is discussed in G. D'Onghia's chapter. A comprehensive review on the threats to CWCs as well as the current situation of the conservation of these ecosystems is presented by Maria del Mar Otero and Pilar Marin. The authors also highlight new perspectives to improve the conservation of these hidden habitats. Besides the direct and mechanical effects of fisheries, which is unquestionably the most important impact currently affecting Mediterranean CWCs, there are also the indirect effects of the anthropogenic activities. Global change is now widely accepted as a fact; the most conspicuous and well-studied effects of global change are warming and ocean acidification (OA), with most research conducted in shallow water environments. During the last two decades, similar studies emerged from the deep-sea realm and most specifically, from CWC communities' research. In this volume, two contributions deal exclusively with the effects of global change on Mediterranean CWCs. Cornelia Maier and co-workers review the Mediterranean CWC research on warming and OA offering also comparisons with results obtained in other areas, whereas Juancho Movilla offers a specific case study focused primarily on the effects of OA in the calcification response of four Mediterranean CWC species. Additionally, S. Reynaud and C. Ferrier-Pagès also highlight the effects of global change on Mediterranean CWCs.

One of the consequences of global change is the spread of non-indigenous species, that is now widely studied in Mediterranean shallow waters. Utilising previous findings and experiences from the Caribbean, Bella Galil tackles the potential effects of non-indigenous species in Mediterranean mesophotic and CWC communities, based on the increasing depth range colonised by non-indigenous species arriving to the Mediterranean through the Suez Canal. The expansion of these species is expected to increase due to global change.

1.9 …Still Much Work to Do

Rapid advances in the research on CWCs in the last two decades guarantee new discoveries and promise exponentially increasing knowledge. Certainly, this knowledge will come with the technological progress made in underwater equipment; however, it also depends on the willingness of governments to finance deep-sea research.

As previously mentioned, to date, reproduction studies on Mediterranean CWC species are completely lacking. The results available from the Atlantic revealed differences in reproductive timing for different geographical regions (e.g., Waller and Tyler 2005; Brooke and Jarnegren 2013). The studies on reproductive traits of Mediterranean CWCs could contribute with further information concerning the reproductive timing, but also the potential influence on CWC reproduction of environmental parameters which are specific for this sea. In species with Atlanto-Mediterranean distribution, such as the ubiquitous *Lophelia pertusa*, knowledge on larval features could also reveal potential differences between conspecifics of both seas. Closely linked to reproductive processes and traits are demographic studies. The chapter on this topic reveals the almost complete ignorance that exists concerning information on CWC population dynamics. It further indicates the need for advances in dating and reproduction studies as well as in software tools to improve the processing of underwater videos – this could enhance the knowledge on this issue. Another useful approach to obtain valuable information would be a continuous monitoring of deep-sea ecosystems; an expensive and challenging approach, although some pioneering examples in the North Atlantic and Pacific Oceans are highly promising. This methodological approach is considered to be fundamental for the understanding of the dynamics of these ecosystems and we are confident that long-term submarine observatories can be deployed in the Mediterranean in the near future. Among the processes, which are still insufficiently investigated globally, is the role of the CWC ecosystems in the geochemical fluxes and carbon cycling. Recently, this gap has also been highlighted for other benthic ecosystems dominated by animals (Rossi et al. 2017). One of the few works conducted on this field in the NE Atlantic revealed that coral communities are hotspots of biomass and carbon cycling along continental margins (van Oevelen et al. 2009). We hope that an increasing number of projects in the Mediterranean will contribute to enhance our knowledge on the functionality of these deep-sea ecosystems in this semi-enclosed sea.

Holistic and seasonal sampling of the deep-sea Mediterranean ecosystems is also needed to better understand the environmental characteristics of CWCs' surroundings, among others, to obtain insights into the Mediterranean CWC trophic ecology. Although several aquaria experiments have already been conducted with CWCs, as well as various studies using stable isotopes (see Carlier et al. 2009; Tsounis et al. 2010; Gori et al. 2015), we still lack sufficient information on the composition of the potential food available in the Mediterranean deep-sea, including differences among the seasons and the potential selectivity of corals for certain prey items.

With regards to other ecophysiological aspects of the Mediterranean CWCs, S. Reynaud and C. Ferrier-Pagès also stress in their chapter the need to gain more knowledge on calcification processes. The current knowledge indicates very different calcification rates obtained for the same species under different environmental conditions. The fact that calcification may also vary with the polyp age demonstrates the need to better understand the influence of the different factors and their synergies on the calcification process. One of the environmental stressors which has already been investigated in Mediterranean CWC communities is OA, and several works (see C. Maier and co-workers in this volume and references therein) revealed the synergic effects of OA and temperature. However, in view of the increasing anthropogenic activities and their impacts on deep-sea ecosystems, studies combining different stressors and its effects on the CWC Mediterranean ecosystems are highly necessary. For instance, local impacts such as high sedimentation levels, which are linked to bottom trawling, drilling and mining activities, should be studied in combination with impacts acting globally or regionally, such as thermal stress or high pCO_2.

Several chapters in this volume revealed that studies on biodiversity have mostly been conducted in the central Mediterranean (see for instance J.L. Rueda and co-workers); which highlights the need to investigate CWC associated fauna in the Mediterranean, notably in the Levantine, and in general in the southern part of the Mediterranean basin.

Furthermore, available biodiversity studies are mostly focused on the megabenthic organisms. Two chapters by Markus Weinbauer and co-workers are dedicated to the microbial communities associated to Mediterranean CWCs. Both chapters highlight the scarce number of studies conducted on microbial communities to date, although available information indicate their very important role in ecosystem functionality, as recently discovered in the "sponge loop" (de Goeij et al. 2013). Even other associated diversity is completely understudied as it is the case for symbiotic relationships, such as mutualism or parasitism in Mediterranean CWCs. Apart from the well-known symbiosis-like relationship between *L. pertusa* and *Eunice norvegica* (Mueller et al. 2013), and some studies conducted in the Norwegian fjords on symbiotic relationships with associated fauna (see Buhl-Mortensen and Buhl- Mortensen 2005), to the best of our knowledge, no works have been published on these topics for Mediterranean CWCs.

The reader will realise that the "Future" section of the book contains fewer chapters than the "Past" and "Present" sections, which reflects the low numbers of studies conducted in predictive models regarding CWC ecosystems. This is also partially attributable to the Mediterranean CWC research where this topic is still in its infancy. To the best of our knowledge, the publication of the first paper on predictive habitat mapping for Mediterranean CWC (Lo Iacono et al. 2018) coincides with the completion of this volume. The chapter by C. Lo Iacono and co-workers presents predictions for the distribution of *L. pertusa* and *Madrepora oculata* in the Cap de Creus canyon (NW Mediterranean). Future basic research will allow the addition of new data to feed predictive models, not only with regard to habitat suitability, but also considering future climate scenarios such as the ones from the Intergovernmental Panel on Climate Change (IPCC). Additionally, further information on species distribution will also enable the performance of species distribution models (SDMs) in Mediterranean CWC ecosystems.

Finally, and this is a general issue regarding deep-sea ecosystems, scientists need to make more of an effort to improve and extend communication with policy makers. The fantastic discoveries made in the last two decades need to be transferred to decision makers. This will promote further research and ensure a rational and sustainable use of deep-sea ecosystems as well as the protection of vulnerable marine ecosystems (VMEs), as is the case for CWC ecosystems.

Several chapters of this book already summarised some of the fundamental functions that these ecosystems play: from the role as hot-spots of associated biodiversity to their function as nursery and refugia for fish and invertebrate species; many of which are of commercial interest. Last but not least, most of the research projects everywhere take place thanks to the citizens. Tax payers contribute to conduct research and hence, as scientists, we are in debt to society as a whole and it is our duty to give our feedback to the general public. Finding the right approaches, words and language to reach people is fundamental to demonstrate the vital role that these hidden ecosystems play in the oceans and thus, their importance and value for us, mankind.

On a final note, a few days before going to press, a taxonomic change occurred of the emblematic white coral *Lophelia pertusa*; the accepted name by WoRMS is now *Desmophyllum pertusum* (Linnaeus 1758).[2] Due to time constrains, it was decided to maintain the former in all sections of the book.

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References

Brooke S, Jarnegren J (2013) Reproductive periodicity of the scleractinian coral *Lophelia pertusa* from the Trondheim Fjord, Norway. Mar Biol 160:139–153

Buhl-Mortensen L, Buhl- Mortensen P (2005) Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 849–879

Carlier A, Le Guilloux E, Olu K, et al (2009) Trophic relationships in a deep Mediterranean cold-water coral bank (Santa Maria di Leuca, Ionian Sea). Mar Ecol Progr Ser 397:125–137

de Goeij JM, van Oevelen D, Vermeij MJ, et al (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. Science 342:108–110

Desbruyères D, Guille A, Ramos J (1972–1973) Bionomie benthique du Plateau continental de la côte catalane espagnole. Vie Milieu XXIII: 335–363

Gage JD, Tyler PA (1992) Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge, 457 pp

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Gori A, Reynaud S, Orejas C, et al (2015) The influence of flow velocity and temperature on zooplankton capture rates by the cold-water coral *Dendrophyllia cornigera*. J Exp Mar Biol Ecol 466:92–97

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[2] Hoeksema, B.; Cairns, S. (2018). World List of Scleractinia. *Lophelia pertusa* (Linnaeus, 1758). Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=135161 on 2018-04-27

Henriet JP, Mol BD, Pillen S, et al (1998) Gas hydrate crystals may help build reefs. Nature 391:648–649

Henry LA, Roberts JM (2016) Global biodiversity in cold-water coral reef ecosystems. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 235–256

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Knittweis L, Aguilar R, Alvarez H, et al (2016) New depth record of the precious red coral *Corallium rubrum* for the Mediterranean. Rapp Comm int Mer Médit 41:463

Lincoln R, Bohshall G, Clark P (1998) A dictionary of ecology, evolution and systematics. Cambridge University Press, Cambridge, 361 pp

Lo Iacono C, Robert K, Gonzalez-Villanueva R, et al (2018) Predicting cold-water coral distribution in the Cap de Creus Canyon (NW Mediterranean): implications for marine conservation planning. Progr Oceanogr. https://doi.org/10.1016/j.pocean.2018.02.012

Mavraki D, Fanini L, Tsompanou M, et al (2016) Rescuing biogeographic legacy data: the “Thor” expedition, a historical oceanographic expedition to the Mediterranean Sea. Biodivers Data J 4:e11054

Mueller CE, Lundälv T, Middelburg JJ, et al (2013) The symbiosis between *Lophelia pertusa* and *Eunice norvegica* stimulates coral calcification and worm assimilation. PLoS One 8:e58660

Pérès JM, Piccard J (1964) Nouveau manuel de bionomie benthique de la mer Mediterranée. Extrait du recueil des travaux de la station marine d’Endoume Bulletin 31. Fasc 47:1–137

Reyss D (1964) Observations faites en soucoupe plongéante dans deux vallées sous-marines de la Mer Catalane: le rech du Cap et le rech Lacaze-Duthiers. Bulletin de l’Institut Océanographique. Fondation Albert I, Prince de Monaco 63:1–8

Reyss D (1972–73) Les canyons sous-marins de la mer catalane le rech du cap et le rech lacaze-duthiers IV - étude synécologique des peuplements de macrofaune benthique. Vie Milieu XXIII:101–142

Riedl R (1963) Fauna und flora der Adria: ein systematischer Meeresfürer für Biologen und Naturfreunde/in der Gemeinschaft von Dr. Erich Abel. Paul Parey, Hamburg, 640 p

Rossi S, Bramanti L, Gori A, et al (2017) Animal forests of the world: an overview. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1–28

Roberts JM, Wheeler A, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334. https://doi.org/10.1017/CBO9780511581588

Taviani M, Vertino A, Lopez Correa M, et al (2011) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603

Tsounis G, Orejas C, Reynaud S, et al (2010) Prey-capture rates in four Mediterranean cold water corals. Mar Ecol Progr Ser 398: 149–155

van Oevelen D, Duineveld G, Lavaleye M, et al (2009) The cold-water coral community as a hot spot for carbon cycling on continental margins: a food-web analysis from Rockall Bank (Northeast Atlantic). Limnol Oceanogr 54:1829–1844

Waller RG, Tyler PA (2005) The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic ocean. Coral Reefs 24:514–522

Part I

Past

Paleoecology of Mediterranean Cold-Water Corals

2

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Abstract

Atlantic-type scleractinian cold-water corals occur in the Quaternary of the Mediterranean basin. Most fossil evidence on-land is Early Pleistocene in age, and occurs in peninsular Italy, Sicily and on some Greek islands, whilst submerged situations are by large late Pleistocene. According to circumstances, the mode of preservation of fossil cold-water coral varies sensibly (from loose corals to micritic limestones) what affects the level of confidence of the paleoecological reconstruction. All known situations point about a bathyal setting for such cold-water coral hosting deposits in the Mediterranean basin, but under many respects the geological record of cold-water coral paleoenvironments is yet largely underworked. Research developments are discussed, with special emphasis on the widespread submarine occurrences which prevail over the on-land cold-water coral legacy.

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Keywords

Cold-water coral · Mediterranean basin · Fossil · Taphonomy · Paleoecology

2.1 Introduction

Understanding the spatio-temporal distribution and functioning of corals inhabiting deep waters is currently a central issue in science because of their value as biodiversity hotspots, ecosystemic services and paleoclimatic potential (Freiwald et al. 2004; Roberts et al. 2006; Armstrong et al. 2014; Robinson et al. 2014; Henry and Roberts 2017; Montagna and Taviani, this volume). These corals are collectively recognised in the literature under the name of deep- (DWC) or cold-water (CWC) corals. Both definitions are somewhat ambiguous, however. Although most such corals are, in fact, established at bathyal depths >200 m, on peculiar situations like fjords they can be found at very shallow bathymetries (Rapp and Sneli, 1999; Försterra et al. 2005; Järnegren and Kutti 2014). On the other hand, these corals are distributed in a temperature range of 4°–14 °C (Freiwald et al. 2009; Roberts et al. 2009) up to 21 °C in the Red Sea (Qurban et al. 2014), what makes the term 'cold' questionable. 'Corals' include cnidarians equipped with mineralised or proteinaceous skeletal parts (Cairns 2007). Conventionally, here we adopt CWC, the term currently enjoying a general acceptance, and restrict our discussion to the sole Scleractinia.

Scleractinians are cnidarians provided with an aragonitic skeleton prone to be fossilised. Comparatively little is published on the paleoecological reconstruction of former CWC environments. As documented by their modern distribution, CWC display a rather patchy distribution in the ocean settling preferentially hard substrates at bathyal depths (Freiwald et al. 2004; Roberts et al. 2006), what partly explains why their overall geological record is scanter than their shallow water counterparts (Cairns and Stanley Jr 1981; Stanley Jr and Cairns 1988; Roberts et al. 2009).

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Fossil extant-type CWC habitats are, in fact, best exposed in contexts where propitious geological situations drive to the uplift of deep-water sediments like compressive scenarios in the Mediterranean or New Zealand (e.g., Squires 1964; Vella 1964; Beu and Climo 1974; Wells 1986; Barrier et al. 1992; Freiwald 2002; Taviani et al. 2005a, b; Titschack and Freiwald 2005; Roberts et al. 2009; Vertino et al. 2014, this volume, with references therein).

Submarine Quaternary CWC are instead relatively common in the ocean (e.g., Ayers and Pilkey 1981; Newton et al. 1987; Taviani et al. 1991, 2007; Wilber and Neumann 1993; Adkins et al. 1998; Frank et al. 2004, 2011a, b; Schröder-Ritzrau et al. 2005; Ross and Nizinski 2007; Wienberg et al. 2009, 2018; Thresher et al. 2011; Douarin et al. 2013). Their preservation ranges from pristine to intensely degraded and bioeroded (Freiwald and Schönfeld 1996; Freiwald and Wilson 1998; Freiwald et al. 2002; Wisshak et al. 2005; Beuck et al. 2007, 2010; Henry and Roberts 2017). Patination by Fe-Mn-oxides is common place whenever CWC got prolonged exposure to seawater (e.g., Mullins et al. 1981; Wilber and Neumann 1993; Taviani 1998; Taviani et al. 2011a). These CWC can even concur to the formation of large to giant coral mounds from the Pliocene onwards (van Weering et al. 2003; Dorschel et al. 2005; Ferdelman et al. 2006a; Kano et al. 2007; Wheeler et al. 2007; Eisele et al. 2008; Comas et al. 2009; Foubert and Henriet 2009; Frank et al. 2009; Thierens et al. 2009, 2013; Wienberg et al. 2010a, b; Henriet et al. 2011; Douarin et al. 2013; Lo Iacono et al. 2014; Raddatz et al. 2014; Wienberg and Titschack 2017).

Because of its geodynamic evolution, the Mediterranean basin is a key-area of global importance where to study past deep-sea biota (Taviani 2002, 2014; Emig and Geistdoerfer 2004). Here, CWC occurrences taxonomically similar to modern counterparts are best known from Neogene to Quaternary sediments located along the Apennine chain in peninsular Italy and Sicily, and on some islands in the Eastern Mediterranean (Di Geronimo 1987; Hanken et al. 1996; Taviani et al. 2005a, b; Titschack et al. 2005, this volume; Roberts et al. 2009; Vertino et al. 2014, this volume; Moissette et al. 2017). By large, those outcrops are of Early Pleistocene age, mostly ascribed to the Sicilian Stage. Late Pleistocene submarine CWC occurrences are instead distributed basin-wide (Zibrowius 1980; Delibrias and Taviani 1985; Taviani et al. 2005a, b, 2011a; McCulloch et al. 2010; Fink et al. 2015).

The so-called 'white corals' *Lophelia pertusa* and *Madrepora oculata sensu* (Pérès and Picard 1964) are still forming at present considerable bioconstructions and accumulations in the Mediterranean basin (Freiwald et al. 2009; Corselli 2010; Taviani et al. 2016; Wienberg and Titschack 2017), thus making this region a significant CWC-carbonate factory (Titschack et al. 2016).

The main architects of extant Mediterranean CWC bioconstructions are the branching scleractinians *L. pertusa* and *M. oculata*. The solitary but often gregarious up to pseudocolonial scleractinian *Desmophyllum dianthus*, genetically almost indistinguishable from the truly colonial *L. pertusa* (Addamo et al. 2016), may contribute substantially to deep-water coral bioconstructions. Other scleractinians such as *Stenocyathus vermiformis*, *Javania cailleti*, *Caryophyllia* spp., and *Dendrophyllia cornigera* often participate to CWC habitats (Freiwald et al. 2009; Vertino et al. 2010; Angeletti et al. 2014; Chimienti et al., this volume; Rueda et al., this volume; Vertino et al., this volume).

A variety of other skeletonised invertebrates, therefore in principle easily fossilisable, co-occurs with the main CWC frame builders among which other cnidarians (calcitic octocorals), molluscs, barnacles, brachiopods, serpulids etc. (Remia and Taviani 2005; Zibrowius and Taviani 2005; Taviani et al. 2009, 2011a; Mastrototaro et al. 2010; Rosso et al. 2010; Sanfilippo et al. 2013; Sartoretto and Zibrowius 2017; Nasto et al. 2018; Rueda et al., this volume).

The occurrence in the Mediterranean basin of extant frame-builders CWC since the Miocene at least has been reported in the literature (Taviani et al. 2005a, b; Vertino et al. 2014). Here we take into consideration only the post-Messinian history as the starting point of the renewed Mediterranean benthic biota (Corselli 2001; Taviani 2003; Sabelli and Taviani 2014; Freiwald, this volume).

The present chapter briefly reviews examples recorded in the literature regarding the paleoecology of Mediterranean scleractinian CWC (Fig. 2.1) with emphasis on the submerged occurrences, and provides hints on current and future research.

2.2 Cold-Water Coral Paleoecology

According to the definition of Brenchley and Harper (1998) 'Paleoecology attempts to discover and elucidate the life habits and relationships of fossil organisms to each other and their surrounding environments'. This goal can be partly achieved by classical paleoecological reconstructions that are aptly based upon the organisms' ecological requirements (Ager 1963). In practice, paleoecology is continuously evolving by gaining advantage of emerging disciplines, improving technologies and methodologies, and by constantly introducing new questions (e.g., Birks 1985, 2008; Hunter 1998; Allmon and Bottjer 2001; Seddon et al. 2014; Smiley and Terry 2017).

As discussed in the present review, the literature considering CWC paleoecology is comparatively scant, reflecting the paucity of outcropping evidence and the relative inaccessibility of the submerged occurrences. Yet, the published studies contemplate both classical and frontier approaches.

Fig. 2.1 Map of the Mediterranean region showing major sites mentioned in the text: yellow circles correspond to outcrop occurrence, white circles to submarine occurrences: (1) Sicily-Calabria; (2) Rhodes-Karpathos; (3) Alboran Sea; (4) Balearic Islands; (5) Tuscan archipelago; (6) Sardinia Channel; (7) Strait of Sicily; (8) Malta Escarpment; (9) northern Ionian Sea; (10) Santa Maria di Leuca; (11) Southern Adriatic; (12) Crete; (13) Hellenic Trough

The CWC habitats are inhabited by a variety of organisms of highly different fossilisation potential. Organisms equipped with mineral parts typically have higher chances to be preserved in the fossil record than soft body ones. The geological survival of fossils depends upon a number of circumstances, and also durable mineral parts are exposed through time to profound alterations up to their total dissolution, biasing the reconstruction of former communities and from there extrapolating past environments. The complex multi-facet filtering action of taphonomic and diagenetic processes at the expense of a CWC community starts immediately *post-mortem*.

2.2.1 Early Taphonomy

Freiwald and Wilson (1998) have documented how complex and multistage are the early taphonomic processes affecting a CWC habitat. As testified by their study of the Sula Ridge CWC complex off Norway, early taphonomic processes encompass the formation of a biofilm and fungi over dead *Lophelia* skeleton, propitious to the precipitation of the oxide patina and then the biofouling by a variety of invertebrates as serpulids, brachiopods, foraminifers and bryozoans. Later taphonomic stages are documented by an increase of sponges and bioerosion. One implication is that a CWC setting may experience many ecological turnovers on a relatively short time-span (centuries to millennia), at times leaving a legacy beyond in the form of body fossils and/or biological activity (traces, borings, scars etc.) suitable to be fossilised.

2.2.2 Diagenesis

The main engineers of CWC habitats are frame-building scleractinian corals which are aragonitic and thus prone to easier *post-mortem* dissolution than, for example, co-occurring calcitic skeletons. The drilling of the giant Pleistocene Challenger Mound in the north Atlantic (IODP 307) has provided a first-hand opportunity to evaluate CWC aragonite loss before late burial alteration and lithification take place. Frank et al. (2011b) hypothesise that the observed selective aragonite dissolution (grain corrosion and fragmentation) is caused by the corrosive action of undersaturated pore waters, formed in response to organic matter oxidation. This process reverberates on the final preservation of aragonite allochems (such as CWC) and delay at the same time the lithification. It could thus bias the final fossil record and potentially the paleoecological assumptions. Although, independently by taxon, all CWC scleractinians are aragonitic, it is likely that their relative preservation potential in face of diagenetic processes varies according to their specific skeletal microstructure and microarchitecture. This aspect, best documented thus far for fossil shallow-water coral reef scleractinians (e.g., Dullo 1987), may be equally valid for CWC and thus needs to be explored since it bears on the ultimate correct paleoecological reconstruction.

2.3 Mode of Fossil Cold-Water Coral Occurrence

The reconstruction of CWC paleoenvironments needs to take into account some specific contour aspects regarding their preservation mode. The approach differs noticeably if fossil CWC are (i) hosted in loose sediment, (ii) plaster rocky substrates or (iii) are embedded in limestone. All such situations are known to occur both in subaerial outcrop and under submerged conditions, and mixed situations are commonplace. Regarding outcrop evidence of the Mediterranean basin, these situations are best met in the Pleistocene CWC record of southern Italy, mostly in northeastern Sicily and Calabria (Barrier et al. 1989; Vertino 2003; Vertino et al. 2013, this volume; Taviani, this volume, with references therein), and on the Greek islands of Rhodes and Karpathos (Titschack et al. 2005; Moissette et al. 2017). Besides these two areas, records of fossil extant CWC are quite sporadic (Montanaro 1931; Placella 1980; Spadini 2015).

In the case of CWC associated with unlithified sediment, individual components, that are often reasonably well preserved within a clay matrix, could be extracted for taxonomic identification and are also available to refined taphonomic assessment (mineralogy, bioerosion, etc.). In principle, this CWC preservation is ideal for quantitative analyses based upon standard volumetric sampling.

We discuss below only the modern literature that approaches, at a various degree of deepening, paleoecological aspects of CWC-bearing deposits. No reference is made at the historical bibliography on fossil extant-type CWC, which can be found in Taviani et al. (2005a, b) and Vertino et al. (2014).

2.3.1 Outcrop

2.3.1.1 Cold-Water Corals Hosted in Loose Sediment

Placella (1979) comments upon the CWC fauna from Archi (Reggio Calabria) containing *Lophelia pertusa* among other deep-sea scleractinians. The author estimates a paleodepth between 1000–1500 m based on the modern distribution of scleractinian corals and temperature up to 11 °C using *Madrepora* as an actualistic example. Ruggieri et al. (1979) report the occurrence of a fauna that includes *L. pertusa* and *Madrepora oculata* in the Pleistocene of Primosole (Siracusa, Sicily) as one of the supporting evidence pointing at bathyal conditions at the time. Di Geronimo (1979) describes a highly diverse Pleistocene bathyal fauna at Valle Palione (Catania, Sicily) containing, among other invertebrates, the 'white corals' *L. pertusa*, *Madrepora* aff. *oculata*, and many other scleractinians such as *Desmophyllum dianthus* (as *D. cristagalli*), *Caryophyllia* spp., *Javania eburnea* (= *J. cailleti*), *Stenocyathus vermiformis*, *Enallopsammia scillae* etc. The quantitative approach based upon the collection of a standard volume of 1 dm^3 of marly sediment is basically limited to the study of the microfauna. With the exception of a single volumetric sample of 3 dm^3 from a sedimentary infilling, the whole of the macrofauna (which includes the CWC) was instead handpicked as seen. The Valle Palione fossil fauna is compared to living habits of extant organisms in the Atlantic and Mediterranean according to the bionomic scheme proposed by Pérès and Picard (1964). Valuable environmental attributes of these Pleistocene communities (trophic structure, salinity, temperature) have been thus derived through this actualistic approach. The Pleistocene succession of Punta Mazza, Capo Milazzo (Sicily) hosts a corallofauna which comprehends small, though frequent, fragments of the colonial *M. oculata* and *E. scillae*, presumably originally attached to pebbles of the underlying conglomerate layer described by Fois (1990). The marly sediment is dominated by soft-bottom solitary corals, such as *Balanophyllia cellulosa* inhabiting at present circalittoral to epibathyal environments of the Mediterranean. The Punta Mazza coral-bearing deposit has been interpreted by Vertino (2003) as to represent an epibathyal setting.

Colella and D'Alessandro (1988) propose that the presence of *L. pertusa* and *M.* aff. *oculata* branches and other megafauna in the Pleistocene megabreccia topping the Monte Torre succession (Calabria) is due to sediment gravity flows, likely in a paleostrait context. These authors report also a third species of extant colonial CWC, *Solenosmilia variabilis*, but this proved to be a misidentification of a misshapen *Lophelia* (Zibrowius 1991).

Pleistocene CWC-bearing deposits also occur on the island of Rhodes (Titschack and Freiwald 2005). Here, *L. pertusa* branches embedded in marly sediment at the Lardos SW Hill site are interpreted by Titschack et al. (2013) as representing a displacement of these corals due to a debris flow in a 'blind' paleocanyon setting. Bromley (2005) produced a comprehensive evaluation of the bioerosion of *Lophelia* branches in the Pleistocene Lindos Bay clay. Some 18 different ichnotaxa have been identified, referred to the activity of boring fungi, polychaetes, sponges and phoronids, attachment scars attributable to foraminifera, brachiopods and bivalves and gnawing marks due to echinoids.

2.3.1.2 Cold-Water Corals Plastering Hard Substrates

Published examples of fossilised CWC plastering hard substrates (such as hardgrounds) are only a few and those are often associated or interspersed with mobile bottoms.

Barrier et al. (1996) describe one such occurrence in the Pleistocene of Lazzàro (Calabria) where individual boulders lay onto clay sediments at the base of a paleoescarpment.

Boulders are fouled by the deep-water scleractinians *L. pertusa*, *M.* aff. *oculata*, *E. scillae*, *D. cristagalli* (= *D. dianthus*), *Caryophyllia sarsiae* and other co-occurring organisms (bivalves, barnacles, octocorals etc.). The paleoecological reconstruction based upon field evidence and the fossil assemblages of both clay sediment and boulders, envisages a bathyal setting at the foot of a submarine escarpment where coral growth was suddenly stopped by rapid silting. A similar situation has been observed at Vallone Catrica, Calabria (Di Geronimo 1987) and in Sicily at Capo Milazzo, San Filippo and Camaro where isolated boulders, presumably fallen from paleocliffs, were exploited by CWC and, in some cases, deep-water giant oysters (Vertino 2003; work in progress). The case-study analysed by Di Geronimo et al. (2005) at Furnari (NW Sicily) is rather interesting and somewhat unique, combining the encrustation of a lithified steep substrate (possibly a former hardground) along a fault plane with the loose infilling within fissures by clayey sediment rich in CWC rubble and a quite diverse associated benthic fauna. The proposed paleoecological reconstruction calls for a situation where the steep substrate was originally settled by CWC, whose basal parts can be still found attached to it and detached remains are now found in the adjacent clayey sediment and fissures.

Early Pleistocene hardgrounds and carbonate surfaces encrusted by extant CWC have been identified by Moissette et al. (2017) on the Sokastro islet and at Levkos, Karpathos islands, Greece. The corallofauna comprehends species requiring hard substrate to settle as well as others living in the sediment. These authors list a number of colonial and solitary scleractinian CWC (*L. pertusa*, *M. oculata*, *Enallopsammia* sp., *Dendrophyllia cornigera*, *D. dianthus*, *S. vermiformis*, *Flabellum alabastrum*, *Caryophyllia sarsiae*, *C. smithii*), as well as isidid corals (*Keratoisis* sp.), *Corallium* sp., molluscs, barnacles, serpulids and bryozoans. Based upon the benthic assemblage, containing not only 'white corals' but also characteristic cirripeds (*Pachylasma giganteum*) and bivalves as the giant deep-sea oyster *Neopycnodonte zibrowii* (see Wisshak et al. 2009) and the large limid *Acesta excavata* (see López Correa et al. 2005), these authors reconstruct an upper bathyal paleoenvironment at an estimated paleodepth of 400–600 m with bottom temperatures cooler than today.

2.3.1.3 Cold-Water Corals Embedded in Limestones

Limestones embedding CWC may show advanced diagenetic processes that could obviously mask primary morphological features preventing coral identification. This holds true for aragonitic scleractinians prone to partial to total dissolution. In the latter case, coral identification is still possible if the fine grain-size of the embedding sediment allows the preservation of the coral outer wall micromorphology (cf. Vertino 2003; Stolarski and Vertino 2007). Several Pleistocene CWC outcrops of northeastern Sicily are considered by Vertino (2003) and Vertino et al. (2013) that provide paleoecological information. Some of the coral-dominated limestones in the surroundings of Messina, are interpreted as bioconstructions in place or as extensive coral rubble aprons (Vertino work in progress). In particular, the succession at 'La Montagna' contains extant CWC whose preservation ranges from almost pristine, and embedded in a semilithified matrix, to partly or completely dissolved up to leave only vugs or molds (Vertino 2003; Vertino et al. 2013). In the view of Barrier et al. (1985), the succession was a large submarine dune to account for bed thickness and presence of mega cross-bedded basal deposits. Titschack et al. (2008) and Vertino et al. (2013) consider the option that La Montagna is, at least partly, a former CWC mound since coral fragments are often large and their abrasion low, suggesting a parautochtonous source instead than intense bottom-current reworking solely. These authors envisage a depositional model that combines an initial submarine-dune phase, then followed by *in situ* accretion with corals baffling sediment and further creating lithified substrate to following growth through early diagenetic processes.

Information that could turn useful in evaluating paleoecological aspects may be derived also by partially or totally dissolved CWC in limestones, through opportune 'recovery' techniques such as molding or microtomographic imaging.

If CWC-bearing limestones are highly lithified, taxonomic and paleoecological information (including presence of symbionts, boring traces, etc.) must be derived from the study of polished and thin sections. A case in point are the Pleistocene limestones containing *L. pertusa*, *M. oculata* and *D. dianthus* reported from Rhodes (St. Paul's Bay limestone) that have been analysed by Titschack and Freiwald (2005). By integrating field evidence, CWC ecological requirements and microborings, Titschack and Freiwald (2005) reconstructed a cliffed rocky environment for the St. Paul's Bay limestone, characterised by the presence of hardgrounds, debris flows and Neptunian dykes in a depth range of 300–500 m. Interestingly, Titschack and Freiwald (2005) present in their study an ecological detail of these ancient CWC habitat clearly pointing out at the presence of the commensal polychaete *Eunice* (Roberts 2005), based upon a thin section of its calcified tube.

Other examples of CWC-Pleistocene limestones, hosting *D. dianthus*, as well as the deep oyster *N. zibrowii*, occur at Punta Gamba di Donna, Punta Milazzo, Sicily (Rosso et al. 2013), but their paleoecology has not been studied in any detail to date. A Pleistocene *Desmophyllum*-limestone interpreted as a representing a paleocliff encrustation at bathyal depths is illustrated by Di Geronimo (1987: Pl 3 fig 4) from the Pleistocene of Vallone Catrica, Calabria. Part of the paleobiological CWC record from the Sokastro islet site also belongs to this category (Moissette et al. 2017, figures 3 and 4).

In summary, the main paleoecological outcome of many published contributions related to outcrop evidence is the reconstruction of the former bathymetry and paleocommunity taxonomic composition. Because of the relatively wide vertical distribution of *L. pertusa*, *M. oculata* and *D. dianthus* in the Mediterranean and elsewhere in the ocean, any paleobathymetric interpretation cannot provide a strict figure but only a range. Noticeably, already Seguenza (1864) correctly understood that the fossil coral fauna from the surrounding of Messina (southern Italy) was of considerable depth, notwithstanding the scarce knowledge on deep-sea ecosystems at that time (Taviani, this volume; Vertino et al., this volume).

In this respect, the reconstruction offered by Di Stefano and Longhitano (2009) of a Pleistocene paleo-strait deposit containing CWC fossil fauna in the Peloritani chain in the Messina area (La Montagna, San Filippo and other classic successions) as formed in a tidal setting is rather difficult to understand. These authors hypothesise, in fact, that deposits containing only deep-water species, including *L. pertusa*, *M. oculata, E. scillae*, *D. cristagalli (= D. dianthus*) and typical bathyal species from other taxonomic groups, formed in a shallow-water context under enhanced water turbidity, disregarding the ecological incongruence embodied by CWC.

At any event, the presence of these deep-water corals and associated fauna has been sufficient to provide a robust support to geodynamic reconstructions, such as the strong uplift of the (paleo) Messina Strait margins in eastern Sicily and southwestern Calabria (e.g., Barrier et al. 1986, 1990, 1992; Montenat et al. 1987).

2.3.2 Submarine Occurrences

Pre-modern CWC are widespread in the Mediterranean basin (Delibrias and Taviani 1985; Taviani et al. 2005a, b; McCulloch et al. 2010; Margreth et al. 2011; Fink et al. 2015), and are often degraded and patinated if exposed to the seafloor (Blanc et al. 1959; Hersey 1965; Selli 1970; Bellaiche et al. 1974; Zibrowius 1981; Remia and Taviani 2005; Gamberi et al. 2006; Rosso et al. 2010; Angeletti and Taviani 2011; Sartoretto and Zibrowius 2017). Extensive U/Th-dating has documented that they are mostly of middle to late Pleistocene covering ages from ca 480 kyrs up to the Holocene, although most dates are post-Last Glacial Maximum (McCulloch et al. 2010; Fink et al. 2015).

Deep-water settings, especially on sloping topography and under the influence of bottom currents, can be the site of a complex process of submarine lithification of the muddy sediment ultimately ending into a hardground (Noé et al. 2006; Rebesco and Taviani, this volume). As for the open ocean, more or less advanced micritisation and subsequent oxide patination are commonly observed in the Mediterranean Sea (Bernoulli and Mc Kenzie 1981; Biju-Duval et al. 1983; Allouc 1990; Remia et al. 2004; Toscano and Raspini 2005; Conti et al. 2013). Cold-water corals are found embedded into hardgrounds (Taviani and Colantoni 1984; Zibrowius and Taviani 2005; Vertino et al. 2010; Angeletti and Taviani 2011; Taviani et al. 2011a), and this may result conservative of the corals (Fig. 2.2), including their original mineralogy by subtracting them at the action of aggressive waters. The hardground itself is an ideal surface for CWC settling (Fig. 2.3), together with other encrusting fauna (Taviani et al. 2005b, 2010, 2011a, b, 2016; Freiwald et al. 2009; Rosso et al. 2010; Angeletti et al. 2014; Sartoretto and Zibrowius 2017). Ecological turnovers are to be expected on a surface exposed for a while in the water column, as often documented by encrusters at different degree of preservation and patination (Fig. 2.2). The temporal discrimination among the settlers of even a single surface would not be possible if not assisted by multiple dating of individual skeletons.

Overall, the main difference from outcrop deposits is that by large these coral communities and associated organisms have never been exposed to taphonomic processes under subaerial conditions, above all leaching by meteoric waters or precipitation of non-marine cements. Thus, with respect to outcrop situations (see Sect. 2.3.1), the mode of occurrence of Late Pleistocene submarine Mediterranean record includes CWC either “Cold-water corals hosted in loose sediment” or “Cold-water corals plastering hard substrates” while the case of “Cold-water corals embedded in limestones” should be considered rather uncommon. This submarine record is quite important for a better assessment of on-land situations because, apart for the poorly-fossilisable components, its fossil legacy is intrinsically close to the original ecological situation since less affected by later, often destructive diagenetic processes. Furthermore, it permits in many cases to precisely date individual components to disclose with confidence subtle ecological turn-over through time, what is at present almost impossible for the time-averaged and undatable Early-Middle Pleistocene and older situations.

In the past, subfossil CWC have been routinely obtained through heavy geological dredges operating on structural highs such as seamounts or escarpments (Selli 1970; Bellaiche et al. 1974; Cita et al. 1979; Taviani and Colantoni 1984; Allouc 1987; Taviani et al. 2005a, b, 2011b; Zibrowius and Taviani 2005; Gamberi et al. 2006, with references therein). For long the modest optical resolution offered by research submersibles did not permit any refined paleoecological appreciation from *in situ* images (see, for examples, the images in Allouc 1987). Thus, paleoecological information was derived for a while by the qualitative inspection of dredged samples examined in the laboratory. An exception is the study by Zibrowius (1981) based upon the Cyana manned submersible and reporting over the subfossilised benthos

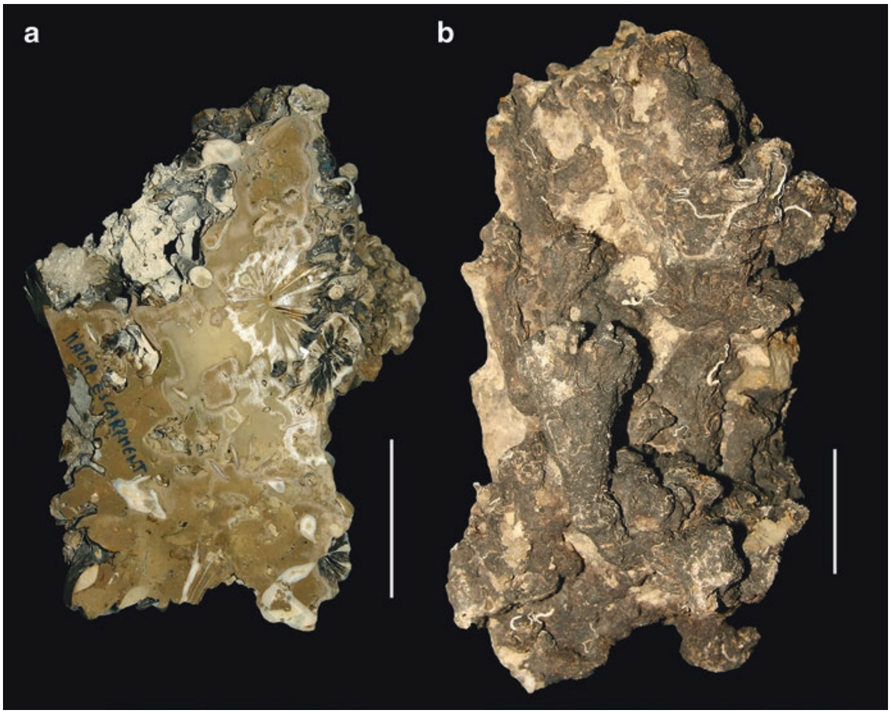

Fig. 2.2 Examples of preservation of fossil CWC from submerged situations in the Mediterranean Sea: (**a**) polished section of a micritic limestone embedding the solitary scleractinian *Desmophyllum dianthus*; external surface patinated by Fe-Mn oxides: Malta Escarpment, ca. 2000 m depth, bar = 5 cm; (**b**) CWC-bearing framestone with large *D. dianthus* coral welded to the surface, observe patination and later encrustation by serpulid polychaetes; northern Ionian Sea (39°03′ N – 18°54′E), 1200 m depth, bar = 5 cm. (Photographs: a, b: © ISMAR-CNR Bologna)

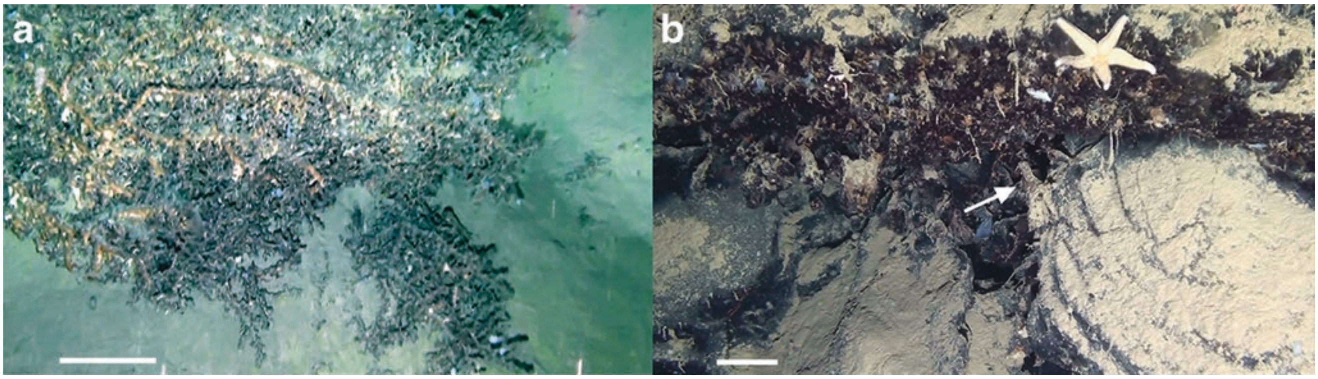

Fig. 2.3 Examples of CWC situations versus coring: (**a**) A loose CWC-canopy partly buried in mud could be targeted for gravity or box-coring; Nora Canyon, Sardinia Channel, −420 m, bar = 20 cm, (**b**) precipitous topographies exposing CWC on hard bedrock are unsuitable to coring, but a paleoecology analysis could be performed through Dohrn Canyon, Gulf of Naples, −390 m; bar = 2 cm. (Photographs: a, b: © ISMAR-CNR Bologna)

(scleractinians, serpulids), inclusive of Atlantic-type CWC, encrusting patinated hardgrounds from the Hellenic Trough. Taviani and Colantoni (1979) analysed the co-occurrence of subfossil *Lophelia, Madrepora* and *Desmophyllum* together with the large bivalve *Lima excavata* (= *A. excavata*) and the corallivorous gastropods *Coralliophila lactuca* (= *C. richardi*) and *C. lamellosa* (= *Hirtomurex squamosus*) in taphocoenoses dredged in the Strait of Sicily and Balearic Sea between 300 and 700 m. In absence of any dating and on the basis of the ecological consistency represented by the frequent and intimate association of such CWC and molluscs at present (see López Correa et al. 2005; Taviani et al. 2009), and of their present distribution in the north Atlantic Ocean, the authors speculate that those taxa participated to former ‘white coral’ communities that inhabited the glacial Pleistocene Mediterranean at temperatures not exceeding 10.4 °C. Taviani and Colantoni (1984) described a Last Glacial fossil assemblage recovered by dredging the Malta-Siracusa escarpment at depths below 2000 m, and characterised by the co-occurrence of the CWC *D. cristagalli* (= *D. dianthus*) and the pectinid *Delectopecten vitreus*. Fossils are embedded within a Fe-Mn-oxide patinated micritic limestone which plasters cliffs of the escarpment. Originally interpreted by the authors as representing a single fossilised biocoenosis, it is instead likely that the bathyal pectinids settled over and inside dead *Desmophyllum* calices, therefore at later stage of colonisation of the substrate. In fact, *D. vitreus* is often but not exclusively associated with fossil (Barrier et al. 1996; Sartoretto and Zibrowius 2017) and recent CWC habitats (Mastrototaro et al. 2010; Panetta et al. 2010; Taviani et al. 2011a).

Manned submersible surveys in the Stoechades Canyon off the Provence coast of France recently documented that cliffs and large boulders between 1700–220 m appear intensely fouled by subfossil black-patinated *D. dianthus*, *C. sarsiae* and *J. cailleti*, plus a number of associated invertebrates such as serpulids (*Neovermilia falcigera* and *Filogranula stellata*), molluscs and octocorals (Sartoretto and Zibrowius 2017). The age of this thanatocoenosis is unknown but, in all likeness, (late?) Pleistocene in analogy with comparable situations in the Mediterranean Sea as the Malta-Siracusa escarpment case-study mentioned above. The case-studies recorded by Taviani and Colantoni (1984), Zibrowius (1991), Taviani et al. (2011a); Sartoretto and Zibrowius (2017) corals plastering hard substrates" and, partly, incipient stages of "Cold-water corals embedded in limestones" categories discussed in the 2.3.1 section.

Late Pleistocene *Madrepora*-dominated reefs occur between 355–410 m offshore the Tuscan archipelago in the Tyrrhenian Sea. Remia and Taviani (2005) describe coral carbonates, part of which oxide-patinated, providing some paleoecological hints. The framestones embed shells of benthic invertebrates like molluscs (coralliophiline and limpet gastropods) and brachiopods (*Megerlia truncata*, *Gryphus vitreus*) consistent with CWC habitats (cf. Taviani et al. 2017). The subfossil CWC frames display also the presence of *Eunice* encalcified tubes denouncing the former presence of this commensal polychaete in the Pleistocene reefs, and ichnologically diagnostic scars and pitting documenting the activity of brachiopods (*Novocrania anomala*) and attached foraminifera, respectively. This case-study (as most of CWC core-evidence, see below) attains at the "(i) Cold-water corals hosted in loose sediment "category discussed in the 'Outcrop' section.

Based upon remotely operated vehicle (ROV) images and bottom samples, Rosso et al. (2010) recognised six 'thanatofacies' at the Santa Maria di Leuca CWC province in the Ionian Sea, established on skeletonised components shed by calcifying organisms. Although not *per se* a real paleoecological study s.s., this exercise has the value to provide snapshots on *post-mortem* CWC-related assemblages formed in a relatively short time span. As introduced before, this kind of information may assist interpretation of time-averaged situations seen in outcrop, difficult to unravel since evidence beyond radiometric dating techniques.

Angeletti and Taviani (2011) reported the peculiar case, from the South Malta CWC province at ca. 680 m water depth, of subfossil Holocene CWC frames (*Madrepora* and *Lophelia*) entrapping shells of corallivorous gastropods (Muricidae-Coralliophilinae, Architectonicidae). The coral frame acted as a taphonomic trap to rare cnidarian-predatory organisms ecologically coherent with a CWC habitat. The final preservation of both corals and molluscs was then enhanced by early submarine lithification and patination.

2.3.3 CWC in Sediment Cores

As seen before, most previous work on submerged CWC sites dealt with hand-samples, often recovered through poorly positioned geological dredging, and at a considerably lesser degree, observation by manned submersibles. The technological and scientific advancement in the exploration of the deep brought a breaking novelty in the field of CWC paleoecology, which is coring.

Cold-water coral grounds are intrinsically difficult to core for the following reasons: (i) They are often located at rocky sites where the predominant substrate discourages any coring attempt, (ii) they may be located on precipitous almost vertical topographies unsuitable to coring, (iii) they may be partly lithified posing a problem to traditional (piston, gravity) coring, (iv) they may be very reduced in size and difficult to locate without visual inspection, making useless random coring, (v) their texture could be very intricate making a coral canopy unsuitable to easy coring (Fig. 2.3).

These caveats and the little interest around CWC until 20 years ago explain the virtual lack of coring documentation for long. Among the few exceptions is the pioneer work by Ayers and Pilkey (1981) on CWC grounds off the US eastern Atlantic margin. Improved mapping techniques (such as multibeam), direct bottom inspection through TV-equipped devices (for example, large box-corer), the assistance provided by ROV in selecting best potential sites, the availability of aptly drilling vessels and new coring techniques (for example MeBo: Freudenthal and Wefer 2007) have disclosed new horizons in the study of CWC by achieving georeferenced successions with their original stratigraphy. Thus, since the mid '90s the scenario has changed considerably and coring (piston, gravity and box) is routine on most research conducted on Atlantic (Dorschel et al. 2005; Rüggeberg et al. 2007; Hebbeln et al. 2008, 2009; Wienberg et al. 2009, 2010a, b, 2018; Frank et al. 2011a; Freiwald et al. 2011; Van Rooij et al. 2011; Douarin et al. 2013; Vandorpe et al. 2017) and Mediterranean CWC (Malinverno et al. 2010; Freiwald et al. 2011; Margreth et al. 2011; Fink et al. 2012, 2013, 2015; Douarin et al. 2014; Titschack et al. 2016; Dubois-Dauphin et al. 2017).

To this, it must be added the successful drillcoring off Ireland of the Challenger Mound (Belgica Mound Province, Porcupine Seabight) during Expedition 307 of the Integrated

Ocean Drilling Program (IODP). A total of three holes (U1316, U1317, U1318) recovered a long record reaching down to the upper Pliocene (Ferdelman et al. 2006b; Kano et al. 2007; Thierens et al. 2009).

Coring makes available to the scientific community an unprecedented archive of CWC-bearing situations prone to be studied under various paleoecological perspectives. To date, most attention on the core record concerns, in fact, the onset/demise of CWC through time, and the identification of possible forcing ecological, climatic and oceanographic factors. Paleoecology here merges, therefore, into paleoceanography with most arguments focusing on the presence or absence of emblematic CWC and their precise chronology. Less has been produced about the response to environmental factors of the biological component in a core record, and holistic studies encompassing the whole fossil content have yet to be produced.

Regarding the Mediterranean, Margreth et al. (2011) reconstruct contour conditions around CWC growth in the mud volcano area of the west Alborán Sea using the core's planktonic and benthic foraminifer record. Finally, Stalder et al. (2015) produced one of the most comprehensive and quantitative study of CWC-bearing cores. By examining quantitatively the abundance of macrofossils (scleractinians, bryozoans and others) and microfossils (foraminifers and ostracods) in cores from the Alborán Sea, the authors reconstruct various environmental factors such as flux and type of nutrients, bottom currents, seawater temperature and density, oxygenation, sediment supply that exert control on CWC growth, turnover or demise through time. All such cases pertain by large to the "(i) Cold-water corals hosted in loose sediment" category discussed previously.

2.4 Paleoenvironmental Information Derivable from Geochemical Signals

The main constraint in interpreting the geochemical signals of the aragonite skeleton of fossil coral remains from subaerial outcrop is the presence of diagenetic alterations. Dissolution and recrystallisation of the skeleton can disrupt the primary geochemical signal, strongly limiting the interpretation of the geochemical proxies. Screening for traces of diagenesis, such as micro-dissolution, secondary cements or aragonite to calcite recrystallisation, is thus a necessary step when investigating the geochemistry of fossil corals long exposed to subaerial conditions (e.g., Janiszewska et al. 2017). Micro-analytical techniques like laser ablation ICP-MS or ion microprobe can partially overcome this limitation through a selective sampling strategy that targets pristine skeletal portions (Montagna and Taviani, this volume).

Valuable environmental information could be extracted through the geochemical composition of fossils, such as CWC (reviewed by Montagna et al. 2011; Robinson et al. 2014; Montagna and Taviani, this volume). This could be, for instance, an important aid and independent approach at determining more precisely variables as seawater temperature, at constraining salinity and nutrient concentration, and understanding response to ocean acidification, but is seldom introduced in a standard paleoecological study. Within the scheme of a modernised approach to paleoecology (Seddon et al. 2014), it is easy to foresee that CWC geochemistry will get more and more momentum.

2.5 Discussion

As seen, not much has been written thus far on the paleoecology of Mediterranean CWC with respect of its enormous potential. Fragmented or specific information on some basic taphonomic or paleoenvironmental aspects predominates with respect to a more comprehensive paleoecological analysis. In principle, the paleoecological analysis of CWC in outcrop appears intrinsically easier than producing similar studies in the deep sea. However, the evidence gained from the study of still-submerged late Pleistocene-Holocene occurrences warns about potential problems in interpreting a fossil situation. U/Th-dating of CWC recovered from a very steep wall from the Balearic escarpment at >900 m may help to elucidate this issue. The sample consisted of two specimens of *Desmophyllum dianthus* one attached on each other, the external one being alive whilst the second was dead (Fig. 2.4). Up to 10,000 years separate the two corals sitting on each other that settle precisely the same spot (Montagna et al. 2006). Only the precise radiometric chronology exposes an otherwise hidden pulsing colonisation of the area, characterised by times of CWC recession. Such type of subtle, albeit relevant ecological turnovers cannot be disclosed in outcrop situations which are beyond the potential of dating techniques.

A modern paleoecological approach to the study of hardground and other rocky substrates encrusted by CWC should consider importing methodologies, with opportune adaptations, typically applied to live communities, in particular habitat mapping by means of ROV (Vertino et al. 2010; Savini et al. 2014; Bargain et al. 2017, 2018; Angeletti et al., this volume-a, this volume-b; Lo Iacono et al., this volume). This would represent a major goal when applied to the most topographically difficult situations, such as steep canyons or walls. The Mediterranean basin provides a number of such sites with known subfossil CWC occurrences, as for example the Balearic Islands margin, the Malta Escarpment, the Crete margin, the Bari Canyon in the Adriatic, and many seamounts in the Tyrrhenian and Ionian seas.

There is an enormous potential for conducting detailed paleoecological analysis on past CWC habitats by using the superb, but largely underworked, record provided by cores.

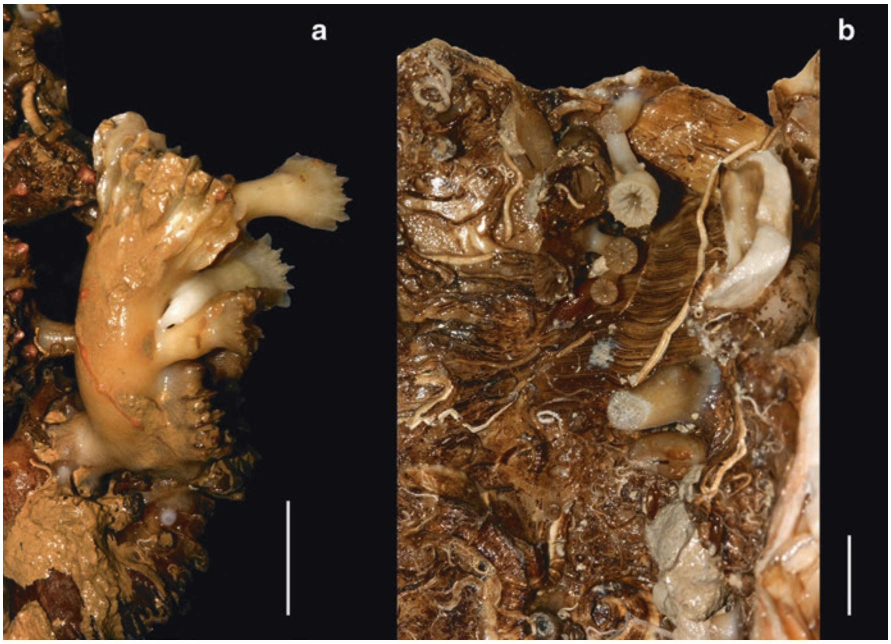

Fig. 2.4 Hand samples showing complex patterns of re-colonisation; (**a**) Living *Desmophyllum* growing on a framestone encrusted by Pleistocene corals; observe differential patination; from a steep wall at 800 m water depth, Balearic Islands; bar = 1 cm; (**b**) multiple generations of solitary corals and serpulids encrusting a fossil internal valve of the giant oyster *Neopycnodonte zibrowii*, Balearic Islands, > 800 m; bar = 1 cm. (Photographs: a, b: © ISMAR-CNR Bologna)

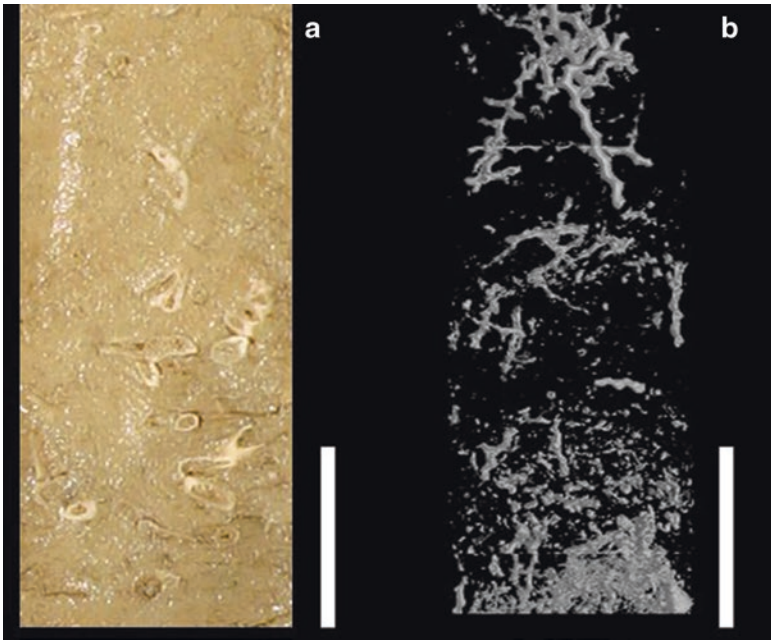

Fig. 2.5 Examples of CWC contained in cores: (**a**) Coral fragments hosted in muddy sediment within a split gravity core (Adriatic Sea), bar = 5 cm; (**b**) computed tomography discloses presence and fabric of CWC inside a core; resolution permits taxonomic assessment at species level (*Madrepora oculata*); Strait of Sicily, Linosa island, −600 m, bar = 5 cm. (Photographs: a, b: © ISMAR-CNR Bologna)

Standard qualitative and quantitative approaches can be now take advantage of computed tomography at the scale of the core (López-Correa et al. 2007; Tanaka and Nakano 2011; Douarin et al. 2014; Victorero et al. 2016; Wienberg and Titschack 2017; Angeletti et al., this volume-b) and of microtomography (Beuck et al. 2007; Färber et al. 2016) at the scale of individual fossils. Computed-tomography images are excellent in providing the 3D spatial arrangement of CWC and any other associated fossil (up to taxonomy at species-level), relevant for the paleoecological reconstruction (Fig. 2.5).

Microtomography instead permits to resolve with great detail hidden internal features, microarchitecture and bioerosion paths (e.g., Beuck et al. 2007; Zapalski and Dohnalik 2013; Lee et al. 2017). Ultimately, its interactive application will allow to study CWC through the creation of 3D digital modeling, the field of virtual paleontology (Sutton et al. 2014).

2.6 Conclusions and Future Research

We have presented and discussed the progress of science and the current perspectives for tackling with CWC paleoecology. Pre-modern, by large Pleistocene, scleractinian CWC occurrences are common place as submarine situations in the whole Mediterranean Sea and, far less as outcrops at specific sites of this basin. Their preservation mode varies considerably what deeply influences the quality of ecological restitution.

The refined paleocological interpretation of CWC occurrences and their functioning through time will greatly benefit by the on-going advancement of knowledge on biological traits of participating organisms (taxonomy, ecology, physiology) in the modern deep-sea habitats. The contribution offered by the other scientific fields, like geochemistry, is further widening the prospects in paleoecology. Certainly, the application of integrated paleoecological approaches would affect positively the reliable analysis of the on-land and submerged situations like those recorded in this chapter.

The implementation of virtual paleontology in the study of CWC will prove instrumental in the understanding at fine resolution of internal coral structures and diagenetic processes, useful to better decipher important paleoecological traits.

New frontiers are obvious in the deep sea. In the specific case of conducting paleoecological research on submerged CWC sites, research gets and will get benefit of the phenomenal advancement of the technological exploration of the deep sea realm. Even to achieve a level of classical paleoecology comparable with the traditional ecological-based studies on-land is a demanding challenge because of environmental and logistic difficulties. This holds particularly true for hard substrates, difficult to sample and typically distributed at complicate submarine topographies in physically stressing conditions. Here, the application of habitat mapping protocols and related technologies may be the first firm point to consider to overcome the problem. By adapting to the specific needs of paleoecology that requires also a spatial quantitative evaluation of the ‘community’ components, an ROV may serve the cause. The pre-requisites are the capability of the ROV to maintain a stable position on the study-site, and the mounting of high definition cameras so to permit a correct taxonomic identification and counting. The definition of a given standard surface (such as a square as in ecology) could be obtained by laser pointers. One limitation is that the taxonomic identification at species level of most organisms (e.g., sponges, some scleractinians, octocorals, bryozoans) is based on the detailed analysis of microscopic features that can be observed only on collected specimens. Accompanying sampling by ROV robotic arms and/or box-coring is therefore still essential for the understanding of structure and functioning of modern deep-sea communities and for the correct interpretation of the corresponding fossil ones. Sampling would be a major challenge when dealing with encrusters on a hardground or on a wall but recovering fossils is a relevant part of a CWC paleoecological assessment. Specifically designed and properly mounted microdrills may be considered for this action whenever a manipulator arm would fail.

In all likeness, drilling will be implemented more and more to sample long sedimentary succession containing CWC, bearing upon improvements in the design of the related equipment as well as on their support vessels.

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References

Addamo AM, Vertino A, Stolarski J, et al (2016) Merging scleractinian genera: the overwhelming genetic similarity between solitary *Desmophyllum* and colonial *Lophelia*. BMC Evol Biol 16:1–17. https://doi.org/10.1186/s12862-016-0654-8

Adkins JF, Cheng H, Boyle EA, et al (1998) Deep-sea coral evidence for rapid change in ventilation of the deep North Atlantic 15,400 years ago. Science 280:725–728

Ager DV (1963) Principles of Palaeoecology. McGraw-Hill, New York

Allmon W, Bottjer DJ (eds) (2001) Evolutionary paleoecology: the ecological context of macroevolutionary change. Columbia University Press, New York, Chichester, p 320

Allouc J (1987) Les paléocommunautés profondes sur fond rocheux du Pléistocène méditerranéen. Description et essai d’interpretation paléoécologique. Geobios 20:241–263

Allouc J (1990) Quaternary crusts on slopes of the Mediterranean Sea: a tentative explanation for their genesis. Mar Geol 94:351–376

Angeletti L, Taviani M (2011) Entrapment, preservation and incipient fossilization of benthic predatory molluscs within deep-water coral frames in the Mediterranean Sea. Geobios 44:543–548

Angeletti L, Taviani M, Canese S, et al (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Medit Mar Sci 15:225–238

Armstrong CW, Foley NS, Kahuic V, et al (2014) Cold-water coral reef management from an ecosystem service perspective. Mar Policy 50:126–134

Ayers MW, Pilkey OH (1981) Piston cores and surficial sediment investigations of the Florida-Hatteras slope and inner Blake plateau. In: Popenoe P (ed) Environmental geologic studies on the southeastern Atlantic outer continental shelf, USGS open file report 81-582-A, pp 5-1–5-89

Bargain A, Marchese F, Savini A, et al (2017) Santa Maria di Leuca Province (Mediterranean Sea): identification of suitable mounds for cold-water coral settlement using geomorphometry proxies and Maxent methods. Front Mar Sci 4:338. https://doi.org/10.3389/fmars.2017.00338

Bargain A, Foglini F, Pairaud I, et al (2018) Predictive habitat modeling in two Mediterranean canyons including hydrodynamic variables. Progr Ocean 169:151–168

Barrier P, Di Geronimo I, Zibrowius H (1985) Sezione plio-pleistocenica della Montagna. Guida alle escursioni. 3° Simposio di Ecologia e Paleoecologia delle Comunità Bentoniche, 3 pp

Barrier P, Di Geronimo I, Lanzafame G (1986) I rapporti tra tettonica e sedimentazione nell'evoluzione recente dell'Aspromonte occidentale (Calabria). Riv Ital Paleontol S 91:537–556

Barrier P, Di Geronimo I, Montenat C, et al (1989) Présence de faunes bathyales atlantiques dans le Pliocène et le Pléistocène de Méditerranée (détroit de Messine, Italie). B Soc Geol Fr 5:787–796

Barrier P, Di Geronimo I, Zibrowius H, et al (1990) Faune Sénégalienne du paléoescarpement du Capo Vaticano (Calabre Meridionale). Implications néotectoniques. Atti IV Simp Ecol Paleoecol Com Bent Sorrento 1–5 Novembre 1988:511–526

Barrier P, Zibrowius H, Lozouet P, et al (1992) Une faune de fond dur du bathyal supérieur dans le Miocène terminal des Cordillères Bétiques (Carboneras, SE, Espagne). Mésogée 51:3–13

Barrier P, Di Geronimo I, La Perna R, et al (1996) Taphonomy of deep-sea hard and soft bottom communities: the Pleistocene of Lazzàro (Southern Italy). In: Meléndez Hevia G, Blasco Sancho MF, Pérez Urresti I (eds) Com II Reun Tafon Fosiliz, Zaragoza 13–15 Jun, pp 39–45

Bellaiche C, Gennesseaux M, Mauffret A, et al (1974) Prélèvements systématiques et caractérisation des réflecteurs acoustiques: nouvelle étape dans la conpréhension de la géologie de la Méditerranée occidentale. Mar Geol 16:M47–M56

Bernoulli D, Mc Kenzie J (1981) Hardground formation in the Hellenic trench: penesaline to hypersaline marine carbonate diagenesis. In: Dercourt J (ed) Programme HEAT, Campagne submersible, les fossée helléniques, 19 aout-15 septembre 1979, Publ CNEXO: Rès Camp Mer 23, pp 197

Beu AG, Climo FM (1974) Mollusca from a recent coral community in Palliser Bay, Cook Strait. N Z J Mar Freshw Res 8:302–332

Beuck L, Freiwald A, Taviani M (2010) Spatio-temporal bioerosion patterns in deep-water scleractinians from off Santa Maria di Leuca (Apulia, Ionian Sea). Deep-Sea Res Part 2 Top Stud Oceanogr 57:458–470

Beuck L, Vertino A, Stepina E, et al (2007) Skeletal response of *Lophelia pertusa* (Scleractinia) to bioeroding sponge infestation visualised with micro-computed tomography. Facies 53:157–176

Biju-Duval B, Morel Y, Baudrimont A, et al (1983) Examples de sedimentation condensée sur les escarpements de la Mer Ionienne (Méditerranée orientale), Observations a partir sui submersible "Cyana". Rev INFP 38:427–438

Birks HJB (1985) Recent and possible future mathematical developments in quantitative palaeoecology. Palaeogeogr Paleoclim Palaeoecol 50:107–147

Birks HJB (2008) Palaeoecology. In: Jørgensen SE (ed) Encyclopedia of ecology. Elsevier, Oxford, p 2623

Blanc JJ, Pérès JM, Picard J (1959) Coraux profonds et thanatocoenoses quaternaires en Méditerranée In: La Topographie et la géologie des profondeurs océaniques. Coll Int CNRS 83:185

Brenchley PJ, Harper DAT (1998) Palaeoecology: ecosystems, environments and evolution. xxv + 402 pp. Chapman & Hall, London/Weinheim/New York/Tokyo/Melbourne/Madras

Bromley RG (2005) Preliminary study of bioerosion in the deep-water coral *Lophelia*, Pleistocene, Rhodes, Greece. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 895–914

Cairns SD (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. Bull Mar Sci 81:311–322

Cairns SD, Stanley GD Jr (1981) Ahermatypic coral banks: living and fossil couterparts. Proc 4th Int Coral Reef Symp Manila 1:611–618

Cita MB, Fantini Sestini N, Salvatorini G, et al (1979) Late Neogene sediments and fossils from the Malta escarpment and their geodynamic significance. Ann Géol Pays Hellen 1:273–283

Colella A, D'Alessandro A (1988) Sand waves, *Echinocardium* traces and their bathyal depositional setting (Monte Torre Paleostrait, Plio-Pleistocene, southern Italy). Sedimentology 35:219–237

Comas M, Pinheiro LM, Ivanov M, et al (2009) Deep-water coral mounds in the Alboran Sea: the Melilla mound field revisited, IOC workshop report 220. UNESCO, Paris, pp 8–9

Conti MA, De Girasoli DE, Frezza V, et al (2013) Repeated events of hardground formation and colonisation by endo-epilithozoans on the sediment-starved Pontine continental slope (Tyrrhenian Sea, Italy). Mar Geol 336:184–197

Corselli C (2001) Change and diversity: the Mediterranean deep corals from the Miocene to the present. In: Faranda FM, Guglielmo L, Spezie G (eds) Mediterranean ecosystems: structures and processes. Springer, Genova, pp 361–366

Corselli C (ed) (2010) The APLABES programme: physical, chemical and biological characterization of deep-water coral ecosystems from the Ionian Sea (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:323–325

Delibrias G, Taviani M (1985) Dating the death of Mediterranean deep-sea scleractinian corals. Mar Geol 62:175–180

Di Geronimo I (1979) Il Pleistocene in facies batiale di Valle Palione (Grammichele, Catania). Boll Malacol 15:85–156

Di Geronimo I (1987) Bionomie des peuplements benthiques des substrats meubles et rocheux plio-quaternaires du Détroit de Messine. Doc Trav IGAL 11:153–169

Di Geronimo I, Messina C, Rosso A, et al (2005) Enhanced biodiversity in the deep: early Pleistocene coral communities from southern Italy. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 61–86

Di Stefano A, Longhitano SG (2009) Tectonics and sedimentation of the lower and middle Pleistocene mixed siliciclastic/bioclastic sedimentary successions of the Ionian Peloritani Mts (NE Sicily, southern Italy): the onset of opening of the Messina Strait. Cent Eur J Geosci 1:33–62

Dorschel B, Hebbeln D, Rüggeberg A, et al (2005) Growth and erosion of a cold-water coral covered carbonate mound in the Northeast Atlantic during the late Pleistocene and Holocene. Earth Planet Sci Lett 233:33–44

Douarin M, Elliot M, Noble SR, et al (2013) Growth of north-East Atlantic cold-water coral reefs and mounds during the Holocene: a high resolution U-series and 14C chronology. Earth Planet Sci Lett 375:176–187

Douarin M, Sinclair DJ, Elliot M, et al (2014) Changes in fossil assemblage in sediment cores from Mingulay reef complex (NE Atlantic): implications for coral reef build-up. Deep-Sea Res Part 2 Top Stud Oceanogr 99:286–296

Dubois-Dauphin Q, Montagna P, Siani G, et al (2017) Hydrological variations of the intermediate water masses of the western Mediterranean Sea during the past 20 ka inferred from neodymium isotopic composition in foraminifera and cold-water corals. Clim Past 13:17–37

Dullo W-C (1987) The role of microarchitecture and microstructure in the preservation of taxonomic closely related scleractinians. Facies 16:11–22

Eisele M, Hebbeln D, Wienberg C (2008) Growth history of a cold-water coral covered carbonate mound – Galway Mound, Porcupine Seabight, NE-Atlantic. Mar Geol 253:160–169

Emig CC, Geistdoerfer P (2004) The Mediterranean deep-sea fauna: historical evolution, bathymetric variations and geographical changes. Carnets de Géologie/Notebooks on Geology, Maintenon, Article 2004/01

Färber C, Titschack J, Schönberg CHL, et al (2016) Long-term macro-bioerosion in the Mediterranean Sea assessed by micro-computed tomography. Biogeosciences 13:3461–3474

Ferdelman TG, Kano A, Williams T, et al (2006a) IODP expedition 307 drills cold-water coral mound along the Irish continental margin. Science reports. Sci Drill 2(March 2006):11–16. https://doi.org/10.2204/iodp.sd.2.02.2006

Ferdelman TG, Kano A, Williams T, et al (2006b) Proceedings of the integrated ocean drilling program 307, Washington, DC, Integrated Ocean Drilling Program Management International, Inc. https://doi.org/10.2204/iodp.proc.307.2006

Fink HG, Wienberg C, Hebbeln D (2012) Oxygen control on Holocene cold-water coral development in the eastern Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96

Fink HG, Wienberg C, De Pol-Holz R, et al (2013) Cold-water coral growth in the Alboran Sea related to high productivity during the late Pleistocene and Holocene. Mar Geol 339:71–82

Fink HG, Wienberg C, De Pol-Holz R, et al (2015) Spatio-temporal distribution patterns of Mediterranean cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) during the past 14,000 years. Deep-Sea Res Part 1 Oceanogr Res Pap 103:37–48

Fois E (1990) Stratigraphy and palaeogeography of the capo Milazzo area (NE Sicily, Italy): clues to the evolution of the southern margin of the Tyrrhenian Basin during the Neogene. Palaeogeogr Paleoclim Palaeoecol 78:87–108

Försterra, Beuck L, Häussermn V, Freiwald A (2005) Shallow-water *Desmophyllum dianthus* (Scleractinia) from Chile: characteristics of the biocoenoses, the bioeroding community, heterotrophic interactions and (paleo)-bathymetric implications. In: Freiwald A, Roberts JM (eds). Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 937–977

Foubert A, Henriet JP (2009) Nature and significance of the recent carbonate mound record. Lect Notes Earth Sci 126

Frank N, Ricard E, Lutringer-Paquet A, et al (2009) The Holocene occurrence of cold-water corals in the NE Atlantic: implications for coral carbonate mound evolution. Mar Geol 266:129–142

Frank N, Freiwald A, López Correa M, et al (2011a) Northeastern Atlantic cold-water coral reefs and climate. Geology 39:743–746

Frank T, Titschack J, Thierens M (2011b) Aragonite loss in a cold-water coral mound: mechanisms and implications. Sedimentology 58:670–690

Frank N, Paterne M, Ayliffe L, et al (2004) Eastern North Atlantic deep-sea corals: tracing upper intermediate water Δ 14C during the Holocene. Earth Planet Sci Lett 219:297–309

Freiwald A (2002) Reef-forming cold-water corals Ocean margin systems. Springer, Berlin, Heidelberg, 365 pp

Freiwald A, Schönfeld J (1996) Substrate pitting and boring pattern of *Hyrrokkin sarcophaga* Cedhagen, 1994 (foraminifera) in a modem deep-water coral reef mound. Mar Micropal 28:199–207

Freiwald A, Wilson JB (1998) Taphonomy of modern deep, cold-temperate water coral reefs. Hist Biol 13:37–52

Freiwald A, Hühnerbach V, Lindberg B, et al (2002) The Sula reef complex, Norwegian shelf. Facies 47:179–200

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs, UNEP-WCMC Biodiversity Series 22. UNEP-WCMC, Cambridge, 86 pp

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Freiwald A, Boetius A, Bohrmann G (2011) Deep water ecosystems of the eastern Mediterranean, Cruise No. 70, Leg 1–3, September 24–December 8, 2006, La Valetta (Malta) – Heraklion (Greece). METEOR-Berichte, 11–5. Leitstelle Deutsche Forschungsschiffe Institut für Meereskunde der Universität Hamburg

Freudenthal T, Wefer G (2007) Scientific drilling with the sea floor drill rig MeBo. Sci Drill 5:63–66

Gamberi F, Marani M, Landuzzi V (2006) Sedimentologic and volcanologic investigation of the deep Tyrrhenian sea: preliminary result of cruise VST02. Ann Geophys 49:767–781

Hanken N-M, Bromley RG, Miller J (1996) Plio–Pleistocene sedimentation in coastal grabens, north-East Rhodes, Greece. Geol J 31:271–296

Hebbeln D, Wienberg C, Beuck L, et al (2008) Report and preliminary results of RV Pelagia cruise 64PE284. Cold-water corals in the Gulf of Cádiz and on coral patch seamount (NE Atlantic). Portimão – Portimão, 18.02. 09.03.2008. Berichte, Fachbereich Geowissenschaften, Universität Bremen 265, Bremen:1–90

Hebbeln D, Wienberg C, Beuck L, et al (2009) Report and preliminary results of RV POSEIDON cruise POS 385 "cold-water corals of the Alboran Sea (western Mediterranean Sea)", Faro – Toulon, May 29–June 16, 2009. Berichte, Fachbereich Geowissenschaften, Universität Bremen 273, Bremen: 1–79

Henriet JP, Spezzaferri S, Samankassou E, et al (2011) Carbonate mounds in shallow and deep time. Mar Geol 282:1–4

Henry LA, Roberts JM (2017) Global biodiversity in cold-water coral reef ecosystems. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 235–256. https://doi.org/10.1007/978-3-319-17001-5_6-1

Hersey JB (1965) Sedimentary basins of the Mediterranean Sea. Colston Pap 17:75–91

Hunter JP (1998) Paleoecology meets ecology on questions of scale. Trend Ecol Evol 13:478–479

Järnegren J, Kutti T (2014) *Lophelia pertusa* in Norwegian waters. What have we learned since 2008? NINA Rep 1028:40

Janiszewska K, Mazur M, Escrig S, et al (2017) Aragonitic scleractinian corals in the cretaceous calcitic sea. Geology 45:319–322

Kano A, Ferdelman TG, Williams T, et al (2007) Age constraints on the origin and growth history of a deep-water coral mound in the Northeast Atlantic drilled during Integrated Ocean drilling program expedition 307. Geology 35:1051–1054

Lee S, Shi GR, Park TYS, et al (2017) Virtual palaeontology: the effects of mineral composition and texture of fossil shell and hosting rock on the quality of X-ray microtomography (XMT) outcomes using Palaeozoic brachiopods. Palaeont Electr 20.2.3T, pp 1–25. palaeo-electronica.org/content/2017/1891-xmt-on-brachiopod-fossils

Lo Iacono C, Gràcia E, Ranero CR, et al (2014) The West Melilla cold-water coral mounds, eastern Alboran Sea: morphological characterization and environmental context. Deep-Sea Res Part 2 Top Stud Oceanogr 99:316–326

López Correa M, Freiwald A, Hall-Spencer J, et al (2005) Distribution and habitats of *Acesta excavata* (Bivalvia: Limidae) with new data on its shell ultrastructure. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 173–205

López-Correa M, Freiwald A, Demuth M (2007) Cold-water corals as climate archives in the ocean depths. Computer tomography of sediment cores provides outstanding insights for geologists SOMATOM sessions, pp 52–54

Malinverno E, Taviani M, Rosso A, et al (2010) Stratigraphic framework of the Apulian deep-water coral province, Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:345–359

Margreth S, Gennari G, Rüggeberg A, et al (2011) Growth and demise of cold-water coral ecosystems on mud volcanoes in the West Alboran Sea: the messages from the planktonic and benthic foraminifera. Mar Geol 282:26–39

Mastrototaro F, D'Onghia G, Corriero G (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the younger Dryas. Earth Plan Sci Lett 298:143–152

Moissette P, Cornée J-J, Quillévéré F, et al (2017) Pleistocene (Calabrian) deep-water corals and associated biodiversity in the eastern Mediterranean (Karpathos Island, Greece). J Quat Sci 32:923–933

Montagna P, McCulloch M, Taviani M, et al (2006) Phosphorus in cold-water corals as proxy for seawater nutrient chemistry. Science 312:1788–1791

Montagna P, Taviani M, Silenzi S, et al (2011) Marine climate archives and geochemical proxies: a review and future investigations on the Mediterranean Sea. In: Brugnoli E, Cavarretta G, Mazzola S, et al (eds) Marine research at CNR, vol DTA/06-2011, pp 809–822

Montanaro E (1931) Coralli pliocenici dell'Emilia. Palaeontogr Ital 31:63–91

Montenat C, Barrier P, Di Geronimo I (1987) The strait of Messina, past and present: a review. Doc et Trav IGAL 11:7–13

Mullins HT, Newton CR, Heath K, et al (1981) Modern deep-water coral mounds north of Little Bahama Bank; criteria for recognition of deep-water coral bioherms in the rock record. J Sediment Res 51:999–1013

Nasto I, Cardone F, Mastrototaro F, et al (2018) Benthic invertebrates associated with subfossil cold-water corals and hardgrounds in the Adriatic Albanian waters (Mediterranean Sea). Turk J Zool 42. https://doi.org/10.3906/zoo-1708-44

Newton CR, Mullins HT, Gardulski A, et al (1987) Coral mounds on the West Florida slope: unanswered questions regarding the development of deep-water banks. PALAIOS 2:359–367

Noé S, Titschack J, Freiwald A, et al (2006) From sediment to rock: diagenetic processes of hardground formation in deep-water carbonate mounds of the NE Atlantic. Facies 52:183–208

Panetta P, Mastrototaro F, Capezzuto F, et al (2010) Size evaluation of *Delectopecten vitreus* (Mollusca, Bivalvia) from Santa Maria di Leuca deep-water coral site (Ionian Sea). Biol Mar Med 17:308–309

Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la mer Méditerranée. Rec Trav Sta Mar Endoume 47:3–137

Placella B (1979) Nuove osservazioni sulla corallofauna delle argille pleistoceniche di Archi (Reggio Calabria). Boll Soc Nat Napoli 87:1–31

Placella B (1980) I coralli pliocenici di Masseria Concarone, Pisticci (Mt). Boll Soc Nat Napoli 89:19–32

Qurban MA, Krishnakumar PK, Joydas TV, et al (2014) *In-situ* observation of deep water corals in the northern Red Sea waters of Saudi Arabia. Deep-Sea Res Part 1 Oceanogr Res Pap 89:35–43

Raddatz J, Rüggeberg A, Liebetrau V, et al (2014) Environmental boundary conditions of cold-water coral mound growth over the last 3 million years in the Porcupine Seabight, Northeast Atlantic. Deep-Sea Res Part 2 Top Stud Oceanogr 99:227–236

Rapp HT, Sneli JA (1999) *Lophelia pertusa* – myths and reality. Abstracts 2nd Nord Mar Sci Meet, Hirtshals, Denmark, 2–4 March 1999

Remia A, Taviani M (2005) Shallow-buried Pleistocene *Madrepora*-dominated coral mounds on a muddy continental slope, Tuscan archipelago, NE Tyrrhenian Sea. Facies 50:419–425

Remia A, Montagna P, Taviani M (2004) Submarine diagenetic products on the sediment-starved Gorgona slope, Tuscan archipelago (Tyrrhenian Sea). Chem Ecol 20:131–153

Roberts JM (2005) Reef-aggregating behaviour by a symbiotic eunicid polychaetes from cold-water corals: do worms assemble reefs? J Mar Biol Assoc UK 85:813–819

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Roberts JM, Wheeler A, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334

Robinson LF, Adkins JF, Frank N, et al (2014) The geochemistry of deep-sea coral skeletons: a review of vital effects and applications for paleoceanography. Deep-Sea Res Part 2 Top Stud Oceanogr 99:184–198

Ross SW, Nizinski MS (2007) State of the U.S. deep coral ecosystems in the Southeastern United States region: Cape Hatteras to the Florida Straits. In: Lumsden SE, Hourigan TF, Bruckner AW, et al (eds) The state of deep coral ecosystems of the United States, NOAA technical memorandum CRCP-3. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Silver Spring, 233 pp

Rosso A, Vertino A, Di Geronimo I, et al (2010) Hard- and soft-bottom thanatofacies from the Santa Maria di Leuca deep-water coral province, recent Mediterranean. Deep-Sea Res Part 2 Top Stud Oceanogr 57:360–379

Rosso A, Sanfilippo R, Sciuto F, et al (2013) Capo Milazzo (Plio-Pleistocene): an overview. In: Rosso A, Sanfilippo R, Sciuto F (eds) Pre-conference field-trip guide, IBA, June 3rd–9th, 2013, p 57

Rüggeberg A, Dullo C, Dorschel B, et al (2007) Environmental changes and growth history of a cold-water carbonate mound (Propeller Mound, Porcupine Seabight). Int J Earth Sci 96:57–72

Ruggieri G, Sprovieri R, Uniti M, et al (1979) Indagini batimetriche sulle argille pleistoceniche (siciliano) di Primosole (Siracusa). Naturalista Siciliano (s V) 3:119–129

Sabelli B, Taviani M (2014) The making of the Mediterranean molluscan biodiversity. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 285–306

Sanfilippo R, Vertino A, Rosso A, et al (2013) *Serpula* aggregates and their role in deep-sea coral communities in the southern Adriatic Sea. Facies 59:663–677

Sartoretto S, Zibrowius H (2017) Note on new records of living Scleractinia and Gorgonaria between 1700 and 2200 m depth in the western Mediterranean Sea. Mar Biodivers 48:4. https://doi.org/10.1007/s12526-017-0829-6

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108. https://doi.org/10.1371/journal.pone.0087108

Schröder-Ritzrau A, Freiwald A, Mangini A (2005) U/Th-dating of deep-water corals from the eastern North Atlantic and the western Mediterranean Sea. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Berlin, Heidelberg, pp 157–172

Seddon AWR, Mackay AW, Baker AG, et al (2014) Looking forward through the past: identification of 50 priority research questions in palaeoecology. J Ecol 102:256–267

Seguenza G (1864) Disquisizioni paleontologiche intorno ai Corallarii fossili delle rocce terziarie del distretto di Messina. Mem R Acc Sci Torino (Ser 2) 21:399–560

Selli R (1970) Ricerche geologiche preliminari nel Mar Tirreno. Giorn Geol 37:1–249

Smiley TM, Terry RC (2017) Palaeoecology: methods. Wiley, Chichester. https://doi.org/10.1002/9780470015902.a0003274.pub2

Spadini (2015) Sclerattiniari del Pliocene senese (Cnidaria, Anthozoa). Mem Acc Scie Siena Fisiocratici:1–159

Squires DF (1964) Fossil coral thickets in Wairarapa. N Z J Paleontol 38:904–915

Stalder C, Vertino A, Rosso A, et al (2015) Microfossils, a key to unravel cold-water carbonate mound evolution through time: evidence from the Eastern Alboran Sea. PLoS One 10:e0140223. https://doi.org/10.1371/journal.pone.0140223

Stanley GD Jr, Cairns SD (1988) Constructional azooxanthellate coral communities; an overview with implications for the fossil record. Palaios 3:233–242

Stolarski J, Vertino A (2007) First Mesozoic record of the scleractinian *Madrepora* from the Maastrichtian siliceous limestones of Poland. Facies 53:67–78

Sutton M, Rahman I, Garwood R (2014) Techniques for virtual paleontology, 1st edn. Wiley Blackwell, Chichester

Tanaka A, Nakano T (2011) Data report: three-dimensional observation and quantification of internal structure of sediment core from Challenger Mound area in the Porcupine Seabight off western Ireland using a medical X-ray CT. In: Ferdelman TG, Kano A, Williams T, et al (eds) IODP, 307. Integrated Ocean Drilling Program Management International, Inc, Washington, DC. https://doi.org/10.2204/iodp.proc.307.209.2009

Taviani M (1998) Axial sedimentation of the Red Sea transitional region (22°–25°N): pelagic, gravity flow and sapropel deposition during the late quaternary. In: Purser BH, DWJ B (eds) Sedimentation and tectonics of rift basins: Red Sea -gulf of Aden. Chapman and Hall, London, pp 467–478

Taviani M (2002) The Mediterranean benthos from late Miocene up to present: ten million years of dramatic climatic and geological vicissitudes. Biol Mar Medit 9:445–463

Taviani M (2003) Shaping the biogeography of the Mediterranean basin: one geologist's perspective. In: 'Marine biogeography of the Mediterranean Sea: patterns and dynamics of biodiversity' Biogeographia, vol 24. Nuova Immagine Ed, Siena, pp 15–22

Taviani M (2014) Marine chemosynthesis in the Mediterranean Sea. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 69–83

Taviani M, Colantoni P (1979) Thanatocoenoses wurmiennes associées aux craux blancs. Rapp Comm Int Mer Médit 25/26:141–142

Taviani M, Bouchet P, Metivier B, et al (1991) Intermediate steps of southwards fauna1 shifts testified by last glacial submerged thanatocoenoses in the Atlantic Ocean. Palaeogeogr Palaeoclim Palaeoecol 86:331–338

Taviani M, López Correa M, Zibrowius H (2007) Last glacial deep-water corals from the Red Sea. Bull Mar Sci 81:361–370

Taviani M, Angeletti L, Dimech M, et al (2009) Coralliophilinae (Mollusca: Gastropoda) associated with deep-water coral banks in the Mediterranean. The Nautilus 123:106–112

Taviani M, Freiwald A, Beuck L (2010) The deepest known occurrence of the precious red coral *Corallium rubrum* (L. 1758) in the Mediterranean Sea. In: Bussoletti E, Cottingham D, Bruckner A, et al (eds) Proceedings of the international workshop on red coral science, management, trade: lessons from the Mediterranean, NOAA technical memorandum CRCP-13. NOAA, Silver Spring, MA, p 87

Taviani M, Vertino A, López Correa M, et al (2011a) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603

Taviani M, Angeletti L, Antolini B, et al (2011b) Geo-biology of Mediterranean deep-water coral ecosystems. In: Brugnoli E, Cavaretta G, Mazzola S, et al (eds) Marine research at CNR, vol DTA/06-2011, pp 705–719

Taviani M, Angeletti L, Beuck L, et al (2016) On and off the beaten track: megafaunal sessile life and Adriatic cascading processes. Mar Geol 375:146–160

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water Coral Province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78

Taviani M, Colantoni P (1984) Paleobiocoenoses profondes a scleractiniaires sur l'escarpement de Malte-Syracuse (Mer Mediterranée): leur structure, leur age et leur signification. Oil Gas Sci Technol 39:547–559

Taviani M, Freiwald A, Zibrowius H (2005a) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Taviani M, Remia A, Corselli C, et al (2005b) First geomarine survey of living cold-water *Lophelia* reefs in the Ionian Sea (Mediterranean basin). Facies 50:409–417

Thierens M, Browning E, Pirlet H, et al (2013) Cold-water coral carbonate mounds as unique palaeo-archives: the Plio-Pleistocene challenger mound record (NE Atlantic). Quat Sci Rev 73:14–30

Thierens MM, Pirlet H, Titschack J, et al (2009) The 2.6 Ma depositional sequence from the challenger cold-water coral carbonate mound (IODP Exp. 307): a unique palaeo-record of Plio-Pleistocene NE Atlantic climate variability. Eos, Trans (Washington, DC) AGU Fall Meet Suppl 90: abstract PP11A-1284

Thresher RE, Adkins J, Thagarajan N (2011) Modal analysis of the deep-water solitary scleractinian, *Desmophyllum dianthus*, on SW Pacific seamounts: inferred recruitment periodicity, growth, and mortality rates. Coral Reefs 30:1063–1070

Titschack J, Freiwald A (2005) Growth, deposition, and facies of Pleistocene bathyal coral communities from Rhodes, Greece. In: Freiwald A, Roberts M (eds) Deep-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 41–59

Titschack J, Bromley RG, Freiwald A (2005) Plio-Pleistocene cliff-bound, wedge-shaped, warm-temperate carbonate deposits from Rhodes (Greece): sedimentology and facies. Sediment Geol 180:29–56

Titschack J, Vertino A, Pino P, et al (2008) Plio-Pleistocene cold-water coral deposits at La Montagna (Messina, Sicily) – submarine dune or cold-water coral mound. The geology of coral-rich carbonate systems: from tropical shallow water to cold, deep-water settings. Capo Sant'Alessio, 5–8 Maggio 2008, p 26

Titschack J, Joseph N, Fietzke J, et al (2013) Record of a tectonically-controlled regression captured by changes in carbonate skeletal associations on a structured island shelf (mid-Pleistocene, Rhodes, Greece). Sediment Geol 283:15–33

Titschack J, Fink HG, Baum D, et al (2016) Mediterranean cold-water corals–an important regional carbonate factory? Depos Rec 2:74–96

Toscano F, Raspini A (2005) Epilithozoan fauna associated with ferro-manganese crustgrounds on the continental slope segment between Capri and li Galli Islands (bay of Salerno, northern Tyrrhenian Sea, Italy). Facies 50:427–441

Vandorpe T, Wienberg C, Hebbeln D, et al (2017) Multiple generations of buried cold-water coral mounds since the Early-Middle Pleistocene Transition in the Atlantic Moroccan Coral Province, southern Gulf of Cádiz. Palaeoclim Palaeogeogr Palaeoecol 485:293–304

Van Rooij D, Blamart D, De Mol L, et al (2011) Cold-water coral mounds on the Pen Duick Escarpment, Gulf of Cadiz: the MiCROSYSTEMS project approach. Mar Geol 282:102–117

van Weering TCE, de Haas H, de Stigter H, et al (2003) Structure and development of giant carbonate mounds at the SW and SE Rockall trough margins, NE Atlantic ocean. Mar Geol 198:67–81

Vella P (1964) Foraminifera and other fossils from late tertiary deep-water coral thickets, Wairarapa, New Zealand. J Paleontol 38:916–928

Vertino A (2003) Sclerattiniari plio-pleistocenici e attuali del Mediterraneo (Sistematica, Biostratinomia e Paleoecologia). Ph D thesis, University of Messina (unpublished), pp 1–306

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396

Vertino A, Stolarski J, Bosellini FR, et al (2014) Mediterranean corals through time: from Miocene to present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 257–274

Vertino A, Titschack J, Rosso A, et al (2013) Messina Strait: CWC Pleistocene deposits from "La Montagna" (Messina). In: Vertino

A, Basso D, Rosso A (eds) Field seminar guide book, COCARDE-ERN workshop and field seminar, Sicily, 23–27 September 2013, p 4

Victorero L, Blamart D, Pons-Brachu E, et al (2016) Reconstruction of the formation history of the Darwin mounds, N Rockall trough: how the dynamics of a sandy contourite affected cold-water coral growth. Mar Geol 378:186–195

Wells PE (1986) Record of an upper Miocene fossil *Goniocorella* coral thicket, Mt. Bruce, Wairarapa, New Zealand. J R Soc N Z 16:139–144

Wheeler AJ, Beyer A, Freiwald A, et al (2007) Morphology and environment of cold-water coral carbonate mounds on the NW European margin. Int J Earth Sci 96:37–56

Wienberg C, Hebbeln D, Fink HG, et al (2009) Scleractinian cold-water corals in the Gulf of Cadiz-first clues about their spatial and temporal distribution. Deep-Sea Res Part 1 Oceanogr Res Pap 56:1873–1893

Wienberg C, Frank N, Mertens KN, et al (2010a) Glacial cold-water coral growth in the Gulf of Cádiz: implications of increased palaeo-productivity. Earth Planet Sci Lett 298:405–416

Wienberg C, Beuck L, Coughlan M, et al (2010b) Report and preliminary results of RV POSEIDON cruise POS400 "CORICON – cold-water corals along the Irish continental margin", Vigo – Cork, June 29–July 15 2010. Berichte, Fachbereich Geowissenschaften, Universität Bremen 275, Bremen: 1–46

Wienberg C, Titschack J, Freiwald A, et al (2018) The giant Mauritanian cold-water coral mound province: oxygen control on coral mound formation. Quat Sci Rev 185:135–152

Wienberg C, Titschack J (2017) Framework-forming scleractinian cold-water corals through space and time: a late quaternary North Atlantic perspective. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 699–732

Wilber RJ, Neumann AC (1993) Effects of submarine cementation on microfabrics and physical properties of carbonate slope deposits, northern Bahamas. In: Rezak R, Lavoie DL (eds) Carbonate Microfabrics. Springer, New York, pp 79–94

Wisshak M, Gektidis M, Freiwald A, et al (2005) Bioerosion along a bathymetric gradient in a cold-temperate setting (Kosterfjord, SW Sweden): an experimental study. Facies Facies 51:93–117

Wisshak M, López Correa M, Gofas S, et al (2009) Shell architecture, element composition, and stable isotope signature of the giant deep-sea oyster *Neopycnodonte zibrowii* sp. n. from the NE Atlantic. Deep-Sea Res Part 1 Oceanogr Res Pap 56:374–407

Zapalski MK, Dohnalik M (2013) Blastogeny in tabulate corals: case studies using X-ray microtomography. Lethaia 46:223–231

Zibrowius (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mém Inst Océanogr Monaco 11:1–284 + 107 plates

Zibrowius H (1981) Thanatocoenose plèistocène profonde à spongiaires et scléractiniaires dans la Fosse Hellénique. J Etud Systémat Evolut Biogéogr Méditerranée, Cagliari. CIESM:133–136

Zibrowius H (1991) Les scléractiniaires du Miocéne au Pléistocène de Sicile et de Calabre de Giuseppe Seguenza (1864, 1880) (Cnidaria, Anthozoa). In: Bonfiglio L (ed) Celebrazione del 1° centenario di Giuseppe Seguenza, naturalista e paleontologo. Convegno di paleontologia e stratigrafia, Messina – Taormina, 22–26 maggio 1989. Atti Acc pelor pericol, Messina, (Classe di scienze fisiche, matematiche e naturali) 67: 75

Zibrowius H, Taviani M (2005) Remarkable sessile fauna associated with deep coral and other calcareous substrates in the Strait of Sicily, Mediterranean Sea. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 807–819

Cross References

Angeletti L, Bargain A, Campiani E, et al (this volume-a) Cold-water coral multiscale habitat mapping: methodologies and perspectives

Angeletti L, Bettuzzi M, Morigi MP (this volume-b) Tomography of cold-water corals (CWC)-bearing cores

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of cold-water coral communities in Mediterranean hard and soft bottoms

Freiwald A (this volume) Messinian Salinity Crisis: What Happened to Cold-Water Corals?

Lo Iacono C, Savini A, Huvenne VAI, et al (this volume) Habitat mapping of cold-water corals in the Mediterranean Sea

Montagna P, Taviani M (this volume) Mediterranean cold-water corals as paleoclimate archives

Rebesco M, Taviani M (this volume) A turbulent story: Mediterranean deep-sea sedimentation and Cold-water coral establishment

Rueda J, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Taviani M (this volume) Changing views about Mediterranean cold-water corals

Titschack J (this volume) Bathyal corals within the Aegean Sea and the adjacent Hellenic trench

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Drop Chapter
Cold-Water Corals in the Mediterranean: A History of Discovery

3

Julian Evans, Leyla Knittweis, Joseph A. Borg,
and Patrick J. Schembri

Abstract

The earliest records of cold-water corals from the Mediterranean Sea date back to the eighteenth century when Linnaeus first described *Madrepora oculata* based on specimens from the central Mediterranean and Tyrrhenian Sea. It was only towards the end of the nineteenth century that cold-water corals were recorded from elsewhere in the Mediterranean, thanks to early research cruises that explored the Mediterranean deep-sea benthos. Although the first records of live cold-water corals date back to the early twentieth century, further observations of living individuals were extremely rare and most records made by the end of the century were actually based on dead or fossil fragments. This led to the idea that extant Mediterranean cold-water coral assemblages are merely relicts of the communities that thrived during the Pleistocene. However, several sites with live framework-forming cold-water coral species were discovered since the year 2000, including six regions identified as cold-water coral provinces given that they support a dense growth of living corals. The emerging picture is that thriving cold-water coral assemblages that are hotspots of deep-sea biodiversity still occur in the Mediterranean, but have a rather punctuate distribution along the circulation path of the Levantine Intermediate Water, which appears to be a main driver for cold-water coral distribution in the Mediterranean.

Keywords

Benthic biodiversity · Coral framework · Historical records · Oceanographic expeditions · Scleractinia

The existence of cold-water corals (CWC), such as the framework-building *Madrepora oculata* Linnaeus 1758 and *Lophelia pertusa* (Linnaeus 1758) and associated solitary coral *Desmophyllum dianthus* (Esper 1794), has been known for at least half a millennium, as attested by the lists of synonymies dating back to the sixteenth century given by Milne Edwards and Haime (1850). The first Mediterranean record is possibly that by Marsilli (1725), whose figure of *M. oculata* could have been based on specimens collected off Marseille (Zibrowius 1980). However, the first confirmed record seems to be by Linnaeus (1758), who named and described *M. oculata* on the basis of specimens collected from the "*Mari Siculo, Tyrrheno*" (central Mediterranean and Tyrrhenian Sea). Linnaeus' type specimens are missing, so it is not clear if his description was based on live, dead, or even fossil fragments. Fossils of several taxa contributing to present-day CWC assemblages date back as far as the Miocene epoch, with these fossil genera being morphologically indistinguishable from extant ones (Taviani et al. 2011). Specimens dredged from the deep sea may represent fossil forms dating back to the Pleistocene, and these are not always easy to tell apart from more recent specimens as they can lack the dark coating of iron-manganese oxides typical of hard material in deep water (Zibrowius 2003). Historical records of CWC based on dead material must therefore be interpreted with caution, particularly since Mediterranean CWC assemblages appear to have had a much more extensive distribution during the Pleistocene than at present.

Until recently, most records of CWC species from the Mediterranean were actually based on dead (or subfossil/fossil) fragments. The earliest such records are of *M. oculata*, and these were most likely based on specimens brought up unintentionally in commercial red coral fisheries by collecting gear which had been lowered into deeper waters; the branches present in various old museum collections generally lack any indication of origin but were probably sourced from the Tyrrhenian Sea and Sicilian waters (Zibrowius 2003). More precise information is available starting from

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the late nineteenth century, based on records made during early research cruises that explored the Mediterranean deep-sea benthos. The history of discovery of CWC in the Mediterranean closely follows that of the deep-sea exploration of this region, starting with the *Porcupine* (1870) expedition, which recorded the presence of both *M. oculata* and *L. pertusa* in the Sicilian Channel (Duncan 1873; see also Taviani, this volume). By the end of the twentieth century, further records were made during cruises by the *Washington* (1881–1883), *Princess-Alice* and *Hirondelle* (1888–1922), *Pola* (1890–1893), *Valdivia* (1898–1899), *Calypso* (1954–1964), *Jean Charcot* (1972–1974), *Hannoun* (1973), *Cryos* (1984), *Suroit* (1995), *Europe* (1996), *Sonne* (1996), and *Urania* (1996–2000) (see Zibrowius 1980, 2003). Most of these records were based on dredged specimens, but direct observations were also made through manned submersibles such as the *Cyana*, *Griffon*, the French bathyscaphe, and Jacques Cousteau's diving saucer (SP350 *Denise*) (Zibrowius 2003).

The first confirmed records of live Mediterranean CWC date back to the early twentieth century: in 1910 *L. pertusa* and *D. dianthus* were found alive on a telegraph cable in the vicinity of Cabo de Gata (Alborán Sea), and subsequently a living specimen of *M. oculata* was collected from off north Sicily in 1922 (see Zibrowius 1980). By the end of the century, the only other records of live individuals of *M. oculata* were those made in canyons near Banyuls (Lacaze-Duthiers canyon) and Marseille (Cassidaigne canyon), and south of Thassos Island in the northern Aegean Sea. Besides the Cabo de Gata specimen, additional records of live *L. pertusa* were even rarer, restricted to off Banyuls, and possibly south of Thassos Island; likewise live *D. dianthus* was only known from Marseille, from off Euboea Island in the Aegean Sea, and from Eratosthenes Seamount south of Cyprus (Zibrowius 2003; Taviani et al. 2005).

Based on their personal observations and other records published by the early 1960s, Pérès and Picard (1964) described the Mediterranean *Biocoenose des "coraux blancs"* (the "white coral" community) as occurring at depths of at least 300 m on hard grounds that are sufficiently sloped to prevent burial through sedimentation, and comprising isolated mounds formed by *M. oculata* and *L. pertusa*, which may be surrounded by depressions where mud settles. However, these authors noted that most of the coral frameworks are actually dead, either entirely or else with only a few living branches at the top. Pérès and Picard (1964) also noted that the dead "sub-fossil" parts are often buried in muddy sediment, and are associated with a rich thanatocoenosis of Pleistocene age, whereas the extant biocoenosis is faunally impoverished, especially compared to that associated with the extensive CWC frameworks of the north-eastern Atlantic. Zibrowius (2003) cautioned that it is unrealistic to compare the species richness of the intensely studied Atlantic CWC communities with that of their much less well-studied Mediterranean counterparts, and that it is unlikely that the Mediterranean "white coral" communities are in fact species poor (for an updated review see Rueda et al., this volume). On the other hand, the dearth of records of live CWC made by the end of the twentieth century supported the notion that extant Mediterranean CWC assemblages are merely relicts of the communities that thrived during the Pleistocene.

In 2000, several living colonies of *M. oculata* and *L. pertusa* and individuals of *D. dianthus* were accidentally collected during experimental fishing operations off Cape Santa Maria di Leuca, representing the only large live *Lophelia*-bearing deep coral area known at the time (Mastrototaro et al. 2002). Just 3 years later, a second area with living *Madrepora–Lophelia–Desmophyllum* CWC was discovered south of Malta, again incidentally during experimental trawl surveys (Schembri et al. 2007). These discoveries led to extensive studies in the areas, including through dedicated oceanographic research cruises such as those by the *R/V Meteor* and *R/V Urania*. In the meantime, several other sites with live framework-forming CWC species were also discovered, extending from the Strait of Gibraltar to Cyprus and including localities in the Alborán Sea, the Gulf of Lions (Cap de Creus, Lacaze-Duthiers, and Cassidaigne canyons), the Ligurian and Tyrrhenian Seas, the central Mediterranean, and the southern Adriatic and northern Aegean Seas (Taviani et al. 2017; Chimienti et al., this volume). While a number of sites presented only patchy or isolated coral occurrences, six areas have been identified as "CWC provinces" (*sensu* Taviani et al. 2011, 2017) due to the dense growth of living corals (generally interspersed with coral-free sediment patches or accumulations of dead corals): the Bari Canyon, Santa Maria di Leuca, south Malta, south Sardinia, Gulf of Lions (Catalan-Provençal-Ligurian canyons), and Melilla CWC provinces (Fig. 3.1). The emerging picture is that thriving CWC assemblages that are hotspots of deep-sea biodiversity still occur in the Mediterranean (Taviani, this volume), but have a rather punctuate distribution along the circulation path of the Levantine Intermediate Water (LIW), which appears to be a main driver for CWC distribution in the Mediterranean (Taviani et al. 2017; Chimienti et al., this volume). Whether this picture will hold true in the future will ultimately depend on the location of any newly discovered CWC sites, which will serve to address the still rather fragmentary knowledge on distribution of CWC in the Mediterranean.

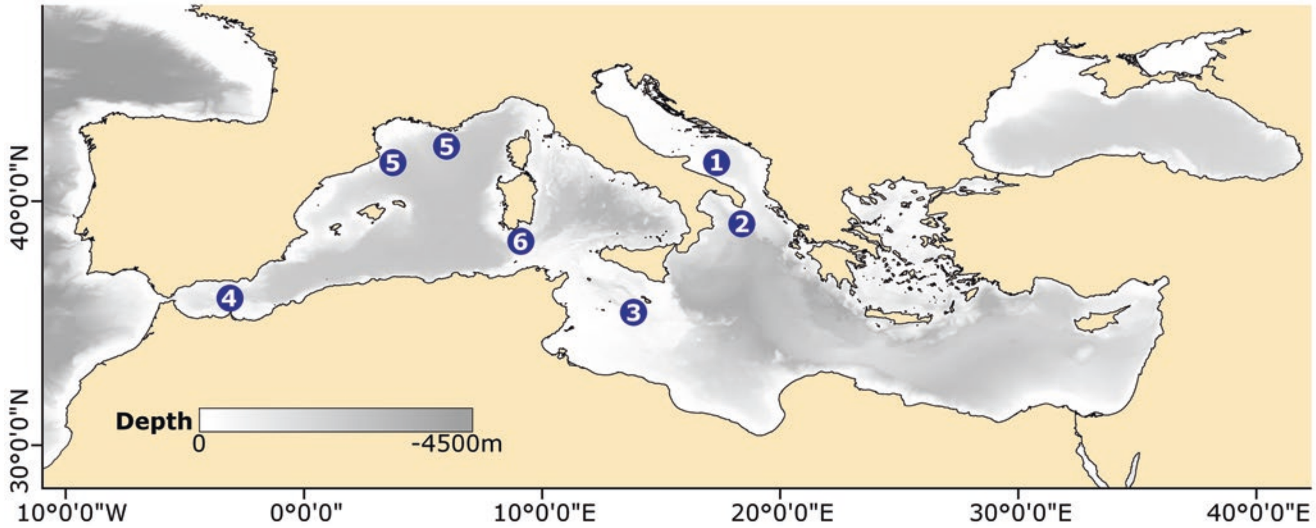

Fig. 3.1 Map of the Mediterranean Sea showing the locations of the six cold-water coral (CWC) provinces recognised to date (numbered blue dots: *1*. Bari Canyon CWC Province; *2*. Santa Maria di Leuca CWC Province; *3*. South Malta CWC Province; *4*. Melilla CWC Province; *5*. Gulf of Lions CWC Province; *6*. South Sardinia CWC Province)

References

Duncan PM (1873) A description of the Madreporaria dredged up during the expeditions of HMS ‘Porcupine’ in 1869 and 1870. Trans Zool Soc Lond 8:303–344. https://doi.org/10.1111/j.1096-3642.1873.tb00560.x

Linnaeus C (1758) Systema naturae per Regna tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I: Regnum animale (10th ed). Laurentius Salvius, Stockholm

Marsilli LF (1725) Histoire physique de la mer. Aux dépens de la Compagnie, Amsterdam

Mastrototaro F, Matarrese A, Tursi A (2002) Un mare di coralli nel Mar Ionio. Biol Mar Medit 9:616–619

Milne Edwards H, Haime J (1850) Recherches sur les Polypiers. Cinquième mémoire: monographie des Oculinides. Ann Sci Nat Zool (sér 3) 13:63–110

Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la mer Méditerranée. Rec Trav Stat Mar Endoume 47:3–137

Schembri PJ, Dimech M, Camilleri M, et al (2007) Living deep-water *Lophelia* and *Madrepora* corals in Maltese waters (Strait of Sicily, Mediterranean Sea). Cah Biol Mar 48:77–83

Taviani M, Freiwald F, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Taviani M, Angeletti L, Antolini B, et al (2011) Geo-biology of Mediterranean deep-water coral ecosystems. In: Brugnoli E, Cavaretta G, et al (eds) Marine research at CNR – 2- marine geology (DTA/06–2011), Dipartamento Terra e Ambiente, Consiglio Nazionale delle Ricerche, Roma, pp 705–719

Taviani M, Angeletti L, Canese S, et al (2017) The “Sardinian cold-water coral province” in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78. https://doi.org/10.1016/j.dsr2.2015.12.008

Zibrowius H (1980) Les scléractiniaires de la Méditerranée et de l’Atlantique nord-oriental. Mém Inst Océanogr (Monaco) 11:1–284

Zibrowius H (2003) The “white coral community”, canyon and seamount faunas of the deep Mediterranean Sea. RAC/SPA – Regional Activity Centre for Specially Protected Areas, Tunis, 39 pp

Cross References

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Taviani M (this volume) Changing views about Mediterranean cold-water corals

4 A Turbulent Story: Mediterranean Contourites and Cold-Water Corals

Michele Rebesco and Marco Taviani

Abstract

Dynamic bottom current regimes govern cold-water corals as well as contourites. We provide an overview of the general aspects of both research fields, with specific attention to the Mediterranean Sea region, which has the particularity to be a climatically-sensitive mid-latitude semi-enclosed basin. In this area there are many examples of along-slope contourite deposits (known as contourite drifts), typically with an along-slope, elongated mounded shape adjacent to a concave moat. Likewise, a number of thriving coral sites, together with sparse occurrences, are present in the central and western Mediterranean, with large coral mounds known so far only in the Alborán Sea. In the Mediterranean Sea both contourite drift and cold-water corals seem mainly related to the Levantine Intermediate Water, but their strict co-existence has still to be ascertained in many cases. Further research should address this aspect and the great potential of combining the two complementary kinds of climate paleo-archives provided by cold-water corals and contourites.

Keywords

Cold-water corals · Contourites · Mediterranean Sea · Bottom currents · Suspended matter

4.1 Introduction

The powerful action of deep-water circulation and its ability to shape the seafloor is a well-known phenomenon since the sixties (Heezen and Hollister 1964). The resulting sedimentary deposits (named contourites by Hollister and Heezen 1972) are defined as sediments deposited or substantially reworked by the persistent action of bottom currents (e.g., Stow et al. 2002a; Rebesco 2005, 2014; Rebesco and Camerlenghi 2008; Rebesco et al. 2014). For "bottom currents" it is meant any "persistent" water current near the seafloor, generally with a net along-slope flow (Fig. 4.1). Contourites were first described in the Atlantic Ocean and many examples have been discovered also in the Mediterranean Sea (e.g. Marani et al. 1993; Reeder et al. 2002; Roveri 2002; Gaudin et al. 2006; Verdicchio et al. 2007; Verdicchio and Trincardi 2008a, b; Amelio and Martorelli 2008; Martorelli et al. 2011; Somoza et al. 2012; Schattner et al. 2015; Pellegrini et al. 2016; Ercilla et al. 2016; Miramontes et al. 2016). The general understanding regarding contourites is steadily improving with increasing recognition that contour currents are major transport and sedimentary processes exerting control on deep-sea sedimentation (Camerlenghi et al. 1997; Giorgetti et al. 2003; Rebesco and Camerlenghi 2008). The progress in the knowledge on these deposits confirms their importance, especially in the fields of paleoclimatology and paleoceanography, slope-stability, geological hazard assessment, and hydrocarbon exploration. Contourite areas are associated with a number of oceanographic processes at different water depths, from abyssal plains to continental shelves (Rebesco et al. 2014). Such processes include, but are not limited to, dense bottom currents, tides, eddies, deep-sea storms, internal waves and tsunamis.

Sustained currents significantly affect the seafloor (resulting in large-scale depositional and erosional contourite features). Though there is consensus about the large-scale, geophysical characteristics of these deposits, the small-scale

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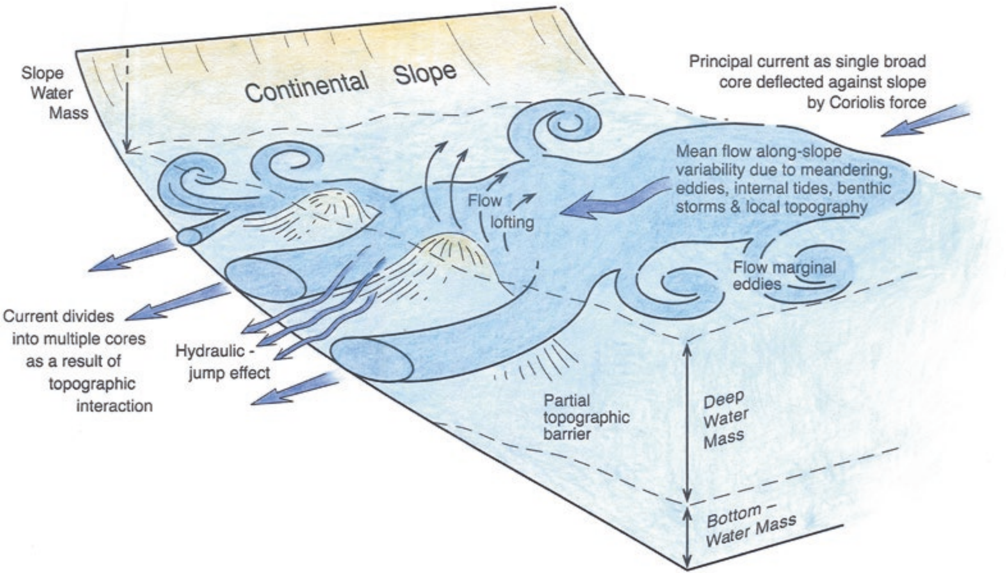

Fig. 4.1 Schematic diagram summarising the principal bottom-current features. (Modified from work by Stow et al. (2008); with permission from © Elsevier)

contourite facies still lack unambiguous and commonly accepted diagnostic criteria, also for distinguishing them from turbidite facies and bottom-current reworked sandy deposits (Rebesco et al. 2014). Most contourite researchers consider extensive bioturbation as the dominant feature (e.g. Gonthier et al. 1984; Stow and Faugères 2008). However, a minority of workers interprets some distinctly laminated sandy deposits as contourites (Hüneke and Stow 2008; Martín-Chivelet et al. 2008; Shanmugam 2008, 2013; Mutti and Carminatti 2012). In those regions of the ocean suitable for cold-water coral (CWC) settlement, bottom currents are also steadily or periodically delivering food particles to sessile suspension-feeders and limit excess silting. A link between contourites and CWCs has been noticed in the Gulf of Mexico (Hübscher et al. 2010), and the distribution of contourites in shallow to intermediate depths may provide a first order indication for the presence of CWCs and *vice versa* (Hebbeln et al. 2016).

We discuss the action of dynamic bottom current regimes with relation to contourites and CWCs by providing a general overview, with a particular attention to the Mediterranean Sea region.

4.2 Hydrographic Setting

The Mediterranean Sea is a semi-enclosed basin, characterised by moderate-energy continental margins and micro-tidal conditions, that communicates with the Atlantic Ocean through the narrow Strait of Gibraltar (Robinson et al. 2001; Hayes et al., this volume).

The Mediterranean is a concentration basin with evaporation exceeding the joined effect of river runoff and precipitation (Skliris, this volume). The circulation is strongly influenced by Atlantic inflow water and by the presence of shallow sills (Miller 1972). In general, modern circulation is anti-estuarine, with a cell in the western Basin and one in the eastern Basin (Lascaratos et al. 1999; Robinson et al. 2001). The relatively fresh and light Mediterranean Surface Water (MSW), entering from the Atlantic, occupies the upper tens of m and interchanges with the salty and relatively warm Levantine Intermediate Water (LIW; Wüst 1961; Fig. 4.2), which forms southeast of Crete, in the eastern Mediterranean Basin (Millot 2009; Pinardi and Masetti 2000; Hecht et al. 1988; Rubino et al. 2012; Bensi et al. 2013).

4.3 Contourite Deposits

In the Mediterranenan Sea there are many examples of along-slope contourite deposits, known as contourite drifts, (Verdicchio and Trincardi 2008a). They are mostly located at intermediate water depths (about 200–600 m) and associated with the LIW (e.g. Marani et al. 1993; Reeder et al. 2002; Roveri 2002; Gaudin et al. 2006; Verdicchio et al. 2007; Verdicchio and Trincardi 2008a, b; Amelio and Martorelli 2008; Martorelli et al. 2011; Somoza et al. 2012; Schattner et al. 2015; Pellegrini et al. 2016; Ercilla et al. 2016; Miramontes et al. 2016). Normally, these relatively shallow water contourite drifts (Fig. 4.3) are similar (either in terms of shape in plan-view and of internal geometry) to the better known oceanic counterparts (Verdicchio and Trincardi

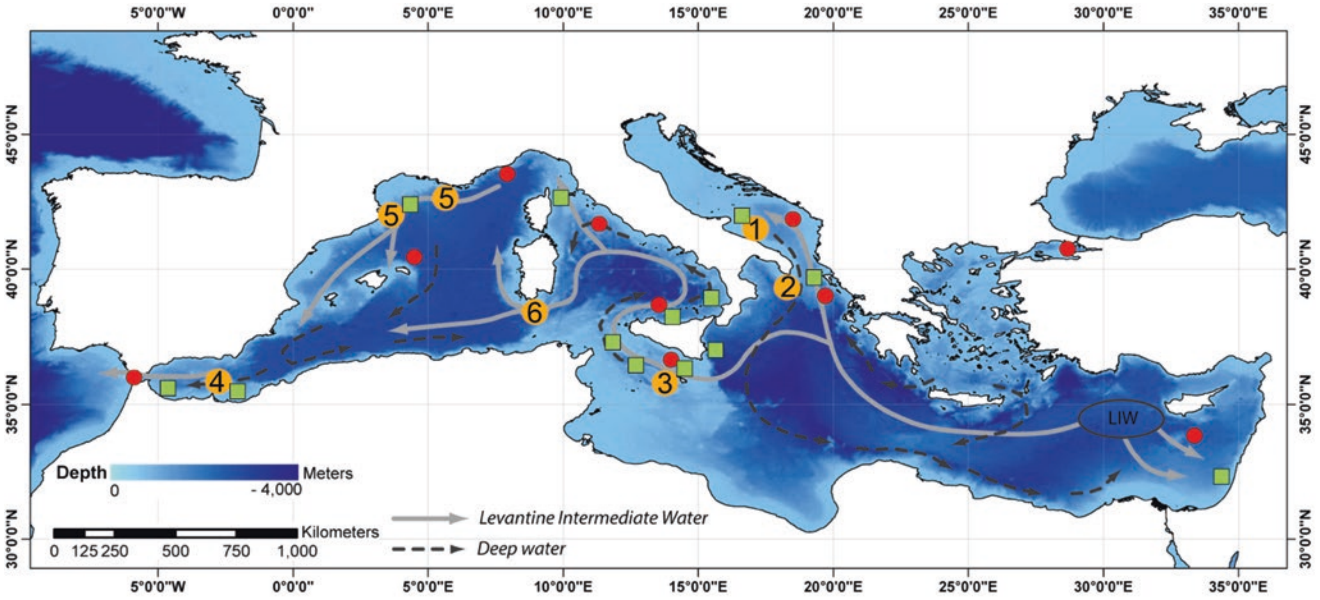

Fig. 4.2 Map of the Mediterranean Sea showing a simplified scheme of water circulation with respect to Levantine Intermediate Water (LIW) and deep water. Rectangles indicate areas with contourite deposits discussed in the text. Main cold water coral (CWC) provinces are identified by numbers: 1 = Bari Canyon; 2 = Santa Maria di Leuca; 3 = South Malta; 4 = Melilla; 5 = Gulf of Lion; 6 = South Sardinia. Red dots refer to minor occurrences of live CWC. (Modified from Taviani et al. 2016. With permission from © Elsevier)

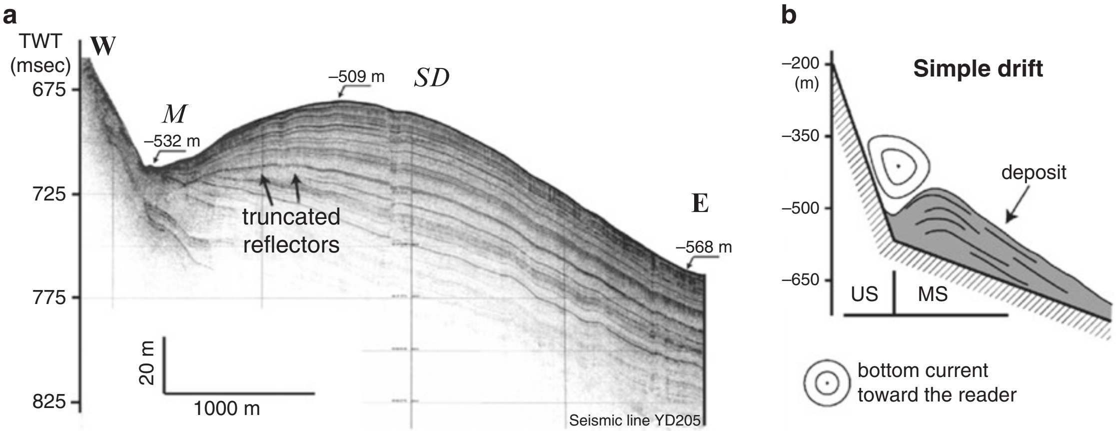

Fig. 4.3 Bottom-current deposit along the slope of the SW Adriatic Margin. (**a**) Chirp-sonar profile showing a separated drift (SD) rimmed, upslope, by a well-defined moat (M). (**b**) Schematic representation of the relationship between bottom-current deposits, erosional areas, changes in slope gradient and seafloor roughness. (From Verdicchio and Trincardi (2006); with permission from © Elsevier)

2008a). In fact, bottom currents are known to construct large accumulations of sediments which vary greatly in location, morphology, size, sediment patterns, construction mechanisms and controls (Faugères and Stow 2008). Typically, contourite drifts have an along-slope, elongated mounded shape, and an adjacent concave moat (Rebesco and Stow 2001). The oceanic drifts (Fig. 4.4) can be more than 100 km wide, several hundreds of kilometres long, up to 2 km thick and have a relief of up to 1.5 km (Rebesco et al. 2014). Their areal extension ranges from *ca.* 100 km^2 (small patch drifts) to >100,000,000 km^2 (giant elongated drifts). As a consequence of shallow water margin physiography and bottom-water circulation, Mediterranean contourite drifts are generally smaller in size and encompassing a shorter deposition interval.

In addition, various depositional and erosional bedforms are generated by bottom currents (Stow et al. 2013). They are highly variable in terms of sediment composition, morphology and dimension, from decimetres to kilometres (Wynn and Masson 2008). The detection of bedforms can be important for the reconstruction of bottom-current velocity (Fig. 4.5) in absence of direct oceanographic measurements (Stow et al. 2009). Contourite deposits vary widely in their lithology, grain size and composition (Shanmugam 2006,

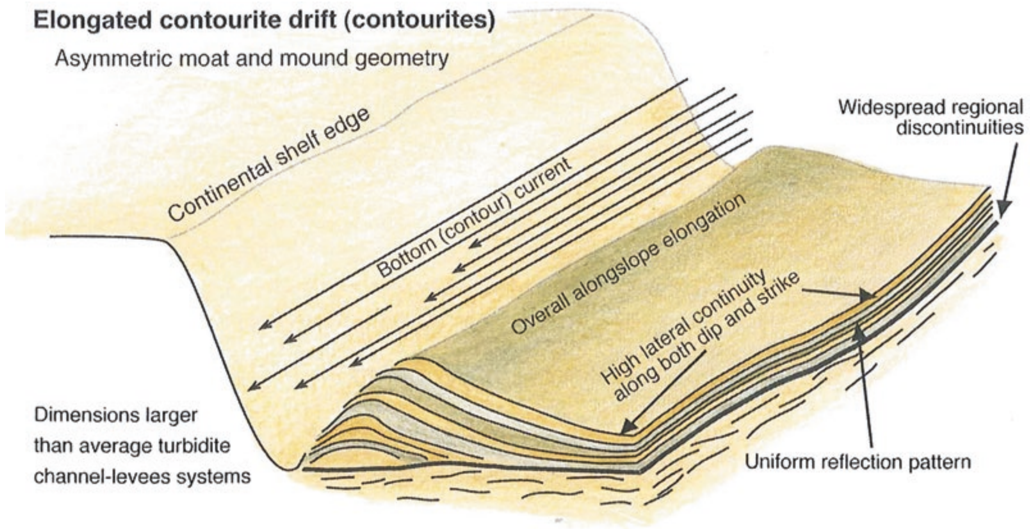

Fig. 4.4 Schematic model showing ideal, large-scale characteristics of oceanic contourite drifts and channel-levee systems. (From Rebesco et al. (2014); with permission from © Elsevier)

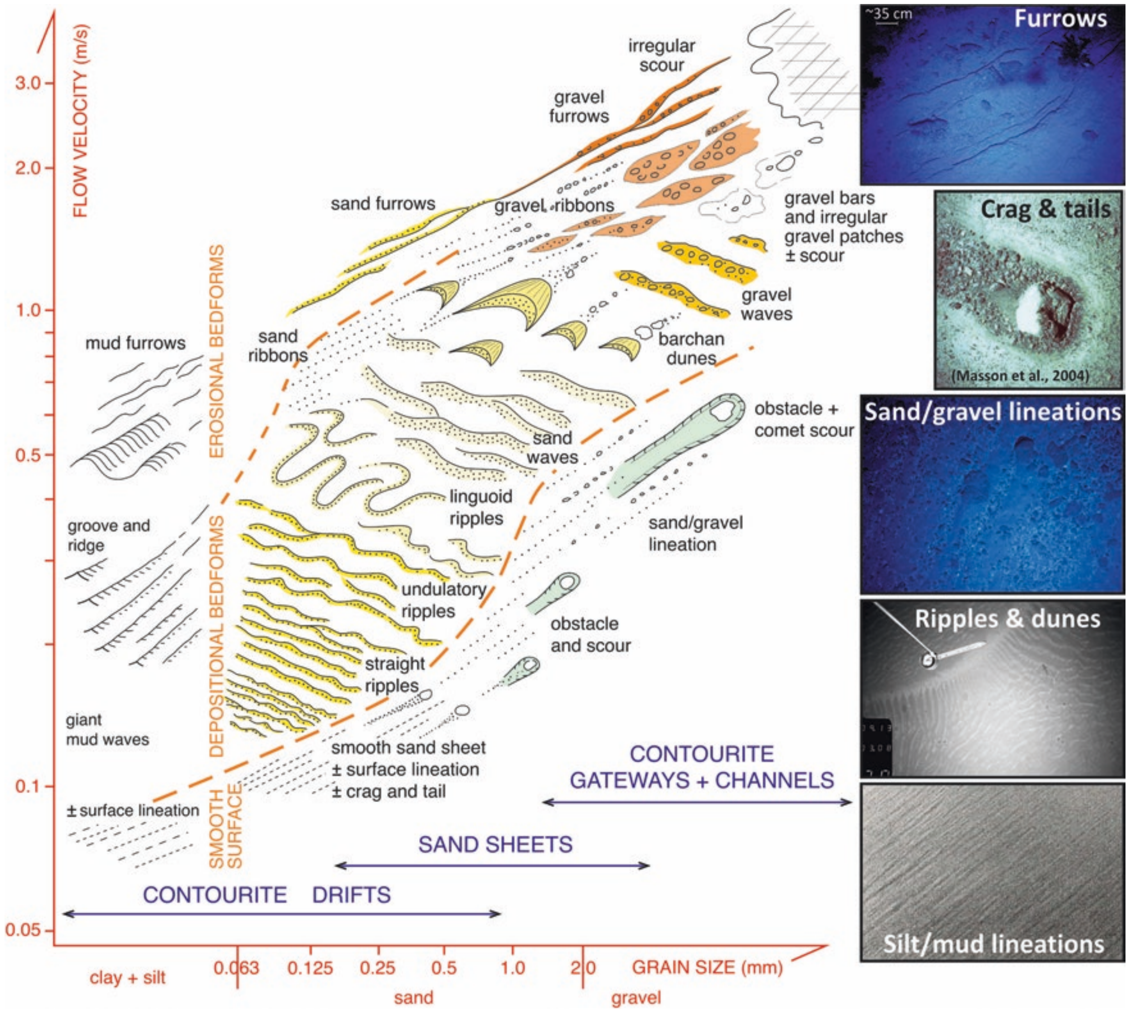

Fig. 4.5 Bedform-velocity matrix for deep-water bottom current systems, showing a schematic representation of bedforms in function of mean grain size of sediment versus flow velocity at or near the seafloor. The matrix was obtained using a large amount of data and has a general validity for all marine basins, including the Mediterranean Sea. (From Rebesco et al. (2014); with permission from © Elsevier)

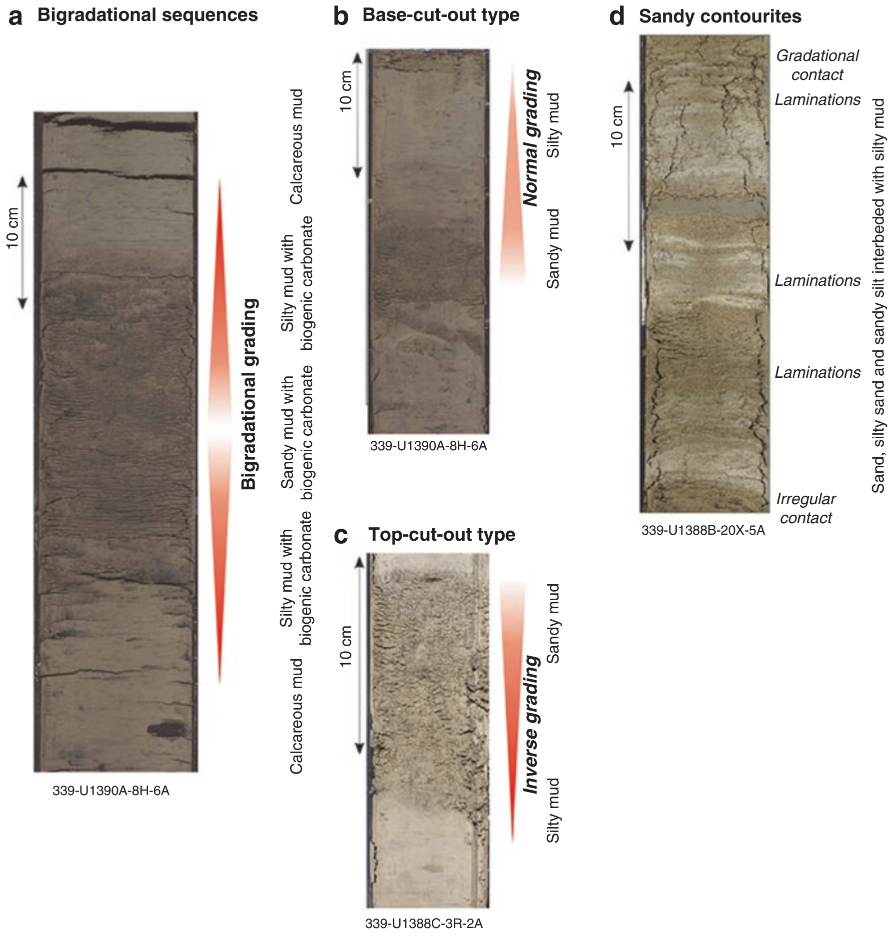

Fig. 4.6 Examples of the principal sedimentary facies for the contourites recovered during IODP Expedition 339 in the Gulf of Cádiz under the influence of the Mediterranean Outflow Water (MOW). (From © Hernández-Molina et al. (2013))

2013; Stow et al. 1996, 1998, 2002b; Stow and Faugères 2008). Most bottom-current deposits show a characteristically mixed composition, including biogenic, terrigenous, volcanoclastic and authigenic components (Stow et al. 2008). Most commonly, contourite deposits (Fig. 4.6) are rather poorly sorted, mud-rich, intensively bioturbated, interlayered with thin fine-grained sandy/silty beds, and show a certain kind of rhythmic stripes (Stow et al. 2002b). Less commonly, sandy contourite deposits have been reported, e.g. in the Gulf of Cádiz (Hanquiez et al. 2007; Hernández-Molina et al. 2014). Finally, both sandy and muddy contourite deposits are relatively frequently associated with CWC habitats (Fig. 4.7; Huvenne et al. 2009; Savini and Corselli 2010; Martorelli et al. 2011; Van Rooij et al. 2011; Henriet et al. 2014; Hebbeln et al. 2015, 2016).

4.4 Currents and Ecosystemic Response

Both contourites and CWCs are dependent from hydrodynamism. Bottom currents are, in fact, one important factor controlling deep-water ecosystems, including CWCs (Van Rooij et al. 2007a; Huvenne et al. 2009; Hebbeln et al. 2016).The CWCs, as sessile suspension feeders, depend on bottom currents delivering food particles (Frederiksen et al. 1992; White et al. 2005; Duineveld et al. 2007). In fact, the likelihood for a coral to catch food particles sinking through the water column (Fig. 4.8) is appreciably enhanced when their trajectory is sub-horizontal in response to the action of a sideways bottom current flow (Dorschel et al. 2007; Davies et al. 2009). Furthermore, if persistent over time, they also help promoting soft sediment induration and lithification turning into firm and hardgrounds thus producing substrates eventually suitable for coral colonisation (Allouc 1990; Remia et al. 2004; Toscano and Raspini 2005; Noé et al. 2006; Conti et al. 2013). Finally, currents may act as conveyor belts for the coral propagules ensuring their dissemination over long distances (Henry et al. 2014). As a matter of fact, prospering CWCs are mostly linked to a vigorous bottom water regime (Van Rooij et al. 2007b; Freiwald et al. 2004, 2009; Hebbeln et al. 2014, 2016; Wienberg and Titschack 2017; Taviani et al. 2016).

Contourites and CWCs are often found in association when subject to dynamic current regimes in shallow to intermediate water depths. In the Atlantic Ocean, Hebbeln et al. (2016) found a clear relationship between contourite sedi-

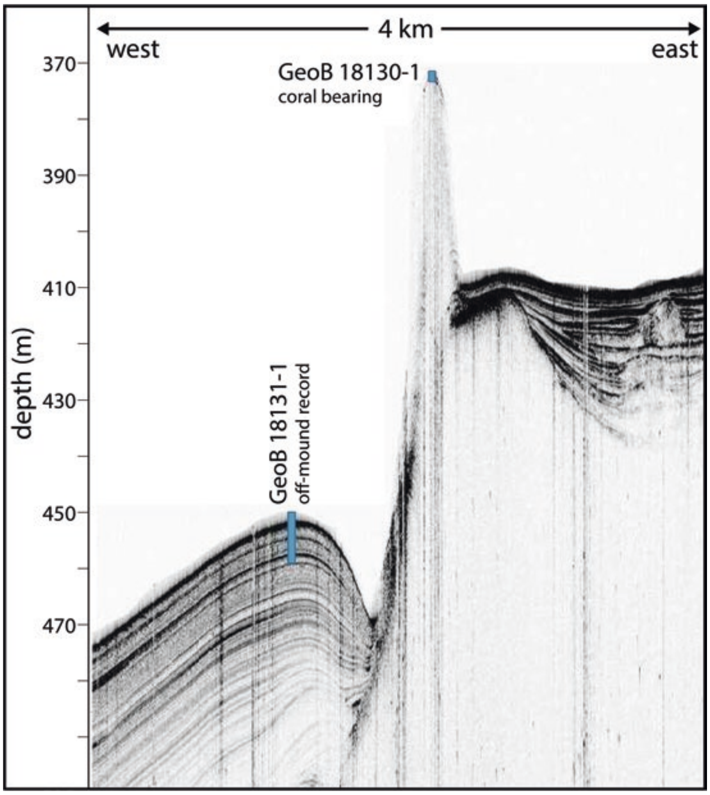

Fig. 4.7 PARASOUND profile across the western rim of the West Melilla Cold-Water Coral Province showing a sediment drift (sampled in core GeoB 18131-1) adjacent to a Cold-Water Coral mound structure (sampled in core GeoB 18130-1). Further to the east a buried Cold-Water Coral mound also appears. (From © Hebbeln et al. (2015))

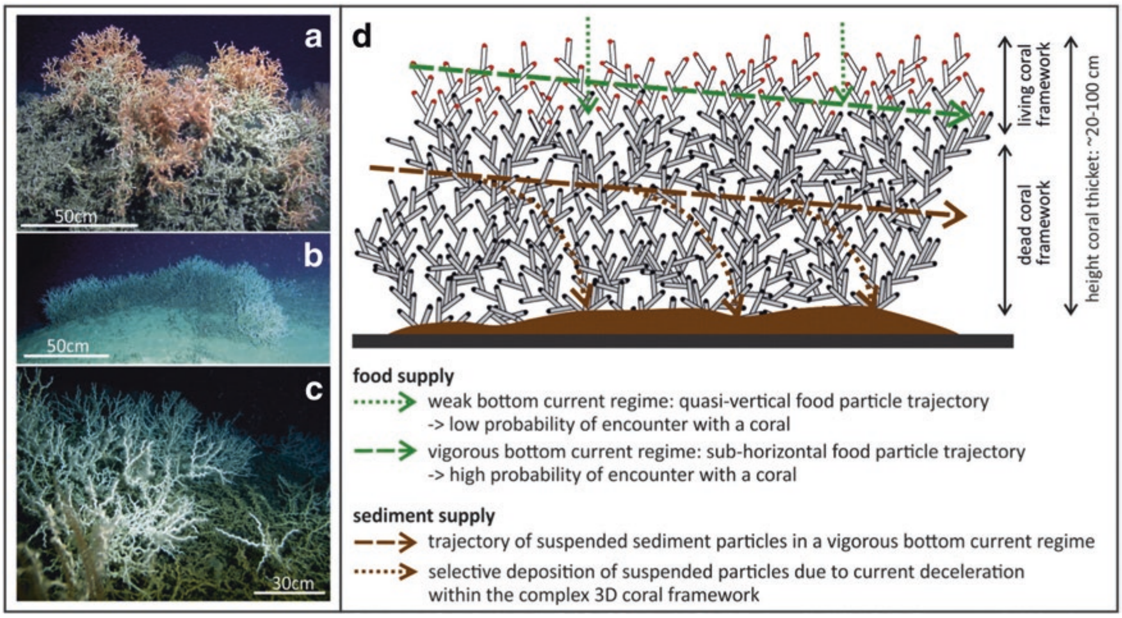

Fig. 4.8 Cold-water coral (CWC) and bottom current interaction. (a–c) CWC framework showing the transition from the living part of the CWC colony growing on top of dead coral framework. See examples from the Irish margin (**a**) and the Campeche margin off Mexico (**b** and **c**). (**d**) Sketch indicating (i) the increasing probability of food particles to be caught by a coral with increasing bottom currents (green arrows) and (ii) the baffling effect of the CWC framework on suspended sediment particles transported along with the bottom currents (brown arrows). (From Hebbeln et al. (2016) with permission from © Elsevier)

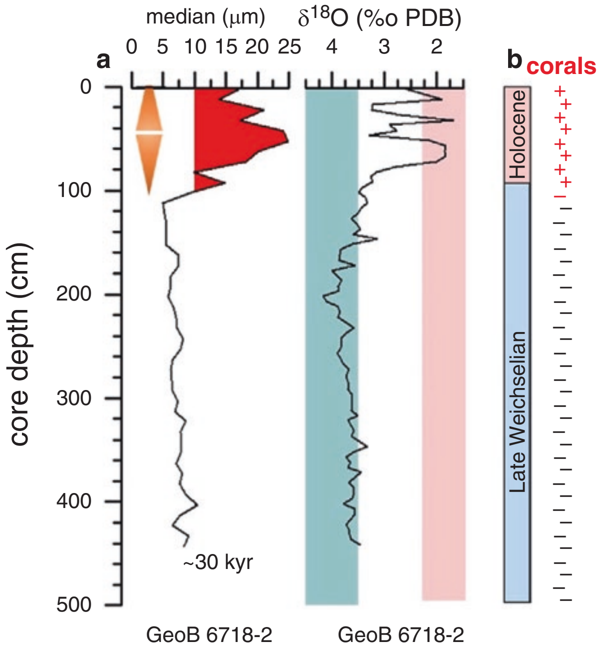

Fig. 4.9 Example of relationship between contourites and coral growth on the Irish margin. (**a**) Median grain-size (showing a Holocene bigradational grading typical of contourite facies; orange arrows) and stable oxygen isotope data (core GeoB 6718–2 in a contourite setting close to Propeller Mound, Porcupine Seabight, Dorschel et al. 2005). (**b**) Regional pattern of the temporal occurrence of cold-water corals along the Irish margin (Frank et al. 2011) with coral growth likely linked to Holocene strong bottom currents, as shown by increased grain-size in (**b**). (From Hebbeln et al. (2016) with permission from © Elsevier)

mentation and CWCs during the Holocene (Fig. 4.9). Of course, this is true below a certain flow velocity threshold, but when the bottom current circulation becomes too vigorous it starts to be erosive and destructive. Contourites are, however, much more widespread than CWC occurrences since the latter are dependent also from productivity in addition to dynamic current regimes.

On the one hand, contourites facies, inferred to reflect long-term changes in the bottom current strength (Stow and Faugères 2008), are valuable high-resolution paleo-archives of climate and environmental changes (Viana and Rebesco 2007; Rebesco et al. 2014). On the other hand, the aragonitic coral skeleton is equally archiving relevant palaeoceanographic information, which can be decoded through opportune geochemical techniques (Cheng et al. 2000; Adkins et al. 2003; Rüggeberg et al. 2008; Montagna et al. 2005, 2011, 2014; López Correa et al. 2010; McCulloch et al. 2012; Robinson et al. 2014; Montagna and Taviani, this volume). In fact, the application of precise U-series and 14C dating to Mediterranean CWC, and trace and minor element geochemistry has already allowed to disclose major variations in their distribution and paleoceanographic contour current conditions in the late Pleistocene to present (Montagna et al. 2006; McCulloch et al. 2010; Fink et al. 2012, 2015). A combined analysis of associated contourites and CWCs may provide the opportunity for a comprehensive understanding of past changes in both climatic and environmental conditions (Hebbeln et al. 2016).

4.5 CWC Establishment

Twenty years plus of research devoted to the study of CWC in the Mediterranean basin permits a comprehensive overview of the main traits of CWC spatio-temporal colonisation in this basin. At present, a number of healthy CWC sites have been identified in the central and western Mediterranean (Southern Adriatic, Northern Ionian, Strait of Sicily, South Sardinian, Ligurian-Provencal-Catalan canyons, Alborán), together with sparse occurrences (Freiwald et al. 2009; Orejas et al. 2009; Vertino et al. 2010; Savini et al. 2010, 2014; Taviani et al. 2011a, 2015, 2016; Madurell et al. 2012; Gori et al. 2013; Angeletti et al. 2014; Fanelli et al. 2017; Wienberg and Titschack 2017; Altuna and Poliseno, this volume; Chimienti et al., this volume; Vertino et al., this volume). The major CWC provinces (*sensu* Taviani et al. 2011a) appear to be on the main track of the LIW (Freiwald et al. 2009; Fink et al. 2015; Taviani et al. 2015, 2016).

The current knowledge suggests that substantial CWC growth took place in the Mediterranean since the Pliocene, after the Messinian Salinity Crisis (Taviani et al. 2005a; Vertino et al. 2014, this volume; Freiwald, this volume). Extant CWC of Atlantic affinity (i.e., the highly emblematic *Lophelia pertusa, Madrepora oculata, Desmophyllum dianthus*) are widespread in the basin since the middle Pleistocene at least, but their spatio-temporal occurrence, persistence or decline in the Mediterranean is marked by regional or local circumstances. For instance, such CWC displayed a basin-wide distribution during the late Pleistocene that included the eastern Basin (Taviani et al. 2011b), but then suffered important regional setbacks driving to their decline or demise. Climatically-driven factors evoked to have impacted on Mediterranean CWC survival are silting (Remia and Taviani 2005; McCulloch et al. 2010), nutrients (Montagna et al. 2006) oxygen (Fink et al. 2012), temperature (McCulloch et al. 2010), productivity (Fink et al. 2013) or their interaction. Whatever is backing the past, present and future history of Mediterranean CWC, one basic tenet is the role of oceanography, what includes the whole current system that is not stable over time since responding to climatic forcers. Sortable silt particle-size data reveal that the Mediterranean intermediate circulation fluctuated on Milankovitch to millennial time-scales between cold / faster (and well-ventilated and deepening) at time of climate degradation (Toucanne et al. 2012). The development of contourite drifts in the Tirrenian and Ionian seas was enhanced after the Middle Pleistocene Transition (700–900 kyr) (Miramontes et al. 2016; Rebesco et al., in prep). The LIV velocity changed in the past with faster bottom currents and greater accumulation of fine sediment during cold periods and sea level low stands (Miramontes et al. 2016). Neodymium isotopic composition record from intermediate depths in the western Mediterranean Sea supports a vigorous deep overturning with a decrease of the deep-water intensity afterward (Dubois-Dauphin et al. 2017). Also suggests that at about 8.7 ka BP western-sourced intermediate water likely replaced LIW that was no longer produced (or heavily reduced) in the eastern basin, potentially supporting a reversal of the Mediterranean circulation.

Coral mounds in the Mediterranean are often represented by small-relief expressions, probably one or few generations of coral growth, or by the colonisation of pre-existing 'mounded' features. This is the case of CWC growth at Santa Maria di Leuca CWC province in the northern Ionian Sea, where *M. oculata* and *L. pertusa* settle over submarine-slumped blocks (Taviani et al. 2005b; Savini and Corselli 2010; Savini et al. 2016; Bargain et al. 2017), or in the southern Adriatic Sea (Freiwald et al. 2009) and Alborán Sea (Wienberg, this volume). Larger features (tens to hundreds meters thick) coral mounds are known at various sites in the Atlantic Ocean (Reed 2002; Kenyon et al. 2003; van Weering et al. 2003; Mienis et al. 2007; Wheeler et al. 2006, 2011; Hebbeln et al. 2015, 2016; Wienberg and Titschack 2017). They are, however, uncommon in the Mediterranean Sea (Wienberg and Titschack 2017; Taviani et al., this volume; Wienberg, this volume). The closest example of Atlantic-type large mounds in the Mediterranean is found in the Alborán Sea (Hebbeln et al. 2009, 2015; Fink et al. 2013; Lo Iacono et al. 2014; Stalder et al. 2015; Wienberg and Titschack 2017). Factors controlling the aggradation of large coral mounds have been reviewed by Wienberg and Titschack (2017) but some aspects still need to be explored in greater detail in the future. Regarding a strict connection between contourites and CWC in the Mediterranean, it can be observed that a spatial relationship seems to date ascertained only at some sites. One clear example is that of the Melilla CWC Province where clusters of CWC mounds are associated with sediment drifts and contourite moats (Hebbeln et al. 2015, Fig. 4.7). Another case is for example that of the southwestern Adriatic Sea whose seabottom is profoundly impinged by bottom currents. A number of impressive bedforms is documented there at bathyal depths, encompassing mudwave fields, barcans and sediment drift mounds (Trincardi et al. 2007; Foglini et al. 2016). The area is site of important coral growth and comprehends the Bari Canyon CWC province thought to be influenced by the North Adriatic Dense (or Deep) Water (Taviani et al. 2015). However, corals like *M. oculata* and *D. dianthus* have been documented also outside the canyon system itself as sparse occurrences on hardgrounds and other suitable substrates under the influence of strong bottoms currents (Freiwald et al. 2009).

Although it has been highlighted the positive feedback of currents, that account for contourites and concomitantly sustain coral growth, it should be contemplated that actively drifting sediment may also cause their ultimate burial if established on their trajectory.

4.6 Conclusions and Future Perspectives

Contourite drift occurrences and major CWC provinces in the Mediterranean Sea appear to be largely controlled by the LIW. However, much is still to be understood since both fields of research are relatively young for the Mediterranean Sea, dating back to some 15 years. Further discoveries are hence expected regarding the likely co-occurrence of contourites and CWCs, and here is where further research is motivated.

It is predictable that substantial CWC growth is present in the area of the Corsica Channel where sediment drifts presence has been documented by Roveri (2002). Although not much CWC evidence has been produced thus far, *Madrepora oculata* does occur indeed alive in the area (M. Taviani, unpublished data), together with now-buried coral mounds (Remia and Taviani 2005). The Strait of Sicily is another area that deserves to be investigated in-depth for a potential relationship between sediment drift and CWC (Martorelli et al. 2011).

The LIW glacial-interglacial variability, observed in sedimentary core records (Toucanne et al. 2012; Miramontes et al. 2016; Dubois-Dauphin et al. 2017) documenting better ventilation and faster bottom water mass movement in cooler times with respect to the early Holocene, provides fertile ground to explore potential responses of CWC as well. Finally, the paleo-climate archives included in contourites and in CWC are synergic and both respond to oceanographic regimes driven by climatic forcing. Further research should hence address the match between the complementary information provided by the two different paleo-archives.

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References

Adkins JF, Boyle E, Curry WB, et al (2003) Stable isotopes in deep-sea corals and a new mechanism for “vital effects”. Geochim Cosmochim Acta 67:1129–1143

Allouc J (1990) Quaternary crusts on slopes of the Mediterranean Sea: a tentative explanation for their genesis. Mar Geol 94:205–238

Amelio M, Martorelli E (2008) Seismo-stratigraphic characters of paleocontourites along the Calabro-Tyrrhenian margin (Southern Tyrrhenian Sea). Mar Geol 252:141–149

Angeletti L, Taviani M, Canese S, et al (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Mediterr Mar Sci 15:225–238

Bargain A, Marchese F, Salvini A, et al (2017) Santa Maria di Leuca Province (Mediterranean Sea): an identification of suitable mounds for probable coral settlements using two statistical methods. Front Mar Sci 4:338. https://doi.org/10.3389/fmars.2017.00338

Bensi M, Rubino A, Cardin V, et al (2013) Structure and variability of the abyssal water masses in the Ionian Sea in the period 2003–2010. J Geophys Res-Oceans 118:931–943

Camerlenghi A, Crise A, Accerboni E, et al (1997) Ten-month observation of the bottom current regime across a sediment drif of the Pacific margin of the Antarctic peninsula. Antarct Sci 9:424–431

Cheng H, Adkins J, Edwards RL, et al (2000) U–Th dating of deep-sea corals. Geochim Cosmochim Acta 64:2401–2416

Conti MA, De Girasoli DE, Frezza V, et al (2013) Repeated events of hardground formation and colonisation by endo-epilithozoans on the sediment-starved pontine continental slope (Tyrrhenian Sea, Italy). Mar Geol 336:184–197

Davies AJ, Duineveld GCA, Lavaleye MSS, et al (2009) Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay reef complex. Limnol Oceanogr 54:620–629

Dorschel B, Hebbeln D, Foubert A, et al (2007) Hydrodynamics and cold-water coral facies distribution related to recent sedimentary processes at Galway mound west of Ireland. Mar Geol 244:184–195

Dorschel B, Hebbeln D, Rüggeberg A, et al (2005) Growth and erosion of a cold-water coral covered carbonate mound in the Northeast Atlantic during the late Pleistocene and Holocene. Earth Planet Sci Lett 233:33–44

Dubois-Dauphin Q, Montagna P, Siani G, et al (2017) Hydrological variations of the intermediate water masses of the western Mediterranean Sea during the past 20 ka inferred from neodymium isotopic composition in foraminifera and cold-water corals. Clim Past 13:17–37

Duineveld GCA, Lavaleye MSS, Bergman MJN, et al (2007) Trophic structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in relation to the near-bottom particle supply and current regime. Bull Mar Sci 81:449–467

Ercilla G, Juan C, Hernández-Molina FJ, et al (2016) Significance of bottom currents in deep-sea morphodynamics: an example from the Alboran Sea. Mar Geol 378:157–170

Fanelli E, Delbono I, Ivaldi R, et al (2017) Cold – water coral *Madrepora oculata* in the eastern Ligurian Sea (NW Mediterranean): historical and recent findings. Aquat Conserv Mar Freshw Ecosys 27:965. https://doi.org/10.1002/aqc.2751

Faugères JC, Stow DAV (2008) Contourite drifts: nature, evolution and controls. In: Rebesco M, Camerlenghi A (eds) Contourites, developments in sedimentology, vol 60. Elsevier, Amsterdam, pp 257–288

Fink HG, Wienberg C, De Pol-Holz R, et al (2015) Spatio-temporal distribution patterns of Mediterranean cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) during the past 14,000 years. Deep-Sea Res Part 1 Oceanogr Res Pap 103:37–48

Fink HG, Wienberg C, De Pol-Holz R, et al (2013) Cold-water coral growth in the Alboran Sea related to high productivity during the late Pleistocene and Holocene. Mar Geol 339:71–82

Fink HG, Wienberg C, Hebbeln D, et al (2012) Oxygen control on Holocene cold-water coral development in the eastern Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96

Foglini F, Campiani E, Trincardi F (2016) The reshaping of the south west Adriatic margin by cascading of dense shelf waters. Mar Geol 375:64–81

Frank N, Freiwald A, López Correa M, et al (2011) Northeastern Atlantic cold-water coral reefs and climate. Geology 39:743–746

Frederiksen R, Jensen A, Westerberg H (1992) The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing. Sarsia 77:157–171

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs, UNEP-WCMC biodiversity series 22. UNEP-WCMC, Cambridge, 86 pp

Gaudin M, Berné S, Jouanneau JM, et al (2006) Massive sand beds attributed to deposition by dense water cascades in the Bourcart canyon head, Gulf of Lions (northwestern Mediterranean Sea). Mar Geol 234:111–128

Giorgetti A, Crise A, Laterza R, et al (2003) Water masses and bottom boundary layer dynamics above a sediment drift of the Antarctic Peninsula Pacific margin. Antarct Sci 15:537–546

Gonthier E, Faugères JC, Stow DAV (1984) Contourite facies of the Faro Drift, Gulf of Cadiz. In: Stow DAV, Piper DJW (eds) Fine grained sediments, deepwater processes and facies. Geological Society special publication, vol 15. Geological Society, London, pp 275–291

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Hanquiez V, Mulder T, Lecroart P, et al (2007) High resolution seafloor images in the Gulf of Cadiz, Iberian margin. Mar Geol 246:42–59

Hebbeln D, Van Rooij D, Wienberg C (2016) Good neighbours shaped by vigorous currents: cold-water coral mounds and contourites in the North Atlantic. Mar Geol 378:171–185

Hebbeln D, Wienberg C, Beuck L, et al (2009) Report and preliminary results of RV POSEIDON cruise POS 385 ‘cold-water corals of the Alboran Sea (western Mediterranean Sea)’. Berichte, Fachbereich Geowissenschaften: Universität Bremen; Faro – Toulon, May 29–June 16, 273, 79 pp

Hebbeln D, Wienberg C, Bartels M, et al (2015) MoccoMeBo climate-driven development of Moroccan cold-water coral mounds revealed by MeBo-drilling: Atlantica vs. Mediterranean settings – Cruise MSM36 – February 18 – March 17, 2014 – Malaga (Spain) – Las Palmas (Spain). MARIA S. MERIAN-Berichte, MSM36, 47 pp, DFGSenatskommission für Ozeanographie, https://doi.org/10.2312/cr_msm36

Hebbeln D, Wienberg C, Wintersteller P, et al (2014) Environmental forcing of the Campeche cold-water coral province, southern Gulf of Mexico. Biogeosciences 11:1799–1815

Hecht A, Pinardi N, Robinson AR (1988) Currents, water masses, eddies and jets in the Mediterranean Levantine Basin. J Phys Oceanogr 18:1320–1353

Heezen BC, Hollister CD (1964) Deep sea current evidence from abyssal sediments. Mar Geol 1:141–174

Henriet JP, Hamoumi N, da Silva AC, et al (2014) Carbonate mounds: from paradox to world heritage. Mar Geol 352:89–110

Henry LA, Frank N, Hebbeln D, et al (2014) Global Ocean conveyor lowers extinction risk in the deep sea. Deep-Sea Res Part 1 Oceanogr Res Pap 88:8–16

Henry LA, Davies AJ, Roberts JM (2010) Beta diversity of cold-water coral reef communities off western Scotland. Coral Reefs 29:427–436

Hernández-Molina FJ, Llave E, Preu B (2014) Contourite processes associated to the Mediterranean outflow water after its exit from the Gibraltar Strait: global and conceptual implications. Geology 10:227–230

Hernández-Molina FJ, Stow DAV, Alvarez-Zarikian C, et al (2013) IODP expedition 339 in the Gulf of Cadiz and off West Iberia: decoding the environmental significance of the Mediterranean outflow water and its global influence. Sci Drill 16:1–11 https://doi.org/10.5194/sd-16-1-2013

Hollister CD, Heezen BC (1972) Geological effects of ocean bottom currents: western North Atlantic. In: Gordon AL (ed) Studies in physical oceanography, vol 2. Gordon and Breach, New York, pp 37–66

Hübscher C, Dullo C, Flögel S, et al (2010) Contourite drift evolution and related coral growth in the eastern Gulf of Mexico and its gateways. Int J Earth Sci (Geol Rundsch) 99:191–206

Hüneke H, Stow DAV (2008) Identification of ancient contourites: problems and palaeoceanographic significance. In: Rebesco M, Camerlenghi A (eds) Contourites, developments in sedimentology, vol 60. Elsevier, Amsterdam, pp 323–344

Huvenne VAI, Van Rooij D, De Mol B, et al (2009) Sediment dynamics and palaeo-environmental context at key stages in the challenger cold-water coral mound formation: clues from sediment deposits at the mound base. Deep-Sea Res Part 1 Oceanogr Res Pap 56:2263–2280

Kenyon NH, Akhmetzhanov AM, Wheeler AJ, et al (2003) Giant carbonate mud mounds in the southern Rockall trough. Mar Geol 195:5–30

Lascaratos A, Roether W, Nittis K, et al (1999) Recent changes in deep water formation and spreading in the eastern Mediterranean Sea: a review. Prog Oceanogr 44:5–36

Lo Iacono C, Gracia E, Ranero C, et al (2014) The West Melilla cold water coral mounds, eastern Alboran Sea: morphological characterization and environmental context. Deep-Sea Res Part 2 Top Stud Oceanogr 99:316–326

López Correa M, Montagna P, Vendrell-Simón B, et al (2010) Stable isotopes (δ18O and δ13C), trace and minor element compositions of recent scleractinians and last glacial bivalves at the Santa Maria di Leuca deep-water coral province, Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:471–486

Madurell T, Orejas C, Requena S, et al (2012) The benthic communities of the cap de Creus canyon. In: Würtz M (ed) Mediterranean submarine canyons: ecology and governance. Gland, Switzerland and Malaga, Spain, IUCN, pp 123–132

Marani M, Argnani A, Roveri M, et al (1993) Sediment drifts and erosion surfaces in the Central Mediterranean: seismic evidence of bottom-current activity. Sediment Geol 82:207–220

Martín-Chivelet J, Fregenal-Martínez MA, Chacón B (2008) Traction structures in contourites. In: Rebesco M, Camerlenghi A (eds) Contourites, developments in sedimentology, vol 60. Elsevier, Amsterdam, pp 159–182

Martorelli E, Petroni G, Chiocci FL (2011) Contourites offshore Pantelleria Island (Sicily Channel, Mediterranean Sea): depositional, erosional and biogenic elements. Geo-Mar Lett 31:481–493

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the younger Dryas. Earth Planet Sc Lett 298:143–152

McCulloch M, Trotter J, Montagna P, et al (2012) Resilience of cold-water scleractinian corals to ocean acidification: boron isotopic systematics of pH and saturation state up-regulation. Geochim Cosmochim Acta 87:21–34

Mienis F, de Stigter HC, White M, et al (2007) Hydrodynamic controls on cold-water coral growth and carbonate-mound development at the SW and SE Rockall trough margin, NE Atlantic ocean. Deep-Sea Res Part 1 Oceanogr Res Pap 54:1655–1674

Miller AR (1972) Speculation concerning bottom circulation in the Mediterranean Sea in. In: Stanley DJ (ed) The Mediterranean Sea: a natural sedimentation laboratory. Hutchinson and Ross, Dowden, pp 37–42

Millot C (2009) Another description of the Mediterranean Sea outflow. Prog Oceanogr 82:101–124

Miramontes E, Cattaneo A, Jouet G, et al (2016) The Pianosa contourite depositional system (northern Tyrrhenian Sea): drift morphology and Plio-quaternary stratigraphic evolution. Mar Geol 378:20–42

Montagna P, McCulloch M, Douville E, et al (2014) Li/Mg systematics in scleractinian corals: calibration of the thermometer. Geochim Cosmochim Ac 132:288–310

Montagna P, McCulloch M, Taviani M, et al (2006) Phosphorus in cold-water corals as a proxy for seawater nutrient chemistry. Science 312:1788–1791

Montagna P, McCulloch M, Taviani M, et al (2005) High-resolution trace and minor element compositions in deep-water scleractinian corals (*Desmophyllum dianthus*) from the Mediterranean Sea and the great Australian bight. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer-Verlag, Berlin, Heidelberg, pp 1109–1126

Montagna P, Silenzi S, McCulloch M, et al (2011) Marine climate archives and geochemical proxies: a review and future investigations on the Mediterranean Sea. In: Brugnoli E, Cavaretta G, et al (eds) Marine research at CNR, Dipartimento Terra e Ambiente, Consiglio Nazionale delle Ricerche, Roma, pp 809–822

Mutti E, Carminatti M (2012) Deep-water sands in the Brazilian offshore basins. AAPG Search and Discovery, Article 30219. http://www.searchanddiscovery.com/documents/2012/30219mutti/ndx_mutti.pdf

Noé S, Titschack J, Freiwald A, et al (2006) From sediment to rock: diagenetic processes of hardground formation in deep-water carbonate mounds of the NE Atlantic. Facies 52:183–208

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the cap de Creus canyon (North-Western Mediterranean): spatial distribution, density and antropogenic impact. Mar Ecol Progr Ser 397:37–51

Pellegrini C, Maselli V, Trincardi F (2016) Pliocene–Quaternary contourite depositional system along the south-western Adriatic margin: changes in sedimentary stacking pattern and associated bottom currents. Geo-Mar Lett 36:67–79

Pinardi N, Masetti E (2000) Variability of the large scale general circulation of the Mediterranean Sea from observations and modelling: a review. Palaeogeogr Palaeoclimatol Palaeoecol 158:153–173

Rebesco M (2005) Contourites. In: Selley RC, Cocks LRM, Plimer IR (eds) Encyclopedia of geology. Elsevier, Oxford, pp 513–527

Rebesco M (2014) Contourites. In: Elias SA (ed) Reference module in earth systems and environmental sciences. Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.09094-1

Rebesco M, Camerlenghi A (eds) (2008) Contourites, developments in sedimentology. Elsevier, Amsterdam, 60:3–10

Rebesco M, Stow DAV (2001) Seismic expression of contourites and related deposits: a preface. Mar Geophys Res 22:303–308

Rebesco M, Hernández-Molina J, van Rooij D, et al (2014) Contourites and associated sediments controlled by deep-water circulation processes: state-of-the-art and future considerations. Mar Geol 352:111–154

Reed JK (2002) Deep-water *Oculina* coral reefs of Florida: biology, impacts, and management. Hydrobiologia 471:43–55

Reeder MS, Rothwell G, Stow DAV (2002) The Sicilian gateway: anatomy of the deep-water connection between east and West Mediterranean basins. In: Stow DAV, Pudsey CJ, Howe JA, et al (eds) Deep-water contourite systems: modern drifts and ancient series, seismic and sedimentary characteristics. Geological Society Memoir, vol 22. The Geological Society, London, pp 171–190

Remia A, Montagna P, Taviani M (2004) Submarine diagenetic products on the sediment-starved Gorgona slope, Tuscan archipelago (Tyrrhenian Sea). Chem Ecol 20:131–153

Remia A, Taviani M (2005) Shallow-buried Pleistocene *Madrepora*-dominated coral mounds on a muddy continental slope, Tuscan archipelago, NE Tyrrhenian Sea. Facies 50:419–425

Robinson AR, Leslie WG, Theocharis A, et al (2001) Mediterranean Sea circulation. In: Steele JH et al (eds) Encyclopedia of ocean sciences. Academic Press, Boston, pp 1689–1706

Robinson LF, Adkins JF, Frank N (2014) The geochemistry of deep-sea coral skeletons: a review of vital effects and applications for palaeoceanography. Deep-Sea Res Part 2 Top Stud Oceanogr 99:184–198

Roveri M (2002) Sediment drifts of the Corsica Channel, northern Tyrrhenian Sea. In: Stow DAV, Pudsey CJ, Howe JA, et al (eds) Deep-water contourite systems: modern drifts and ancient series, seismic and sedimentary characteristics. Geological Society Memoir, vol 22. The Geological Society, London, pp 191–208

Rubino A, Falcini F, Zanchettin D (2012) Abyssal undular vortices in the eastern Mediterranean basin. Nat Commun 3:1836. https://doi.org/10.1038/ncomms1836

Rüggeberg A, Fietzke J, Liebetrau V (2008) Stable strontium isotopes (δ88/86Sr) in cold-water corals—a new proxy for reconstruction of intermediate ocean wáter temperatures. Earth Planet Sci Lett 269:570–575

Savini A, Corselli (2010) High-resolution bathymetry and acoustic geophysical data from Santa Maria di Leuca cold water coral province (Northern Ionian Sea-Apulian continental slope). Deep-Sea Res Part 2 Top Stud Oceanogr 57:326–344

Savini A, Corselli C, Loubrieu B, et al (2010) Deep sea habitat mapping at the Sant Maria di Leuca cold water coral province: results from small to large scale seafloor mapping at one representative site. Rapp Comm Int Mer Medit 39:62

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108

Savini A, Marchese F, Verdicchio G (2016) Submarine slide topography and the distribution of vulnerable marine ecosystems: a case study in the Ionian Sea (Eastern Mediterranean). In: Lamarche G, Mountjoy J, Bull S, et al (eds) Submarine mass movements and their consequences: 7th international symposium, advances in natural and technological hazards research. Springer International Publishing, pp 163–170

Schattner U, Gurevich M, Kanari M, et al (2015) Levant jet system—effect of post LGM seafloor currents on Nile sediment transport in the eastern Mediterranean. Sediment Geol 329:28–39

Shanmugam G (2006) Deep-water processes and facies models: implications for sandstone petroleum reservoirs: 5 (handbook of petroleum exploration and production). Elsevier Science, 496 pp

Shanmugam G (2008) Deep-water bottom currents and their deposits. In: Rebesco M, Camerlenghi A (eds) Contourites, developments in sedimentology, vol 60. Elsevier, Amsterdam, pp 59–81

Shanmugam G (2013) New perspectives on deep-water sandstones: implications. Pet Explor Dev 40:316–324

Somoza L, Medialdea T, León R, et al (2012) Structure of mud volcano systems and pockmarks in the region of the Ceuta Contourite depositional system (western Alborán Sea). Mar Geol 332–334:4–26

Stalder C, Vertino A, Rosso A, et al (2015) Microfossils, a key to unravel cold-water carbonate mound evolution through time: evidence from the eastern Alboran Sea. PLoS One 10:e0140223

Stow DAV, Faugères JC (2008) Contourite facies and the facies model. In: Rebesco M, Camerlenghi A (eds) Contourites, developments in sedimentology, vol 60. Elsevier, Amsterdam, pp 223–256

Stow DAV, Hernández-Molina FJ, Llave E, et al (2013) The Cadiz Contourite Channel: Sandy contourites, bedforms and dynamic current interaction. Mar Geol 343:99–114

Stow DAV, Hernández-Molina FJ, Llave E, et al (2009) Bedform-velocity matrix: the estimation of bottom current velocity from bedform observations. Geology 37:327–330

Stow DAV, Hunter S, Wilkinson D, et al (2008) The nature of contourite deposition. In: Rebesco M, Camerlenghi A (eds) Contourites, developments in sedimentology, vol 60. Elsevier, Amsterdam, pp 143–156

Stow DAV, Pudsey CJ, Howe JA, et al (eds) (2002a) Deep-water contourite systems: modern drifts and ancient series, seismic and sedimentary characteristics. Geological Society Memoir, vol 22. The Geological Society, London

Stow DAV, Ogawa Y, Lee IT, et al (2002b) Neogene contourites, Miura-Boso forearc basin, SE Japan. In: Stow DAV, Pudsey CJ, Howe JA, et al (eds) Deep-water contourite systems: modern drifts and ancient series, seismic and sedimentary characteristics. Geological Society Memoir, vol 22. The Geological Society, London, pp 409–419

Stow DAV, Reading HG, Collinson J (1996) Deep seas. In: Reading HG (ed) Sedimentary environments, 3rd edn. Blackwell Science, Oxford, pp 395–453

Stow DAV, Taira A, Ogawa Y, et al (1998) Volcaniclastic sediments, process interaction and depositional setting of the Mio-Pliocene Miura group, SE Japan. Sediment Geol 115:351–381

Taviani M, Angeletti L, Antolini B, et al (2011a) Geo-biology of Mediterranean deep-water coral ecosystems. In: Brugnoli E, Cavaretta G, et al (eds) Marine research at CNR, Dipartimento Terra e Ambiente, Consiglio Nazionale delle Ricerche, Roma, pp 705–720

Taviani M, Vertino A, López Correa M, et al (2011b) Pleistocene to recent scleractinian deep-water corals and coral facies in the eastern Mediterranean. Facies 57:579–603

Taviani M, Angeletti L, Beuck L, et al (2016) On and off the beaten track: megafaunal sessile life and Adriatic cascading processes. Mar Geol 375:146–160

Taviani M, Angeletti L, Canese S, et al (2015) The "Sardinian cold-water Coral Province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61. https://doi.org/10.1016/j.dsr2.2015.12.008

Taviani M, Freiwald A, Zibrowius H (2005a) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 37–156

Taviani M, Remia A, Corselli C, et al (2005b) First geo-marine survey of living cold-water *Lophelia* reefs in the Ionian Sea (Mediterranean basin). Facies 50:409–417

Toscano F, Raspini A (2005) Epilithozoan fauna associated with ferro-manganese crustgrounds on the continental slope segment between Capri and li Galli Islands (bay of Salerno, northern Tyrrhenian Sea, Italy). Facies 50:427–441

Toucanne S, Jouet G, Ducassou E, et al (2012) A 130,000-year record of Levantine intermediate water flow variability in the Corsica trough, western Mediterranean Sea. Quat Sci Rev 33:55–73

Trincardi F, Foglini F, Verdicchio G, et al (2007) The impact of cascading currents on the Bari canyon system, SW-Adriatic margin (Central Mediterranean). Mar Geol 246:208–230

Van Rooij D, Blamart D, De Mol L (2011) Cold-water coral mounds on the pen Duick escarpment, gulf of Cadiz: the MiCROSYSTEMS project approach. Mar Geol 282:102–117

Van Rooij D, Blamart D, Richter T, et al (2007a) Quaternary sediment dynamics in the Belgica mound province, porcupine Seabight: ice-rafting events and contour current processes. Int J Earth Sci 96:121–140

Van Rooij D, Blamart D, Kozachenko M, et al (2007b) Small mounded contourite drifts associated with deep-water coral banks, porcupine Seabight, NE Atlantic ocean. In: Viana AR, Rebesco M (eds) Economic and palaeoceanographic importance of contourite deposits. Geological Society Memoir, vol 276. The Geological Society, London, pp 225–244

van Weering TCE, de Haas H, Akhmetzanov AM, et al (2003) Giant carbonate mounds along the porcupine and SW Rockall trough margins. In: Mienert J, Weaver P (eds) European margin sediment dynamics: side-scan sonar and seismic images. Springer, Berlin, Heidelberg, pp 211–216

Verdicchio G, Trincardi F (2006) Short-distance variability in slope bed-forms along the southwestern Adriatic margin (Central Mediterranean). Mar Geol 234:271–292

Verdicchio G, Trincardi F (2008a) Shallow-water contourites. In: Rebesco M, Camerlenghi A (eds) Contourites, developments in sedimentology, vol 60. Elsevier, Amsterdam, pp 409–434

Verdicchio G, Trincardi F (2008b) Mediterranean shelf-edge muddy contourites: example from Gela and south Adriatic basins. Geo-Mar Lett 28:137–151

Verdicchio G, Trincardi F, Asioli A (2007) Mediterranean bottom-current deposits: an example from the southwestern Adriatic margin. In: Viana AR, Rebesco M (eds) Economic and palaeoceanographic significance of contourite deposits. Geological Society Memoir, vol 276. The Geological Society, London, pp 199–224

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396

Vertino A, Stolarski J, Bosellini F, et al (2014) Mediterranean corals through time: from Miocene to present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 257–274

Viana AR, Rebesco M, (Eds) (2007) Economic and palaeoceanographic significance of contourite deposits. Geological Society Memoir, vol 276. The Geological Society, London

Wheeler AJ, Beyer A, Freiwald A, et al (2006) Morphology and environment of cold-water coral carbonate mounds on the NW European margin. Int J Earth Sci 96:37–56

Wheeler AJ, Kozachenko M, Henry LA, et al (2011) The Moira mounds, small cold-water coral banks in the porcupine Seabight, NE Atlantic: part A—an early stage growth phase for future coral carbonate mounds? Mar Geol 282:53–64

White M, Mohn C, de Stigter H, et al (2005) Deep water coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall trough, NE Atlantic. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 503–514

Wienberg C, Titschack J (2017) Framework-forming scleractinian cold-water corals through space and time: a late quaternary North Atlantic perspective. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1–35

Wüst G (1961) On the vertical circulation of the Mediterranean Sea. Geophys Res 66:3261–3271

Wynn RB, Masson DG (2008) Sediment waves and bedforms. In: Rebesco M, Camerlenghi A (eds) Contourites, developments in sedimentology, vol 60. Elsevier, Amsterdam, pp 289–300

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals.

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals.

Freiwald A (this volume) Messinian salinity crisis: what happened to cold-water corals?

Hayes R, Schroeder K, Poulain PM, et al (this volume) Review of the circulation and characteristics of intermediate water masses of the Mediterranean--implications for cold-water coral habitats.

Montagna P, Taviani M (this volume) Mediterranean cold-water corals as paleoclimate archives.

Skliris N (this volume) The Mediterranean is getting saltier: from the past to the future.

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals.

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold water corals.

Wienberg C (this volume) A deglacial cold-water coral boom in the Alborán Sea: from coral mounds and species dominance.

Drop Chapter Messinian Salinity Crisis: What Happened to Cold-Water Corals?

5

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Abstract

The fate of bathyal coral communities prior, during and after the environmentally devastating Messinian Salinity Crisis is briefly reviewed. The Messinian Salinity Crisis has created a geologically short-termed but massive disruption to marine life in the Late Miocene Mediterranean Sea. First signs of deteriorating environmental conditions begun about 7.15 Ma ago with a successive reduction of water mass exchange between the open Atlantic Ocean the Mediterranean Sea and progressively diminishing deep-water ventilation in the remaining Mediterranean basins. The resulting deposition of three massive evaporite sequences causes a vivid debate until today on the degree of desiccation ranging from a complete dry-out to a much milder course of events in the Late Miocene marine realm. The sudden marine reflooding via the newly formed Gibraltar gateway at 5.33 Ma abruptly terminated the ecological crisis and gave way to fully marine conditions in the Mediterranean Sea. The preservation and the fate of bathyal corals during this event is fragmentary and still understudied. Existing knowledge indicate that most of the bathyal coral genera and species are present or re-appeared in the Early Pliocene (Zanclean) and that major losses in species richness appeared much later during the advent of the Pliocene.

Keywords

Cold-water corals · Messinian salinity crisis · Miocene · Pliocene · Bathyal

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Introduction

The fate of cold-water corals (CWC) thriving in bathyal environments during the advent of the Messinian Salinity Crisis (MSC) is poorly constrained and deserves appreciation. The MSC represents an extraordinary and extreme event that affected the whole Late Miocene Mediterranean Sea by the deposition of more than a million cubic kilometers of salt within probably less than 700 ka (CIESM 2008; Roveri et al. 2014a). Main trigger was a tectonically-driven continuous restriction of water exchange with the Atlantic Ocean through the former Betic and Rifean corridors, added by coeval climatic forcings and their feedbacks on sea-level fluctuations (Krijgsman et al. 1999). Since the introduction of the concept of the MSC by Selli (1954), the search for its causes and effects stimulated numerous geologic disciplines and research programs. The usually most considered MSC scenario implies high-amplitude sea-level oscillations in the range of about 1500 m of the Mediterranean Sea up to its complete desiccation ("shallow water – deep basin model" of Hsü et al. 1973).

However, even after 65 years of intense research, major questions remain unsolved and new discoveries open alternative thoughts and views (see Roveri et al. 2014a, b; 2016 and Vai 2016). The cataclysmic MSC paradigm is now challenged by an alternative scenario which suggests a "milder" MSC evolution by assuming the presence of a permanent water body in the Mediterranean during the entire MSC and the formation of subaqueous evaporite precipitation in the deep basins (Roveri et al. 2016 for review).

A major obstacle is a still unavailable comprehensive stratigraphic framework linking the physically disconnected onshore and offshore sedimentary sequences. Geophysical seismic explorations of MSC sequences which are buried under Plio-Quaternary sediments in the deep basins still await precise stratigraphic calibration and correlation through deep-sea drilling campaigns in the future.

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The Temporal Sequence of the MSC

The prelude of the Messinian evaporite deposition started with the narrowing of the two Atlantic-Mediterranean gateways, the Betic and the Rifean corridors, already in the Late Tortonian. Progressively restricted water exchange and shallowing depths led to a reduced circulation and a subsequent drop of deep-water ventilation in the Mediterranean short after the Tortonian-Messinian boundary at 7.15 Ma (Kouwenhoven et al. 2003; Seidenkrantz et al. 2000). Probably enhanced by increasing surface salinities, the calcareous plankton as well as deep-water foraminifer communities experienced a sudden drop in diversity at 6.7 Ma (Blanc-Valleron et al. 2002; Kouwenhoven et al. 2003; Sierro et al. 2003). The following stepwise disruption has led to three differentially developed main stages which characterise the MSC (CIESM 2008; Manzi et al. 2013; Roveri et al. 2014a, b, c): First, evaporates precipitated in shallow basins bordering the deep offshore main basins from 5.97 to 5.60 Ma. Second, evaporite deposition progressed towards the deepest depocenters and affected the main basins from 5.60 to 5.54 Ma (Roveri et al. 2016). The third stage started in shallow basins with selenite and laminar gypsum evaporates (Manzi et al. 2009) followed by a widespread shift to the Lago Mare deposits at 5.42 Ma (Roveri et al. 2008), fed by fresh- and brackish water supply from the surrounding Mediterranean hinterland and from Paratethyan seaways. The restricted-marine Messinian episode terminated abruptly at 5.33 Ma with the reflooding of the Mediterranean through the newly formed Strait of Gibraltar. This event marked the stratigraphic boundary to the Zanclean series of the Pliocene and brought back fully marine conditions within short time. However, there is an increasing body of evidence that marine incursions, indicated by fully marine fishes, already started along with the Lago Mare during the latest Messinian (Carnevale et al. 2006, 2008). This questions a complete isolation of the Mediterranean basins from marine influx during the whole course of the MSC and argues for at least periodical connections to the open ocean (Roveri et al. 2014b; Vai 2016).

The Impact of MSC on CWCs

Several authors have analysed the broad-scale fossil record of scleractinian corals including those which thrived in bathyal depths from Miocene to Pleistocene peri-Mediterranean outcrops and associated museum collections (Corselli 2001; Taviani et al. 2005; Vertino et al. 2014, this volume). The generic diversity of CWC show no significant changes when comparing pre-Messinian with Zanclean outcrops, whereas a more pronounced decline of CWC genera and species can be traced during the advent of the Plio-Pleistocene.

In general, bathyal CWC-bearing deposits in the Mediterranean pre-Messinian are poorly studied and provided so far punctuated information only. As today, the bathyal mud-dominated paleoenvironments provided habitat for mostly solitary CWC, whereas hard substrates facilitated the colonisation of colonial, or potentially constructional, CWC species.

Apparently, pre-Messinian CWC peaked in the Burdigalian-Langhian (20.44 to 15.97 Ma) with more than 30 genera, including the colonial framework constructors *Lophelia, Madrepora* and *Enallopsammia*, known from bathyal marl deposits of the Turin Hills, northern Italy (summarised in Vertino et al. 2014 and further references therein, Fig. 5.1a). A circalittoral to upper bathyal example of a Late Tortonian CWC occurrence is preserved in the Calcare di Mendicino of the Amanthea Basin, Calabria, Italy (Mastandrea et al. 2002). This coral bank, 5–8 m thick and approximately several hundred meters wide, was constructed solely by *Oculina* and *Dendrophyllia* and intercalated with subaqueous dune sands deposited in a vigorous current regime of a paleo-strait. Other, poorly known but rich dendrophyllid coral assemblages are preserved from deeper water deposits of Serravallian-Tortonian (13.65–7.25 Ma) age in the Salento area (Vertino, personal communication and Fig. 5.1b). The only intra-Messinian example displaying a hard-substrate bathyal CWC environment is preserved in sedimentary dikes at Carboneras, eastern Betics, Spain, known as Brèche Rouge (Barrier et al. 1991; Montenat et al. 2000). These sediment pockets contain a snapshot of a bathyal CWC assemblage comprising scleractinians (*Madrepora, Dendrophyllia, Desmophyllum, Caryophyllia, Javania, Balanophyllia, Flabellum*), gorgonians and stylasterids.

Assumingly, along with the progressive reduction of deep-water ventilation in the Mediterranean basins due to a disruption of water exchange with the Atlantic, the fidelity and diversity of benthic organisms became negatively affected by the spread of stagnant and oxygen-poor deep water conditions. In some basins, the lack of deep-water oxygenation gave way to the deposition of euxinic black shales during the advent of the MSC. Such a devastating evolution that has fostered the local extinction of benthic life is documented in the hemipelagic Sant'Agata Fossili Formation, a bathyal mud paleoenvironment from the Piedmont Basin (Corselli 2001; Dela Pierre et al. 2011).

Even under the assumption of a permanent water body scenario during the MSC in the Mediterranean (see Roveri et al. 2016), available seawater chemistry data based on strontium isotopes (Flecker et al. 2002; Roveri et al. 2014c) show at least during the second and third MSC stages a

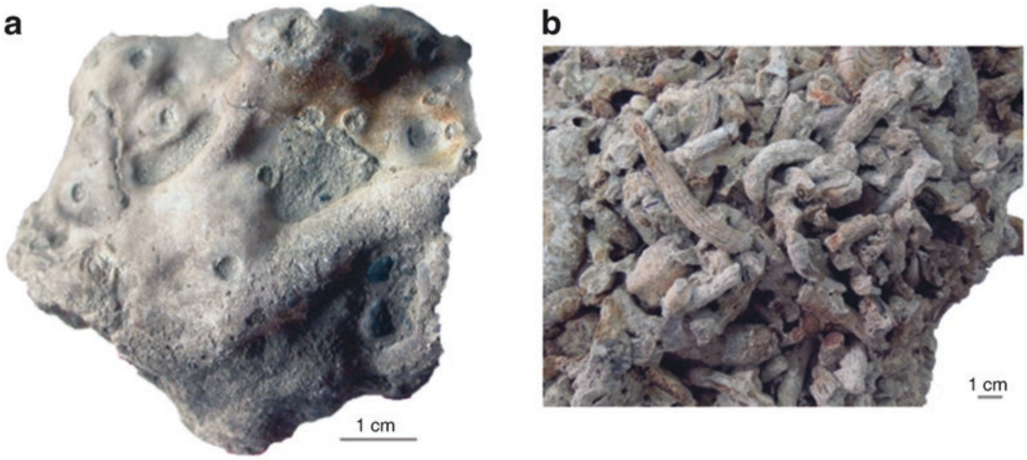

Fig. 5.1 (**a**) *Madrepora oculata* of Early-Middle Miocene (Burdigalian-Langhian) age from Baldissero, Turin Hills, Italy (identified by A. Vertino from the Museum of Natural History Collection, University of Torino). (**b)** Dendrophyllid rudstone of Middle-Upper Miocene (Serravallian-Tortonian) age from Salento Peninsula, Italy (identified by A. Vertino from the University of Modena & Reggio Emilia Collection). (Images courtesy of © Agostina Vertino)

strong decoupling from open-Atlantic water (5.60–5.33 Ma), thus limiting a survival window for bathyal CWC considerably. Also the short-lived marine incursions during the brackish Lago Mare depositional sequences as precursors of the upcoming Zanclean reflooding event did not yield benthic bathyal calcareous organisms other than euryhaline fishes (Grunert et al. 2016). This leaves us with the fundamental question of a species' potential to re-occupy previously disturbed or hostile environments. Along with the Zanclean reflooding, fully marine conditions and well-ventilated cool and deep-water circulation rapidly established, thus enabling the re-immigration of CWCs via the Gibraltar gateway during the advent of the Zanclean (5.33–3.6 Ma) (Russo 1980).

To conclude, there is increasing evidence that the isolation of the Mediterranean basins from water exchange with the open ocean during the MSC was not as complete and enduring as previously thought. However, the paleoenvironmental conditions for deep-sea communities became worse and the stepwise reduction in ventilation, productivity and circulation was accompanied by a loss in diversity of other benthic organisms, such as foraminifera. Moreover, the local deposition of black shales must have annihilated benthic life. These drastic changes must have impacted CWC communities as well. However, Vertino et al. (2014) pointed out that the most dramatic reductions in generic diversity of Mediterranean CWCs did happen much later, at the end of the Pliocene and at the end of the Pleistocene, and not after the MSC.

References

Barrier P, Zibrowius H, Lozouet P, et al (1991) Une faune de fond dur du bathyal supérieur dans le Miocène Terminal des Cordillères Bétiques (Carboneras, SE Espagne). Mésogée 51:3–13

Blanc-Valleron MM, Pierre C, Caulet JP, et al (2002) Sedimentary, stable isotope and micropaleontological records of paleoceanographic change in the Messinian Tripoli formation (Sicily, Italy). Palaeogeogr Palaeoclimatol Palaeoecol 185:255–286

Carnevale G, Landini W, Sarti G (2006) Mare versus Lago-mare: marine fishes and the Mediterranean environment at the end of the Messinian salinity crisis. J Geol Soc 163:75–80

Carnevale G, Longinelli A, Caputo D, et al (2008) Did the Mediterranean marine reflooding precede the Mio–Pliocene boundary? Paleontological and geochemical evidence from upper Messinian sequences of Tuscany, Italy. Palaeogeogr Palaeoclimatol Palaeoecol 257:81–105

CIESM (2008) The Messinian salinity crisis from mega-deposits to microbiology. In: Briand F (ed) A consensus report, CIESM workshop monographs 33

Corselli C (2001) Change and diversity: the Mediterranean deep corals from the Miocene to the present. In: Faranda FM, Guglielmo L, Spezie G (eds) Mediterranean ecosystems: structures and processes. Springer, Milano, pp 361–366

Dela Pierre F, Bernardi E, Cavagna S, et al (2011) The record of the Messinian salinity crisis in the tertiary Piedmont Basin (NW Italy): the Alba section revisited. Palaeogeogr Palaeoclimatol Palaeoecol 310:238–255

Flecker R, de Villiers S, Ellam RM (2002) Modelling the effect of evaporation on the salinity– ^{87}Sr/^{86}Sr relationship in modern and ancient marginal-marine systems: the Mediterranean Messinian salinity crisis. Earth Planet Sci Lett 203:221–233

Grunert P, Harzhauser M, Rosenthal Y, et al (2016) Estuarine Lago Mare fauna from the tertiary Piedmont Basin indicates episodic Atlantic/Mediterranean exchange during the final stage of the Mediterranean salinity crisis. Palaeogeogr Palaeoclimatol Palaeoecol 457:70–79

Hsü KJ, Ryan WBF, Cita MB (1973) Late Miocene desiccation of the Mediterranean. Nature 242:240–244

Kouwenhoven TJ, Hilgen FJ, Van der Zwaan GJ (2003) Late Tortonian – early Messinian stepwise disruption of the Mediterranean-Atlantic connections: constraints from benthic foraminiferal and geochemical data. Palaeogeogr Palaeoclimatol Palaeoecol 198:303–319

Krijgsman W, Hilgen FJ, Raffi I, et al (1999) Chronology, causes, and progression of the Messinian salinity crisis. Nature 400:652–655

Manzi V, Lugli S, Roveri M, et al (2009) A new facies model for the upper gypsum of Sicily (Italy): chronological and paleoenvironmental constraints for the Messinian salinity crisis in the Mediterranean. Sedimentology 56:1937–1960

Manzi V, Gennari R, Hilgen F, et al (2013) Age refinement of the Messinian salinity crisis onset in the Mediterranean. Terra Nova 25:315–322

Mastandrea A, Muto F, Neri R, et al (2002) Deep-water coral banks: an example from the “Calcare di Mendicino” (upper Miocene, northern Calabria, Italy). Facies 47:27–42

Montenat C, Ott d’Estevou P, Leyrit H, et al (2000) The Brèche rouge of Carboneras. An example of late Miocene volcanic megabreccia deposited in a deep-marine basin controlled by wrench tectonics (Eastern Betics, Spain). In: Leyrit H, Montenat C (eds) Volcaniclastic rocks from magmas to sediments. CRC Press, Boca Raton, pp 193–215

Roveri M, Bertini A, Cosentino D, et al (2008) A high-resolution stratigraphic framework for the latest Messinian events in the Mediterranean area. Stratigraphy 5:323–342

Roveri M, Flecker R, Krijgsman W, et al (2014a) The Messinian salinity crisis: past and future of a great challenge for marine sciences. Mar Geol 352:25–58

Roveri M, Manzi V, Bergamasco A, et al (2014b) Dense shelf water cascading and Messinian canyons: a new scenario for the Mediterranean salinity crisis. Am J Sci 314:751–784

Roveri M, Lugli S, Manzi V, et al (2014c) High-resolution strontium isotope stratigraphy of the Messinian deep Mediterranean basins: implications for marginal to central basins correlation. Mar Geol 349:113–125

Roveri M, Gennari G, Lugli S, et al (2016) The Messinian salinity crisis: open problems and possible implications for Mediterranean petroleum systems. Pet Geosci 22:283–290

Russo A (1980) The psychrospheric coral fauna from the lower Pliocene of northern Italy. Acta Palaeontol Pol 25:613–617

Seidenkrantz MS, Kouwenhoven TJ, Jorissen FJ, et al (2000) Benthic foraminifera as indicators of changing Mediterranean–Atlantic water exchange in the late Miocene. Mar Geol 163:387–407

Selli R (1954) Il Bacino del Metauro Giornale di Geologia 24:1–294

Sierro FJ, Flores JA, Francés G, et al (2003) Orbitally controlled oscillations in planktic communities and cyclic changes in western Mediterranean hydrography during the Messinian. Palaeogeogr Palaeoclimatol Palaeoecol 190:289–316

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Vai GB (2016) Over half a century of Messinian salinity crisis. Bol Geol Min 127:625–641

Vertino A, Stolarski J, Bosellini FR, et al (2014) Mediterranean corals through time: from Miocene to present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 257–274

Cross Reference

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Drop Chapter
Did Quaternary Climate Fluctuations Affect Mediterranean Deep-Sea Coral Communities?

6

Agostina Vertino and Cesare Corselli

Abstract

Despite our limited current knowledge on fossil Mediterranean deep-sea corals, data collected so far hint at a strong influence of climate modifications on the distribution and diversity of these organisms through the Quaternary. Several species still living in the North Atlantic became extinct in the Mediterranean Sea at the Pleistocene-Holocene boundary, and the highest cold-water coral mound accretion rates known so far occurred during the last deglacial phase. Thermal variations of deep-sea waters have certainly affected distribution and survival of the most stenothermic coral species. However, changes in other environmental variables (such as current intensity, food supply and sediment rate, oxygenation), influenced by climate forcing, seem to have highly contributed to the decreased diversity of deep-sea corals and reduced accretion rate of coral mounds through the Quaternary. In order to precisely correlate the observed modifications of paleoassemblages with climate fluctuations, additional research effort needs to be conducted on both emerged and submerged coral deposits.

Keywords

Deep-sea corals · Mediterranean · Quaternary · Paleoclimate · Basin-scale extinction

The Mediterranean is a marginal sea with limited communication with the Atlantic Ocean. Due to its small volume to surface area ratio, and being confined between continents, it is much more responsive to climate change than the open ocean (Rohling et al. 2009; Schroeder et al. 2017). Recent projections reveal that significant changes in the Mediterranean region climate (warming between 1.5 and 2 °C and decrease of precipitation of about 5%) might happen in the next few decades (Gualdi et al. 2013) threatening the highly diverse ecosystems of this "miniature ocean" (UNEP 2010, Marbà et al. 2015; Maier et al., this volume; Movilla, this volume). Similar phenomena, at variable timescale and magnitudes, occurred also through the geologic history of the Mediterranean Sea, inducing remarkable paleoceanographic modifications (e.g., Rohling et al. 2009; Abrantes et al. 2012; Rogerson et al. 2012). As highlighted by several authors, climate changes combined with the complex tectonic evolution of this basin strongly influenced composition and spatial distribution of shallow- and deep-sea benthic ecosystems in the last million years (e.g., Di Geronimo et al. 1996; Corselli 2001; Taviani 2002; Emig and Geistdoerfer 2004; Hayward et al. 2009, Monegatti and Raffi, 2010; Sabelli and Taviani 2014; Vertino et al. 2014; Chefaoui et al. 2017; Freiwald, this volume).

The Mediterranean geological record provides clear evidence that the deep-sea coral fauna was severely affected by palaeoceanographic modifications through the Quaternary (Di Geronimo 1979; Zibrowius 1987; Vertino 2003; Di Geronimo et al. 2005; Stalder et al. 2015; Fink et al. 2015; Moissette et al. 2017; Vertino et al., this volume; Wienberg, this volume; Titschack, this volume). However the triggering factors that led to the flourishing and decline phases of these organisms are still under study.

The current coral fauna of the Mediterranean Sea can be considered as an impoverished North Atlantic fauna, especially in the deep-sea (Zibrowius 1980, Altuna and Poliseno, this volume). Focusing on the order Scleractinia, almost all known species (33) live also in the NE Atlantic but only 12

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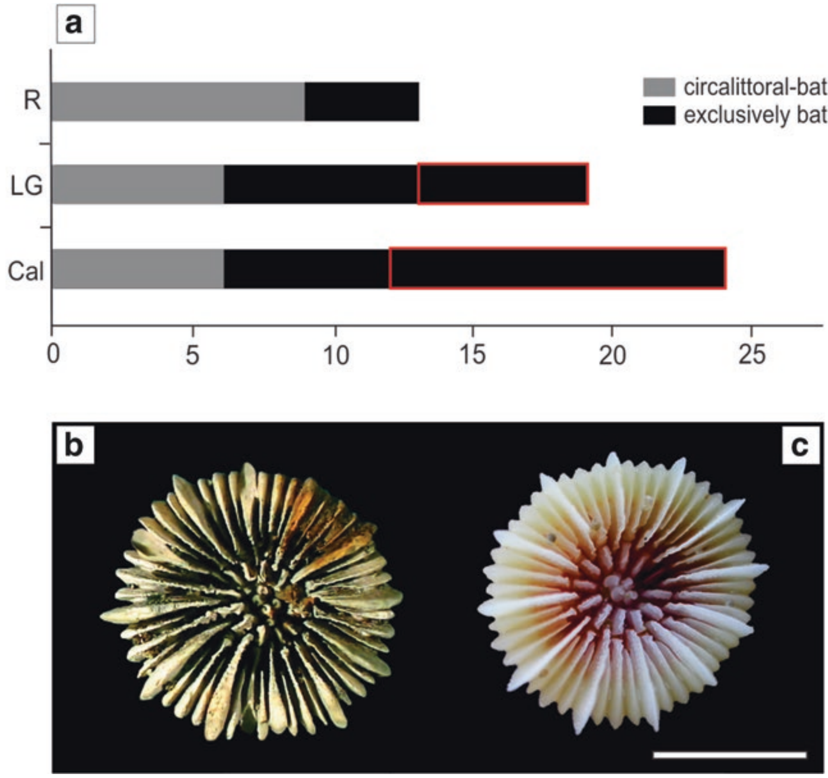

Fig. 6.1 (**a**) Number of Mediterranean scleractinian coral species (from circalittoral to bathyal environment or exclusively bathyal), as known so far, in the Early Pleistocene (Calabrian stage: Cal), in the Late Glacial epoch (LG, data to be confirmed) and in the modern sea (R: Recent). Red rectangle: psychrospheric species. (**b-c**) The psychrospheric species *Caryophyllia coronata* (= *Caryophyllia sarsiae*) from (**b**) Early Pleistocene, Messina (southern Italy) and (**c**) the modern NE Atlantic, Porcupine Seabight (POS 316_525, 1039 m water depth). (Photographs © Agostina Vertino)

and 7 species are known alive at depth higher than 200 m in the western and eastern Mediterranean, respectively, and among them only 4 (3 in the E Mediterranean) are exclusive to bathyal biocoenoses. A similar trend can be observed in other skeletonised coral groups, such as the octocoral families Coralliidae and Isididae and the hydrozoan Stylasteridae. Each is represented by a single species in the modern Mediterranean (*Corallium rubrum*, *Isidella elongata* and *Errina aspera*) but is much more diverse in the bathyal environments of the NE Atlantic (see Altuna and Poliseno and references therein, this volume).

Richer Atlantic-like deep-sea coral communities were instead flourishing in the Early Pleistocene Mediterranean, as shown by fossil deposits cropping out along the coasts of the Messina Strait (MS) (Vertino 2003; Di Geronimo et al. 2005), recently ascribed to the Calabrian stage (Di Stefano and Longhitano 2009), and the island of Karpathos (Moissette et al. 2017). The MS coral buildups, dominated by *Lophelia pertusa*, and mud-dominated "inter-mound" deposits hosted several species extinct in the modern Mediterranean. Considering only the representatives of the phylum Cnidaria ascribable to bathyal environments, at least 6 species belonging to the above mentioned Isidiidae, Coralliidae and Stylasteridae families, and 14 scleractinian species that were thriving on deep-sea Pleistocene seafloors are absent in the modern Mediterranean (Fig. 6.1a). Among these species it is worth mentioning both typical soft-bottom taxa, such as representatives of the genera *Stephanocyathus, Fungiacyathus, Deltocyathus, Flabellum* and the subgenus *Caryophyllia (Ceratocyathus),* and hard-bottom taxa, such as *Caryophyllia coronata*, Seguenza 1864 (= *Caryophyllia sarsiae*, Zibrowius 1980) (Fig. 6.1b-c) and *Enallopsammia scillae* (Seguenza 1864) (= *Enallopsammia rostrata*, Pourtalès, 1878). The former were living on clay- to silt-dominated seafloors and represent the highest number of extinct species, the latter colonised instead fault escarpments, large boulders or were associated to CWC bioconstructions dominated by the species *L. pertusa* (Vertino 2003; Di Geronimo et al. 2005; Taviani et al., this volume). Over 70% of the Early Pleistocene Mediterranean deep-sea species live today in NE Atlantic seafloors (Fig. 6.2a) and many of them are "psychrospheric" taxa, i.e. exclusively known in very deep marine environments at water temperature lower than 10 °C (Fig. 6.1a). Instead ~ 60% of these species (including all psychrospheric taxa) are absent in the modern Mediterranean (Figs. 6.1a and 6.2a).

The increased severity and duration of climate oscillations since the mid-Pleistocene transition (Head and Gibbard 2005; Capotondi et al. 2016), (2) the (quasi-) periodical sapropel formation and related dysoxic to anoxic conditions in the eastern Mediterranean deep-sea floors (Rohling et al. 2015) and (3) the Heinrich and the Dansgaard–Oeschger stadial and interstadial events of the Late Pleistocene (Cacho et al. 2002, 2006; Morabito et al. 2014 with references) had certainly a profound effect on the Mediterranean deep-sea

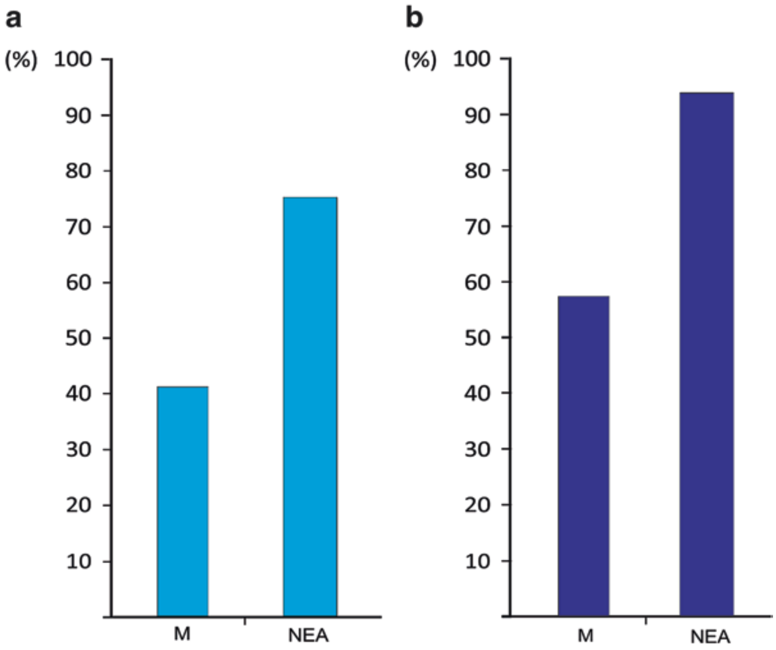

Fig. 6.2 (**a**) Percentage of deep-sea scleractinian coral species known in Early Pleistocene deposits from Italy and Greece, still living in the Mediterranean (M) and in the North-East Atlantic (NEA). (**b**) Percentage of deep-sea species, known thus far in the Mediterranean during the Late Glacial Epoch, still living in the Mediterranean (M) and in the North-East Atlantic (NEA)

benthic biota. However, due to the current lack of knowledge of post-Calabrian deep-sea paleocommunities until the last 50 kyr BP (McCulloch et al. 2010; Fink et al. 2015; Vertino et al., this volume), robust hypotheses on the impact of Quaternary climate oscillations on deep-sea coral diversity and spatial distribution cannot be drawn. What is known so far is that (1) at least around 60% of the deep-sea Calabrian species were still present in the basin until the "late glacial" (LG) epoch,[1] (2) over 90% of the LG species are still living in the NE Atlantic (Fig. 6.2b) and (3) almost half of them are known only as fossils in the Mediterranean (Fig. 6.2b). Moreover, LG scleractinians include around 30% of Atlantic species (such as *Schizocyathus fissilis, Flabellum macandrewi, Eguchipsammia cornucopia*) that have not been found in Early Pleistocene deposits thus far.

When and why all psychrospheric species disappeared from the Mediterranean is not clear yet. The narrow thermal range tolerated by these organisms today lead us to hypothesise that lower temperatures than 13–14 °C, typical of modern Mediterranean bathyal seafloors, occurred both during the Calabrian stage and the Late Glacial period. This hypothesis is supported by the modern thermal range of other species (also extinct in the Mediterranean) belonging to molluscs, bryozoans, polychaetes, crinoids and ostracods found associated to the Pleistocene psychrospheric scleractinians (e.g., Di Geronimo et al. 1996, 2005; Rosso and Di Geronimo 1998; Sciuto 2012; Borghi et al. 2014). Several authors have related the reduction until the basin-scale extinction of Pleistocene Mediterranean psychrospheric species to the remarkable temperature increase after the Younger-Dryas period and the establishment of the current homothermal conditions in deep-water environments (e.g., Di Geronimo et al. 1996; Corselli 2001; Taviani 2002). However, temperature modification cannot be considered as the only cause of the deep-sea fauna impoverishment at the Pleistocene-Holocene transition. In fact, it would not explain the disappearance from the Mediterranen of less stenothermic Atlantic species, such as *S. fissilis* and *E. cornucopia,* that could tolerate temperature of around 13 °C (Zibrowius pers. comm.).

Concerning Mediterranean frame-building cold-water coral (CWC) species, the modern cosmopolitan distribution of the most common species (Cairns et al. 1999) and their persistence in this basin since the Neogene (Vertino et al., this volume), hint at a their rather high tolerance for environmental changes. Nevertheless, recent experimental studies focused on *L. pertusa, Madrepora oculata* and *Dendrophyllia cornigera* have highlighted the sensitivity, and above all, the species-specific physiological response of these organisms to sudden thermal modifications. *D. cornigera* seems to be more tolerant to temperature increase (Naumann et al. 2013; Gori et al. 2014, 2016) than *L. pertusa* (Brooke et al. 2013) and the latter species appears to acclimate better to low temperatures (< 10 °C) than *M. oculata* (Naumann et al. 2013, 2014). These results are consistent with the spatial distribution of the three species through the Quaternary. At present, *M. oculata* and *D. cornigera* characterise Mediterranean lower circalittoral and bathyal bioconstructions, respectively. *L. pertusa* can co-occur in Mediterranean bathyal habitats but is much more

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[1] The total number of species ascribed herein to the "LG epoch" derives from literature and must be confirmed. It includes species whose skeletons have been radiometrically dated (Delibrias and Taviani 1985; McCulloch et al. 2010) but also taxa that have been ascribed to the LG period based on the age of the sediment in which they were embedded (Allouc 1987; Corselli and Bernocchi 1990; Vertino 2003).

common in the NE Atlantic, especially at lower temperature. As far as we know, *Lophelia*-dominated communities flourished in the Mediterranean during the Early Pleistocene (Vertino 2003) and in specific intervals of the last 20 kyr (see Wienberg, this volume and Vertino et al., this volume, with references): 1) at the boundary between the Bølling-Allerød (BA) warm interstadial and the Younger-Dryas (YD) cooling event and at 2) the beginning of the Holocene. These *Lophelia* "golden ages" seem to correspond to maximum coral mound accretions (Wienberg, this volume) and are apparently not always in-phase with surface paleotemperature oscillations. Coral mound accretion rates seem to be more influenced by interrelated environmental variables (highly affected by climate modifications), such as primary productivity, current intensity, food and sediment supply, water oxygenation (Remia and Taviani 2005; McCulloch et al. 2010; Fink et al. 2012, 2013, 2015; Stalder et al. 2015), than directly by thermal constrains. Only the switch between *Lophelia*- to *Madrepora*/*Dendrophyllia*-dominated assemblages observed at the Pleistocene-Holocene transition in Mediterranean coral mounds (Malinverno et al. 2010; Stalder et al. 2015; Wienberg, this volume), apparently diachronous in the eastern and western basins (Vertino et al., this volume), could be partly explained with increased temperature at the sea bottoms.

In conclusion, the Mediterranean deep-sea coral fauna certainly underwent marked modifications through the Quaternary. Nevertheless, our current knowledge is not sufficient to precisely correlate the observed changes with climate oscillations. Data collected thus far hint that all "psychrospheric" species (but not only) disappeared from the Mediterranean at the last glacial-interglacial transition; but further radiometric dating is needed to support this hypothesis. Moreover, it is not clear yet if (1) the deep-sea coral diversity decline was synchronous in the whole basin, (2) comparable demise events also occurred during previous glacial-interglacial transitions of the Quaternary, (3) there is any correlations between the coral diversity impoverishment and the switch between the dominant frame-building corals (*Lophelia* vs. *Madrepora*) at the Pleistocene-Holocene boundary. Some of these open questions can be answered by carrying out further in-depth chronological, paleoecological, sedimentological and geochemical proxy studies on emerged and submerged coral-rich deposits.

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References

Abrantes F, Voelker A, Sierro F, et al (2012) Paleoclimate variability in the Mediterranean region. In: Lionello P (ed) The climate of the Mediterranean region. Elsevier, Amsterdam, pp 1–86

Allouc J (1987) Les paléocommunautés profondes sur fond rocheux du Pléistocène méditerranéen. Description et essai d'interpretation paléoécologique. Geobios 20:241–263

Borghi E, Garilli V, Bonomo S (2014) Plio-Pleistocene Mediterranean bathyal echinoids: evidence of adaptation to psychrospheric conditions and affinities with Atlantic assemblages. Palaeontol Electronica 17.3:1–26

Brooke S, Ross SW, Bane JM, et al (2013) Temperature tolerance of the deep-sea coral *Lophelia pertusa* from the southeastern United States. Deep-Sea Res Part 2 Top Stud Oceanogr 92:240–248

Cacho I, Grimalt JO, Canals M (2002) Response of the western Mediterranean Sea to the rapid climatic variability that occurred during the last 50,000 years: a molecular biomarker approach. J Mar Syst 33–34:253–272

Cacho I, Shackleton N, Elderfield H, et al (2006) Glacial rapid variability in deep-water temperature and δ^{18}O from the western Mediterranean Sea. Quat Sci Rev 25:3294–3311

Cairns SD, Hoeksema BW, van der Land J (1999) List of extant stony corals. Atoll Res Bull 59:13–45

Capotondi L, Girone A, Lirer F (2016) Central Mediterranean mid-Pleistocene paleoclimatic variability and its association with global climate. Palaeogeogr Palaeoclimatol Palaeoecol 442:72–83

Chefaoui RM, Duarte CM, Serrão EA (2017) Palaeoclimatic conditions in the Mediterranean explain genetic diversity of *Posidonia oceanica* seagrass meadows. Sci Rep 7:2732. https://doi.org/10.1038/s41598-017-03006-2

Corselli C (2001) Change and diversity: the Mediterranean deep corals from the Miocene to the present. In: Faranda FM, Guglielmo L, Spezie G (eds) Mediterranean ecosystems: structures and processes. Springer, Italia, Genova, pp 361–366

Corselli C, Bernocchi A (1990) Paleocommunities of the last glacial from the Sardinia continental slope: a paleoceanography problem. Atti 4° Simp Ecol Paleoecol Comun Bent Sorrento, 1–5 Novembre 1988, Mus Nat Sci Nat, Torino, pp 575–595

Delibrias G, Taviani M (1985) Dating the death of Mediterranean deep-sea scleractinian corals. Mar Geol 62:175–180

Di Geronimo I (1979) Il Pleistocene in facies batiale di Valle Palione (Grammichele, Catania). Boll Malacol 15:85–156

Di Geronimo I, La Perna R, Rosso A (1996) The Plio-Quaternary evolution of the Mediterranean deep sea benthos: an outline. In: La Méditerranée: variabilités climatiques, environnement et biodiversité, Actes du Colloque Scientifique 6–7 Avril 1995. Maison de l'Environnement de Montpellier, Montpellier, pp 286–290

Di Geronimo I, Messina C, Rosso A, et al (2005) Enhanced biodiversity in the deep: early Pleistocene coral communities from southern Italy. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin, pp 61–86

Di Stefano A, Longhitano SG (2009) Tectonics and sedimentation of the lower and middle Pleistocene mixed siliciclastic/bioclastic sedimentary successions of the Ionian Peloritani Mts (NE Sicily, southern Italy). Cent Eur J Geosci 1:33–62

Emig C, Geistdoerfer P (2004) The Mediterranean deep-sea fauna: historical evolution, bathymetric variations and geographical changes. Carnets Geol 4:A01. https://doi.org/10.4267/2042/3230

Fink H, Wienberg C, Hebbeln D, et al (2012) Oxygen control on Holocene cold-water coral development in the Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96

Fink H, Wienberg C, De Pol-Holz R, et al (2013) Cold-water coral growth in the Alboran Sea related to high productivity during the late Pleistocene and Holocene. Mar Geol 339:71–82

Fink H, Wienberg C, De Pol-Holz R, et al (2015) Spatio-temporal distribution patterns of Mediterranean cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) during the past 14,000 years. Deep-Sea Res Part 1 Oceanogr Res Pap 103:37–48

Gori A, Reynaud S, Orejas C, et al (2014) Physiological performance of the cold-water coral *Dendrophyllia cornigera* reveals its preference for temperate environments. Coral Reefs 33:665–674

Gori A, Ferrier-Pagès C, Hennige SJ, et al (2016) Physiological response of the cold-water coral *Desmophyllum dianthus* to thermal stress and ocean acidification. PeerJ 4:e1606. https://doi.org/10.7717/peerj.1606

Gualdi S, Somot S, Li L, et al (2013) The CIRCE simulations. Regional climate change projections with realistic representation of the Mediterranean Sea. Bull Am Meteorol Soc 94:65–81

Hayward BW, Sabaa AT, Kawagata S, et al (2009) The early Pliocene re-colonisation of the deep Mediterranean Sea by benthic foraminifera and their pulsed late Pliocene–middle Pleistocene decline. Mar Micropaleontol 71:97–112

Head MJ, Gibbard PL (eds) (2005) Early-middle Pleistocene transitions—the Land-Ocean evidence, In: Geological Society, London, Special Publication, 247, 326 pp

Malinverno E, Taviani M, Rosso A, et al (2010) Stratigraphic framework of the Apulian deep-water coral province, Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:345–359

Marbà N, Jordà G, Agustí S, et al (2015) Footprints of climate change on Mediterranean Sea biota. Front Mar Sci 2:56. https://doi.org/10.3389/fmars.2015.00056

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the Younger Dryas. Earth Planet Sci Lett 298:143–152

MMoissette P, Cornée JJ, Quillévéré F (2017) Pleistocene (Calabrian) deep-water corals and associated biodiversity in the eastern Mediterranean (Karpathos Island, Greece). J Quat Sci 32(7). https://doi.org/10.1002/jqs.2966

Monegatti P, Raffi S (2010) The Messinian marine molluscs record and the dawn of the eastern Atlantic biogeography. Palaeogeogr Palaeoclimatol Palaeoecol 297:1–11

Morabito S, Milia A, Sprovieri, et al (2014) A multidisciplinary approach for reconstructing the stratigraphic framework of the last 40 ka in a bathyal area of the eastern Tyrrhenian Sea. Glob Planet Change 123: 121–138

Naumann MS, Orejas C, Ferrier-Pagès C (2013) High thermal tolerance of two Mediterranean cold-water coral species maintained in aquaria. Coral Reefs 32:749–754

Naumann MS, Orejas C, Ferrier-Pagès C (2014) Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. Deep-Sea Res Part 2 Top Stud Oceanogr 99:36–41

Remia A, Taviani M (2005) Shallow-buried Pleistocene Madrepora-coral mounds on a muddy continental slope, Tuscan archipelago, NE Tyrrhenian Sea. Facies 50:419–425

Rogerson M, Rohling EJ, Bigg GR, et al (2012) Paleoceanography of the Atlantic-Mediterranean exchange: overview and first quantitative assessment of climatic forcing. Rev Geophys 50:RG2003. https://doi.org/10.1029/2011RG000376

Rohling EJ, Abu-Zied R, Casford JSL, et al (2009) The Marine Environment: present and past. In: Woodward JC (ed) The physical geography of the Mediterranean. Oxford University Press, Oxford, pp 33–67

Rohling EJ, Marino G, Grant K (2015) Mediterranean climate and oceanography and the periodic development of anoxic events (sapropels). Earth Sci Rev 143:62–97

Rosso A, Di Geronimo I (1998) Deep-sea Pleistocene Bryozoa of southern Italy. Geobios 31:303–317

Sabelli B, Taviani M (2014) The making of the Mediterranean molluscan biodiversity. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 285–306

Schroeder K, Chiggiato J, Josey SA, et al (2017) Rapid response to climate change in a marginal sea. Sci Rep 7:4065. https://doi.org/10.1038/s41598-017-04455-5

Sciuto F (2012) New ostracod species from lower Pleistocene sediments from capo Milazzo (NE Sicily). Boll Soc Paleontol Ital 51:117–125

Seguenza G (1864) Disquisizioni paleontologiche intorno ai Corallarii fossili delle rocce terziarie del distretto di Messina. Mem R Acc Sci Torino (Ser 2) 21:399–560

Stalder C, Vertino A, Rosso A, et al (2015) Microfossils, a key to unravel cold-water carbonate mound evolution through time: evidence from the eastern Alboran Sea. PLoS One 10:e0140223

Taviani M (2002) The Mediterranean benthos from late Miocene up to present: ten million years of dramatic climatic and geologic vicissitudes. Biol Mar Medit 9:445–463

UNEP-MAP-RAC/SPA (2010) Impact of climate change on marine and coastal biodiversity in the Mediterranean Sea: current state of knowledge. In: Ben Haj S, Limam A, RAC/SPA Edit, Tunis, pp 1–28

Vertino A (2003) Sclerattiniari plio-pleistocenici ed attuali del Mediterraneo. PhD dissertation (unpublished), University of Messina, 306 pp

Vertino A, Stolarski J, Bosellini FR, et al (2014) Mediterranean corals through time: from Miocene to present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 257–274

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mém Inst Océanogr Monaco 11:284

Zibrowius H (1987) Scléractiniaires et Polychètes Serpulidae des faunes bathyales actuelle et plio-pléistocène de Méditerranée. Doc et Trav IGAL 11:255–257

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Freiwald A (this volume) Messinian salinity crisis: what happened to cold-water corals?

Maier C, Weinbauer MG, Gattuso JP (this volume) Fate of Mediterranean scleractinian cold-water corals as a result of global climate change. A synthesis

Movilla J (this volume) A case study: variability in the calcification response of Mediterranean cold-water corals to ocean acidification

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals

Titschack J (this volume) Bathyal corals within the Aegean Sea and the adjacent Hellenic trench

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Wienberg C (this volume) A deglacial cold-water coral boom in the Alborán Sea: from coral mounds and species dominance

Drop Chapter
A Deglacial Cold-Water Coral Boom in the Alborán Sea: From Coral Mounds and Species Dominance

7

Claudia Wienberg

Abstract

The two scleractinian cold-water corals *Lophelia pertusa* and *Madrepora oculata* are widely distributed in the Alborán Sea. They have been found (alive and fossil) on seamounts, volcanic ridges and mud volcanoes, and they formed coral mounds in the geological past. While the cold-water corals show a reduced occurrence during the last glacial period, they experienced a boom since the last deglaciation until the Early Holocene. The proliferation of cold-water corals during this time is expressed in very high vertical mound aggradation rates of >400 cm kyr^{-1}. Since the mid-Holocene coral mound aggradation significantly slowed-down, which is ascribed to the reduced occurrence of cold-water corals likely supplemented by a reduced sediment supply. During the Holocene, a shift in coral species dominance towards a *M. oculata*-dominated cold-water coral community becomes apparent. It is speculated that in comparison to *L. pertusa*, *M. oculata* has a higher tolerance against the increasing Holocene bottom water temperatures, but is not efficient in building-up mounds likely attributed to its thinly branching framework.

Keywords

Lophelia pertusa · *Madrepora oculata* · Deglaciation · Coral mound · Mound aggradation · Environmental tolerance · Alborán Sea

The Alborán Sea (AS) comprises the westernmost part of the Mediterranean Sea, which is bordered by the Spanish and Moroccan continental margins (Fig. 7.1a). The AS is a very narrow basin (180 × 330 km) and water depths are shallower than 2000 m. It has a complex seafloor topography with three sub-basins separated by volcanic ridges and seamounts (Muñoz et al. 2008). The two prominent framework-forming scleractinian cold-water corals (CWC), *Lophelia pertusa* and *Madrepora oculata*, are widely distributed in the AS comprising living and fossil occurrences (Fig. 7.1a; see also Chimienti et al., this volume; Vertino et al., this volume). They are a common member of the faunal community colonising various seamounts and ridges (Palomino et al. 2015 and references therein; see Rueda et al., this volume; Lo Iacono et al., this volume). They are also associated to a rather exceptional habitat as they have been encountered on some of the mud volcanoes within a large mud diapir province in the western AS (Margreth et al. 2011; Palomino et al. 2018). However, *L. pertusa* and *M. oculata* do not just occur as single living colonies or as scattered small-sized accumulations of coral rubble and dead framework on topographic highs, both species also formed substantial accumulations on the seafloor, which over thousands of years developed to mound- or ridge-like seabed structures of tens of metres in height. Such coral mounds are composed of skeletal remnants of both species (and other benthic organisms) and sediments. Their formation depends on a well-balanced interplay between sustained coral growth, the development of a coral framework with a high sediment baffling capacity, and the continuous supply of sediments which stabilises the biogenic construction (Wienberg and Titschack 2017).

In the northern AS, up to 9-m-high mounds grouped into provinces have been reported from southeast of Málaga and north of the Chella bank in water depths between 150 and 250 m (Muñoz et al. 2008). Potential mound structures are also reported from some seamounts (e.g., Herradura, Chella) and from the Alborán ridge (Fig. 7.1a; Lo Iacono et al. 2008; Palomino et al. 2011; Lo Iacono et al., this volume). However, all these reports are mainly based on acoustic data and a definite evidence that these structures are formed by CWC is still lacking. For mounds discovered in the southern AS, it is

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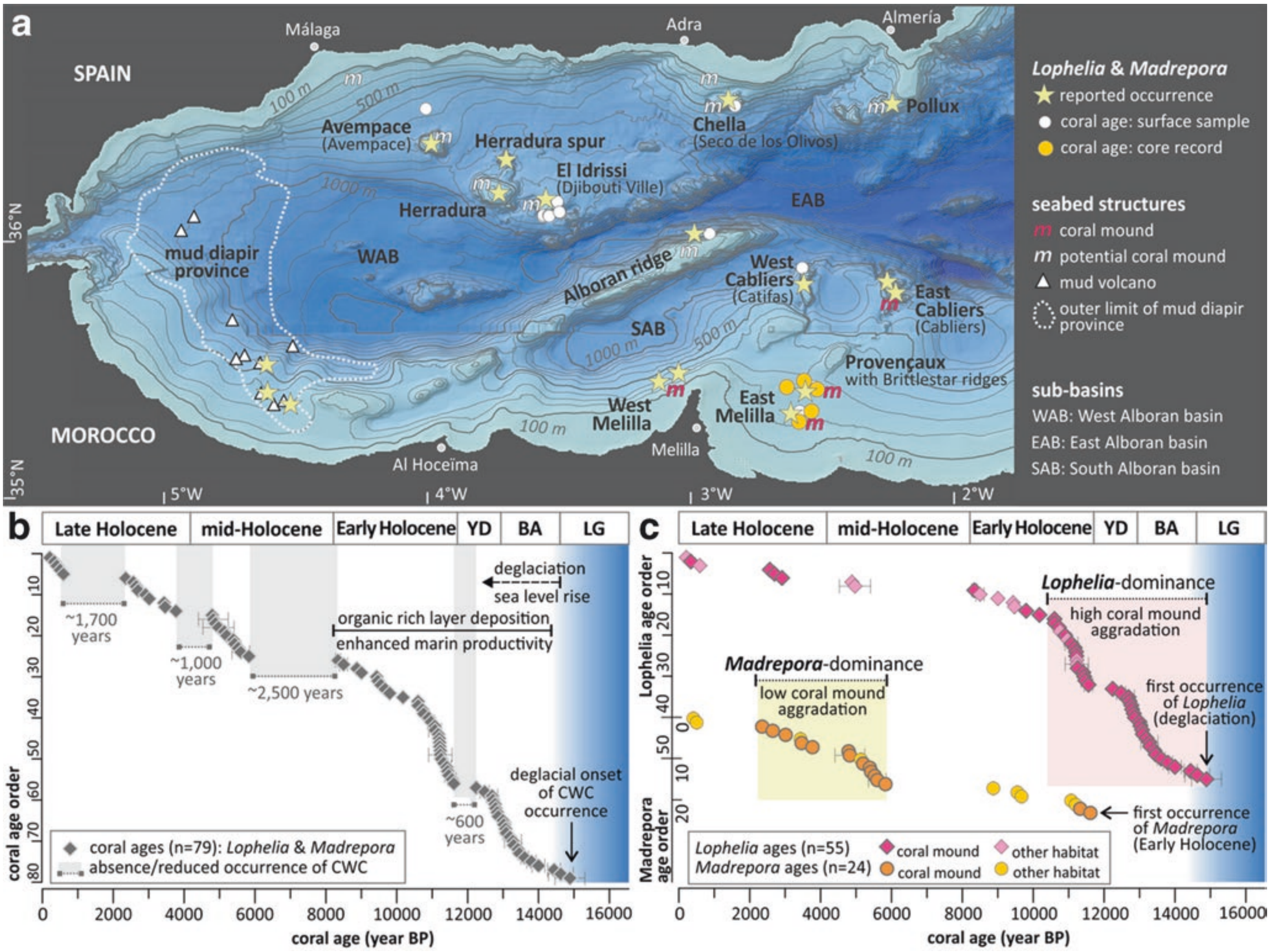

Fig. 7.1 (**a**) Bathymetric map of the Alborán Sea (data source: http://www.emodnet-hydrography.eu) showing its volcanic ridges, seamounts/banks (alternative names found in literature are given in brackets), and mud volcanoes. Displayed are reported live/fossil occurrences of *Lophelia pertusa* and *Madrepora oculata*, coral mounds formed by both species, and sites from which coral ages are available (note: core records from the East Cabliers bank and the West Melilla province are indicated but not considered for the coral age plots shown in b and c as they are not published yet). (**b**) Complete coral age dataset obtained for *L. pertusa* and *M. oculata* collected in the Alborán Sea (note: two recently published glacial ages of 28,560 and 43,040 years BP obtained for *L. pertusa* are not displayed, see Dubois-Dauphin et al. 2016). (**c**) Separation between *L. pertusa* (pink) and *M. oculata* (orange) ages. Ages that derived from coral mounds and from other habitats are indicated. See legend for symbol code; see text for references. *YD* Younger Dryas, *BA* Bølling-Allerød, *LG* late glacial period

already proven by video observations and long sediment cores that substantial parts of these structures have been build up by *L. pertusa* and *M. oculata*. The East Melilla province comprises coral mounds with different morphologies (Hebbeln, this volume). In the north, steep and elongated ridges (Brittlestar ridges I to III) are attached to the southern edge of the Provençaux bank (Fig. 7.1a). They have heights of 50–150 m and rise to water depths of 250–450 m (Fink et al. 2013). Their morphology and orientation might point to a tectonic-related origin, but a recent drilling campaign revealed that at least the upper 70 m of these ridges are made up of coral-sediment-deposits (Hebbeln et al. 2015). *Lophelia pertusa* and *M. oculata* still colonise these ridges today though in low numbers and as small and scattered colonies. To the south at water depths below 300 m, a field with oval to curved coral mounds (height: > 20 m) occurs, followed by a cluster with elongated mounds (height: < 20 m) with some of them being partly buried by sediments (Hebbeln, this volume). The West Melilla province, situated 50 km westward of the East Melilla province (Fig. 7.1a), comprises >100 mounds, which are organised in two clusters, occur in water depths of 300–590 m, and have heights of 10–45 m. The mounds have an asymmetrical to circular shape and some of them are completely buried by sediments (Lo Iacono et al. 2014). No living CWC are found today on these mounds (Lo Iacono et al. 2016). A third coral mound site exists to the north of the Melilla provinces on the East Cabliers bank (Fig. 7.1a), which is a 25-km-long N-S oriented structurally controlled volcanic ridge. Substantial coral accumulations have been deposited on the crest of this structure, which rises today to water depths of 250–710 m. In the northern portion, living occurrences of *L. pertusa* and *M. oculata* were observed (Lo Iacono et al. 2016).

Many efforts have been conducted to gain information about the past occurrence of *L. pertusa* and *M. oculata* in the AS. Until the present day, ~80 datings have been published for both species (Fig. 7.1b). This dataset contains datings obtained from CWC fragments collected from the seabed surface (n = 35), which mainly originate from seamounts (see compilation by Fink et al. 2015 and references therein), while the majority of ages (n = 47) derive from core records retrieved from coral mounds along the Moroccan margin (Fink et al. 2013; Stalder et al. 2015; Dubois-Dauphin et al. 2016; unpubl. Data Wienberg). Overall, sediment cores collected from coral mounds are crucial to reconstruct recurring periods of sustained coral colonisation on these mounds (see Angeletti et al., this volume), and thus, to identify periods of enhanced vertical mound aggradation under suitable environmental conditions (Wienberg and Titschack 2017). The number of CWC ages obtained for the AS is still rather low but will potentially significantly increase in the near future with respect to ongoing studies for which more than 100 new datings are expected for the East and West Melilla provinces, and the East Cabliers bank (Krengel et al. 2015; Lo Iacono et al. 2016; Wang et al. 2016). However, the available dataset already reveals a distinct pattern regarding the past occurrence of *L. pertusa* and *M. oculata*.

During the last glacial period, a reduced occurrence of both species in the AS is assumed as only two glacial ages have been obtained so far (see Dubois-Dauphin et al. 2016), which comprise just 2% of all available ages. However, the low number of glacial coral ages could also be ascribed to the lack of appropriate core material covering longer timescales. Yet, preliminary dating results obtained from 70-m-long drill cores collected from the East Melilla province (Hebbeln et al. 2015) revealed that there was indeed no sustained occurrence of *L. pertusa* and *M. oculata* lasting since ~100,000 years BP until the last deglaciation, thus a time span covering the last glacial, and part of the preceding interglacial (Krengel et al. 2015). There is a conspicuous common start-up phase for their occurrence coinciding with the onset of the Bølling-Allerød (BA) warm interval at ~14,600 years BP (Fig. 7.1b), which marked the onset of the last deglaciation with a post-glacially rising sea level (Fink et al. 2013; Stalder et al. 2015; Lo Iacono et al. 2016; see Vertino et al., this volume and references therein). The first post-glacial period of pronounced coral occurrence lasted until the mid-Younger Dryas (~12,200 years BP) and is followed by a second boost roughly covering the entire Early Holocene (11,600–8,300 years BP; Fig. 7.1b). Both periods of pronounced coral occurrence coincided with intensified intermediate water mass circulation and enhanced productivity in the surface ocean increasing the availability of food for CWC (Cacho et al. 2002; Fink et al. 2013, 2015; Stalder et al. 2015). Concurrent with the onset of the mid-Holocene occurs a relevant gap in the age dataset (Fig. 7.1b). This ~2,500-years-lasting temporary reduced occurrence of CWC was likely related to a significant decrease in productivity after 9,000 years BP, which occurred concurrent to the termination of the organic rich layer deposition in the AS (Fink et al. 2015; Cacho et al. 2002). After ~5,800 years BP, CWC seem to be present in the AS until the present-day, except from two gaps at the transition from the mid- to Late Holocene and during the Late Holocene (Fig. 7.1b). Overall, all presently observed age gaps need to be considered with care as the lack of dating does not necessarily indicate the complete absence of CWC but clearly document phases of reduced CWC occurrence in the AS. Moreover, as the majority of coral ages derive from the East Melilla province, it cannot be excluded that the identified temporal pattern might slightly differ for other coral sites in the AS.

The identified temporal pattern in the general occurrence of CWC in the AS is even more clearly displayed in core records obtained from individual coral mounds, and is explicitly expressed in the varying vertical aggradation rates estimated for these mounds. Coral mounds of the East Melilla province show highest aggradation rates of >400 cm kyr^{-1} for the last deglaciation and up to ~300 cm kyr^{-1} for the Early Holocene (Fink et al. 2013; Stalder et al. 2015; Titschack et al. 2016). These values are in the upper range of aggradation rates obtained so far for other coral mound areas in the North Atlantic (see compilation by Wienberg and Titschack 2017), and preliminary results of mound records of the West Melilla province and the East Cabliers bank seem to display a very similar pattern (Lo Iacono et al. 2016; Wang et al. 2016). During the late Younger Dryas and the mid- to Late Holocene, mound aggradation rates decreased noticeably to values of ~30–50 cm kyr^{-1} and < 20 cm kyr^{-1}, respectively. Thus, although CWC still colonised the East Melilla mounds during these time intervals, mound aggradation slowed-down or even stagnated. This reduction in mound aggradation can be explained by the environmental change to less favourable conditions for the corals themselves, but might also be the consequence of a reduced sediment supply.

A third species-related pattern comes up when considering ages obtained for *L. pertusa* and *M. oculata* separately (Fig. 7.1c). Periods of pronounced CWC occurrence associated with high coral mound aggradation rates during the last deglaciation and the Early Holocene relate to ages obtained for *L. pertusa*, while *M. oculata* seems to have been largely absent from the AS before the onset of the Holocene. On the contrary, since the mid-Holocene, *M. oculata* seems to dominate over *L. pertusa* (Fig. 7.1c). A similar pattern is also shown by faunal analyses based on mound records, which revealed that *M. oculata* becomes more abundant since the Early Holocene eventually culminating in a *M. oculata*-dominated coral community (Stalder et al. 2015; Lo

Iacono et al. 2016). Moreover, as the dominance of *M. oculata* coincides with periods of low mound aggradation rates (Fig. 7.1c), it can be speculated that this species is not as successful and efficient in building-up mounds as *L. pertusa*. This might be explained by the thinly branching framework formed by *M. oculata* which does not allow a sufficient baffling of sediment and therefore might inhibit enhanced vertical mound aggradation.

It is still not known which environmental change triggered the obvious shift in coral species dominance during the Holocene in the AS. It might be the consequence of the increasing bottom water temperatures to which *M. oculata* is likely to be more tolerant, as it occurs preferentially in warmer waters (8.5–10 °C), while *L. pertusa* seems to dominate in colder waters (6.5–8 °C; Wienberg and Titschack 2017). This assumption is further supported by experimental studies showing that both species have their specific thermal preferences and tolerances, with *M. oculata* showing acclimatisation capacity toward the presumed CWC upper thermal tolerance limit of 14 °C (Naumann et al. 2014). Overall, this highlights that a detailed knowledge of bio-ecological dynamics of the CWC species adopted for stratigraphic studies is of utmost importance when interpreting coral age datasets in a regional, climatological and palaeoceanographic context (see also Vertino et al., this volume).

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References

Cacho I, Grimalt JO, Canals M (2002) Response of the western Mediterranean Sea to rapid climatic variability during the last 50,000 years: a molecular biomarker approach. J Mar Syst 33–34:253–272

Dubois-Dauphin Q, Bonneau L, Colin C, et al (2016) South Atlantic intermediate water advances into the north-East Atlantic with reduced Atlantic meridional overturning circulation during the last glacial period. Geochem Geophys Geosyst 17:2336–2353

Fink HG, Wienberg C, De Pol-Holz R, et al (2015) Spatio-temporal distribution patterns of Mediterranean cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) during the past 14,000 years. Deep-Sea Res Part 1 Oceanogr Res Pap 103:37–48

Fink HG, Wienberg C, De Pol-Holz R, et al (2013) Cold-water coral growth in the Alboran Sea related to high productivity during the late Pleistocene and Holocene. Mar Geol 339:71–82

Hebbeln D, Wienberg C, Cruise Participants (2015) Report and preliminary results of R/V MARIA S. MERIAN Cruise MSM36 "MoccoMeBo". Malaga-Las Palmas, 18.02.-17.03.2014. MERIAN-Reports, 47 pp, DFG-Senatskommission für Ozeanographie. https://doi.org/10.2312/cr_msm36

Krengel T, Frank N, Hemsing F, et al (2015) Growth of cold-water corals in the Gulf of Cádiz and the Alboran Sea from two cores obtained through drilling (MSM36-MoccoMeBo). In: Abstracts of the 1st international carbonate mound conference, Monte Veritá, 1–5 November 2015

Lo Iacono C, Gràcia E, Diez S, et al (2008) Seafloor characterization and backscatter variability of the Almería Margin (Alboran Sea, SW Mediterranean) based on high-resolution acoustic data. Mar Geol 250:1–18

Lo Iacono C, Gràcia E, Ranero CR, et al (2014) The West Melilla cold water coral mounds, eastern Alboran Sea: morphological characterization and environmental context. Deep-Sea Res Part 2 Top Stud Oceanogr 99:316–326

Lo Iacono C, Huvenne VAI, Gonzalez LV, et al (2016) Living reefs and CWC mounds in the Alboran Sea (Western Mediterranean). Holocene evolution and present-day conditions. In: Abstracts of the 6th international symposium on deep-sea corals, Boston, 11–16 September 2016

Margreth S, Gennari G, Rüggeberg A, et al (2011) Growth and demise of cold-water coral ecosystems on mud volcanoes in the west Alboran Sea: the messages from the planktonic and benthic foraminifera. Mar Geol 282:26–39

Muñoz A, Ballesteros M, Montoya I, et al (2008) Alborán Basin, southern Spain. Part I: Geomorphology. Mar Petrol Geol 25:59–73

Naumann MS, Orejas C, Ferrier-Pagès C (2014) Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. Deep-Sea Res Part 2 Top Stud Oceanogr 99:36–41

Palomino D, Alonso B, Lo Iacono C, et al (2015) Seamounts and Seamount-like structures of the Alborán Sea. In: Würtz M, Rovere M (eds) Atlas of the Mediterranean seamounts and seamount-like structures. IUCN, Gland, Málaga, pp 21–58

Palomino D, Vázquez J-T, Ercilla G, et al (2011) Interaction between seabed morphology and water masses around the seamounts on the Motril marginal plateau (Alboran Sea, western Mediterranean). Geo-Mar Lett 31:465–479

Stalder C, Vertino A, Rosso A, et al (2015) Microfossils, a key to unravel cold-water carbonate mound evolution through time: evidence from the eastern Alboran Sea. PLoS One 10:e0140223

Titschack J, Fink HG, Baum D, et al (2016) Mediterranean cold-water corals – an important regional carbonate factory? Depos Rec 2:74–96

Wang H, Wienberg C, Titschack J, et al (2016) Past cold-water coral growth in the West Melilla cold-water Coral Province, Alboran Sea, related to high food availability. Rapp Comm Int Mer Médit 41:58

Wienberg C, Titschack J (2017) Framework-forming scleractinian cold-water corals through space and time: a late Quaternary North Atlantic perspective. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 699–732. https://doi.org/10.1007/978-3-319-17001-5_16-1

Cross References

Angeletti L, Bettuzzi M, Morigi MP (this volume) Tomography of cold-water corals – bearing cores

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Hebbeln D (this volume) Highly variable submarine landscapes in the Alborán Sea created by cold-water corals

Lo Iacono C, Savini A, Huvenne VAI, et al (this volume) Habitat mapping of cold-water corals in the Mediterranean Sea

Palomino D, Rueda JL, Vázquez JT, et al (this volume) Cold-water corals in fluid venting submarine structures

Rueda J, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean Cold-water corals

Drop Chapter
Highly Variable Submarine Landscapes in the Alborán Sea Created by Cold-Water Corals

8

Dierk Hebbeln

Abstract

Impressive seafloor structures formed by cold-water corals characterise parts of the seafloor in the southeastern Alborán Sea, forming the East Melilla Cold-Water Coral Mound Province. These geomorphological features are composed of a mixture of cold-water coral fragments and hemipelagic sediments, displaying typical coral mound deposits. Along a N-S transect across the Mediterranean Moroccan margin, extending for up to ~25 km, three belts of very differently shaped mound structures occur. Their morphologies and dimensions vary considerably, ranging from up to 20-km-long and 150-m-high steep ridges to elongated and arcuate mounds of a few hundred meters in diameter and up to 40 m in height. Obviously, different interacting drivers, including tectonics and hydrodynamics, must have been involved at a variable scale in shaping these fascinating submarine landscapes in the past.

Keywords

Cold-water coral mounds · Alborán Sea · Multibeam echosounder bathymetry · Mound shape · Tectonics · Hydrodynamics

Over millennia and longer time scales, framework-forming cold-water corals (CWC) are able to trigger the development of large geo-bioconstructions known as coral mounds (Roberts et al. 2006; Wienberg and Titschack 2017). As ecosystem engineers, CWC are key organisms to form highly diverse ecosystems in the deep sea, providing a habitat for many other marine organisms (Roberts et al. 2006). Given the availability of suspended sediments, the baffling effect of CWC frameworks favors an enhanced sediment deposition in comparison to the surrounding seabed (Wienberg and Titschack 2017). Combined with the high carbonate production of CWC and accompanying species this results within millennia in the creation of sometimes impressive mound structures, affecting the large-scale heterogeneity of the seafloor (Lo Iacono et al. 2018). The development of these coral mounds, which largely consist of fossil CWC assemblages embedded in hemipelagic sediments (Dorschel et al. 2005; Titschack et al. 2016), is very sensitive to climatic variations. As the delivery of food particles to feed the sessile CWC and sediments to fill and stabilise the biogenic framework construction are prerequisites for mound formation, the occurrence of these structures usually is linked to rather strong and turbulent hydrodynamics (Mienis et al. 2014; Hebbeln and Samankassou 2015; Wienberg and Titschack 2017). Consequently, geologic records show that CWC mounds typically co-occur with contouritic deposits (Hebbeln et al. 2016; Rebesco and Taviani, this volume).

Although CWC have been found all over the Atlantic basin from the shelf down to the mid-Atlantic ridge (Mortensen et al. 2008), coral mounds, due to their dependency on sediment supply (e.g., Hebbeln et al. 2016), are restricted to the continental margins of the Atlantic Ocean and occur from Ireland (Kenyon et al. 2003) southward to Argentina (Muñoz et al. 2012). They range in height from just a few meters to >300 m (Mienis et al. 2006), and are found sometimes as isolated features or mostly grouped in large clusters or provinces covering hundreds to even thousands of square kilometers (e.g., de Mol et al. 2002, Hebbeln et al. 2014, Vandorpe et al. 2017). Due to the high accumulation rates, mound deposits potentially provide very high-resolution paleoarchives and might even preserve stratigraphic records that are lacking in the neighboring sedimentary succession (Hebbeln et al. 2016). These paleoarchives document the development of the CWC ecosystem through time as well as any related changes of the ambient environmental setting – both of which can be reconstructed through paleoceanographic approaches (e.g., Dorschel et al.

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2005; Kano et al. 2007; Wienberg et al. 2018; Montagna and Taviani, this volume).

Whereas CWC communities are widespread in the Mediterranean Sea (Freiwald et al. 2009; Chimienti et al., this volume), only few coral mound sites have been described up to now. Such coral mounds with heights generally <25 m occur (i) in the Ionian Sea off Santa Maria de Leuca (Taviani et al. 2005; Savini and Corselli 2010), (ii) south off Pantelleria Island in the Sicily Channel (Martorelli et al. 2011), (iii) in the Tyrrhenian Sea (Remia and Taviani 2005), and (iv) in the northern Alborán Sea, from where several small mound structures have been reported (Muñoz et al. 2008; Lo Iacono et al. 2008, this volume), although evidence for their true nature (formed by CWC, bryozoans or others) is partly still lacking.

The most impressive coral mound province of the Mediterranean Sea has been described from the southern Alborán Sea. Framed in the west by the West Melilla CWC Province (WMCP) with mounds reaching heights of up to 50 m (Lo Iacono et al. 2014) and in the northeast by the Cabliers Mounds (Lo Iacono et al. 2018), the East Melilla CWC Province (EMCP, Fig. 1) comprises coral mounds displaying an impressive variety of shapes and sizes, partly reaching heights of >100 m. Located off the Moroccan coast east off the Spanish enclave Melilla, the EMCP was first mentioned by Comas and Pinheiro (2007) and described in more detail by Fink et al. (2013).

While in the WMCP no living corals have been observed, scattered occurrences of the two most common CWC, *Lophelia pertusa* and *Madrepora oculata*, have been reported from the EMCP (Hebbeln et al. 2009; Fink et al. 2013). Very high mound aggradation rates of several meters per thousand years during the last deglaciation and the Early Holocene clearly document much more favorable living conditions for the CWC in the EMCP during the past (Fink et al. 2013; Wienberg, this volume).

Here, a high resolution bathymetric map of the EMCP is presented to document a large variety of submarine landscapes triggered and maintained within millennia by CWC growth (Fig. 8.1). The bathymetric dataset consists of multibeam echosounder data obtained with a KONGSBERG EM1002 operating at 95 kHz during the MSM36 cruise in 2014, aboard the RV Maria S. Merian (Hebbeln et al. 2015). It shows a huge variability of remarkable seabed features, which are arranged in three east-west-trending belts between the shallow Banc de Provençaux to the north (a volcanic structure of Miocene age; Ammar et al. 2007), and the Moroccan coast to the south (Fig. 8.1b). (i) In the northern sector of this region, the three so-called Brittlestar Ridges (Hebbeln et al. 2009; Fink et al. 2013) are attached to the southern edge of the Banc de Provençaux (Fig. 8.1c), (ii) southward, a cluster of at least 25 coral mounds with oval to arcuate shape occurs on an area with a gently rising flat sea floor (Fig. 8.1d), (iii) finally, the southernmost belt comprises sinuous to elongated coral ridges, stretching on average in a NW-SE direction and being partly buried (Fig. 8.1e).

Each mound and ridge structure that was sampled by gravity and/or box corers (n > 13), is clearly identified as a coral mound/ridge through the composition of its deposits comprising CWC fragments and hemipelagic sediments (Fig. 8.2; Hebbeln et al. 2009, 2015; Fink et al. 2013; Stalder et al. 2015). At four sites (Brittlestar Ridges I and III, Mole and Dragon Mounds; see Fig. 8.1b), drill cores obtained with the Bremen seafloor drill rig MeBo confirmed the CWC mound nature of these structures even down to drill depths of 33–70 m (Hebbeln et al. 2015). Consequently, it is assumed that the totality of the mound and ridge structures identified in the EMCP are build-up by CWC.

The three Brittlestar Ridges in the north are very long and steep coral ridges, rising 50–150 m above the surrounding sea floor between 475 and 375 m and stretching from over 3 km to almost 20 km in length (Fig. 8.1b, c). Interestingly, although they are all attached to the southern edge of the Banc de Provençaux, they extend into very different directions (Brittlestar Ridge (BR) I: beginning southward and turning southeastward, BR II: southwestward, BR III: beginning southwestward and turning WNW-ward). The elongated shape of coral mounds is often controlled by a dominant unidirectional bottom current (e.g., Messing et al. 1990; Correa et al. 2012; Hebbeln et al. 2014), which due to the varying directions of the Brittlestar ridges appears rather unlikely here. Nevertheless, although probably not controlling the shape of the ridges, strong bottom currents clearly had a role in their development, as demonstrated by the distinct moats found at the base of the ridges. Moats are most pronounced and deep around Brittlestar Ridge I, which point to a stronger bottom current impact to this easternmost ridge – at least for the most recent development that is best reflected in the present-day seabed morphology.

Peculiar features of the western Brittlestar Ridge III are the abrupt changes in direction of partly almost 90° that are occasionally observed along its crest (Fig. 8.1b). This configuration might hint to a tectonic control of the orientation and extension of the ridges, especially as the dominant directions to the SE and the SW follow the main regional fault directions (Ammar et al. 2007; Martínez-García et al. 2011). However, the drill cores obtained from the Brittlestar Ridges I and III confirm their CWC mound nature down to maximum drill depths of 70 m and 30 m, respectively (Hebbeln et al. 2015), indicating that tectonics probably only played a role of a pre-conditioning factor for mounds to initiate, by providing a hardground for the first CWC communities to settle.

Separated by a seabed area barren of any mound structures, a cluster with oval- to arcuate-shaped mounds occurs to the south of the Brittlestar Ridges, in water depths of 230–

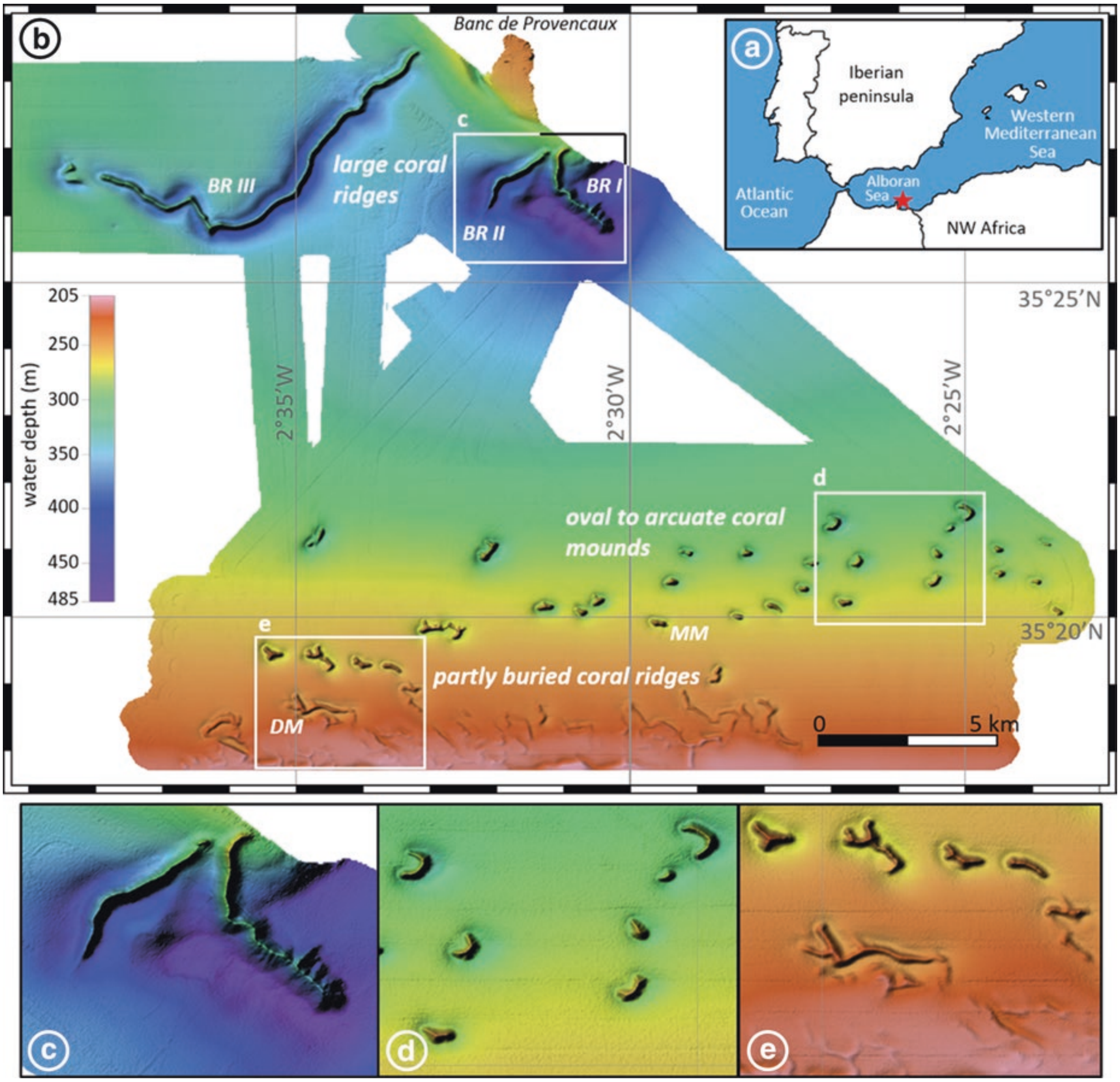

Fig. 8.1 The East Melilla Cold-Water Coral Mound Province (EMCP): (**a**) Overview map showing the location of the EMCP in the Alborán Sea. (**b**) Multibeam bathymetric map of the EMCP (25 m grid resolution) showing the three main morphotypes of coral ridges/mounds which are arranged along east-west trending belts. White rectangles indicate the position of the detailed maps in (**c**) (**d**) and (**e**); (*BR* Brittlestar Ridge, *MM* Mole Mound, *DM* Dragon Mound). (**c**) to (**e**) Detailed multibeam bathymetric maps (10 m grid resolution; approx. 4.5 km wide) showing each of the main coral ridge/mound type (for location see (**a**))

320 m (Fig. 8.1b, d). These mounds are much smaller compared to the Brittlestar ridges as their longest axes just reach few hundreds of meters. These mounds display very steep flanks, often reaching slope angles of >30°. Average heights above the seafloor range between 20 and 40 m, and even more if the depressions of the surrounding moats are considered. The extensions of these moats (Fig. 8.1d) point to bottom currents predominantly moving along northwest-southeast directions, however, without any clear indication to either NW- or SE-directed bottom currents.

These oval/arcuate mounds are distributed across an ENE-WSW direction, with their shapes gradually changing to extended, almost ridge-like, structures towards WSW, where they get closest to the ridges of the southernmost zone (Fig. 8.1b). The intermediate shape of these slightly elongated mounds – between oval- and ridge-like mounds – occurs where both morphotypes come closest to each other, pointing to an environmental control on the mound shapes.

In the southernmost part of the EMCP, coral ridges arranged in an E-W trending belt in water depths of 200–240 m rise to only ~10 m above the surrounding sea floor (Fig. 8.1b, e). Vanishing towards the south, these ridges appear to get buried by a thin veneer of sediments. The

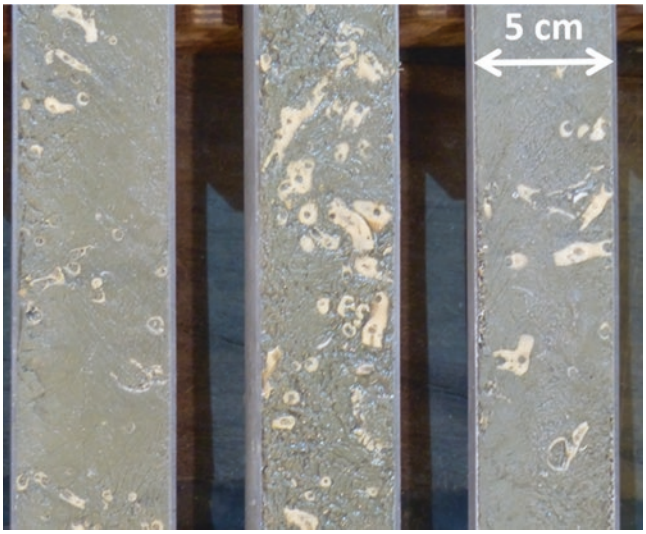

Fig. 8.2 Coral mound sediments composed of the typical mixture of cold-water coral fragments and hemipelagic sediments drilled with the MeBo (Bremen Sea Floor Drill Rig) at site GeoB 18110 on the Mole Mound (see Fig. 8.1), in the East Melilla Cold-Water Coral Province (EMCP)

sinuous (and partly branched) coral ridges predominantly stretch over up to 5 km along NW-SE directions and are also partly accompanied by well-defined moats. Here, the almost parallel directions of the ridges might point to a hydrodynamic control of their shape. Interestingly, the dominant shapes and moats of both of the southern coral mound/ridge types point to the same current directions (NW-SE) controlling their shape. Their very different shapes might be due to different current intensities, either at the two different depth levels or during different periods in the geological past.

The variety of the coral mounds and ridges shaping the submarine landscape in the EMCP points to different (or differently acting) drivers of coral mound formation. Within an area of only ~25 km in a N-S extension (Fig. 8.1), the sequence from probably tectonically driven long and steep ridges in the north via oval to arcuate mounds in the central part to most likely hydrodynamically controlled elongated ridges in the south provide evidence on the small-scale dynamics of submarine landscape formation. Nevertheless, future studies on these structures have to provide more detailed information on the drivers of these processes to fully unravel the formation history of these fascinating submarine landscapes.

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References

Ammar A, Mauffret A, Gorini C, et al (2007) The tectonic structure of the Alboran margin of Morocco. Rev Soc Geol España 20:247–271

Comas M, Pinheiro LM (2007) Discovery of carbonate mounds in the Alboran Sea: the Melilla mound field. In: Abstract for the first MAPG international convention, Conference & Exhibition Marrakech Convention Center, 28–31 October 2007

Correa TBS, Grasmueck M, Eberli GP, et al (2012) Variability of cold-water coral mounds in a high sediment input and tidal current regime, Straits of Florida. Sedimentology 59:1278–1304

De Mol B, Van Rensbergen P, Pillen S, et al (2002) Large deep-water coral banks in the Porcupine Basin, southwest of Ireland. Mar Geol 188:193–231

Dorschel B, Hebbeln D, Rüggeberg A, et al (2005) Growth and erosion of a cold-water coral covered carbonate mound in the Northeast Atlantic during the late Pleistocene and Holocene. Earth Planet Sci Lett 233:33–44

Fink HG, Wienberg C, De Pol-Holz R, et al (2013) Cold-water coral growth in the Alboran Sea related to high productivity during the late Pleistocene and Holocene. Mar Geol 339:71–82

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Hebbeln D, Samankassou E (2015) Where did ancient carbonate mounds grow — in bathyal depths or in shallow shelf waters? Earth Sci Rev 145:56–65

Hebbeln D, Wienberg C, Cruise Participants (2009) Report and preliminary results of RV POSEIDON Cruise POS 385 “Cold-Water Corals of the Alboran Sea (western Mediterranean Sea)”, Faro – Toulon, May 29–June 16, 2009: Berichte, Fachbereich Geowissenschaften, Universität Bremen, 273, urn:nbn:de:gbv:46-ep000106508

Hebbeln D, Wienberg C, Wintersteller P, et al (2014) Environmental forcing of the Campeche coldwater coral province, southern Gulf of Mexico. Biogeosciences 11:1799–1815

Hebbeln D, Wienberg C, Cruise Participants (2015) Climate-driven development of Moroccan cold-water coral mounds revealed by MeBo-drilling: Atlantic vs. Mediterranean settings – Cruise report to R/V Maria S. Merian expedition MSM 36. https://doi.org/10.2312/cr_msm36

Hebbeln D, Van Rooij D, Wienberg C (2016) Good neighbours shaped by vigorous currents: cold-water coral mounds and contourites in the North Atlantic. Mar Geol 378:114–126

Kano A, Ferdelman TG, Williams T, et al (2007) Age constraints on the origin and growth history of a deep-water coral mound in Northeast Atlantic drilled during integrated ocean drilling program expedition 307. Geology 35:1051–1054

Kenyon NH, Akhmetzhanov AM, Wheeler AJ, et al (2003) Giant carbonate mounds in the southern Rockall Trough. Mar Geol 195:3–50

Lo Iacono C, Gràcia E, Diez S, et al (2008) Seafloor characterization and backscatter variability of the Almería margin (Alboran Sea, SW Mediterranean) based on high-resolution acoustic data. Mar Geol 250:1–18

Lo Iacono C, Gràcia E, Ranero CR, et al (2014) The West Melilla cold water coral mounds, eastern Alboran Sea: morphological characterization and environmental context. Deep-Sea Res Part 2 Top Stud Oceanogr 99:316–326

Lo Iacono C, Savini A, Basso D (2018) Cold-water carbonate bioconstructions. In: Micallef A, Krastel S, Savini A (eds) Submarine geomorphology. Springer, Cham, pp 425–455. https://doi.org/10.1007/978-3-319-57852-1_22

Martínez-García P, Soto J, Comas M (2011) Recent structures in the Alboran ridge and Yusuf fault zones based on swath bathymetry and sub-bottom profiling: evidence of active tectonics. Geo-Mar Lett 31:19–36

Martorelli E, Petroni G, Chiocci FL, et al (2011) Contourites offshore Pantelleria Island (Sicily Channel, Mediterranean Sea): depositional, erosional and biogenic elements. Geo-Mar Lett 31:481–493

Messing CG, Neumann AC, Lang JC (1990) Biozonation of deep-water lithoherms and associated hardgrounds in the northeastern Straits of Florida. PALAIOS 5:15–33

Mienis F, van Weering T, de Haas H, et al (2006) Carbonate mound development at the SW Rockall trough margin based on high resolution TOBI and seismic recording. Mar Geol 233:1–19

Mienis F, Duineveld GCA, Davies AJ, et al (2014) Cold-water coral growth under extreme environmental conditions, the cape lookout area, NW Atlantic. Biogeosciences 11:2543–2560

Mortensen PB, Buhl-Mortensen L, Gebruk AV, et al (2008) Occurrence of deep-water corals on the mid-Atlantic ridge based on MAR-ECO data. Deep-Sea Res Part 2 Top Stud Oceanogr 55:142–152

Muñoz A, Ballesteros M, Montoya I, et al (2008) Alborán Basin, southern Spain. Part I: Geomorphology. Mar Petrol Geol 25:59–73

Muñoz A, Cristobo J, Rios P, et al (2012) Sediment drifts and cold-water coral reefs in the Patagonian upper and middle continental slope. Mar Petrol Geol 36:70–82

Remia A, Taviani M (2005) Shallow-buried Pleistocene Madrepora-dominated coral mounds on a muddy continental slope, Tuscan Archipelago, NE Tyrrhenian Sea. Facies 50:419–425

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Savini A, Corselli C (2010) High-resolution bathymetry and acoustic geophysical data from Santa Maria di Leuca cold water coral province (Northrn Ionian Sea – Apulian continental slope). Deep-Sea Res Part 2 Top Stud Oceanogr 57:326–344

Stalder C, Vertino A, Rosso A, et al (2015) Microfossils, a key to unravel cold-water carbonate mound evolution through time: evidence from the eastern Alboran Sea. PLoS One 10:e0140223

Taviani M, Remia A, Corselli C, et al (2005) First geo-marine survey of living cold-water Lophelia reefs in the Ionian Sea (Mediterranean basin). Facies 50:409–417

Titschack J, Fink HG, Baum D, et al (2016) Mediterranean cold-water corals – an important regional carbonate factory? Depos Rec 2:74. https://doi.org/10.1002/dep2.14

Vandorpe T, Wienberg C, Hebbeln D, et al (2017) Multiple generations of buried cold-water coral mounds since the Early-Middle Pleistocene Transition in the Atlantic Moroccan Coral Province, southern Gulf of Cádiz. Palaeogeogr Palaeoclimatol Palaeoecol 485:293–304

Wienberg C, Titschack J (2017) Framework-forming scleractinian cold-water corals through space and time: a late quaternary North Atlantic perspective. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 699–732. https://doi.org/10.1007/978-3-319-17001-5_16-1

Wienberg C, Titschack J, Freiwald A, et al (2018) The giant Mauritanian cold-water coral mound province: oxygen control on coral mound formation. Quat Sci Rev 185:135–152

Cross References

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Lo Iacono C, Savini A, Huvenne VAI, et al (this volume) Habitat Mapping of Cold-Water Corals in the Mediterranean Sea

Montagna P, Taviani M (this volume) Mediterranean cold-water corals as paleoclimate archives

Rebesco M, Taviani M (this volume) A turbulent story: Mediterranean contourites and cold-water corals

Wienberg C (this volume) A deglacial cold-water coral boom in the Alborán Sea: from coral mounds and species dominance

9

Spatio-Temporal Distribution of Mediterranean Cold-Water Corals

Agostina Vertino, Marco Taviani, and Cesare Corselli

Abstract

Cold-water corals have inhabited the Mediterranean basin since at least the Miocene, undergoing important modifications through time. Most information regarding pre-Pleistocene occurrences of extant cold-water coral species still relies on ancient literature records in need to be updated according to modern taxonomic and chronostratigraphic concepts. In this chapter, Neogene and Quaternary coral records are discussed. Many occurrences have been revised from the taxonomic point of view through the analysis of historical museum collections, newly collected specimens and original species descriptions and illustrations. In particular, this study summarises the current state of knowledge on Mediterranean frame-building cold-water corals and associated solitary species from the Miocene onwards. Several growth and demise phases, as well as changes in composition of dominant species have been observed so far. A shift from *Dendrophyllia*- to "Atlantic-like" *Lophelia*-dominated paleocommunities occurred at the Pliocene – Pleistocene boundary. "Golden ages" for the species *Lophelia pertusa*, and large bioconstructions formed by this coral, are thus far known in the Early Pleistocene (Calabrian stage), at the boundary Bølling- Allerød – Younger Dryas and in the Early Holocene (at least in the western basin). A large knowledge gap currently exists between the end of the Calabrian stage and the last 50 kyr BP. Several Atlantic deep-sea species (including frame-building and "psychrosperic" cold-water corals), common in the Early Pleistocene, disappeared in the Mediterranean after the Late Pleistocene, but how and when this event occurred is not known yet. Further studies need to be carried out to understand if there is any correlation between this deep-sea basin-scale extinction and the decline of *Lophelia*-dominated bioconstructions observed in the late Younger-Dryas and after the Early Holocene. In order to fill knowledge gaps on the fossil record of Mediterranean cold-water corals and to fully exploit the valuable potential of these organisms as palaeoenvironmental archives, the setup of a comprehensive open access database, including quality-controlled data on both modern and fossil species, is highly recommended. This would also provide a useful tool for managing, valorising and preserving the unique, yet undervalued paleontological heritage of the Mediterranean regions.

Keywords

Cold-water coral · Mediterranean · Neogene · Quaternary · Deep-sea · Bioconstruction

9.1 Introduction

The mineralised skeleton of cold-water corals (CWC), such as Scleractinia, Coralliidae, Isididae and Stylasteridae, is suitably preserved in the fossil record providing important information on ancient deep-sea paleoenvironments (e.g., Vertino 2003; Roberts et al. 2009; Robinson et al. 2014;

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Taviani et al., this volume; Montagna and Taviani, this volume; Angeletti et al., this volume). A crucial role in this regard is played by frame-building scleractinian species, like *Lophelia pertusa* and *Madrepora oculata*. These species construct considerable carbonate structures, hosting a variety of associated mineralised macro- and microorganisms, only in certain environmental conditions (Freiwald et al. 2004; Roberts et al. 2009; Henry and Roberts 2016; Wienberg and Titschack 2017; Rueda et al., this volume; Weinbauer et al., this volume).

The genera *Lophelia* and *Madrepora* boast a significant geological antiquity, with representatives being known since the Mesozoic (Cretaceous) (*Madrepora*: Stolarski and Vertino 2007) and Cainozoic (Miocene) (*Lophelia*: Roberts et al. 2009 and references therein), respectively. At present *Lophelia pertusa* and *Madrepora oculata* play a pivotal role in engineering CWC bioconstructions in the Atlantic and Mediterranean (e.g., Freiwald et al. 2004; Taviani et al. 2005b; Roberts et al. 2009; Corselli 2010; see Altuna and Poliseno, this volume; Chimienti et al., this volume) although the two species display a wider geographical distributional range (see Roberts et al. 2009). They are generally associated with other habitat-forming corals of lower frame-building potential, like the solitary gregarious *Desmophyllum dianthus,* the colonial *Dendrophyllia cornigera* and, restricted to the NE Atlantic, *Dendrophyllia alternata, Eguchipsammia cornucopia*, and *Enallopsammia scillae* (= *rostrata* = *amphelioides*) (Zibrowius 1980; Roberts et al. 2009 and references therein). Additionally, solitary scleractinian species, such as *Caryophyllia aradasiana* (= *calveri*) and *Stenocyathus vermiformis* in the Mediterranean, and *Caryophyllia coronata* (= *sarsiae*) in the NE Atlantic, are typical components of *Lophelia*-*Madrepora* bioconstructions (e.g., Zibrowius 1980; Freiwald et al. 2009; Mastrototaro et al. 2010; Angeletti et al. 2014; Taviani et al. 2017; Vertino et al. 2015; Altuna and Poliseno, this volume; Chimienti et al., this volume; Rueda et al., this volume). Most of these species are known in the Quaternary (Vertino 2003; Taviani et al. 2011) and, some of them, in the Neogene record of the Mediterranean (Taviani et al. 2005a; Vertino et al. 2014). However, the exact geographic location and precise age of fossil CWC occurrences on-land is lacunose in many cases, and taxonomic identification often dubious since many records refer to old literature accounts. Data regarding the spatio-temporal distribution of submerged Late Quaternary CWC in the Mediterranean Sea are still limited but much more accurate because based on samples obtained using recent advanced positioning systems. Moreover, thanks to the general good preservation of Late Pleistocene and Holocene corals, it is possible to directly date coral skeletons using radiometric techniques (e.g., McCulloch et al. 2010; Fink et al. 2015; Wienberg and Titschack 2017).

This chapter aims at providing an updated overview of the known occurrences of constructional CWC species and associated solitary ones in the peri-Mediterranean region through the Neogene and Quaternary. These coral records are reported on a georeferenced map and most of them are taxonomically revised based upon the analysis of historical museum collections, newly collected specimens and original species descriptions and illustrations. This is the first step towards setting a much needed database of fossil and recent CWC in the Mediterranean basin.

9.2 Material and Methods

The spatio-temporal data presented herein derive from the critical analysis of modern and ancient published literature (Appendices 9.1, 9.2 and 9.3; Fig. 9.3) and direct observations of Miocene to Holocene Mediterranean coral specimens (Figs. 9.1 and 9.2). This study focuses on the most common extant frame-building CWC taxa (Fig. 9.1) (*Lophelia pertusa, Madrepora oculata, Enallopsammia scillae*, the genus *Dendrophyllia,* with morphotypes resembling modern deep-sea species) and associated solitary scleractinians (Fig. 9.2) (*Desmophyllum dianthus, Caryophyllia coronata, Caryophyllia calveri, Stenocyathus vermiformis* and the genus *Javania*) that have characterised Mediterranean deep-sea bioconstructions during the Quaternary and whose occurrence is known since the Miocene. Museum collections of Miocene to Early Pleistocene fossil corals, critically examined in this study for their CWC material, are listed in Vertino et al. (2014) and updated in the acknowledgements section of the present chapter. Additional analyses were performed on submerged Quaternary specimens held in the Department of Environmental and Earth Sciences, University of Milano-Bicocca (Italy) and the Institute of Marine Sciences – CNR, Bologna (Italy).

The on-land CWC occurrences reported in Fig. 9.3 and Appendix 9.1 are not comprehensive: they include only the scleractinian species mentioned above and exclusively literature citations taxonomically reviewed in recent years. The accuracy of the geographic location of the analysed on-land sites is highly variable. In some cases only a generic geographic description was given in old publications, therefore exact geographic coordinates are not always available. The radiometric coral ages reported in Figs. 9.4 and 9.5 (Appendices 9.2 and 9.3) derive from the literature: Hersey (1965), Zibrowius (1980, 1981), Taviani and Colantoni (1984), Delibrias and Taviani (1985), Schröder-Ritzrau et al. (2005), Malinverno et al. (2010), McCulloch et al. (2010), Angeletti and Taviani (2011), Frank et al. (2011), Taviani et al. (2011), Fink et al. (2012, 2013, 2015), Stalder et al. (2015), Titschack et al. (2016), and Dubois-Dauphin et al. (2016, 2017). In order to compare radiocarbon ages, ^{14}C data not included in Fink et al. (2015), were re-calibrated by using the Marine13 calibration curve (Reimer et al. 2013) of the Oxcal 4.3.2 software (Bronks Ramsey 2009) assum-

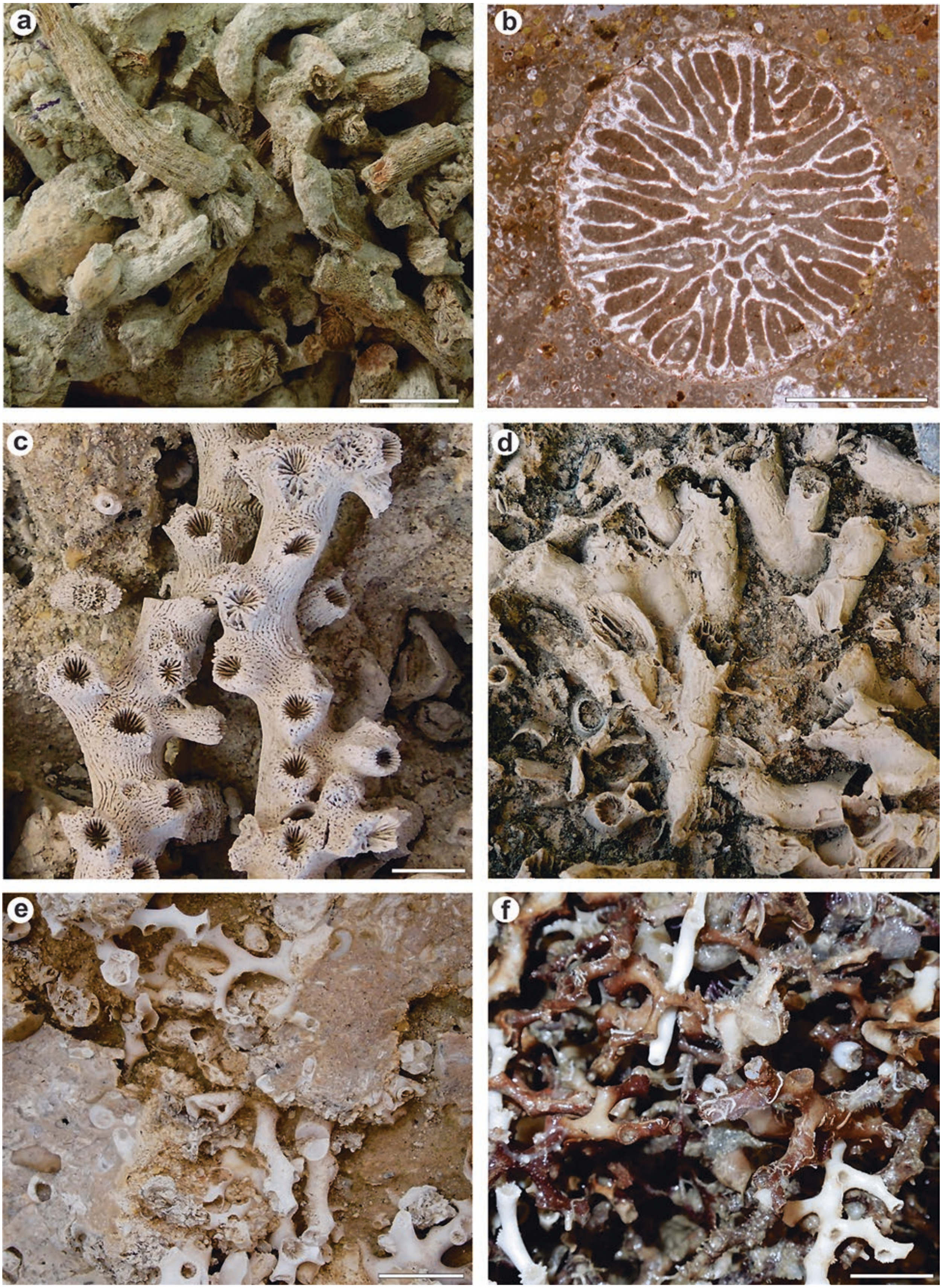

Fig. 9.1 Miocene to Holocene examples of Mediterranean frame-building cold-water corals (CWC). (**a** and **b**) *Dendrophyllia* cf. *cornigera* (Miocee, Serravallian-Upper Tortonian, surroundings of Lecce, southern Italy); see Vescogni et al. 2018; (**a**) Fossil coral rubble, scale bar 2 cm; (**b**) Transversal section of a juvenile corallite, scale bar 0.5 cm. (**c**) *Enallopsammia scillae* (Early Pleistocene, "La Montagna", Messina, southern Italy), scale bar 1 cm. (**d**) *Lophelia pertusa* (Early Pleistocene, "La Montagna", Messina, southern Italy), scale bar 2 cm. (**e**) Fossil coral rubble dominated by tiny branches of *Madrepora oculata* (Early Pleistocene, San Filippo, Messina, southern Italy), scale bar 1 cm. (**f**) Fresh-looking to dark-coated fragments of *Madrepora oculata* on the surface of a box-core samples (MD194 cruise, BC 3471) collected at 314 m depth in the Alboran Sea (Holocene), scale bar 2 cm

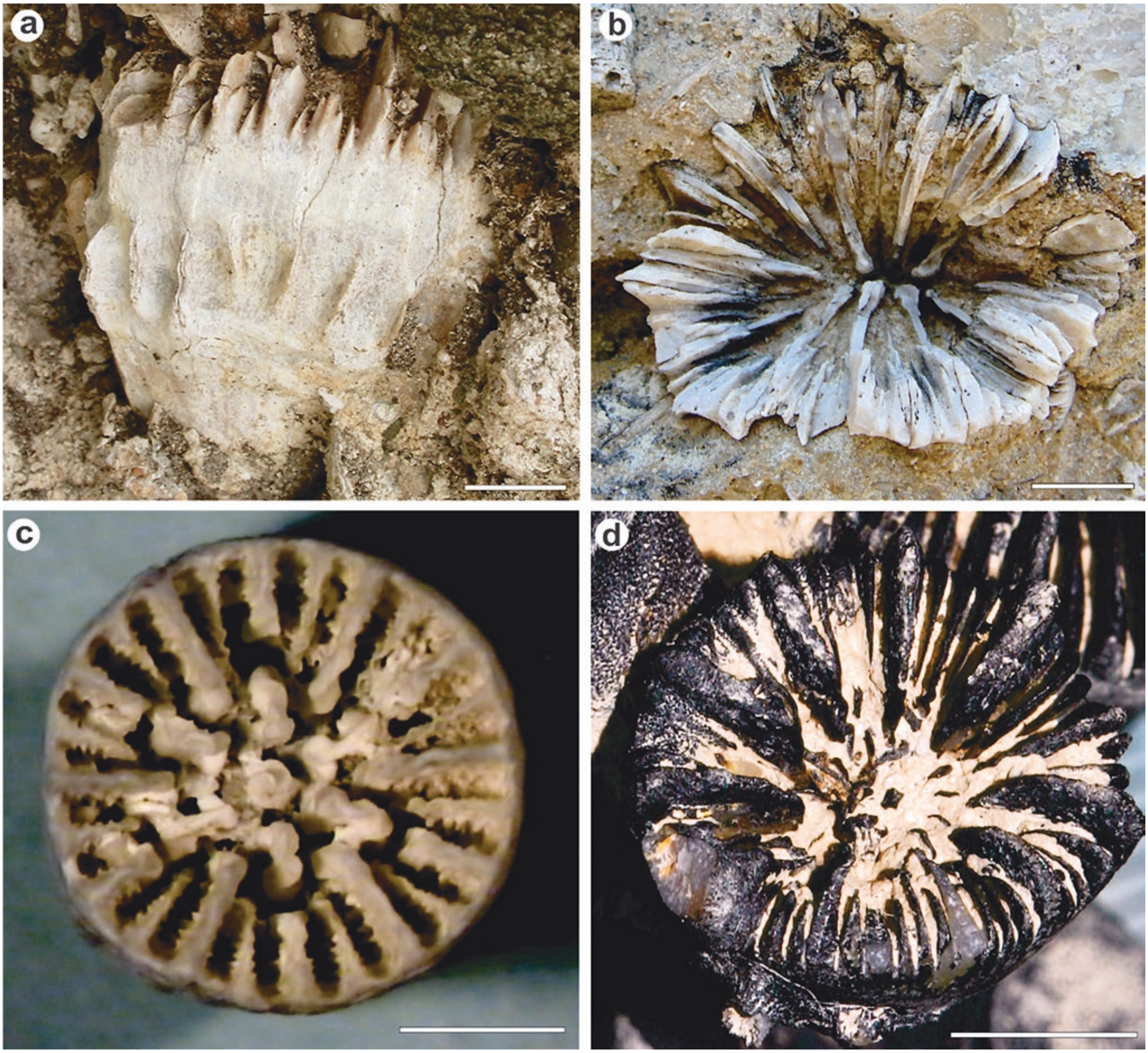

Fig. 9.2 Miocene to Late Pleistocene examples of Mediterranean solitary corals associated with frame-building CWC. (**a** and **b**) Lateral (**a**) and distal (**b**) view of large specimens of the gregarious species *Desmophyllum dianthus*, embedded in coral rudstones (**a**: Early Pleistocene, Trapani, Messina, southern Italy; **b**: Early Pleistocene, Capo Milazzo, southern Italy), scale bar 1 cm. (**c**) Distal view of a well preserved corallite of *Stenocyathus vermiformis* (Early Pleistocene, Gravitelli, Messina, southern Italy), scale bar 2 mm; (**d**) Black coated specimen of *Caryophyllia coronata* collected off-shore Crete at 2133 m depth (GECO cruise, 50) (Late Pleistocene), scale bar 1 cm

ing a reservoir effect of ~400 years (Siani et al. 2001), and are reported as Median Probability Age (MPA) (Appendix 9.2). This procedure has been followed also for data published over 30 years ago by Hersey (1965), Zibrowius (1980), (1981), and Taviani and Colantoni (1984). However, due to the little methodological information provided by these authors on the obtained ^{14}C data, the related calibrated ages (indicated with an asterisk in Fig. 9.4 and Appendix 9.2) must be taken with caution.

Scleractinian taxonomy follows WoRMS Editorial Board (2017), with the exception of *Caryophyllia sarsiae* Zibrowius, 1980, *Caryophyllia calveri* Duncan, 1873 and *Enallopsammia rostrata* (Pourtalès, 1878) that, according to Vertino (2003) and following the Principle of Priority of the International Code of Zoological Nomenclature (ICZN) [Art. 23.1], are named herein as *Caryophyllia coronata* Seguenza, 1864, *Caryophyllia aradasiana* Seguenza, 1864 and *Enallopsammia scillae* (Seguenza, 1864), respectively. Based on comprehensive molecular and morphological analyses, Addamo et al. (2015a), Addamo (this volume) highlighted the extreme similarity between the scleractinian species *D. dianthus* and *L. pertusa* (99.8% of mitochondrial

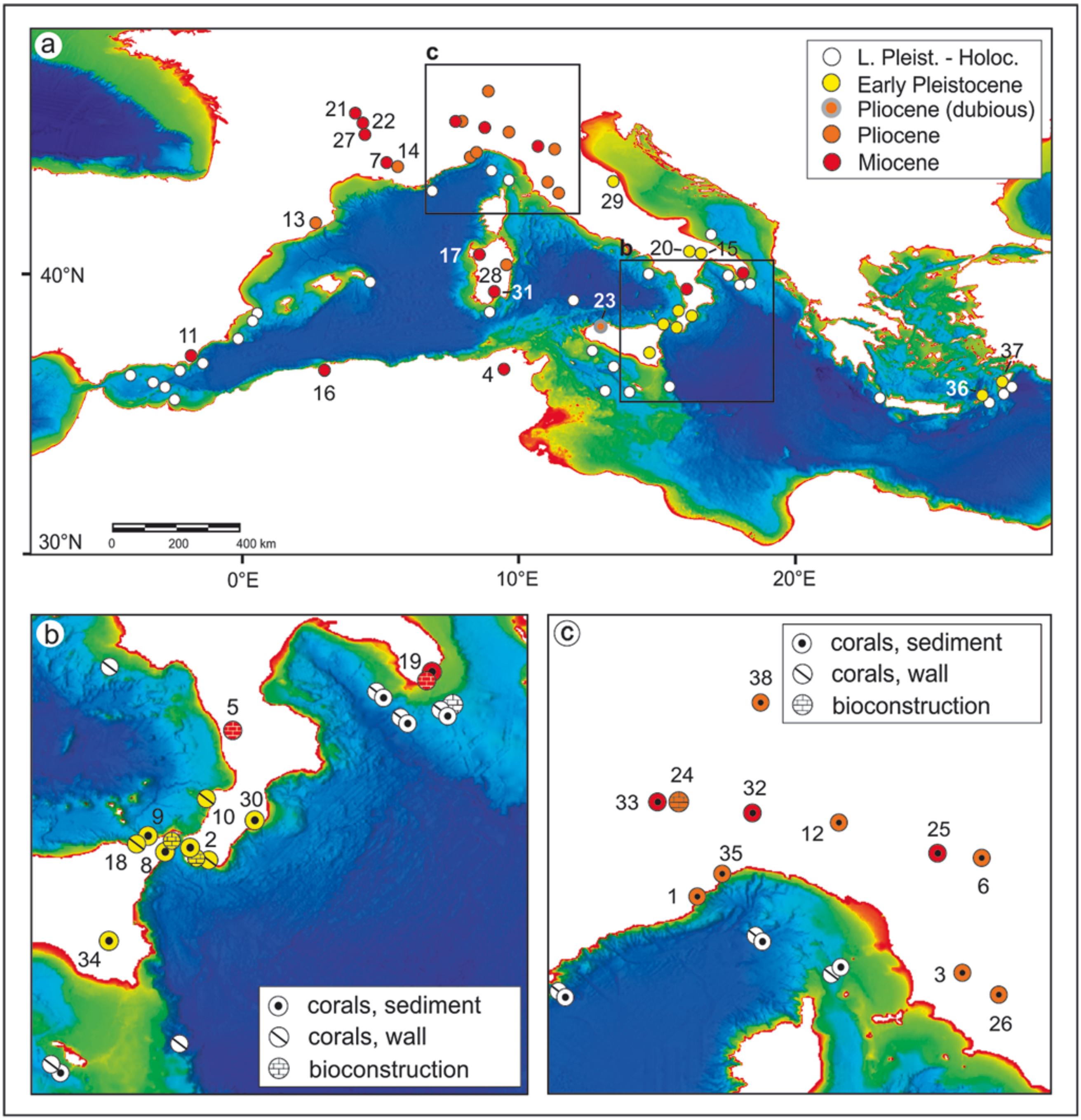

Fig. 9.3 (**a**) Overview map showing the spatio-temporal distribution of the on-land and submerged CWC sites mentioned in the text and/or listed in Appendices 9.1, 9.2 and 9.3. (**b** and **c**) Detail of southern Italy (**b**) and northern Italy (**c**) including basic information on the most common (paleo)habitats: coral colonies and/or fragments sparse in fine-grained siliciclastic deposits or mud-dominated sediment and boulders; corals encrusting subvertical walls and overhangs; coral frameworks forming bioconstructions. Map source ESRI. Numbers refer to the CWC sites listed in Appendix 9.1

nucleotides and 97% of microsatellite sequence are identical). This finding strongly suggests that, despite their different growth forms (solitary *vs.* colonial), these two species should be ascribed to a single genus and, following the ICZN Principle of Priority, *L. pertusa* should be named as *Desmophyllum pertusum*. Nevertheless, in this chapter we maintain the traditional division due to ongoing genetic research on modern specimens and pending taxonomic revision of fossil species historically assigned to these genera. The terms zooxanthellate, azooxanthellate, constructional (= frame-building) and non-constructional are used in the text following the definition by Schumacher and Zibrowius (1985) and the words circalittoral and bathyal are adopted *sensu* Pérès and Picard (1964) (see Altuna and Poliseno, this volume).

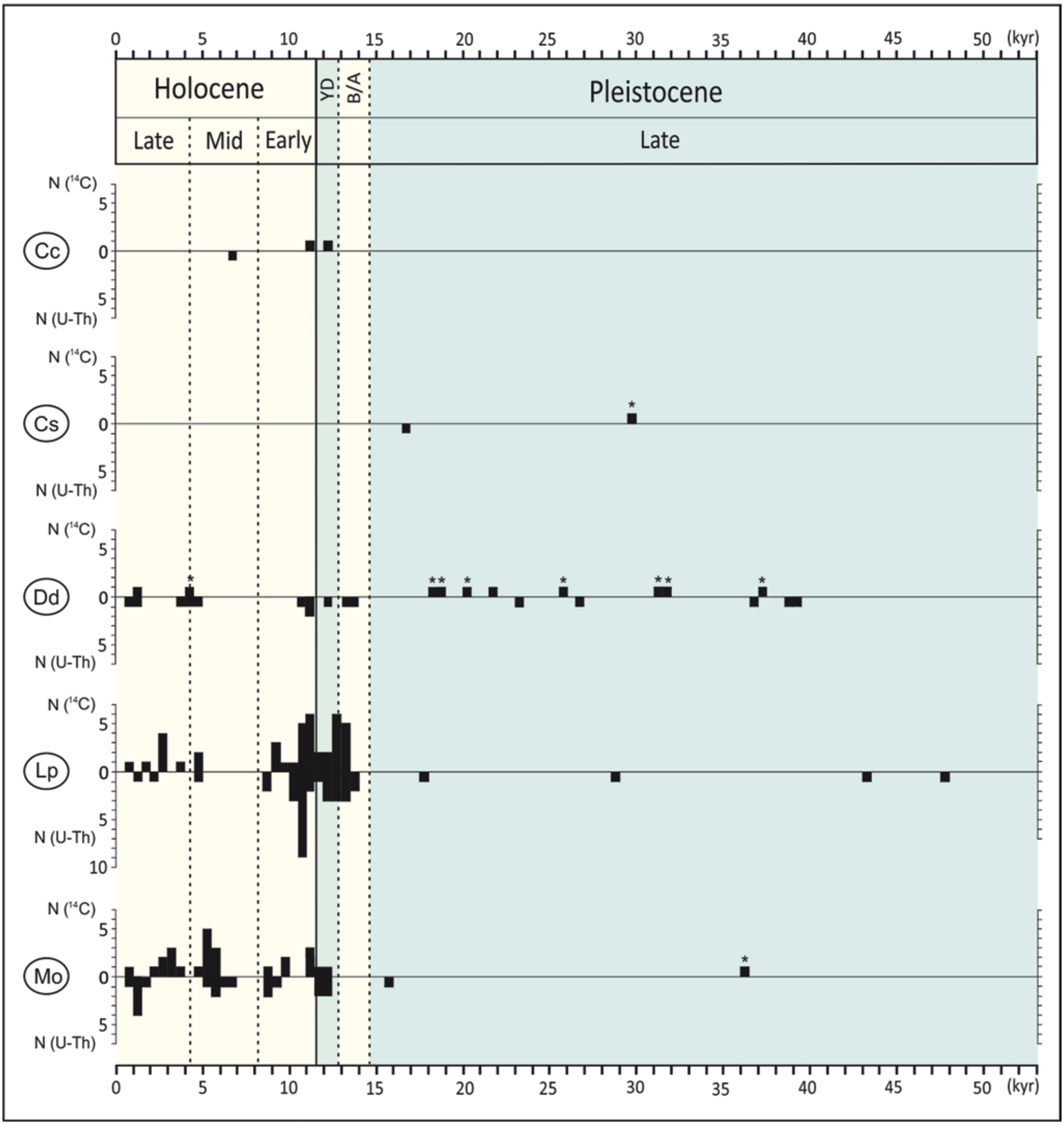

Fig. 9.4 Distribution of radiometric ages of Late Pleistocene and Holocene Mediterranean coral specimens collected from submerged cold-water coral sites of the Mediterranean Sea. Coral compilation from the literature; see references in the text and complete age list in Appendices 9.2 and 9.3. The width of each black bar corresponds to 500 years. The height of each black bar corresponds to the number (N) of coral specimens (dated through ^{14}C or U-Th) whose age is included in those 500 years. Cs *Caryophyllia sarsiae (=coronata)*, Cc *Caryophyllia calveri*, Dd *Desmophyllum dianthus*, Lp *Lophelia pertusa*, Mo *Madrepora oculata*. Asterisks indicate ^{14}C coral ages published in the 1980s that must be treated with caution

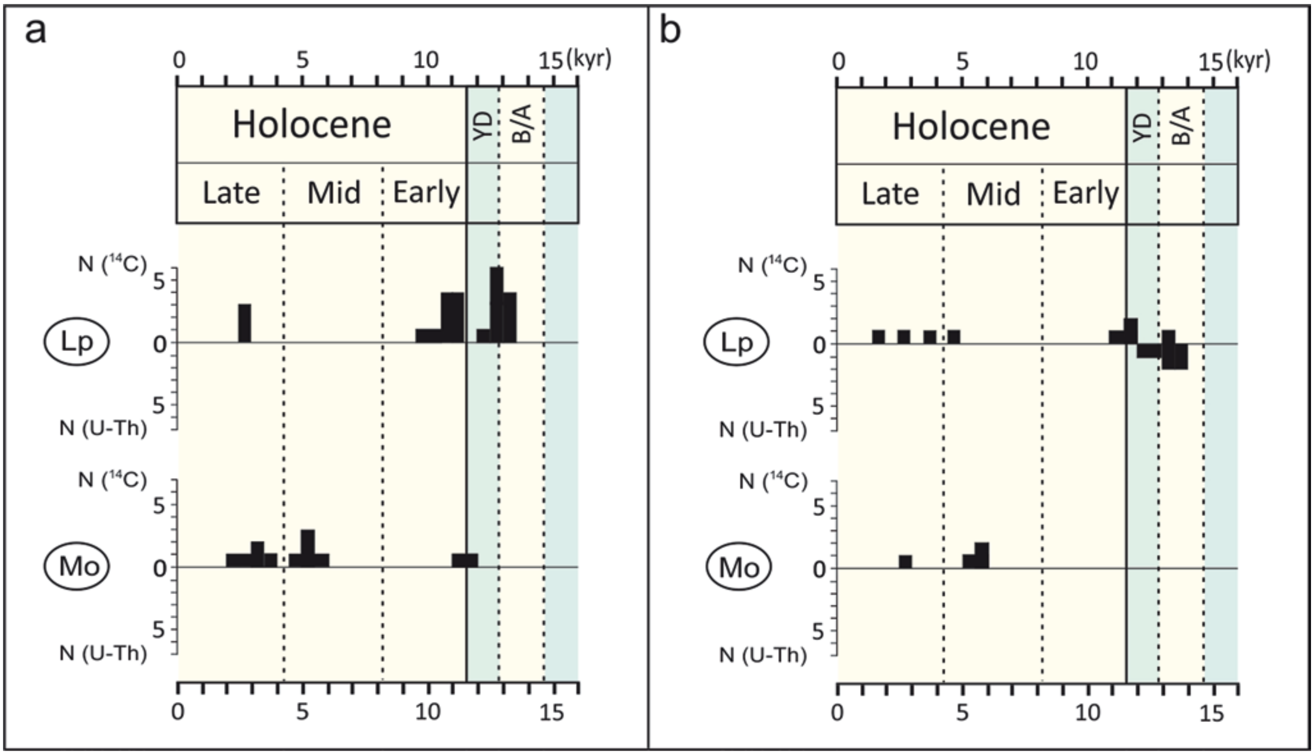

Fig. 9.5 Ages of *L. pertusa* (Lp) and *M. oculata* (Mo) collected from the Melilla coral mounds (**a**) and the Santa Maria di Leuca mounds (**b**) in the last 16 kyr. The width of each black bar corresponds to 500 years. The height of each black bar corresponds to the number of coral specimens (dated through ^{14}C and/or U-Th) whose age is included in those 500 years

These adjectives are applied to fossil species, and/or assemblages, based on the actualistic assumption that the ecological requirements of extant taxa have not drastically changed through geological time. Finally, the adjective deep is used in this chapter to indicate low circalittoral to bathyal (paleo) environments.

9.3 Cold-Water Corals Through Geological Times

9.3.1 Key Study Sites

Fossil occurrences of CWC are known since the Miocene in several peri-Mediterranean localities. Among the examined sites (Appendices 9.1, 9.2 and 9.3; Fig. 9.3), there are some exceptional ones in terms of outcrop extension and exposure and/or preservation and diversity of the fossil assemblages. They are shortly described in the following paragraphs and suggested as target sites for more detailed taxonomic, stratigraphic and paleoecological analyses combining traditional and advanced techniques, such as the use of geochemical proxies, when possible.

9.3.1.1 Miocene

One of the richest regions in terms of specimens and species abundance of Miocene corals is located in northern Italy. In particular, the diversified coral assemblages of the "Collina di Torino" (TH = Turin Hills) deposits have been the focus of taxonomic and paleoecological studies carried out in the eighteenth century by Sismonda (1871) and De Angelis (1894) and later by Zuffardi-Comerci (1932) and Chevalier (1961). Some of the "Helvetian" fossil coral localities mentioned by Chevalier (1961) (Valle Ceppi, Val Sanfrà, Monte Cappuccini) have been recently assigned to the Burdigalian "Termofourà Formation" and the Langhian "Baldissero Formation" (Zunino and Pavia 2009). The richest fossiliferous layers of the TH formations correspond to conglomerate lenses interbedded with silt-clay deposits, described by Chevalier (1961) as a "mélange" of "hermatypic and ahermatypic forms". Based upon taxonomic and taphonomic arguments on mollusc assemblages in the Termofourà and Baldissero Formations, it has been hypothesised that the shallow-water components were transported down basin through gravity processes in submarine canyons, and got mixed with deeper water faunal elements (Zunino and Pavia 2009 and references therein). Through the ongoing revision of the historical coral collection held at the Museum of Natural History of the Torino University and of newly collected specimens from the "Valle Ceppi" and "Val Vergnana" localites, we have ascertained that the TH deposits contain several CWC specimens, most of which represented by solitary corals typical of muddy to fine sandy deposits. Among frame-building CWC, the genus *Dendrophyllia* is rather common and some fragments show size and shape comparable to that of the modern species *D. cornigera*. Other dendrophylliids, identified as *Enallopsammia scillae* in the historical collections, belong indeed to the genus *Enallopsammia* but are indicated herein as *Enallopsammia* cf. *scillae* due to the larger size of their corallites with respect to the Pleistocene Mediterranean and modern Atlantic species. Several specimens originally named as "*Amphihelia*" and *"Diplohelia"* (Zuffardi-Comerci 1932; Chevalier 1961) can be ascribed to the modern species *M. oculata* (Fig. 14.4h in Vertino et al. 2014). Moreover, the skeletal features of most coralla of *Desmophyllum*, ascribed by Chevalier (1961) to 16 distinct species, fall within the high intraspecific variability of the modern species *D. dianthus* (Addamo et al. 2015b). So far, coral fragments belonging to the species *L. pertusa* and *S. vermiformis* have not been found in the Miocene TH deposits. *Javania* has been cited in ancient literature but its presence has still to be ascertained. Several *Caryophyllia* specimens have been collected from the Early Miocene TH deposits but their identification at species level has not been revised yet.

Northern Italy is also well known for several Upper Miocene fossil sites containing well preserved azooxanthellate corals. The Tortonian deep-sea coral fauna is scarce in the TH region but rather common, diversified and exceptionally well preserved in other locations, such as Tortona, Stazzano, Sant'Agata Fossili, Montebaranzone, Montegibbio (De Angelis 1894; Simonelli 1896; Montanaro 1929; Zuffardi-Comerci 1937; Chevalier 1961; Corselli 2001). These sites are mostly characterised by marly and sandy deposits containing typical soft-bottom dwelling solitary corals, belonging to the genera *Balanophyllia (Eupsammia), Flabellum, Ceratotrochus, Trochocyathus, Deltocyathus, Stephanophyllia* etc. (Vertino et al. 2014 and references therein). However, several fragments of colonial, and potentially frame-building corals are also known from these sites. Most probably these colonial corals used skeletal remains of other organisms as substrate for the settlement of their larvae. In particular, specimens comparable to *D. cornigera* are relatively common in marly deposits of both Piedmont and Emilia Romagna sites and skeletal fragments identifiable as *M. oculata* (cited in the literature as *Amphihelia*), *E.* cf. *scillae* and *D. dianthus* have been cited in at least one of the Tortonian localities of northern Italy (Appendix 9.1).

Of particular interest are the coral assemblages of the Tortonian "Calcare di Mendicino" (CM), located at Belsito, in Calabria (southern Italy), where bioconstructed CWC limestones up to 3 m in thickness occur (Mastandrea et al. 2002). Through thin section analysis Mastandrea et al. (2002) identified the dominant corals as *Dendrophyllia* and *Oculina* and clearly showed the common presence of associated stylasterid specimens. Due to the almost complete aragonite dissolution, scleractinians were not identified at species level. However, further detailed analyses of the coral inner and outer moulds may provide important additional taxonomic details. The only other known occurrence of Miocene CWC rudstones is located in the surrounding of Leuca, Apulia (southern Italy), where a very dense accumulation of dendrophylliid (including *Dendrophyllia* cf. *cornigera*, Fig. 9.1a, b) and caryophylliid corals form a much thinner layer, up to 25 cm in thickness, corresponding to the condensed lower Serravallian-upper Tortonian phosphate-rich deposit known in the literature as "*Aturia* Layer" (Föllmi et al. 2015; Vescogni et al. 2018). Finally, dendrophyliids branches (likely *Dendrophyllia* spp.) occur embedded in methanogenetic limestones from various sites in the northern Apennines such as the sites Ca' Fornace in the Sintria Valley, Ravenna and Montepetra Forlì, in Emilia-Romagna (Kiel et al. 2018; Taviani unpublished data).

Lastly, it is worth citing the exceptionally well preserved, abundant and diversified CWC fauna of the Messinian "brèche rouge" of Carboneras (SE Spain), dated to the Messinian stage (Barrier et al. 1991), whose paleobiological value has been recognised by several authors (e.g. Taviani et al. 2005a; Roberts et al. 2009; Freiwald, this volume). Scleractinians, gorgonians (Coralliidae, Isididae, Primnoidae) and stylasterids (the most diversified known so far in the fossil record) were living in a heterogeneous deep seafloor characterised by both hard and soft substrates (Barrier et al. 1991). The hard substrate, consisting of fragmented volcanic rocks, provided a suitable colonisable surface for a diverse stylasterid community including at least 14 species, 10 of which known in the NE Atlantic and 4 living today only in Indo-Pacific regions and the tropical Atlantic (Barrier et al. 1991). Also among the scleractinians, two of the over ten recognised genera living today in the NE Atlantic, are known only in the modern bathyal fauna of the western Atlantic and in Indo-Pacific regions. Like in other Miocene sites, the family Dendrophylliidae is rather common and at least three species of *Dendrophyllia* collected in the Carboneras outcrop are ascribable to deep-sea N Atlantic taxa (Barrier et al. 1991). Fragments of the frame-building genera *Madrepora* and *Desmophyllum* also occur but there is no evidence of bioconstructions. Interestingly, the number of CWC species collected from the "brèche rouge" is much higher than the species number that could be found by dredging modern coral-dominated NE Atlantic bathyal seafloors. The high CWC diversity observable in the Carboneras deposits may have been possibly amplified by time-averaging processes. However, a comparable number of species could be found today in coral-rich deep-sea environments of the tropical Atlantic and in some Indo-Pacific regions (Barrier et al. 1991; Cairns 2007).

9.3.1.2 Pliocene

Most deep-sea azooxanthellate scleractinian genera known so far are solitary soft-bottom dwelling forms (De Angelis 1893, 1894, 1895; Osasco 1895; Simonelli 1895, 1896; Zuffardi-Comerci 1927, 1937; Montanaro 1931; Dieni and Omenetto 1960; Chevalier 1961; Russo 1980) ascribable, or comparable, to modern taxa living in muddy to fine sandy seafloors (Vertino et al. 2014). The dominance of these corals is probably only apparent, being biased by the overwhelming abundance of Pliocene marly and clayey bottoms (e.g. "Argille Azzurre Fm") with respect to hard bottom substrates. Frame-building CWC species are reported in several Pliocene localities of northern Italy (De Angelis 1894; Osasco 1895; Simonelli 1895; Montanaro 1929, 1931; Chevalier 1961; Corselli 1997; Spadini 2015), and Sardinia (Chevalier 1962) as well as in the Vaucluse region (France) and in Catalonia (Spain) (Chevalier 1961) (Appendix 9.1). In all these cases corals have been recorded as fragments within fine-grained siliciclastic deposits. The Pliocene sediments of the Siena Basin (SB) are particularly important for the diversity of azooxanthellate corals and the very good preservation state of most skeletons, some of which are probably still preserved as aragonite. A recent review of the fossil Scleractinia contained in the Zanclean-Piacenzian deposits of the SB (Spadini 2015) lists 19 scleractinian genera living today preferentially, or exclusively, in circalittoral to bathyal environments. In particular, the following frame-building species are reported: dendrophylliid specimens comparable to *D. cornigera,* the species *E. scillae* and *D. dianthus* (indicated as "*Desmophyllum* sp."). Additionally, Spadini (2015) reports the first occurrence in the Mediterranean Pliocene of the tiny species *S. vermiformis*, a recurrent taxon associated with Pleistocene to recent "White Coral" communities (Vertino 2003; Freiwald et al. 2009; Mastrototaro et al. 2010; Rosso et al. 2010; Taviani et al. 2011, 2017; Angeletti et al. 2014; Altuna and Poliseno, this volume; Chimienti et al., this volume). Colonial and solitary CWC, among which dendrophylliids (including *Enallopsammia* cf. *scillae*, Vertino unpublished data) and Caryophylliidae, are mentioned from the Stirone River chemoherm in the northern Apennines in the Parma province (Monegatti et al. 2001; Cau et al. 2015). Another remarkable Pliocene CWC site is located in the surroundings of Marmorito (Piedmont, northern Italy) (Appendix 9.1); where coral rudstones are dominated by *D. dianthus* and *E. scillae*. They contain secondarily also *Caryophyllia cyathus* and other dendrophylliids. Though corals are preserved only as moulds, they can be identified at species level through macro- and micromorphology analysis of casts. Several taxonomic characters (size, shape, branching typology, number of septa, imprint of wall microarchitecture) hint also at the presence of *L. pertusa* in the Marmorito deposits.

Most Pliocene CWC occurrences from southern Italy and from the eastern Mediterranean (e.g., Seguenza 1880; De Stefano 1899; Barrier 1984, 1987; Roux et al. 1988; Barrier et al. 1989; Hanken et al. 1996) have been recently ascribed to Early Pleistocene deposits (Vertino et al. 2003; Di Geronimo et al. 2005; Titschack and Freiwald 2005; Di Stefano and Longhitano 2009).

9.3.1.3 Early-Middle Pleistocene

The most remarkable CWC outcrops so far known in the peri-Mediterranean region are located in southern Italy and are particularly abundant along the margin of the Messina Strait (Seguenza 1864, 1880; Di Geronimo 1987; Zibrowius 1987; Barrier et al. 1989; Roux et al. 1988; Di Geronimo et al. 2005; Vertino 2003; Vertino et al. 2014; Taviani et al., this volume and references therein). These deposits emerged due to strong regional uplift since the middle Pleistocene. Their facies heterogeneity seems to be related to a complex paleo-strait physiography characterised by several micro-basins that evolved independently through time (Barrier 1987). In particular, in the surrounding of the city of Messina, CWCs occur within two main facies groups, (1) Carbonate-dominated Facies (CF) and (2) Siliciclastic-dominated Facies (SF) (Vertino et al. 2013). The CF group is characterised by CWC rudstones laterally evolving into carbonate muddy sands and calcarenites. The rudstones consist almost exclusively of skeletal fragments of frame-building deep-water scleractinians, such as *L. pertusa, M. oculata, E. scillae* and *D. dianthus* (Figs. 9.1c–e and 9.2a, b) and have been interpreted as, at least partly, in-place bioconstructions. They include several other associated species (e.g. *C. coronata,* and secondarily, *C. aradasiana*, *S. vermiformis, Dendrophyllia* spp.), all living today in NE Atlantic bathyal environments but some of them lacking in the modern Mediterranean (Vertino 2003; Vertino et al. 2014; Vertino and Corselli, this volume; Altuna and Poliseno, this volume). These bioconstructed deposits interfinger with floatstones characterised by mudstone to packstones matrix and dominated by isidid octocorals and brachiopods and/or bryozoans and echinoderms. The CF CWC species characterise also the lateral and overlying SF facies that consist mostly of marly and silty clays and, locally, show evidences of chaotic mass deposits. In these siliciclastic-dominated deposits frame-building coral species are commonly scattered within the fine-grained sediment whereas soft-bottom species, such as *Caryophyllia communis* and *Flabellum* spp., can be rather common. These deposits are rich in frame-building species only in the vicinity of large boulders and/or paleoescarments whose original surface can be still encrusted by hard-bottom fauna (coral basal parts, cemented bivalves, serpulids, bryozoans etc.) (Barrier 1987; Vertino 2003; Di Geronimo et al. 2005; Taviani et al., this volume and references therein). Early Pleistocene CWC are known from emerged deposits of other Mediterranean regions, but our knowledge on frame-building species is thus far limited to Italian locations (e.g., Barrier 1987; Placella 1978, 1980; Di Geronimo 1979; Cantalamessa et al. 1987, 1997; Caldara et al. 1993; Di Geronimo et al. 2005), Rhodes (Titschack and Freiwald 2005; Titschack et al. 2008; Titschack, this volume), and Karpathos (Moissette et al. 2017) (Fig. 9.3; Appendix 9.1). The age of the CWC-rich deposits, dated so far, from these three localities has been ascribed to the Calabrian stage (Di Stefano and Longhitano 2009; Titschack and Freiwald 2005; Moissette et al. 2017). Some outcrops from north-eastern Sicily, containing scattered highly bioeroded and mechanically abraded CWC, are probably younger (Middle Pleistocene, Biozone MNN19f) but their coral content seems to be reworked from older beds. The only other information about Middle Pleistocene CWC known hitherto in the Mediterranean derives from research in progress on submerged coral mounds of the Alborán Sea, drilled using the Bremen Seafloor Drill Rig (MeBo) (Hebbeln et al. 2015; Krengel et al. 2017; Wienberg, this volume). In this area large seabed structures made up by CWC occur from 230 to 450 m water depth (Fink et al. 2013, 2015; Lo Iacono et al. 2014a, b; Stalder et al. 2015; Wienberg and Titschack 2017; Wienberg, this volume).

9.3.1.4 Late Pleistocene (Last 50 kyrs) - Holocene

Thanks to the recent increased interest in the study of submerged CWC mounds and the large number of deep-sea coral specimens dated using radiometric techniques, our knowledge on Late Pleistocene and Holocene CWC has highly improved in the last years. As summarised by McCulloch et al. (2010) and Fink et al. (2015), and updated by 28 coral ages later obtained by further investigation (Stalder et al. 2015; Titschack et al. 2016; Dubois-Dauphin et al. 2016, 2017), the oldest dated frame-building Mediterranean CWC specimens (*L. pertusa*) is around 50 kyrs old (Fig. 9.4; Appendix 9.3). As underlined by Fink et al. (2015), almost all coralla of *L. pertusa* and *M. oculata* dated so far have resulted to be younger than 14 kyrs (Fig. 9.4). However, these ages have been obtained by dating coral specimens collected through dredging, box-coring, grabbing and gravity coring of the upper few meters of seafloor sediment (Appendices 9.2 and 9.3).

The Alborán Sea represents the most spectacular CWC mound region known so far in the Mediterranean Sea, both for the wide extension of the mounds (Fink et al. 2013, 2015; Lo Iacono et al. 2014a, b; Wienberg, this volume) and for the diversified fossil and modern fauna associated to frame-building coral communities (Lo Iacono et al. 2014b, 2016; Stalder et al. 2015; Lo Iacono et al. 2016; Wienberg, this volume). The largest coral mounds of the Eastern Melilla Coral Province seem to be dated back to the Middle Pleistocene (Krengel et al. 2017), but data collected so far from superficial deposits indicate that frame-building CWC (at least *L. pertusa*) were common between ~13.5 and 12.5 and ~11.5 and 10.5 kyr BP (Fig. 9.5a; Appendices 9.2 and 9.3), with an apparent decline phase between ~12.2 and ~11.6 kyr BP (Wienberg, this volume). These flourishing coral periods correspond to the highest aggradation rates observed thus far in the carbonate mounds of the Melilla Province and have been correlated to intensified intermediate water mass circulation and enhanced productivity in the Alborán Sea (Wienberg, this volume and reference therein).

The Santa Maria di Leuca (SML) Province is the second widest CWC mound area known in the Mediterranean. It is located in the eastern basin, along the upper slope of the Apulian continental margin, at water depth ranging between ~400 and 1000 m (Taviani et al. 2005b; Savini and Corselli 2010; Savini et al. 2014; Chimienti et al., this volume). Recent studies highlighted the presence of 5820 mound-like morphologies over a total area of approximately 600 km^2, potentially colonised by CWC (dead or alive) (Savini et al. 2014). Less than 40% radiometric ages of colonial CWC have been obtained so far from the eastern basin and less than 20 from the SML province (Fig. 9.5b). Data collected from the upper 3–4 m of the SML mounds indicate the presence of up to ~1.5 m thick coral-dominated deposits that, in the lower part, are rich in *L. pertusa* branches. The latter were dated back to a period ranging from ~14 to ~11.5 kyr BP (McCulloch et al. 2010; Malinverno et al. 2010; Fink et al. 2012). Fink et al. (2012) ascribed the absence of CWC during the Early to Mid-Holocene, in two cores from the SML mounds, to low-oxygen conditions (~2 ml l^{-1}) estimated on the basis of the relative abundance of selected deep-infaunal foraminiferan species. These authors assumed moreover a direct relationship between the demise of CWC mound accretion in the SML province, from 11.4 to 5.9 cal kyr BP, and the formation of the organic-rich sapropel S1 in deeper waters of the eastern Mediterranean basin. Corals seem to re-appear in the SML province around 6 kyr BP with the dominance of *M. oculata* over *L. pertusa* (Malinverno et al. 2010), as typical of the modern Mediterranean Sea CWC communities (Chimienti et al., this volume).

Particularly interesting are the Late Pleistocene solitary CWC "micro-buildups", known from ~1000 to well over 2000 m, such as (1) the *Desmophyllum* clusters encrusting the Malta-Siracusa Escarpment (MSE) (Taviani and Colantoni 1984; Delibrias and Taviani 1985) and rocky walls of the Sicily Strait (SS) (Vertino 2003) and (2) the *Caryophyllia-Desmophyllum* aggregations known offshore Crete (Taviani et al. 2011). The latter coral clusters are formed by unusually large and thick-walled specimens of *D. dianthus* and *C. coronata* (=*sarsiae*) (Fig. 9.2d) growing on each other. *D. dianthus* is still living in several localities of the modern Mediterranean (Altuna and Poliseno, this volume; Aymà et al., this volume; Chimienti et al., this volume; Fourt et al., this volume; Lastras et al., this volume) and, as shown in Fig. 9.4, has been more or less constantly present in this basin in the last 40 kyr. However, the Holocene and modern *Desmophyllum* morphotypes show a relatively small size and a much thinner wall than the "giant" ones from the MSE, SS and Crete. Moreover, they do not form aggregations with *Caryophyllia coronata.* The age of thick-walled *Desmophyllum* from the MSE seems to be comprised between 30 and 15 kyr BP (Taviani and Colantoni 1984; Delibrias and Taviani 1985) and the only two ages available for the species *C. coronata* (one of them collected as a "micro-buildup" offshore Crete) fall within the same time interval (16,600 ± 180, McCulloch et al. 2010 and ~26,000, Zibrowius 1980). *C. coronata* is currently known as fossil in the Mediterranean (Vertino 2003; Vertino and Corselli, this volume) but it is associated with the deep-sea *Lophelia-Madrepora-Desmophyllum* communities of the NE Atlantic; it is quite common in the Porcupine Seabight at depth ranging between 600 and 1000 m and temperature lower than 10 °C (Vertino et al. 2015).

9.4 Spatio-Temporal Patterns of Key Cold-Water Coral Species

The observations carried out so far on the spatio-temporal distribution of the key species *L. pertusa, M. oculata, D. dianthus, D. cornigera, E. scillae, C. aradasiana, C. coronata* and *Stenocyathus vermiformis* are summarised in Figs. 9.3, 9.4, and 9.5 and, only regarding on-land outcrops, in Table 9.1. It should be noted that the values reported in Table 9.1 have to be considered with caution because affected by sampling bias and outcrop availability, especially regarding the Pliocene (see Sect. 9.3.1.2). Considering the spatial distribution, most of the Miocene and Pliocene CWC deposits known so far have been observed in the central and western side of the Mediterranean (Fig. 9.3). However these deposits are dominated by silt and clays and contain mostly soft-bottom corals (Vertino 2003). Instead, thanks to recent regional strong uplifts, Early Pleistocene CWC paleo-habitats abundantly crop out in the southeastern side of the Mediterranean, mostly in southern Italy and Greece (see Sect. 9.3.1.3). According to Table 9.1, with exception of *Dendrophyllia cornigera*, the occurrences of all species examined herein is much higher in the Early Pleistocene than in the Miocene and Pliocene.

Extensive Atlantic-like CWC communities, dominated by *L. pertusa*, commonly associated with *M. oculata*, C. *coronata* and *E. scillae*, were thriving in the Mediterranean during the Early Pleistocene. From around 1 million year up to ~ 50 kyr BP there is an important gap of information. Almost nothing is known about CWC though ongoing studies on coral mounds from the Alborán Sea hint at the establishing of the largest mounds in the Middle Pleistocene (Krengel et al. 2017; Wienberg, this volume). Much more is known about the last 50 kyr though information on *Madrepora* and *Lophelia* are almost completely lacking before the last 14 kyr (Fig. 9.4). According to Fink et al. (2015) these two species seem to have suddenly "(re-) appeared" in the Bølling-Allerød period in the Mediterranean basin. However, although very rarely reported so far, *Lophelia* and *Madrepora* are known between 50 and 15 kyr (Appendices 9.2 and 9.3; Fig. 9.4)

Table 9.1 Number of occurrences (= on-land sites) of the most common extant frame-building deep-sea scleractinian species, and associated solitary ones, from Miocene to Early Pleistocene deposits of peri-mediterranean regions. Data from Appendix 9.1

	Miocene	Pliocene	Early Pleistocene
Lophelia pertusa[a]	2	1	24
Madrepora oculata[a]	6	4	26
Desmophyllum dianthus[b]	2	2	18
Dendrophyllia cornigera[b]	13	7	11
Enallopsammia scillae[b] (f)	3	2	14
Caryophyllia aradasiana[c]	2?	1	8
Caryophyllia coronata[c] (f)	2?	0	11
Stenocyathus vermiformis[c]	0	1	14

(f): species known only as fossil (until the Late Pleistocene) in the Mediterranean but still living in deep-sea environments of the NE Atlantic Ocean

[a] Colonial species commonly fusing their skeletons; high frame-building potential

[b] Solitary gregarious and colonial species, the latter rarely fuse their branches; moderate frame-building potential

[c] Solitary species associated to frame-building CWC; no frame-building potential

in this basin. Moreover, most branches dated so far were collected in the upper 1–2 m of sediment. This means that, based on the current available data, the presence of Mediterranean *Lophelia-Madrepora* communities before the last deglaciation cannot be excluded.

By combining all ages (last 50 kyr) of *M. oculata* and *L. pertusa* published thus far (Fig. 9.4), it is evident the highly frequent occurrence of *L. pertusa* during the late Bølling-Allerød, the early Younger Dryas and in the Early Holocene. The distribution and number of coral ages (Fig. 9.4), confirmed by observations carried out on sediment cores from both eastern and western Mediterranean coral mounds (Malinverno et al. 2010; Stalder et al. 2015; Fink et al. 2012, 2013, 2015), indicate "switches" in the dominance of the most common frame-building coral species (*L. pertusa vs M. oculata*). This is particularly evident after ~10 kyr BP in the western Mediterranean, when *Lophelia* underwent a sharp demise. After this age, though suffering temporary declines, *M. oculata* became the dominant species of the Mediterranean and it remains so to this day (e.g. Taviani et al. 2005a; Freiwald et al. 2009; Vertino et al. 2010; Gori et al. 2013; Fourt et al. 2017). This compositional change in CWC, corresponding to a remarkable decrease in mound accretion rate in the Alboran Sea (Wienberg, this volume), has been explained by Stalder et al. (2015) with the better tolerance of *M. oculata* to higher temperature and unstable environmental conditions established at the Pleistocene-Holocene boundary. This coral switch is observable also in the eastern Mediterranean where the decline of *L. pertusa* seems to occur earlier. However the low number of coral ages obtained so far does not allow to draw robust conclusions in this part of the basin. The occurrence of *L. pertusa* in the Holocene could be overestimated because the thick skeleton of this species is generally preferred to the thinner one of *Madrepora* for radiometric dating.

The comparison between ages of *Lophelia* and *Madrepora* specimens specifically collected from CWC mounds located in the western and eastern Mediterranean (Fig. 9.5a, b), highlights a similar distributional trend. The wider gap observed in the eastern basin in the Early and Mid-Holocene should be ascertained with the analysis of additional samples, but the hypothesis of a direct relation with the sapropel S1, put forward by Fink et al. (2012), seems at the moment the most plausible explanation. Due to the larger number of specimens, the lack of corals between ~9 and 6 kyr observed in the western Mediterranean mounds (Fig. 9.5a, see also Wienberg, this volume) is more reliable and has been explained by Fink et al. (2015) as a consequence of the decrease of productivity at the onset of the Mid-Holocene, resulting in a more oligotrophic regime in the western basin (Bárcena et al. 2001; Cacho et al. 2002; Jimenez-Espejo et al. 2008; Fink et al. 2013).

Other temporal modifications can be observed considering the species examined in this study. *C. coronata* and *E. scillae*, like other stenothermic bathyal species living today exclusively in deep and cold (<10 °C) seafloors of the NE Atlantic, seem to have become extinct at the end of the Pleistocene (Zibrowius 1987; Corselli 2001; Vertino 2003; Di Geronimo et al. 2005; Vertino and Corselli, this volume). Moreover, circalittoral-bathyal species, such as *C. aradasiana (= calveri)* and *S. vermiformis* have become more common in association with frame-building CWC in the Holocene (Vertino pers. observ.). In particular, *C. calveri* is always associated with modern *Madrepora-Lophelia-Desmophyllum* communities of the Mediterranean (e.g. Altuna and Poliseno, this volume; Rueda et al., this volume) and seems to have occupied the ecological niche inhabited by *C. coronata* in the Pleistocene (and still today in the NE Atlantic). The extinction of stenothermic bathyal species in the Mediterranean has been explained by several authors with the shift from psychrosphere to thermosphere conditions of the Mediterranean Sea, as a consequence of the transition from glacial to interglacial age (Benson 1972; Russo 1980; Di Geronimo et al. 1996; Corselli 2001). This is in agreement with the two available ages of *C. coronata* (Fig. 9.4) and to the ages of coral clusters formed by this species and "giant" *Desmophyllum* (Delibrias and Taviani 1985; Taviani et al. 2011). However, further CWC dating is needed to confirm this hypothesis (see Vertino and Corselli, this volume).

In modern CWC habitats, coral accretion and sediment accumulation is highly influenced by local environmental changes, such as micro-current regimes (see Hayes et al., this volume). This makes these environments extremely heterogeneous at spatial scale, even within few meters, and the reconstruction of their evolution through time very complex to be determined based on limited samples. A very large amount of fossil data is needed to put forward robust hypotheses about modifications of CWC abundance and composition through time in relation to broad-scale environmental changes. For instance, the high number of *Lophelia* occurrences in the Early Holocene (especially in the western Mediterranean), reported in recent studies (e.g. McCulloch et al. 2010; Fink et al. 2015) and summarised herein, seem to contradict the previous general hypothesis of frame-building CWC demise during deglacial periods. Moreover, the inference by Fink et al. (2015) regarding the "pronounced 1,400-yrs-lasting gap in the occurrence of *L. pertusa*" during the YD in the Alborán basin has been denied by the almost contemporaneous study carried out by Stalder et al. (2015) that has ascertained the presence of this species in the YD by dating additional specimens.

9.5 Conclusive Remarks and Future Perspectives

The data compilation presented in this chapter includes information on the most important frame-building species of the Mediterranean since the Miocene. It clearly depicts the profound changes overcome by CWC in the highly dynamic Mediterranean basin (Taviani 2002), in response to a variety of mutating oceanographic and climatic scenarios. As disclosed by precise dating in the Late Pleistocene-Holocene, important demise or recolonisation events can take place even at short temporal scales (less than 10^3), almost impossible to discriminate in older situations.

This chapter highlights the improved knowledge gained on Late Pleistocene CWC through radiometric dating of over 150 coral specimens (Appendices 9.2 and 9.3; Fig. 9.4), but it also calls attention to the need for further studies, especially on older coral occurrences, to properly interpret modifications through geological time. For several exceptional Neogene and Quaternary on-land CWC sites, further taxonomic, paleoecological and chronostratigraphic data are still required. Additionally, with exception of the outcrops from southern Italy (recently accurately mapped) precise locations of most outcrops are still lacking.

The hypothesis put forward by Vertino et al. (2014) about a major modification underwent by azooxanthellate coral fauna at the Pliocene – Pleistocene boundary gets further support by the increase of Atlanto-Mediterranean species (*L. pertusa, M. oculata, D. dianthus, E. scillae, C. aradasiana* and *C. coronata*) shown in Table 9.1. Thus far, truly CWC bioconstructions (*Lophelia-Madrepora* dominated), comparable to the modern ones, have not been recorded in Miocene deposits. The only CWC buildups known in this epoch are dominated by dendrophylliid corals (Mastandrea et al. 2002; Vescogni et al. 2018). The presence of *L. pertusa* has been ascertained in the Upper Pliocene Marmorito bioconstructions, dominated by *Enallopsammia* and *Desmophyllum*, but in these limestones *Lophelia* occurs only as a secondary component. On the basis of the data collected so far, there is no evidence of *Lophelia*-dominated bioconstructions before the Calabrian stage when, as testified by the remarkable fossil CWC legacy of southern Italy, the branching frame-building coral was associated to several Atlantic stenothermic bathyal species belonging to the order Scleractinia (such as *C. coronata*, *E. scillae*) and to several other taxonomic groups (Di Geronimo et al. 1996; Vertino 2003).

Our analysis points out a significant gap in knowledge on Mediterranean CWC for the long time interval period comprised between ~1 million year (younger emerged CWC outcrop) and 50 kyr ago. This gap is going to be partly solved by the study of drilled submerged coral mounds (Wienberg, this volume). As to the last 50 kyr, the spatio-temporal distribution of *D. dianthus, L. pertusa* and *M. oculata* appears to be quite different (Fig. 9.4; Appendices 9.2 and 9.3). Thirteen occurrences of *D. dianthus* have been reported before the B / A period, between around 39 and 14.6 kyr BP and most of them are referred to thick-walled specimens, locally associated to *C. coronata*, collected at depth higher than 1000 m. Instead only 2 of the 50 dated specimens of *M. oculata* and 4 of the 78 dated ones of *L. pertusa* have resulted to be older than the Bølling-Allerød interstadial (B/A). This species-specific temporal distribution pattern can be real, thus reflecting the absence of the two colonial species before the B/A, or affected by a selection sampling bias due to the fact that in the Mediterranean both live and dead/fossil *Desmophyllum* is more common on walls and overhangs (Aymà et al., this volume; Lastras et al., this volume) than the other two species. All *Desmophyllum* specimens older than 14 kyr were indeed collected through rock dredging along escarpments where, due to little sediment accumulation, it is likely to find very old specimens still exposed on the surface or covered by a thin muddy drape. The same is true also for the four specimens of *Lophelia* and *Madrepora* older than 14 kyr that were in fact collected through rock dredging (Appendices 9.2 and 9.3). Instead, only specimens younger than 14 kyr were obtained through grabbing, box-coring or gravity coring (shorter than 5 m) from coral mounds (Appendices 9.2 and 9.3). This means that it is more likely to collect *Desmophyllum* older than 14 kyr than *Lophelia* or *Madrepora* and that further sampling effort is needed to verify the actual absence of these two colonial corals before the B/A interstadial, apparently ascertained in the western basin (Wienberg, this volume).

Interestingly, all thick-walled and large *Desmophyllum* specimens as well as *Desmophyllum-Caryophyllia coronata* aggregations collected so far at depth higher than 1000 m seem to have disappeared with the end of the last glacial period. This basin-scale extinction at the Pleistocene-Holocene boundary is coeval to the disappearance from the Mediterranean of several Atlantic stenothermic bathyal species belonging to cnidarians, molluscs, bryozoans, serpulids etc. (Di Geronimo et al. 1996, 2005; Vertino 2003; Vertino et al. 2014). This bathyal species impoverishment could be explained as the direct consequence of temperature increase in the deep sea or, more likely, as the indirect effect of more complex oceanographic modifications occurred at the glacial-interglacial transition (Vertino and Corselli, this volume).

As for the last 14 kyr, the data collection presented herein combined with observations performed on sediment cores (Malinverno et al. 2010; Stalder et al. 2015; Wienberg, this volume) hint at a "golden age" of *L. pertusa* as frame-building coral until ~11 and ~10 kyr BP in the eastern and western Mediterranean, respectively (Figs. 9.4 and 9.5). The end of the flourishing *Lophelia* period is concurrent with lowered mound accretion rates (Wienberg, this volume) and the subsequent general demise (until around 6 kyr BP) of CWC bioconstructors from Mediterranean mound provinces (Figs. 9.4 and 9.5). This has been explained with the concurrent formation of sapropel S1 in the eastern basin (Fink et al. 2012) and productivity decrease/unstable environmental conditions in the western one (Fink et al. 2013, 2015; Stalder et al. 2015; Wienberg, this volume). However, further analyses are needed to define the exact age of development and decline phases of Mediterranean frame-building CWC and to put forward robust conclusions on their modifications through time.

The high intraspecific variability and phenotypic plasticity of scleractinians has recurrently caused the misidentification of colonial fragments belonging to the same species, or even to the same specimen, as distinct taxa. This is particularly true for ancient papers focused on fossil assemblages often composed by few well preserved corals and mostly preserved as small fragments. The arbitrary establishment of new species, based on rare, poorly preserved and fragmented specimens, combined with the poor knowledge of the intraspecific variability of modern deep-sea corals, have generated through time the development of a huge number of unreliable (morpho)species names. Therefore, coral occurrences obtained from the literature must be carefully revised according to modern views on scleractinian systematics before being used for (paleo)biogeographic and (paleo)ecological reconstructions.

On the basis of these observations, as suggested by Wienberg and Titschack (2017), one of the most important steps to do in the near future is to establish a comprehensive open access database including all possible data (taxonomy, ecology, paleoecology, geographic distribution etc.) on both modern and fossil (on-land and submerged) CWC. This database should comprise also solitary forms that, if well preserved, can provide very important paleoenvironmental information. Special care should be given to the quality control of the information entered in the database and very clear standardised procedures should be established for sample collection and analyses. Precise information regarding the collection sites could also be useful to put forward effective plans for management and protection of the unique natural resources of the Mediterranean, including (1) the highly diverse and vulnerable CWC bioconstructions of the modern sea (Otero and Marin, this volume) and (2) the exceptional paleontological heritage occurring on-land.

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References

Addamo AM, Martínez-Baraldés I, Vertino A, et al (2015a) Morphological polymorphism of *Desmophyllum dianthus* (Anthozoa: Hexacorallia) over a wide ecological and biogeographic range: stability in deep habitats? Zool Anz 259:113–130

Addamo AM, Vertino A, Stolarski J, et al (2015b) Merging scleractinian genera: the overwhelming genetic similarity between solitary *Desmophyllum* and colonial *Lophelia*. BMC Evol Biol 16:108

Angeletti L, Taviani M (2011) Entrapment, preservation and incipient fossilization of benthic predatory molluscs within deep-water coral frames in the Mediterranean Sea. Geobios 44:543–548

Angeletti L, Taviani M, Canese S, et al (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Mediterr Mar Sci 15:263–273

Bárcena MA, Cacho I, Abrantes F, et al (2001) Paleoproductivity variations related to climatic conditions in the Alboran Sea (western Mediterranean) during the last glacial-interglacial transition: the diatom record. Palaeogeogr Palaeoclimatol, Palaeoecol 167:337–357

Barrier P (1984) Évolution tectono-sédimentaire pliocène et pléistocène du détroit de Messine. (Italie). Dissertation, University of Marseille-Luminy

Barrier P, Casale V, Costa B, et al (1986) La sezione plio-pleistocenica di Pavigliana (Reggio Calabria). Boll Soc Paleontol Ital 25:107–144

Barrier P (1987) Stratigraphie des dépôts pliocènes et quaternaires du Détroit de Messine. Doc Trav IGAL 11:59–81

Barrier P, Di Geronimo I, Montenat C, et al (1989) Présence de faunes bathyales atlantiques dans le Pliocène et le Pléistocène de Méditerranée (détroit de Messine, Italie). Boll Soc Géol France 5:787–796

Barrier P, Zibrowius H, Lozouet P, et al (1991) Une faune de fond dur du bathyal supérieur dans le Miocène terminal des Cordillères Bétiques (Carboneras, SE, Espagne). Mésogée 51:3–13

Barrier P, Di Geronimo I, La Perna R, et al (1996) Taphonomy of deep-sea hard and soft bottom communities: the Pleistocene of Lazzàro (southern Italy). In: Meléndez G, Blasco MF, Pérez I (eds) Communication Reunion de Tafonomia y Fosilización, Zaragoza, 1996

Benson RH (1972) Ostracods as indicators of threshold depth in the Mediterranean during the Pliocene. In: Stanley DJ (ed) The Mediterranean Sea: A Natural Sedimentation Laboratory, pp 63–73

Bronk C (2009) Bayesian analysis of radiocarbon dates. Radiocarbon 51:337–360

Cacho I, Grimalt JO, Canals M (2002) Response of the Western Mediterranean Sea to rapid climatic variability during the last 50,000 years: a molecular bio- marker approach. J Mar Syst 33–34:253–272

Cairns SD (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. Bull Mar Sci 81:311–322

Caldara M, Ciaranfi N, Marino M (1993) I depositi Plio-Pleistocenici al bordo dell'Appenino Meridionale tra Oliveto Lucano e Garaguso (Basilicata). Boll Soc Geol Ital 112:893–908

Cantalamessa G, Centamore E, Cristallini C, et al (1987) Nuovi dati sulla Geologia dell'area di Porto S. Giorgio (Ascoli Piceno, Marche). Geol Rom 26:359–369

Cantalamessa G, Didaskalou P, Micarelli A, et al (1997) Depositional environments and microfaunal associations in the Sicilian of the Periadriatic Marche Basin (Central Italy). Boll Soc Paleontol Ital 36:123–134

Cau S, Franchi F, Roveri M, et al (2015) The Pliocene-age Stirone River hydrocarbon chemoherm complex (Northern Apennines, Italy). Mar Pet Geol 66:582–595

Chevalier JP (1961) Récherches sur les Madréporaires et les formations récifales Miocene de la Méditerranée occidentale. Mém Soc Géol Fr 40:1–562

Chevalier JP (1962) Les Madréporaires du Pliocène d'Orosei (Nuoro, Sardaigne). Bull Soc Géol France 3:266–270

Corselli C (1997) Il mare in fondo al pozzo: i fossili pliocenici del Pozzo Bagoderi di Malnate. Quaderni del sistema museale Alta Valle Olona, Varese, 77 pp

Corselli C (2001) Change and diversity: the Mediterranean deep corals from the Miocene to the Present. In: Faranda FM, Guglielmo L, Spezie G (eds) Mediterranean ecosystems: structures and processes. Springer, Geneva, pp 361–366

Corselli C (2010) The APLABES programme: physical chemical and biological characterization of deep water coral ecosystems from the Ionian Sea (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr, 99, 0–169

De Angelis G (1893) I zoantari fossili dei dintorni di Roma. Boll Soc Geol Ital 12:1–25

De Angelis G (1894) I Corallari dei terreni terziari dell'Italia settentrionale, Collezione Michelotti, Museo Geologico della Regia Università di Roma. Atti R Accad Lincei Sci Fis Nat 1:164–280

De Angelis G (1895) Descripción de los Antozoos fósiles pliocénicos de Cataluña. Mem R Accad Cienc Artes Barcelona 3:1–25

De Stefano G (1899) Le argille a *Coenopsammia scillae* Seguenza e le sabbie marine della contrada Corvo in Reggio di Calabria. Atti Accad Gioenia Sci Nat, Ser 4:12: 1–12: 9

Delibrias G, Taviani M (1985) Dating the death of Mediterranean deep-sea scleractinian corals. Mar Geol 62:175–180

Di Geronimo I (1979) Il Pleistocene in facies batiale di Valle Palione (Grammichele, Catania). Boll Malacol 15:85–156

Di Geronimo I (1987) Bionomie des peuplements benthiques des substrats meubles et rocheux plio-quaternaires du Détroit de Messine. Doc Trav IGAL 11:153–169

Di Geronimo I, La Perna R, Rosso A (1996) The plio-quaternary evolution of the Mediterranean deep sea benthos: an outline. In: La Méditerranée: variabilités climatiques, environnement et biodiversité, Actes du Colloque Scientifique, Montpellier, 6–7 Avril 1995

Di Geronimo I, D'atri A, La Perna R, et al (1997) The Pleistocene bathyal section of Archi (Southern Italy). Boll Soc Paleontol Ital 36:189–212

Di Geronimo I, Messina C, Rosso A, et al (2005) Enhanced biodiversity in the deep: early pleistocene coral communities from southern Italy. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin, pp 61–86

Di Stefano A, Longhitano SG (2009) Tectonics and sedimentation of the Lower and Middle Pleistocene mixed siliciclastic/bioclastic sedimentary successions of the Ionian Peloritani Mts (NE Sicily, Southern Italy): the onset of opening of the Messina Strait. Cent Eur J Geosci. https://doi.org/10.2478/v10085-009-0002-y

Dieni J, Omenetto P (1960) Studio di una macrofauna del Pliocene inferiore di Orosei. Riv Ital Paleontol 66:605–618

Dubois-Dauphin Q, Bonneau L, Colin C, et al (2016) South Atlantic intermediate water advances into the North-east Atlantic with reduced Atlantic meridional overturning circulation during the last glacial period. Geochem Geophys Geosyst 17:2336–2353

Dubois-Dauphin Q, Montagna P, Siani G, et al (2017) Hydrological variations of the intermediate water masses of the western Mediterranean Sea during the past 20 ka inferred from neodymium isotopic composition in foraminifera and cold-water corals. Climate Past 13:17–37

Fink H, Wienberg C, Hebbeln D, et al (2012) Oxygen control on Holocene cold-water coral development in the Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96

Fink H, Wienberg C, De Pol-Holz R, et al (2013) Cold-water coral growth in the Alborán Sea related to high productivity during the Late Pleistocene and Holocene. Mar Geol 2013 339:71–82

Fink HG, Wienberg C, De Pol-Holz R, et al (2015) Spatio-temporal distribution patterns of Mediterranean cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) during the past 14,000 years. Deep-Sea Res Part 1 Oceanogr Res Pap 103:37–48

Föllmi KB, Hofmann H, Chiaradia M, et al (2015) Miocene phosphate-rich sediment in Salento (southern Italy). Sediment Geol 327:55–71

Fourt M, Goujard A, Pérez T, et al (2017) Guide de la faune profonde de la mer Méditerranée. Museum National d'Histoire Naturelle, Paris, p 184

Frank N, Freiwald A, Lopez Correa M, et al (2011) Northeastern Atlantic cold-water coral reefs and climate. Geology 39:743–746

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs. UNEP-WCMC Biodiversity Series 22. Cambridge, UK

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the central Mediterranean revealed by ROV surveys. Oceanography 22:58–74

Hanken NM, Bromley RG, Miller J (1996) Plio–Pleistocene sedimentation in coastal grabens, north-east Rhodes, Greece. Geol J 31:271–296

Hebbeln D, Wienberg C, Frank N (2015) The development of cold-water coral mounds along the Moroccan Atlantic and Mediterranean margins revealed by MeBo drillings. In: Abstracts of the EGU General Assembly, Vienna, 12–17 April 2015

Henry LA, Roberts M (2016) Global biodiversity in cold-water coral reef ecosystems. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests, pp 1–21

Hersey JB (1965) Sedimentary basins of the Mediterranean Sea. In: Whitard WF, Bradshaw W (eds) Submarine geology and geophysics. Proceedings of 17th symposium of the Colston Research Society, London, pp 75–91

Jimenez-Espejo FJ, Martinez-Ruiz F, Rogerson M, et al (2008) Detrital input, productivity fluctuations, and water mass circulation in the westernmost Mediterranean Sea since the last glacial maximum. Geochem Geophys Geosyst 9:1–19. https://doi.org/10.1029/2008GC002096

Kiel S, Sami M, Taviani M (2018) A serpulid-*Anodontia*-dominated methane-seep deposit from the Miocene of northern Italy. Acta Palaeontol Pol https://doi.org/10.4202/app.00472.2018

Krengel T, Wienberg C, Eichstaedter C, et al (2017) Climate-related formation of coldwater coral mounds in the Alborán Sea since the mid-Pleistocene transition. In: Abstracts of the GOLDSCHMIDT 2017, Paris, 13–18 August 2017

Lo Iacono C, Gracia E, Ranero C, et al (2014a) The West Melilla cold water coral mounds, Eastern Alborán Sea: morphological characterization and environmental context. Deep-Sea Res Part 2 Top Stud Oceanogr 99:316–326

Lo Iacono C, Gonzalez LV, Huvenne VAI, et al (2014b) Morphology and shallow stratigraphy of the West Melilla and Cabliers CWC Mounds (Alborán Sea). Preliminary insights from the GATEWAYS MD194 Cruise. In: Abstracts of the 2nd deep-water circulation congress, Ghent, 10–12 September 2014

Lo Iacono C, Huvenne VAI, Gonzalez LV, et al (2016) Living reefs and CWC mounds in the Alborán Sea (Western Mediterranean). Holocene evolution and present-day conditions. In: Abstracts of the 6th international symposium on deep-sea corals, September 2016, Boston, pp 11–16

Malinverno E, Taviani M, Rosso A, et al (2010) Stratigraphic framework of the Apulian deep-water coral province, Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:345–359

Mastandrea A, Muto F, Neri C, et al (2002) Deep-water coral banks: an example from the "Calcare di Mendicino" (Upper Miocene, Northern Calabria, Italy). Facies 47:27–42

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral ecosystem off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the Younger Dryas. Earth Planet Sci Lett 298:143–152

Moissette P, Cornée JJ, Quillévéré F (2017) Pleistocene (Calabrian) deep-water corals and associated biodiversity in the eastern Mediterranean (Karpathos Island, Greece). J Quat Sci. https://doi.org/10.1002/jqs.2966

Monegatti P, Raffi S, Roveri M, et al (2001) One day trip in the outcrops of Castell'Arquato Plio-Pleistocene Basin: from the Badland of Monte Giogo to the Stirone River. In: Monegatti P, Cecca F, Raffi S (eds) Proocedings of the international conference paleobiogeography & paleoecology, Piacenza e Castell'Arquato, 2001

Montanaro E (1929) Coralli tortoniani di Montegibbio (Modena). Boll Soc Geol Ital 48:107–127

Montanaro E (1931) Coralli pliocenici dell'Emilia. Palaeontogr Ital 31:63–91

Osasco E (1895) Di alcuni corallari pliocenici del Piemonte e della Liguria. Atti R Accad Sci Torino 31:225–238

Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la Méditerranée. Rec Trav Stat mar Endoume 31:137

Placella B (1978) Nuove osservazioni sulla corallofauna delle argille pleistoceniche di Archi (Reggio Calabria). Boll Soc Nat Napoli 87:1–23

Placella B (1980) I coralli pliocenici di Masseria Concarone – Pisticci (Mt). Boll Soc Nat Napoli 89:19–32

Reimer PJ, Bard E, Bayliss A, et al (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55(4):1869–1887

Roberts JM, Wheeler A, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334. https://doi.org/10.1017/CBO9780511581588

Robinson LF, Adkins JF, Frank NA, et al (2014) The geochemistry of deep-sea coral skeletons: a review of vital effects and applications for palaeoceanography. Deep-Sea Res Part 1 Oceanogr Res Pap 99:184–198

Rosso A, Vertino A, Di Geronimo I, et al (2010) Hard- versus soft-bottom thanatofacies from the Santa Maria di Leuca deep-water coral province, recent Mediterranean. Deep-Sea Res Part 2 Top Stud Oceanogr 57:360–379

Roux M, Barrier P, Di Geronimo I, et al (1988) Découverte de Crinoïdes pédonculés bathyaux d'origine atlantique dans le Pliocène supérieur et le Pleistocène moyen méditerranéen: conséquences biogéographiques. C R Acad Sci Paris 307:259–364

Russo A (1980) The psychrospheric coral fauna from the lower Pliocene of northern Italy. Acta Palaeont Pol 25:614–617

Savini A, Corselli C (2010) High-resolution bathymetry and acoustic geophysical data from Santa Maria di Leuca Cold Water Coral province (northern Ionian Sea-Apulian continental slope). Deep-Sea Res Part 2 Top Stud Oceanogr 57:326–344

Savini A, Vertino A, Beuck L, et al (2014) Mapping cold-water coral habitats at different scales within the northern Ionian Sea (central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e91447. https://doi.org/10.1371/journal.pone.0087108

Schröder-Ritzrau A, Freiwald A, Mangini A (2005) U/Th-dating of deep-water corals from the eastern North Atlantic and the western Mediterranean Sea. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin, pp 691–700

Schumacher H, Zibrowius H (1985) What is hermatypic? A redefinition of ecological groups in corals and other organisms. Coral Reefs 4:1–9

Seguenza G (1864) Disquisizioni paleontologiche intorno ai Corallarii fossili delle rocce terziarie del distretto di Messina. Mem R Acc Sci Torino (Ser 2) 21:399–560

Seguenza G (1880) La formazione terziaria nella provincia di Reggio (Calabria). Atti R Accad Lincei Sci Fis Nat 6:1–446

Siani G, Paterne M, Michel E, et al (2001) Mediterranean sea surface radiocarbon reservoir age changes since the last glacial maximum. Science 294(5548):1917–1920

Simonelli V (1895) Gli Antozoi pliocenici del Ponticello di Savena presso Bologna. Paleont Ital 1:149–168

Simonelli V (1896) Antozoi neogenici del Museo Parmense. Paleont Ital 2:185–201

Sismonda E (1871) Matériaux pour servir à la paléontologie du terrain tertiaire du Piémont. Memorie della Reale Accademia delle scienze di Torino, vol 2, pp 257–361

Spadini (2015) Sclerattiniari del Pliocene senese (Cnidaria, Anthozoa). Accademia delle Scienze di Siena detta dei Fisiocratici, p 159

Stalder C, Vertino A, Rosso A, et al (2015) Microfossils, a key to unravel cold-water carbonate mound evolution through time: evidence from the Eastern Alborán Sea. PLoS One 10:e0140223. https://doi.org/10.1371/journal.pone.0140223

Stolarski J, Vertino A (2007) First Mesozoic record of the scleractinian Madrepora from the Maastrichtian siliceous limestones of Poland. Facies 53:67–78

Taviani M (2002) The Mediterranean benthos from late Miocene up to present: ten million years of dramatic climatic and geologic vicissitudes. Biol Mar Medit 9:445–463

Taviani M, Colantoni P (1984) Paléobiocenoses profondes a scléractiniaires sur l'escarpement de Malte-Syracuse (Mer Méditerranée): leur structure, leur âge et leur signification. Rev Inst Fr Pétr 39:547–552

Taviani M, Corselli C, Remia A, et al (2005a) First geo-marine survey of living cold-water *Lophelia* reefs in the Ionian Sea (Mediterranean basin). Facies 50:409–417

Taviani M, Freiwald A, Zibrowius H (2005b) Deep-coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin, pp 137–156

Taviani M, Vertino A, López-Correa M, et al (2011) Pleistocene to Recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78

Titschack J, Freiwald A (2005) Growth, deposition, and facies of Pleistocene bathyal coral communities from Rhodes, Greece. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin, pp 41–59

Titschack J, Nelson CS, Beck T (2008) Sedimentary evolution of a late Pleistocene temperate red algal reef (Coralligène) on Rhodes, Greece: correlation with global sea-level fluctuations. Sedimentology 55:1747–1776

Titschack J, Fink HG, Baum D, et al (2016) Mediterranean cold-water corals–an important regional carbonate factory? Depositional Rec 2:74–96

Vertino A (2003) Sclerattiniari plio-pleistocenici ed attuali del Mediterraneo. PhD dissertation, University of Messina

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396

Vertino A, Titschack J, Rosso A, et al (2013) Messina Strait: CWC Pleistocene deposits from "La Montagna" (Messina). In: Vertino A, Basso D, Rosso A (eds) Field seminar guide book. Proceedings of the COCARDE-ERN Workshop and Field Seminar, Sicily, 2013

Vertino A, Stolarski J, Bosellini FR, et al (2014) Mediterranean corals through time: from Miocene to present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 257–274

Vertino A, Spezzaferri S, Rueggeberg A, et al (2015) An overview on cold-water coral ecosystems and facies. In: Spezzaferri S, Rueggeberg A, Stalder C (eds) Atlas of benthic foraminifera from cold-water coral reefs. Cushman Foundation Special Publication, vol 44, pp 12–19

Vescogni A, Vertino A, Bosellini F, et al (2018) New paleoenvironmental insights on the Miocene condensed phosphatic layer of Salento (southern Italy) unlocked by the coral-mollusc fossil archive. Facies 64. https://doi.org/10.1007/s10347-018-0520-9

Wienberg C, Titschack J (2017) Framework-forming scleractinian cold-water corals through space and time: a late Quaternary North Atlantic perspective. In: Rossi S, Bramanti L, Gori A et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 699–732

World Register of Marine Species (2017) http://www.marinespecies.org at VLIZ. https://doi.org/10.14284/170. Accessed Jan 2018

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mém Inst Océanogr Monaco 11:0–284

Zibrowius H (1981) Thanatocoenose pléistocène profonde à Spongiaires et Scléractiniaires dans la Fosse Hellenique. In: Journées d'études sur la systérnatique évolutive et la biogéographie en Méditerranée, 27th CIESM, Cagliari, 1980

Zibrowius H (1987) Scléractiniaires et Polychètes Serpulidae des faunes bathyales actuelle et plio-pléistocène de Méditerranée. Doc et Trav IGAL 11:255–257

Zuffardi-Comerci R (1927) Faunetta di corallari pliocenici dell'isola di Rodi. Atti R Acad Sci Torino 63:231–237

Zuffardi-Comerci R (1932) Corallari-Zoantari fossili del Miocene della "Collina di Torino". Paleont Ital 23:86–132

Zuffardi-Comerci R (1937) Contributo dato dai corallari – durante i periodi geologici – alla formazione dei terreni calcarei d'Italia. Riv Ital Paleontol Stratigr 43:9–35

Zunino M, Pavia G (2009) Lower to Middle Miocene molluscan assemblages from the Torino Hills (NW Italy): synthesis of new data and chronostratigraphical arrangement. Riv Ital Paleontol 66:349–370

Cross References

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Drop Chapter Bathyal Corals Within the Aegean Sea and the Adjacent Hellenic Trench

10

Jürgen Titschack

Abstract

Within the Aegean Sea and the adjacent Hellenic trench, 128 records of bathyal corals (>200 m water depth; only 6% recorded alive) are described so far, comprising 13 species. Further fossil occurrences of these corals are documented from 10 outcrops on Crete and Rhodes. *Caryophyllia calveri*, *Caryophyllia sarsiae*, *Dendrophyllia cornigera*, *Desmophyllum dianthus*, *Javania cailleti*, *Lophelia pertusa*, *Madrepora oculata*, *Schizocyathus fissilis*, *Stenocyathus vermiformis* and *Trochocyathus mediterraneus* predominate in water depths >200 m. Although *Caryophyllia smithii*, *Guynia annulata* and *Paracyathus pulchellus* also occur in deeper waters, they are mainly reported from shallower water depths. Radiogenic dates obtained from various deep-water species imply their presence in this region since the mid-Pleistocene, however most dates exhibit ages since the last glacial maximum. All bathyal coral species are predominantly found on steep escarpments and topographic highs in coarse sediments or on hard substrates along the steep structured slope of the Hellenic Trench off Crete, Karpathos and Rhodes. A similar environment setting is reconstructed for the fossil occurrences on Rhodes.

Keywords

Bathyal corals · Cold-water corals · Aegean Sea · Hellenic trench · Eastern Mediterranean Sea

Twenty-seven scleractinian species, two of which zooxanthellate, have been documented so far from the Aegean Sea and the adjacent Hellenic trench in the eastern Mediterranean (Zibrowius 1979, 1987; Vafidis et al. 1997; Morri et al. 2000; Gerovasileiou et al. 2009, 2015; Salomidi et al. 2010, 2013; Taviani et al. 2011; Çinar et al. 2014). Among these, 13 species have been reported from bathyal water depths (exceeding 200 m; Fig. 10.1a). From a total of 128 findings in bathyal depths, only 8 records refer to living corals comprising specimens of *Caryophyllia smithii* Stokes and Broderip, 1828, *Dendrophyllia cornigera* (Lamarck, 1816), *Stenocyathus vermiformis* (Pourtalès, 1868) and *Desmophyllum dianthus* (Esper, 1794) (see also Fig. 10.1a; Table 10.1; see Altuna and Poliseno, this volume). All other reports refer to dead specimens or to specimens of which the status is not entirely clear. *Caryophyllia calveri* Duncan, 1873, *Caryophyllia sarsiae* Zibrowius, 1974, *D. cornigera*, *D. dianthus*, *Javania cailleti* (Duchassaing and Michelotti, 1864), *Lophelia pertusa* (Linnaeus, 1758), *Madrepora oculata* Linnaeus, 1758, predominate in water depths >200 m; *Schizocyathus fissilis* Pourtalès, 1874, *S. vermiformis* and *Trochocyathus mediterraneus* Zibrowius, 1980, are only reported from water depths >400 m (Table 10.1). *Caryophyllia smithii*, *Guynia annulata* Duncan, 1872 and *Paracyathus pulchellus* (Philippi, 1842) are only rarely reported from bathyal water depths (6 records) but occur frequently in water depths <200 m (35 records; 24 living, not indicated in Fig. 10.1a). Only *L. pertusa*, *M. oculata* and *D. cornigera* are colonial. *L. pertusa*, *M. oculata* and *D. dianthus* form the white coral community or '*Biocoenose des coraux blanc*', well-known from the entire Mediterranean Sea (*sensu* Pérès and Picard 1964; Freiwald et al. 2009; see Altuna and Poliseno, this volume; Chimienti et al., this volume).

All bathyal coral species are predominantly found along the eastern Hellenic Arc off Crete, Karpathos and Rhodes within the northern Levantine Sea (Taviani et al. 2011). This region is characterised by steep slopes that are highly structured by submarine canyons (Fig. 10.1a; Harris and Whiteway

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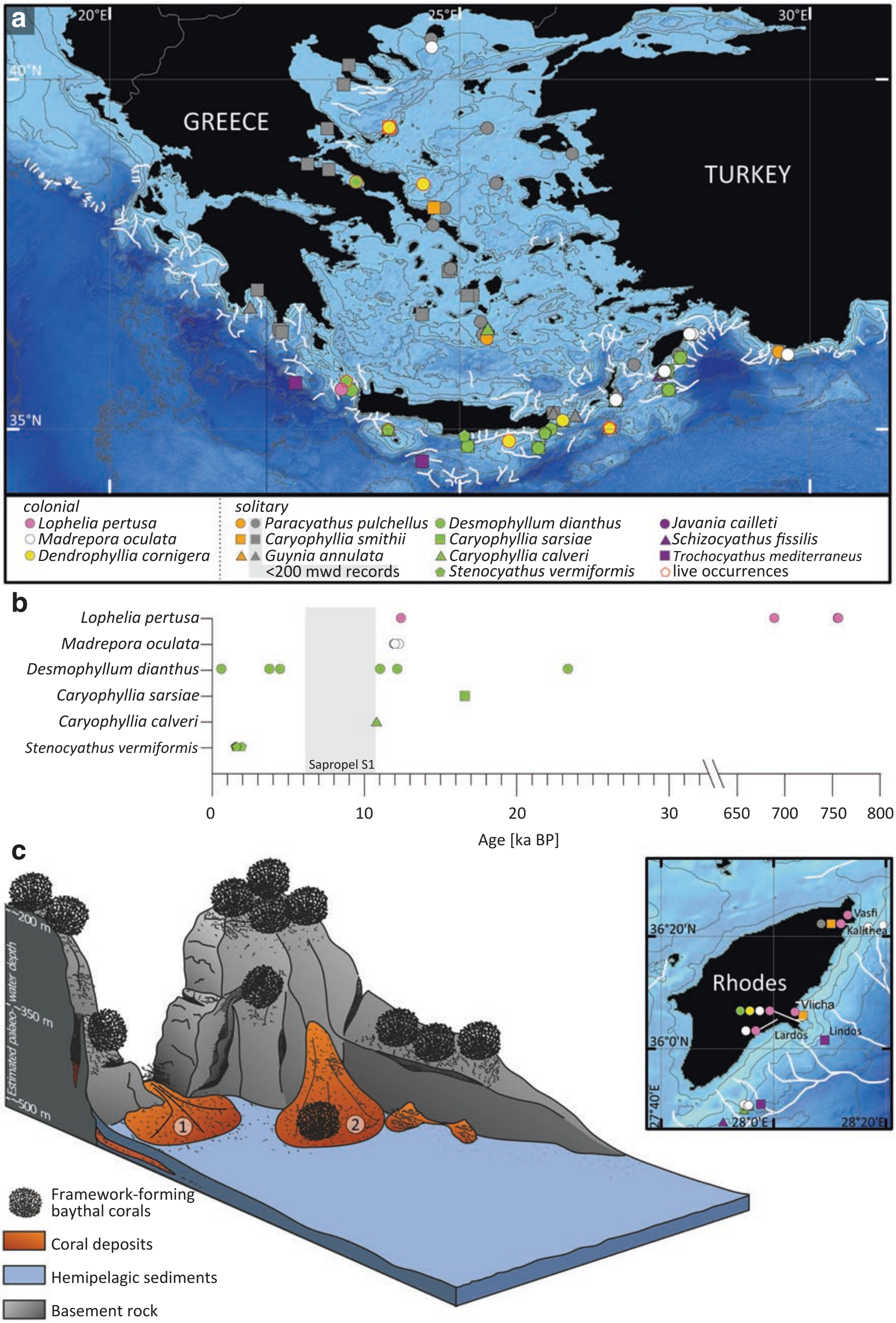

Fig. 10.1 (**a**) Map of the Aegean Sea and the adjacent Hellenic trench. All bathyal coral occurrences are indicated (red symbol boundaries indicate living occurrences; for data see Table 10.1). White lines indicate canyons (Harris and Whiteway 2011). Bathymetry: http://www.emodnet.eu/bathymetry. (**b**) Available coral ages from the study area. Duration of Sapropel S1 is indicated (for data sources see text). (**c**) Palaeoenvironmental reconstruction of Rhodesian bathyal coral occurrences. Bathyal coral deposits form predominately at the base of the steep palaeorelief as debris flow (1) and debris fall (2) deposits. (Modified after Titschack and Freiwald 2005; outcrop positions indicated in map; for data sources see Table 10.2)

Table 10.1 Records of bathyal corals within the Aegean Sea and the adjacent Hellenic trench compiled from various sources

Area	Station	Gear	Latitude [°N]	Longitude [°E]	Depth [m]	*CoralSpecies*	Facies	Status	Reference
Off Milos		**–**	**36.6417**	**24.4613**	**90**	***Caryophyllia smithii***	**On oceanographic instrument**	**Live**	**Morri et al. (2000)**
SSW of Chryssi Island		–	34.8330	25.7020	520–620	*Dendrophyllia cornigera*	RB, C rubble	Live	Smith et al. (2009)
SE of Crete	GECO-56	*D*	35.0022	26.2972	378–773	*?Desmophyllum*	Gravel/Breccia	Dead	Taviani et al. (2011)
NE of Rhodes	GECO-89	*G*	36.3607	28.2807	328–376	*Caryophyllia calveri*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-84	*D*	35.8298	27.9277	354–753	*Caryophyllia calveri*	Den rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-84	*D*	35.8298	27.9277	354–753	*Caryophyllia calveri*	C rubble	Unknown	Taviani et al. (2011)
E of Crete	GECO-55	*D*	35.1277	26.4685	366–647	*Caryophyllia calveri*	Den rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-85	*D*	35.8323	27.9262	403–762	*Caryophyllia calveri*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-85	*D*	35.8323	27.9262	403–762	*Caryophyllia calveri*	C rubble	Unknown	Taviani et al. (2011)
S of Karpathos	GECO-22	*G*	35.4167	27.2247	453–455	*Caryophyllia calveri*	L-M rubble	Unknown	Taviani et al. (2011)
S of Karpathos	GECO-18	*D*	35.4123	27.2233	453–550	*Caryophyllia calveri*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-28	*G*	35.4175	27.2248	460–461	*Caryophyllia calveri*	L-M rubble	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-77	*G*	35.8330	27.9215	465–506	*Caryophyllia calveri*	L-M rubble	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-80	*G*	35.8300	27.9225	477–482	*Caryophyllia calveri*	*Stenocyathus* rubble	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-82	*G*	35.8193	27.9128	493–507	*Caryophyllia calveri*	?	Dead	Taviani et al. (2011)
S of Crete	GECO-50	*D*	34.7637	25.1142	1408–2133	*Caryophyllia sarsiae*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-76	*D*	35.5623	27.9825	1445–2268	*Caryophyllia sarsiae*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-64	*D*	35.8353	27.9618	1458–1963	*Caryophyllia sarsiae*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Crete	GECO-54	*D*	34.7368	26.1187	1741–2179	*Caryophyllia sarsiae*	Des-C framestone	Dead	Taviani et al. (2011)
S of Karpathos	GECO-21	*G*	35.4138	27.2243	451–452	*Caryophyllia sarsiae*	L-M rubble	Dead	Taviani et al. (2011)
E of Rhodes	GECO-75	*D*	36.0252	28.1510	922–1640	*Caryophyllia sarsiae*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-84	*D*	35.8298	27.9277	354–753	*Dendrophyllia cornigera*	Den rubble	Dead	Taviani et al. (2011)
E of Crete	GECO-55	*D*	35.1277	26.4685	366–647	*Dendrophyllia cornigera*	Den rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-22	*G*	35.4167	27.2247	453–455	*Dendrophyllia cornigera*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-28	*G*	35.4175	27.2248	460–461	*Dendrophyllia cornigera*	L-M rubble	Dead	Taviani et al. (2011)
S of Crete	GECO-50	*D*	34.7637	25.1142	1408–2133	*Desmophyllum dianthus*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-76	*D*	35.5623	27.9825	1445–2268	*Desmophyllum dianthus*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-64	*D*	35.8353	27.9618	1458–1963	*Desmophyllum dianthus*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Crete	GECO-54	*D*	34.7368	26.1187	1741–2179	*Desmophyllum dianthus*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-79	*G*	35.8353	27.9113	284–284	*Desmophyllum dianthus*	L-M rubble	Dead	Taviani et al. (2011)
NE of Rhodes	GECO-89	*G*	36.3607	28.2807	328–376	*Desmophyllum dianthus*	L-M rubble	Dead	Taviani et al. (2011)
E of Crete	GECO-55	*D*	35.1277	26.4685	366–647	*Desmophyllum dianthus*	Den rubble	Dead	Taviani et al. (2011)
SE of Crete	GECO-56	*D*	35.0022	26.2972	378–773	*Desmophyllum dianthus*	N-Des framestone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-85	*D*	35.8323	27.9262	403–762	*Desmophyllum dianthus*	L-M rubble	Dead	Taviani et al. (2011)
W of Crete	GECO-7	*D*	35.5688	23.3072	426–968	*Desmophyllum dianthus*	N-Des framestone	Unknown	Taviani et al. (2011)
S of Karpathos	GECO-21	*G*	35.4138	27.2243	451–452	*Desmophyllum dianthus*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-22	*G*	35.4167	27.2247	453–455	*Desmophyllum dianthus*	L-M rubble	Unknown	Taviani et al. (2011)
S of Karpathos	GECO-18	*D*	35.4123	27.2233	453–550	*Desmophyllum dianthus*	M-L rudstone	Dead	Taviani et al. (2011)
S of Karpathos	GECO-18	*D*	35.4123	27.2233	453–550	*Desmophyllum dianthus*	L-M rubble	Dead	Taviani et al. (2011)

(continued)

Table 10.1 (continued)

Area	Station	Gear	Latitude [°N]	Longitude [°E]	Depth [m]	*CoralSpecies*	Facies	Status	Reference
S of Karpathos	GECO-28	*G*	35.4175	27.2248	460–461	*Desmophyllum dianthus*	L-M rubble	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-77	*G*	35.8330	27.9215	465–506	*Desmophyllum dianthus*	M-L rudstone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-77	*G*	35.8330	27.9215	465–506	*Desmophyllum dianthus*	L-M rubble	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-80	*G*	35.8300	27.9225	477–482	*Desmophyllum dianthus*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-81	*G*	35.8190	27.9147	496–510	*Desmophyllum dianthus*	–	Dead	Taviani et al. (2011)
W of Crete	GECO-8	*D*	35.5603	23.4488	743–1334	*Desmophyllum dianthus*	N-Des framestone	Unknown	Taviani et al. (2011)
SE of Crete	GECO-41	*D*	34.9475	26.2158	761–781	*Desmophyllum dianthus*	Gravel/Breccia	Dead	Taviani et al. (2011)
E of Rhodes	GECO-75	*D*	36.0252	28.1510	922–1640	*Desmophyllum dianthus*	Des-C framestone	Dead	Taviani et al. (2011)
S of Karpathos	**GECO-36**	***rd***	**35.5260**	**27.2233**	**126–142**	***Guynia annulata***	**Fine sed. with octocoral axes**	**Dead**	**Taviani et al.** (2011)
S of Crete	GECO-13	G	34.9987	23.9755	219–226	*Guynia annulata*	Fine sed. with octocoral axes	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-79	*G*	35.8353	27.9113	284–284	*Guynia annulata*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-85	*D*	35.8323	27.9262	403–762	*Javania cailleti*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-18	*D*	35.4123	27.2233	453–550	*Javania cailleti*	L-M rubble	Dead	Taviani et al. (2011)
NE of Rhodes	GECO-90	*G*	36.3665	28.3247	1208–1208	*Lophelia pertusa*	L-M rubble	Dead	Taviani et al. (2011)
NE of Rhodes	GECO-89	*G*	36.3607	28.2807	328–376	*Lophelia pertusa*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-84	*D*	35.8298	27.9277	354–753	*Lophelia pertusa*	Den rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-85	*D*	35.8323	27.9262	403–762	*Lophelia pertusa*	M-L rudstone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-85	*D*	35.8323	27.9262	403–762	*Lophelia pertusa*	L-M rubble	Dead	Taviani et al. (2011)
W of Crete	GECO-7	*D*	35.5688	23.3072	426–968	*Lophelia pertusa*	N-Des framestone	Dead	Taviani et al. (2011)
S of Karpathos	GECO-33	*D*	35.4370	27.2388	450–450	*Lophelia pertusa*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-21	*G*	35.4138	27.2243	451–452	*Lophelia pertusa*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-22	*G*	35.4167	27.2247	453–455	*Lophelia pertusa*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-18	*D*	35.4123	27.2233	453–550	*Lophelia pertusa*	M-L rudstone	Dead	Taviani et al. (2011)
S of Karpathos	GECO-18	*D*	35.4123	27.2233	453–550	*Lophelia pertusa*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-28	*G*	35.4175	27.2248	460–461	*Lophelia pertusa*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-77	*G*	35.8330	27.9215	465–506	*Lophelia pertusa*	M-L rudstone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-77	*G*	35.8330	27.9215	465–506	*Lophelia pertusa*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-80	*G*	35.8300	27.9225	477–482	*Lophelia pertusa*	L-M rubble	Dead	Taviani et al. (2011)
NE of Rhodes	GECO-90	*G*	36.3665	28.3247	1208–1208	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-29	*D*	35.4157	27.2267	173–521	*Madrepora oculata*	M-L rudstone	Dead	Taviani et al. (2011)
S of Karpathos	GECO-29	*D*	35.4157	27.2267	173–521	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-79	*G*	35.8353	27.9113	284–284	*Madrepora oculata*	M-L rudstone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-79	*G*	35.8353	27.9113	284–284	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
NE of Rhodes	GECO-89	*G*	36.3607	28.2807	328–376	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-85	*D*	35.8323	27.9262	403–762	*Madrepora oculata*	M-L rudstone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-85	*D*	35.8323	27.9262	403–762	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-33	*D*	35.4370	27.2388	450–450	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-21	*G*	35.4138	27.2243	451–452	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-22	*G*	35.4167	27.2247	453–455	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)

S of Karpathos	GECO-18	*D*	35.4123	27.2233	453–550	*Madrepora oculata*	M-L rudstone	Dead	Taviani et al. (2011)
S of Karpathos	GECO-18	*D*	35.4123	27.2233	453–550	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-28	*G*	35.4175	27.2248	460–461	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-77	*G*	35.8330	27.9215	465–506	*Madrepora oculata*	M-L rudstone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-77	*G*	35.8330	27.9215	465–506	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-80	*G*	35.8300	27.9225	477–482	*Madrepora oculata*	L-M rubble	Dead	Taviani et al. (2011)
S of Crete	GECO-13	G	34.9987	23.9755	219–226	*Paracyathus pulchellus*	Fine sed. with octocoral axes	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-83	*G*	35.7827	27.8508	1119–1125	*Schizocyathus fissilis*	Fine sed. with octocoral axes	Unknown	Taviani et al. (2011)
NE of Rhodes	GECO-90	*G*	36.3665	28.3247	1208–1208	*Stenocyathus vermiformis*	L-M rubble	Dead	Taviani et al. (2011)
S of Crete	GECO-13	G	34.9987	23.9755	219–226	*Stenocyathus vermiformis*	Fine sed. with octocoral axes	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-79	*G*	35.8353	27.9113	284–284	*Stenocyathus vermiformis*	L-M rubble	Unknown	Taviani et al. (2011)
NE of Rhodes	GECO-89	*G*	36.3607	28.2807	328–376	*Stenocyathus vermiformis*	L-M rubble	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-84	*D*	35.8298	27.9277	354–753	*Stenocyathus vermiformis*	Den rubble	Dead	Taviani et al. (2011)
E of Crete	GECO-55	*D*	35.1277	26.4685	366–647	*Stenocyathus vermiformis*	S rubble	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-85	*D*	35.8323	27.9262	403–762	*Stenocyathus vermiformis*	L-M rubble	Unknown	Taviani et al. (2011)
S of Karpathos	GECO-33	*D*	35.4370	27.2388	450–450	*Stenocyathus vermiformis*	L-M rubble	Unknown	Taviani et al. (2011)
S of Karpathos	GECO-21	*G*	35.4138	27.2243	451–452	*Stenocyathus vermiformis*	L-M rubble	Dead	Taviani et al. (2011)
S of Karpathos	GECO-22	*G*	35.4167	27.2247	453–455	*Stenocyathus vermiformis*	L-M rubble	Unknown	Taviani et al. (2011)
S of Karpathos	GECO-18	*D*	35.4123	27.2233	453–550	*Stenocyathus vermiformis*	L-M rubble	Unknown	Taviani et al. (2011)
S of Karpathos	GECO-28	*G*	35.4175	27.2248	460–461	*Stenocyathus vermiformis*	L-M rubble	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-77	*G*	35.8330	27.9215	465–506	*Stenocyathus vermiformis*	L-M rubble	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-80	*G*	35.8300	27.9225	477–482	*Stenocyathus vermiformis*	S rubble	Unknown	Taviani et al. (2011)
SE of Rhodes	GECO-82	*G*	35.8193	27.9128	493–507	*Stenocyathus vermiformis*	?	Dead	Taviani et al. (2011)
SE of Crete	GECO-48	*D*	34.9125	25.0668	630–680	*Stenocyathus vermiformis*	Fine sed. with octocoral axes	Unknown	Taviani et al. (2011)
SE of Crete	GECO-41	*D*	34.9475	26.2158	761–781	*Stenocyathus vermiformis*	Gravel/Breccia	Dead	Taviani et al. (2011)
S of Crete	GECO-50	*D*	34.7637	25.1142	1408–2133	*Trochocyathus mediterraneus*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Rhodes	GECO-64	*D*	35.8353	27.9618	1458–1963	*Trochocyathus mediterraneus*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Crete	GECO-54	*D*	34.7368	26.1187	1741–2179	*Trochocyathus mediterraneus*	Des-C framestone	Dead	Taviani et al. (2011)
E of Rhodes	GECO-75	*D*	36.0252	28.1510	922–1640	*Trochocyathus mediterraneus*	Des-C framestone	Dead	Taviani et al. (2011)
SE of Crete	GECO-41	*D*	34.9475	26.2158	761–781	*Undetermined Caryophylliidae*	Gravel/Breccia	Unknown	Taviani et al. (2011)
Akrotiri Athos	Stat. 139a	*T*	40.1310	24.3850	180–200	*Desmophyllum dianthus*	–	Unknown	Vafidis et al. (1997)
Off Limenaria Thasos I.	Stat. 168b	*T*	40.4570	24.5990	300–350	*Lophelia pertusa*	–	Unknown	Vafidis et al. (1997)

(continued)

Table 10.1 (continued)

Area	Station	Gear	Latitude [°N]	Longitude [°E]	Depth [m]	*CoralSpecies*	Facies	Status	Reference
Off Limenaria Thasos I.	Stat. 168b	*T*	40.4570	24.5990	300–350	*Madrepora oculata*	–	Unknown	Vafidis et al. (1997)
SE of Lesvos	**Stat. 200b**	***trawl***	**38.9390**	**26.6050**	**70–90**	***Paracyathus pulchellus***	**Maerl**	**Unknown**	**Vafides et al. (1997)**
S of Karpathos	75/D40	–	35.0200	27.1383	600	*Caryophyllia calveri*	–	Dead	Zibrowius (1979)
SE of Kastellórizon	SME 1014	–	36.0694	29.6833	366–381	*Caryophyllia calveri*	Yellowish fine sed.	Dead	Zibrowius (1979)
NW of Thira	SME 765	–	36.4417	25.4000	375–394	*Caryophyllia calveri*	Fine ash	Dead	Zibrowius (1979)
NE Gulf of Pagasitikos	**SME 1538**	–	**39.3000**	**23.1083**	**55–62**	***Caryophyllia smithii***	**Yellowish grey sand**	**Live**	**Zibrowius** (1979)
Knimis channel	**SME 1533**	–	**38.7917**	**22.8250**	**58–61**	***Caryophyllia smithii***	**Muddy gravel**	**Live**	**Zibrowius** (1979)
N Euboean Gulf	**SME 1529**	–	**38.7117**	**23.1250**	**62**	***Caryophyllia smithii***	**Grey muddy sand**	**Live**	**Zibrowius** (1979)
NW Gulf of Cassandra	**SME 1560**	–	**40.2056**	**23.4153**	**73**	***Caryophyllia smithii***	**Slightly sandy mud**	**Unknown**	**Zibrowius** (1979)
S of Paros	**SME 835**	–	**36.9181**	**25.1806**	**88**	***Caryophyllia smithii***	**Coralligène**	**Live**	**Zibrowius** (1979)
Betw. Paros and Antiparos	**SME 836**	–	**36.9139**	**25.1028**	**100–102**	***Caryophyllia smithii***	**Coralligène**	**Unknown**	**Zibrowius** (1979)
Off Cape Cassandra	**SME 1564**	–	**39.9290**	**23.3400**	**100**	***Caryophyllia smithii***	**Grey mud**	**Unknown**	**Zibrowius** (1979)
Gulf of Kalamata	**SME 728**	–	**36.9917**	**22.1083**	**110**	***Caryophyllia smithii***	**Coarse detritic sed.**	**Dead**	**Zibrowius** (1979)
NW of Cape of Matapan	**SME 715**	–	**36.4306**	**22.4236**	**115–120**	***Caryophyllia smithii***	**Coarse detritic sed.**	**Dead**	**Zibrowius** (1979)
S of Syros	**SME 814**	–	**37.2889**	**24.8694**	**115**	***Caryophyllia smithii***	**HG**	**Live**	**Zibrowius** (1979)
NW of Cape of Matapan	**SME 721**	–	**36.3889**	**22.4528**	**120–137**	***Caryophyllia smithii***	**Coarse detritic sed.**	**Live**	**Zibrowius** (1979)
Betw. Syros and Serfopoula	**SME 843**	–	**37.2583**	**24.8375**	**160**	***Caryophyllia smithii***	**HG and sandy-muddy sed.**	**Live**	**Zibrowius** (1979)
NE Crete	**67/9**	–	**35.2333**	**26.3333**	**180**	***Caryophyllia smithii***	**Muddy sand with biogenic elements**	**Dead**	**Zibrowius** (1979)
Betw. Alonnisos and Kira Panagia	**SME 1545**	–	**39.3069**	**23.9958**	**185**	***Caryophyllia smithii***	**Muddy sand**	**Live**	**Zibrowius** (1979)
SE plane off Cape Kalireas	SME 792	–	38.1667	24.6278	300	*Caryophyllia smithii*	Light grey fine sed.	Dead	Zibrowius (1979)
Betw. Panagia and Alonissos	SME 1544	–	39.3139	23.9911	200–270	*Caryophyllia smithii*	Muddy coarse sand	Live	Zibrowius (1979)
SW of Antpsara	SME 805	–	38.5056	24.4750	420	*Dendrophyllia cornigera*	HG	Live	Zibrowius (1979)
S of Karpathos	75/D40	–	35.0200	27.1383	600	*Dendrophyllia cornigera*	–	Live	Zibrowius (1979)
Betw. Panagia and Alonissos	SME 1544	–	39.3139	23.9911	200–270	*Dendrophyllia cornigera*	Muddy coarse sand	Live	Zibrowius (1979)
N Euboean Gulf	SME 1525	–	38.5367	23.5183	230–275	*Desmophyllum dianthus*	–	Live	Zibrowius (1979)
W of Thira	**67/61**	–	**36.4300**	**25.3260**	**60**	***Guynia annulata***	**Seafloor with concretions of calc. algae**	**Dead**	**Zibrowius** (1979)
Gulf of Kalamata	**SME 731**	–	**36.7517**	**22.0042**	**82–91**	***Guynia annulata***	**Coarse detritic sed.**	**Live**	**Zibrowius** (1979)
NE Crete	**67/9**	–	**35.2333**	**26.3333**	**180**	***Guynia annulata***	**Muddy sand with biogenic elements**	**Dead**	**Zibrowius** (1979)

Strait of Kasos	**SME 747**	**–**	**35.2000**	**26.6500**	**180**	***Guynia annulata***	**Muddy detrtic sed. with rarely calc. algae**	**Live**	**Zibrowius (1979)**
SE of Kastellórizon	SME 1014	–	36.0694	29.6833	366–381	*Lophelia pertusa*	Yellowish fine sed.	Dead	Zibrowius (1979)
SE of Kastellórizon	SME 1014	–	36.0694	29.6833	366–381	*Madrepora oculata*	Yellowish fine sed.	Dead	Zibrowius (1979)
Betw. Karpathos and Rhodes	**67/20**	**–**	**35.9267**	**27.4850**	**60–80**	***Paracyathus pulchellus***	**Concretions of calc. algae**	**Live**	**Zibrowius (1979)**
S of Thasos	**SME 1587**	**–**	**40.5770**	**24.5870**	**60–70**	***Paracyathus pulchellus***	**Muddy sand with some blocs**	**Live**	**Zibrowius (1979)**
W of Thira	**SME 775**	**–**	**36.3722**	**25.3556**	**73**	***Paracyathus pulchellus***	**Coralligène**	**Live**	**Zibrowius (1979)**
Betw. Euboea and Andros	**SME 795**	**–**	**38.1583**	**24.6153**	**90**	***Paracyathus pulchellus***	**Muddy coarse gravel, calc. algae**	**Live**	**Zibrowius (1979)**
E of Lindos, Rhodes	**SME 1012**	**–**	**36.0811**	**28.1167**	**92**	***Paracyathus pulchellus***	**Sandy and gravely mud, calc. algae**	**Live**	**Zibrowius (1979)**
S of Syros	**SME 816**	**–**	**37.3042**	**24.8667**	**100**	***Paracyathus pulchellus***	**Coralligène, partly dead**	**Live**	**Zibrowius (1979)**
S of Syros	**SME 815**	**–**	**37.2944**	**24.8639**	**104**	***Paracyathus pulchellus***	**Coralligène**	**Dead**	**Zibrowius (1979)**
Betw. Alonnisos and Kira Panagia	**SME 1547**	**–**	**39.2778**	**24.0306**	**108–112**	***Paracyathus pulchellus***	**Coralligène de plateau**	**Live**	**Zibrowius (1979)**
Betw. Euboea and Andros	**SME 794**	**–**	**38.1611**	**24.7833**	**110**	***Paracyathus pulchellus***	**Muddy sand with coarse clasts, calc. algae**	**Live**	**Zibrowius (1979)**
NW of Thirasia	**67/32**	**–**	**36.5383**	**25.2967**	**110–128**	***Paracyathus pulchellus***	**Clay and concretions of calc. Algae**	**Live**	**Zibrowius (1979)**
Johnston Bank	**SME 1640**	**–**	**39.3033**	**25.3914**	**120–150**	***Paracyathus pulchellus***	**Muddy sand**	**Live**	**Zibrowius (1979)**
SW of Antipsara	**SME 801**	**–**	**38.5167**	**25.5167**	**120–130**	***Paracyathus pulchellus***	**Muddy organic gravel**	**Live**	**Zibrowius (1979)**
SW of Thira	**SME 774**	**–**	**36.3528**	**25.3292**	**128–146**	***Paracyathus pulchellus***	**Gravel of calc. algae**	**Live**	**Zibrowius (1979)**
Betw. Euboea and Andros	**SME 791**	**–**	**37.9194**	**24.6139**	**148**	***Paracyathus pulchellus***	**Sandy-muddy detritic sed.**	**Live**	**Zibrowius (1979)**
SE of Kastellórizon	SME 1020	–	36.1070	29.5510	421	*Paracyathus pulchellus*	Yellowish to greyish fine sed.	Dead	Zibrowius (1979)
S of Thira	SME 758	–	36.2958	25.3847	265–284	*Paracyathus pulchellus*	Grey mud with volcanic fragments	Dead	Zibrowius (1979)
SW of Anticythère	64/75	–	35.7000	23.3833	360	*Stenocyathus vermiformis*	Gravely muddy sand	Live	Zibrowius (1979)
S of Karpathos	75/D40	–	35.0200	27.1383	600	*Stenocyathus vermiformis*	–	Live	Zibrowius (1979)
SE of Kastellórizon	SME 1014	–	36.0694	29.6833	366–381	*Stenocyathus vermiformis*	Yellowish fine sed.	Dead	Zibrowius (1979)
Santorin	–	–	36.4417	25.4000	357–394	*Caryophyllia calveri*	–	Unknown	Zibrowius (1980)
Hellenic trench SE of Kythira	–	–	35.6667	22.6500	2000–2150	*Trochocyathus mediterraneus*	–	Unknown	Zibrowius (1980)
S of Crète	–	–	34.5420	24.4600	2100–2500	*Trochocyathus mediterraneus*	–	Unknown	Zibrowius (1980)

Occurrences in water depths <200 m are highlighted in bold

Area: *Betw.* between; Gear: *D* dredge, *T* trawl, *G* grab; Facies: *C Caryophyllia*, *Den Dendrophyllia*, *Des Desmophyllum dianthus*, *HG* Hardground, *L Lophelia*, *M Madrepora*, *N Neopycnodonte*, *RB* rock bottom, *S*: *Stenocyathus*, *sed.* sediment, *calc.* calcareous

Table 10.2 Bathyal coral occurrences in outcrops in the region of the Aegean Sea and the adjacent Hellenic trench compiled from various sources

Area	Latitude [°N]	Longitude [°E]	Species	Facies	Reference
Crete, Phalasarna	35.5019	23.5778	*Stenocyathus vermiformis*	–	Shaw et al. (2008)
Rhodes, Kallithea	36.3752	28.2354	*Caryophyllia smithii*	Lindos Bay Formation	Nielsen et al. (2006)
Rhodes, Kallithea	36.3752	28.2354	*Lophelia pertusa*	Cape Arkhangelos Formation	Nielsen et al. (2006)
Rhodes, Lardos SW Hill	36.0886	28.0096	*Lophelia pertusa*	Lindos Bay Formation	Titschack et al. (2013)
Rhodes, Lardos SW Hill	36.0886	28.0096	*Madrepora oculata*	Lindos Bay Formation	Titschack et al. (2013)
Rhodes, Lindos Bay type locality	36.0999	28.0869	*Caryophyllia smithii*	Lindos Bay Formation	Hanken et al. (1996)
Rhodes, Lindos Road Section	36.0834	28.0838	*Caryophyllia* sp.	St. Paul's Formation	Titschack et al. (2005)
Rhodes, Lindos Road Section	36.0834	28.0838	*Dendrophyllia cornigera*	St. Paul's Formation	Titschack et al. (2005)
Rhodes, Lindos Road Section	36.0834	28.0838	*Desmophyllum dianthus*	St. Paul's Formation	Titschack et al. (2005)
Rhodes, Lindos Road Section	36.0834	28.0838	*Lophelia pertusa*	St. Paul's Formation	Titschack et al. (2005)
Rhodes, Lindos Road Section	36.0834	28.0838	*Madrepora oculata*	St. Paul's Formation	Titschack et al. (2005)
Rhodes, St. Paul's Bay	36.0865	28.0889	*Caryophyllia* sp.	St. Paul's Formation	Titschack and Freiwald (2005)
Rhodes, St. Paul's Bay	36.0865	28.0889	*Dendrophyllia cornigera*	St. Paul's Formation	Titschack and Freiwald (2005)
Rhodes, St. Paul's Bay	36.0865	28.0889	*Desmophyllum dianthus*	St. Paul's Formation	Titschack and Freiwald (2005)
Rhodes, St. Paul's Bay	36.0865	28.0889	*Lophelia pertusa*	St. Paul's Formation	Titschack and Freiwald (2005)
Rhodes, St. Paul's Bay	36.0865	28.0889	*Madrepora oculata*	St. Paul's Formation	Titschack and Freiwald (2005)
Rhodes, Tsunami Bay	36.0832	28.0897	*Lophelia pertusa*	St. Paul's Formation	Titschack and Freiwald (2005)
Rhodes, Tsunami Bay	36.0832	28.0897	*Madrepora oculata*	St. Paul's Formation	Titschack and Freiwald (2005)
Rhodes, Vasfi	36.4018	28.2214	*Lophelia pertusa*	Lindos Bay Formation	Moissette and Spjeldnæs (1995)
Rhodes, Vlycha Bay	36.1098	28.0641	*Lophelia pertusa*	Lindos Bay Formation	Kuhn (1998)

2011) where the corals occur on steep escarpments and topographic highs (Taviani et al. 2011). While *J. cailleti*, *S. fissilis* and *T. mediterraneus* seem to be restricted to this region, *L. pertusa* and *M. oculata* are also once and *D. cornigera*, *D. dianthus* and *C. calveri* frequently reported from the Aegean Sea (Fig. 10.1a; Zibrowius 1979; Vafidis et al. 1997). *Caryophyllia smithii*, *G. annulata* and *P. pulchellus* are more or less randomly distributed over the entire Aegean Sea when their shallow-water occurrences are included (Fig. 10.1). Most reports of the coral-associated facies refer to coarse grained deposits, including coral rubble and (muddy) gravel deposits, and hard substrates, such as hardgrounds and coralligenous deposits (Zibrowius 1979).

The knowledge about the temporal occurrence of bathyal corals is restricted to the Hellenic trench and Hellenic arc islands (Fig. 10.1b). Only 21 ^{230}Th/U and ^{14}C dates exist to date and were obtained from the species *D. dianthus* (n = 6), *S. vermiformis* (n = 5), *L. pertusa* (n = 4), *M. oculata* (n = 4), *C. calveri* (n = 1) and *C. smithii* (n = 1) (paired ^{230}Th/U – AMS^{14}C dates obtained from one coral specimen presented in McCulloch et al. (2010) are counted as one date; Fig. 10.1b; McCulloch et al. 2010; Shaw et al. 2010; Taviani et al. 2011; Titschack et al. 2013). The available dates of offshore-collected corals and corals collected on Crete show ages ranging from 0.6 to 23.4 ka (Fig. 10.1b). Three older ages of *L. pertusa* fragments from outcrops on the island of Rhodes date back to the Middle Pleistocene (690–760 ka; Titschack et al. 2013) and point to the fact that *L. pertusa* and *M. oculata* were already earlier present in this region. Coral ages since the last glacial maximum show a pronounced age gap between 4.5 and 10.8 ka, which roughly coincide with the sapropel S1 formation in the deep eastern Mediterranean Sea (see Vertino et al., this volume). This temporal pattern is consistent with the observations by Fink et al. (2012) who suggested a temporary extinction of *L. pertusa* and *M. oculata* within the Santa Maria di Leuca coral province (Apulian margin, northern Ionian Sea, 500–900 m water depth) most likely due to a strongly reduced bottom water oxygen concentration, which was linked to the sapropel S1 formation. A similar control might also be suggested for the bathyal corals along the Hellenic trench. However, the current database is by far too limited to draw any conclusion with certainty.

Fossil scleractinian occurrences are described from various Greek islands along the Hellenic Arc. In particular, shallow corals are frequently mentioned (especially *Cladocora caespitosa* (Linnaeus 1767) in: Pirazzoli et al. 2004; Kershaw et al. 2005; Cooper et al. 2007; Titschack et al. 2008; Drinia et al. 2010; Mastronuzzi et al. 2014) while fossil remains of bathyal corals represent a rarity and are solely described from the island of Crete (1 outcrop; *S. vermiformis*; e.g., Shaw and Jackson 2010) and Rhodes (9 outcrops; Table 10.2). On Rhodes, all framework-forming bathyal corals (*L. pertusa*, *M. oculata* and *D. cornigera*) and further solitary corals (including species from shallower water depths: *Balanophyllia (Balanophyllia) europaea* (Risso, 1826), *D. dianthus*, *S. vermiformis*, *Stephanophyllia* sp., *Caryophyllia* spp. and flabellid corals) are present (Jüssen 1890; Bukowski 1899; Hanken et al. 1996; Titschack and Freiwald 2005; Titschack et al. 2005; Nielsen et al. 2006). The framework-forming corals occur within debris fall or debris flow deposits that occur close to or at the foot of bedrock cliffs (Hanken et al. 1996; Spjeldnæs and Moissette 1997; Titschack and Freiwald 2005; Titschack et al. 2005, 2013). The bedrock topography, which resembles the palaeorelief during the deposition of the coral deposits, was interpreted by Titschack et al. (2013) as submarine canyon systems. This palaeorelief might have been very similar to the modern situation off SE Rhodes (Fig. 10.1a, see also Taviani et al. 2011).

Taviani et al. (2005) highlighted the importance of an active tectonic setting with high uplift rates for the exposure of framework-forming bathyal corals on land – possibly the reason for their rare fossil documentation. So far framework-forming bathyal coral-bearing deposits emerged on land are only known from the Cook Strait, New Zealand (e.g., Squires 1964; Wells 1986), from Norwegian fjords (e.g. Mikkelsen et al. 1982) and from several regions within the Mediterranean Sea (e.g. Krautworst and Brachert 2003; Taviani et al. 2005; Vertino et al. 2014 and references within these publications). All these regions were characterised by a steep rough topography during the lifetime of the corals, in which submarine cliffs and submarine canyons provide their preferential habitats. Re-deposition by mass-wasting events (debris flows, debris falls, etc.) and final deposition at the foot of submarine cliffs and along the inner margins of submarine canyons present a common fate of corals within this palaeoenvironmental setting (Fig. 10.1c). The world-wide sparsity of emerged framework-forming bathyal coral-bearing deposits, as well as submarine cliff- and submarine canyon-related deposits in general, make these occurrences especially worthy for protection, potentially as PaleoPark (Lipps 2009). On Rhodes, already two localities with remains of the white coral community were considerably affected by building activities (Moissette and Spjeldnæs 1995; Titschack et al. 2005) highlighting the urgency of their protection in this region.

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References

Bukowski G (1899) Geologische Uebersichtskarte der Insel Rhodus. Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt 48:517–688

Çinar ME, Yokeş M, Açik S, et al (2014) Check-list of Cnidaria and Ctenophora from the coasts of Turkey. Turk J Zool 38:677–697

Cooper FJ, Roberts GP, Underwood CJ (2007) A comparison of 103–105 year uplift rates on the South Alkyonides Fault, central Greece: Holocene climate stability and the formation of coastal notches. Geophys Res Lett 34:L14310

Drinia H, Koskeridou E, Antonarakou A, et al (2010) Benthic foraminifera associated with the zooxanthellate coral *Cladocora* in the Pleistocene of the Kos island (Aegean Sea, Greece): sea level changes and palaeoenvironmental conditions. In: 12th international Congress of the Geological Society of Greece, vol 43, pp 613–619

Fink HG, Wienberg C, Hebbeln D, et al (2012) Oxygen control on Holocene cold-water coral development in the eastern Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Gerovasileiou V, Koutsoubas D, Voultsiadou E, et al (2009) Biodiversity in submarine caves of Lesvos Island (NE Aegean Sea): preliminary results. In: 9th symposium on oceanography & fisheries, 2009 – proceedings, vol 1, pp 660–664

Gerovasileiou V, Chintiroglou C, Vafidis D, et al (2015) Census of biodiversity in marine caves of the eastern Mediterranean Sea. Mediterr Mar Sci 16:245–265

Hanken N-M, Bromley RG, Miller J (1996) Plio-Pleistocene sedimentation in coastal grabens, north-east Rhodes, Greece. Geol J 31:393–418

Harris PT, Whiteway T (2011) Global distribution of large submarine canyons: geomorphic differences between active and passive continental margins. Mar Geol 285:69–86

Jüssen E (1890) Über pliocäne Korallen von der Insel Rhodus. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Wien, mathematisch-naturwissenschaftliche Classe 99:13–24

Kershaw S, Guo L, Braga JC (2005) A Holocene coral-algal reef at Mavra Litharia, Gulf of Corinth, Greece: structure, history, and applications in relative sea-level change. Mar Geol 215:171–192

Krautworst UMR, Brachert TC (2003) Sedimentary facies during early stages of flooding in an extensional basin: the Brèche Rouge de Carboneras (Late Miocene, Almería/SE Spain). Int J Earth Sci 92:610–623

Kuhn E (1998) Rhodos. Fossilien 98:198–199

Lipps JH (2009) PaleoParks: Our paleontological heritage protected and conserved in the field worldwide. In: Lipps JH, Granier BRC (eds) Carnets de Géologie/Notebooks on geology, Brest, pp 1–10. http://paleopolis.rediris.es/cg/CG2009_BOOK_03/CG2009_BOOK_03_Chapter01.pdf

Mastronuzzi G, Calcagnile L, Pignatelli C, et al (2014) Late Holocene tsunamogenic coseismic uplift in Kerkira Island, Greece. Quat Int 332:48–60

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the Younger Dryas. Earth Planet Sci Lett 298:143–152

Mikkelsen N, Erlenkeuser H, Killingley JS, et al (1982) Norwegian corals: radiocarbon and stable isotopes in *Lophelia pertusa*. Boreas 11:163–171

Moissette P, Spjeldnæs N (1995) Plio-Pleistocene deep-water bryozoans from Rhodes, Greece. Palaeontology 38:771–799

Morri C, Vafidis D, Peirano A, et al (2000) Anthozoa from a subtidal hydrothermal area of Milos Island (Aegean Sea), with notes on the construction potential of the scleractinian coral *Madracis pharensis*. Ital J Zool 67:319–325

Nielsen JK, Hanken N-M, Nielsen JK, et al (2006) Biostratigraphy and palaeoecology of the marine Pleistocene of Rhodes, Greece: Scleractinia, Serpulidae, Mollusca and Brachiopoda. Bull Geosci 81:173–196

Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la Mer Méditerranée. Recueil des Travaux de la Station Marine d'Endoume, Marseille Bulletin 31, Fasc. 47:1–137

Pirazzoli PA, Stiros SC, Fontugne M, et al (2004) Holocene and Quaternary uplift in the central part of the southern coast of the Corinth Gulf (Greece). Mar Geol 212:35–44

Salomidi M, Zibrowius H, Issaris Y, et al (2010) *Dendrophyllia* in Greek waters, Mediterranean Sea, with the first record of *D. ramea* (Cnidaria, Scleractinia) from the area. Mediterr Mar Sci 11:189–194

Salomidi M, Katsanevakis S, Issaris Y, et al (2013) Anthropogenic disturbance of coastal habitats promotes the spread of the introduced scleractinian coral *Oculina patagonica* in the Mediterranean Sea. Biol Invasion 15:1961–1971

Shaw B, Ambraseys NN, England PC, et al (2008) Eastern Mediterranean tectonics and tsunami hazard inferred from the AD 365 earthquake. Nat Geosci 1:268–276

Shaw B, Jackson J (2010) Earthquake mechanisms and active tectonics of the Hellenic subduction zone. Geophys J Int 181:966–984

Shaw B, Jackson JA, Higham TFG, et al (2010) Radiometric dates of uplifted marine fauna in Greece: implications for the interpretation of recent earthquake and tectonic histories using lithophagid dates. Earth Planet Sci Lett 297:395–404

Smith C, Sakellariou D, McCoy F, et al (2009) Deep coral environments south of Crete. Πανελλήνιο Συμπόσιο Ωκεανογραφίας & Αλιείας 2009—Πρακτικά. Τόμος 1:666–668

Spjeldnæs N, Moissette P (1997) Celleporid (Bryozoan) thickets from the upper Pliocene of the island of Rhodes, Greece. In: James NP, JAD C (eds) Cool-water carbonates. SEPM (Society for Sedimentary Geology), Tulsa, pp 263–270

Squires DF (1964) Fossil coral thickets in Wairarapa, New Zealand. J Paleontol 38:904–915

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin, pp 137–156

Taviani M, Vertino A, López-Correa M, et al (2011) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603

Titschack J, Freiwald A (2005) Growth, deposition, and facies of Pleistocene bathyal coral communities from Rhodes, Greece. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin, pp 41–59

Titschack J, Bromley RG, Freiwald A (2005) Plio-Pleistocene cliff-bound, wedge-shaped, warm-temperate carbonate deposits from Rhodes (Greece): sedimentology and facies. Sediment Geol 180:29–56

Titschack J, Nelson CS, Beck T, et al (2008) Sedimentary evolution of a Late Pleistocene temperate red algal reef (Coralligène) on Rhodes, Greece: correlation with global sea-level fluctuations. Sedimentology 55:1747–1776

Titschack J, Joseph N, Fietzke J, et al (2013) Record of a tectonically-controlled regression captured by changes in carbonate skeletal associations on a structured island shelf (mid-Pleistocene, Rhodes, Greece). Sediment Geol 283:15–33

Vafidis D, Koukouras A, Voultsiadou-Koukoura E (1997) Actinaria, Corallimorpharia, and Scleractinia (Hexacorallia, Anthozoa) of the Aegean Sea, with a checklist of the Eastern Mediterranean and Black Sea species. Isr J Zool 43:55–70

Vertino A, Stolarski J, Bosellini FR, et al (2014) Mediterranean corals through time: from Miocene to Present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 257–274

Wells PE (1986) Record of an Upper Miocene fossil *Goniocorella* coral thicket, Mt. Bruce, Wairarapa, New Zealand. J R Soc N Z 16:139–144

Zibrowius H (1979) Campagne de la Calypso en Méditerranée nord-orientale (1955, 1956, 1960, 1964). 7. Scléractiniaires. Annales de L'Institut Océanographique, Paris 55, Supplement: 7–28

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. In: Mém Inst Oceanogr Monaco, vol 11, p 284

Zibrowius H (1987) Scléractiniaires et polychètes serpulidae des faunes bathyales actuelle et plio-pléistocène de Méditerranée. Documents et Travaux de l'Instiut Géologique Albert de Lapparent 11:255–257

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

11

Mediterranean Cold-Water Corals as Paleoclimate Archives

Paolo Montagna and Marco Taviani

Abstract

Scleractinian cold-water corals preserve in their aragonite skeleton information on the past changes of the physico-chemical properties of the seawater in which they grew. Such information is stored as geochemical signals, such as changes in trace elements concentration (B/Ca, Li/Mg, P/Ca, Sr/Ca, Ba/Ca, U/Ca) or stable and radiogenic isotopes composition (δ^{11}B, δ^{13}C, δ^{18}O, ^{14}C, εNd), that are usually converted into environmental parameters using empirical calibration equations. The aragonite skeleton of cold-water corals is sufficiently uranium-rich to be suitable for U-series dating, providing precise and accurate ages for the last 600–700 kyrs. This opens the possibility to obtain reconstructions of key oceanographic parameters for the intermediate and deep water masses at sub-decadal scale resolution for climatically-relevant time windows in the past. However, part of the geochemical signal incorporated into the coral skeleton is modulated by the physiology of the coral, which complicates the interpretation of the geochemical proxies. This "vital effect" needs to be taken into account and corrected for to obtain reliable reconstructions of past changes in seawater temperature, pH and nutrient content. On the other hand, these biologically-induced geochemical signals can be used to investigate the processes controlling coral biomineralisation and better understand the resilience of cold-water corals to environmental and climate changes.

In the recent years, Mediterranean cold-water corals have been targeted for geochemically-oriented studies and their trace elements and isotopes composition has contributed significantly to developing and understanding new and established coral proxies. Living in an environment characterised by relatively warm seawater temperatures (13–14 °C) and high pH (8.1), the Mediterranean cold-water corals provide the end-member geochemical composition useful to derive empirical calibration equations. In particular, the analysis of several specimens of the cold-water corals species *Lophelia pertusa, Madrepora oculata* and *Desmophyllum dianthus* live-collected in the western, central and eastern Mediterranean Sea, has contributed to the development of the Li/Mg thermometer, boron isotopes pH proxy and P/Ca nutrient proxy, as well as a better understanding of the neodymium isotopic composition of cold-water corals as a water mass tracer. A multi-proxy approach has been recently applied to precisely U/Th-dated cold-water corals fragments from coral-bearing sediment cores retrieved in the western and central Mediterranean Sea, showing large changes in the dynamics of the intermediate waters during the Holocene. Further investigations of fossil cold-water corals specimens from different Mediterranean locations will open new perspectives on the reconstruction of past changes in the physico-chemical properties of sub-surface waters and their potential role in modifying the Mediterranean climate.

Keywords

Geochemical proxies · Paleoclimate · Natural archives · Cold-water corals · Mediterranean Sea

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11.1 Introduction

In the Mediterranean Sea, anthropogenically-induced changes observed at the sea surface, such as the increasing temperature and acidification, propagate fast towards the intermediate and deep layers of the basin due to the very active Mediterranean overturning circulation. Indeed, hydrographic data going back to 1950–1960 indicate increasing sub-surface temperature values for both the western and eastern Mediterranean basins (Bethoux and Gentili 1996; Tsimplis and Baker 2000; Rixen et al. 2005). Hydrographic and modelling data for the Mediterranean Sea suggest that this basin is also experiencing a large increase in ocean acidification (OA) compared to the other world areas (Touratier and Goyet 2011; Flecha et al. 2015; Hassoun et al. 2015; Marcellin Yao et al. 2016; Maier et al., this volume; Movilla, this volume), although uncertainties still exist in the anthropogenic pH change of the Mediterranean deep waters (Palmiéri et al. 2015).

Understanding whether these recent observed modifications and trends in seawater temperature and carbonate chemistry are the result of anthropogenic activities or are part of the natural climate variability requires long-term (i.e. multidecadal to centennial and millennial) time series that extend beyond the relatively short instrumental period, especially for seawater pH changes. Seawater temperature and salinity data for the intermediate and deep waters in the Mediterranean Sea are restricted to the last ~60–70 years (e.g. Painter and Tsimplis 2003) and are very discontinuous in time and space, limiting their use in deriving long-term changes in the past. Moreover, only few continuous and relatively long (~20–30 years) time series of thermohaline properties exist in this basin (see Schroeder et al. 2013 and references therein). The scarcity of historical data is even more critical for the seawater carbonate system (e.g. pH, alkalinity, dissolved inorganic carbon), with the first high-quality measurements being conducted at the beginning of the 2000s (e.g. M51/2 cruise in 2001 on board R/V *Meteor*; Schneider et al. 2007).

The existing historical datasets are then too short to accurately attribute climate trends to natural or anthropogenic processes. Consequently, the only way to extend the instrumental record back in time is by using proxy-based reconstructions. Intermediate and deep water physico-chemical properties can be documented from the geochemistry of CWC that has been proved useful to provide paleoclimate reconstructions at centennial to decadal-scale resolution (Adkins et al. 1998; Montagna et al. 2005; Robinson et al. 2014). Pioneer geochemical contributions mainly focused on coupled U/Th and ^{14}C measurements of the aragonite skeleton of cold-water corals (CWC) to investigate ocean ventilation (Adkins et al. 1998; Mangini et al. 1998) as well as oxygen and carbon isotopes and trace elements for water mass temperature reconstructions or biomineralisation studies (Emiliani et al. 1978; Smith et al. 2000; Adkins et al. 2003; Rollion-Bard et al. 2003; Montagna et al. 2005; Shirai et al. 2005).

In recent years, an increasing number of studies involving new geochemical proxies such as isotopes (εNd), Δ^{14}C, U/Th and trace elements, have targeted Mediterranean CWC as paleo-archives of climate history (e.g. Montagna et al. 2005, 2006; McCulloch et al. 2010; Dubois-Dauphin et al. 2017) (Fig. 11.1). In particular, the Mediterranean has been the prime locus where to test trace and minor elemental composition of CWC with respect to paleoclimate (Montagna et al. 2005), especially triggered by the recent accessibility and availability of a large coral collection and the use of more advanced analytical instruments such as the new generation of mass spectrometers and protocols established for the investigation of tropical (e.g. Sinclair et al. 1998; Fallon et al. 1999; Corrège 2006) and temperate (Silenzi et al. 2005; Montagna et al. 2007) corals. For instance, the application of a laser ablation ICP-MS system to CWC was pivotal in ensuring precise and fast analytical possibilities on small samples and producing a great volume of data. Its successful use in tropical coral geochemistry (e.g. Sinclair et al. 1998) prompted its application to Mediterranean temperate zooxanthellate corals (Montagna et al. 2007). Lastly, the availability of large collections of recent and subfossil CWC provided all the needed material to experiments. All such conspired for producing the first geochemical screening of trace and minor elements in modern and late Pleistocene *Desmophyllum dianthus* corals from the central Mediterranean Sea (Montagna et al. 2005). This set the pace for all subsequent studies on Mediterranean CWC using both trace elements, stable and radiogenic isotopes (Montagna et al. 2006, 2008a, b, 2010, 2014; López Correa et al. 2010; McCulloch et al. 2010, 2012b; Dubois-Dauphin et al. 2017). The paleoclimate-oriented geochemical research on CWC is in full development and still is a frontier discipline, with applications using specimens from the Atlantic, Indian, Pacific and Southern oceans (see Robinson et al. 2014 and references therein). Overall, investigation of geochemical signals in CWC can provide a rare opportunity to put recent anthropogenically-driven changes of key seawater parameters (e.g. T, carbonate chemistry, nutrient content) into the context of the natural variability.

Scope of this chapter is to overview the many facets linked to the geochemistry of Mediterranean CWC for paleoclimate- and biomineralisation-oriented studies, discussing achievements, flaws and promising developments.

This chapter will not address recent studies on the proliferation and demise of Mediterranean CWC in the past linked to specific environmental conditions, such as changes in seawater temperature, oxygen content, carbonate chemistry, nutrient content or sedimentation regime (Malinverno et al. 2010; Margreth et al. 2011; McCulloch et al. 2010; Taviani et al. 2011; Fink et al. 2012, 2013, 2015), as these long-term coral population dynamics based on geochronological data are discussed in other chapters of the book (see Vertino et al., this volume; Wienberg, this volume; Vertino and Corselli, this volume; Taviani et al., this volume).

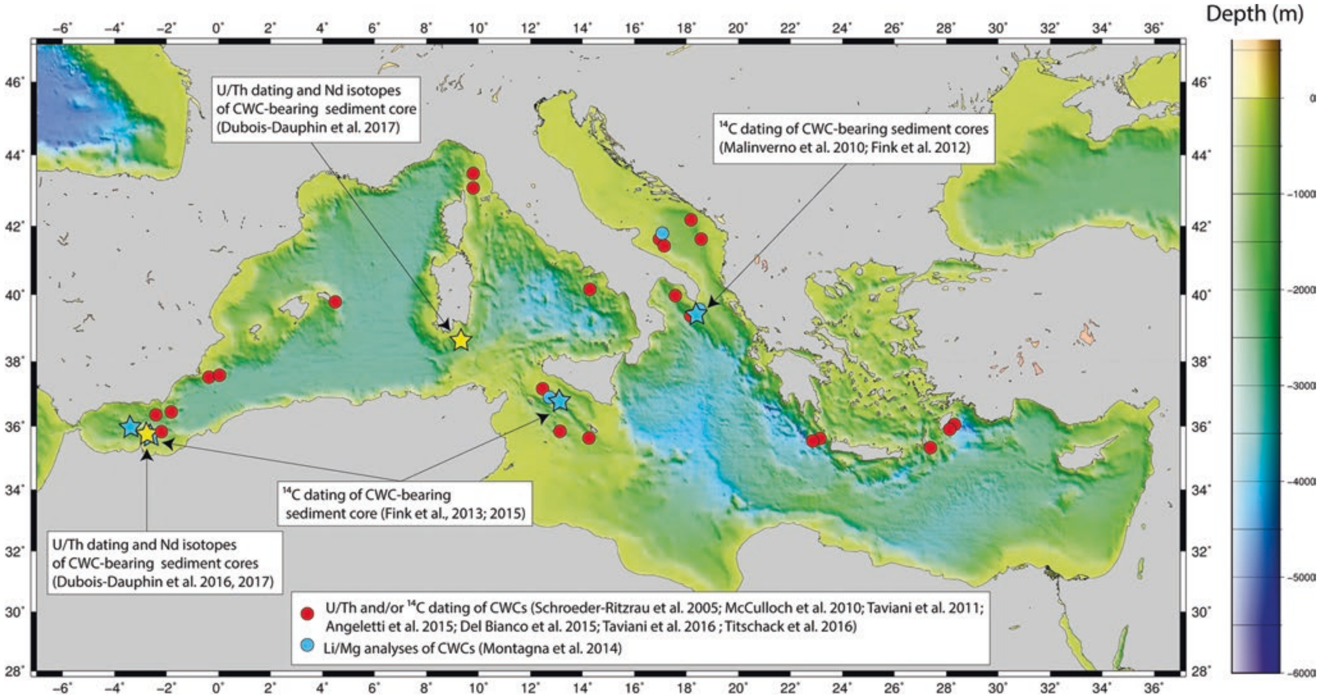

Fig. 11.1 Locations in the Mediterranean Sea where CWC were collected for geochemical analyses (U/Th and ^{14}C dating, Nd isotopes and Li/Mg ratios; Schröder-Ritzrau et al. 2005; Malinverno et al. 2010; McCulloch et al. 2010; Taviani et al. 2011, 2016; Fink et al. 2012, 2013, 2015; Montagna et al. 2014; Angeletti et al. 2015; Del Bianco et al. 2015; Dubois-Dauphin et al. 2016, 2017; Titschack et al. 2016)

11.2 Cold-Water Corals as Paleoclimate Archives: Environmental *vs.* Biologically-Induced Geochemical Signals

CWC are particularly attractive candidates for paleoceanographic applications given they inhabit diverse environments, from the shallow-water Sub-Antarctic and Chilean fjords to great ocean depth worldwide (Roberts et al. 2006). CWC occur as extensive reef structures, coral carbonate mounds, or coral patches and have a relatively large size skeleton (from few cm to 30–40 cm) that can be sub-sampled for multiple geochemical proxies. The slow growth rate, especially for solitary species like *Desmophyllum dianthus* (~1 mm/year; Cheng et al. 2000), allows reconstructing subdecadal scale variability of intermediate water chemistry during century-long time slices. CWC can therefore capture rapid changes in the dynamics of intermediate water masses at unprecedented resolution (e.g. Eltgroth et al. 2006). This unique possibility resides from the ability of CWC to incorporate into their skeleton trace elements and isotopes reflecting seawater temperature (e.g. Li/Mg), nutrient content (P/Ca), pH and dissolved inorganic carbon (boron isotopes, B/Ca, U/Ca), ventilation age (coupled ^{14}C and U/Th) and water mass tracing (Nd isotopes, εNd). Moreover, the aragonite skeleton of CWC persists in the fossil record and can be radiometrically dated by U/Th, ^{14}C, ^{210}Pb and ^{226}Ra techniques (Cheng et al. 2000; Adkins et al. 2004; Frank et al. 2004; Douville et al. 2010a; Sabatier et al. 2012).

Although highly promising, the geochemical signals contained in the aragonite skeleton of CWC can be difficult to interpret due to the presence of post-mortem alteration processes such as Fe – Mn oxide coatings and biologically-induced modifications, commonly known as “vital effects”. The metabolic activity of the organism partly drives the uptake of geochemical proxies in the coral skeleton and obscures the primary environmental signals, complicating the interpretation of climatic records. First micro-scale investigations of the CWC skeleton using micro-drilling system or laser ablation ICP-MS showed a strong elemental and isotopic heterogeneity at fine scale resolution, linked to the coral microstructures (e.g. Rollion-Bard et al. 2003; Montagna et al. 2005; Shirai et al. 2005). The skeleton of scleractinian corals is composed mainly of two structural units: centers of calcification (COCs) also known as centers of rapid accretion (CRA) or early mineralisation zones (EMZ) and the fibrous aragonite (FA) also known as thickening deposits (Stolarski 2003; Cuif and Dauphin 2005; Nothdurft and Webb 2007; Lartaud et al., this volume). Both units are assumed to be controlled to varying degrees by the coral physiology and display different geochemical compositions. In particular, COCs show systematically lower δ^{18}O, δ^{13}C, δ^{11}B and U/Ca values and higher Mg/Ca, Li/Ca, P/Ca and Ba/Ca ratios compared to the fibrous aragonite (Montagna et al. 2005, 2008a, 2014; Blamart et al. 2007; Rollion-Bard and Blamart 2014). It is clear that sub-sampling different coral portions having distinctive proportions of COCs *vs*. FA leads to different geochemical results and eventually contrasting paleoclimate reconstructions. Several approaches have been developed to correct for this biological overprint (e.g. Trotter et al. 2011; McCulloch et al. 2012a, b; Montagna et al. 2014; see below). On the contrary, other coral tracers and dating methods like $\Delta^{14}C$, U-series and Nd isotopes (εNd) do not suffer from "vital effect" and can be used to reconstruct the ventilation rate and the water mass dynamics of the intermediate/bathyal waters without performing any correction.

11.3 Geochemistry of the Mediterranean Cold-Water Corals

11.3.1 U/Th, ^{14}C and Nd Isotopes Measurements to Constrain the Water Mass Dynamics

^{14}C ventilation of water masses and intermediate and deep-water circulation rates can be evaluated from the radiocarbon activity ratio ($\Delta^{14}C$) of CWC in the past, which reflects the radiocarbon content of the seawater dissolved inorganic carbon (DIC) (Adkins et al. 2002). $\Delta^{14}C$ is calculated by coupling precise U/Th dating with radiocarbon measurements using the formula:

$$\Delta^{14}C_{deepwater} = \left(\frac{e^{-\frac{^{14}C\_age}{LibbyMeanLife}}}{e^{-\frac{U/Th\_age}{TrueMeanLife}}} - 1 \right) \times 1000$$

(Adkins and Boyle 1997), where the conventional Libby Mean Life of ^{14}C is 8033 years and the True Mean Life is 8266 years (Stuiver and Polach 1977). This equation derives from the definition of the measured $^{14}C/^{12}C$ ratio (see Adkins and Boyle 1997 for full details of the equations). The ^{14}C content of the coral reflects both the ocean dissolved inorganic carbon ^{14}C content and the age of the coral itself. By correcting the radiocarbon content of the coral for the aging component, the radiocarbon activity ratio of the water mass at the time the coral lived can be extracted. The $\Delta^{14}C$ can then be compared to the contemporaneous atmosphere and surface global ocean $\Delta^{14}C$ records using for example the IntCal 13 and Marine 13 curves (Reimer et al. 2013) to examine rates of water mass circulation and atmosphere-ocean carbon exchange or ^{14}C ventilation. The $\Delta^{14}C$ of the corals is often express as $\Delta\ \Delta^{14}C$, which is the difference between the $\Delta^{14}C$ of the sample and the $\Delta^{14}C$ of the contemporaneous atmosphere. However, this term does not take into account rapid changes in atmospheric $\Delta^{14}C$ and a better representation of the past ocean circulation can be achieved by using the epsilon value (Hines et al. 2015):

$$\varepsilon = \left(\left[\frac{\frac{\Delta^{14}C_{sample}}{1000} + 1}{\frac{\Delta^{14}C_{atm}}{1000} + 1} \right] - 1 \right) \times 1000$$

McCulloch and co-authors provided the first $\Delta^{14}C$ results from CWC collected at different water depths in the Mediterranean Sea, spanning the last ~20 kyrs (McCulloch et al. 2010). As reported by the authors, most of the corals $\Delta^{14}C$ values lie on or only slightly below or above the Marine surface 04 curve, which is the data set published by Hughen and co-authors in 2004 and used to calibrate radiocarbon ages for the ocean (Hughen et al. 2004). The $\Delta^{14}C$ data of McCulloch et al. (2010) suggest equilibrium with surface waters and generally well ventilated intermediate and deep waters in the Mediterranean Sea. The only exception is represented by two *Lophelia pertusa* specimens dated at ~12.5 kyrs from the Ionian Sea with $\Delta^{14}C$ values that fall significantly below the marine curve (~70–80‰), likely indicating conditions of water mass isolation derived from a reduction of deep-water formation in the Adriatic Sea (McCulloch et al. 2010). Here, the $\Delta^{14}C$ values of 23 coral samples reported in McCulloch et al. (2010) that cover the last 12 kyrs have been plotted against the more recent IntCal 13 atmospheric and Marine 13 $\Delta^{14}C$ curves (Reimer et al. 2013) and converted into epsilon units (Fig. 11.2). Most of the reconstructed $\Delta^{14}C$ values of the intermediate and deep waters follow the atmosphere at almost constant offset and more than 80% of the calculated $\Delta^{14}C$ overlap within error with the Marine surface 13 curve. The mean epsilon value of the corals (−47.6 ± 10‰; mean ± 1σ SD) is similar to the mean difference between Marine 13 and IntCal 13 curves (−43.1 ± 5‰; Fig. 11.2), suggesting no major changes in the intermediate-deep water ventilation of the Mediterranean Sea during the last 12 kyrs. During the sapropel S1 event (~10.5-6 cal kyrs BP; De Lange et al. 2008), characterised by anoxic bottom water conditions and weakening or shutdown of intermediate and deep-water formation in the eastern Mediterranean basin (e.g. Rohling et al. 2015; Tesi et al. 2017; Vertino et al., this volume), the $\Delta^{14}C$ and epsilon values of the CWC do not indicate reduced water mass circulation (Fig. 11.2). However, the two samples dated at ~ 7 and 9 kyrs were collected at intermediate depths in the Balearic Sea where ventilation conditions have not likely changed during the last 12 kyrs (Dubois-Dauphin et al., 2017). In order to track potential variations of the intermediate water ventilation associated to the sapropel S1 event, studies should be focused on CWC collected in the central-eastern Mediterranean Sea at water depths corresponding to the Levantine Intermediate Water (LIW) or the Eastern Mediterranean Deep water (EMDW) (see for example Fink et al. 2012). Moreover, reliable reconstructions of ventilation rates in the past require water mass tracers that can be used to identify mixing ratio of distinct water masses, such as the nutrient proxy P/Ca (Montagna et al. 2006; see below) or the water mass provenance tracer εNd (e.g. Copard et al. 2010; van de Flierdt et al. 2010). A very recent study investigated Nd isotopes in Mediterranean CWC spanning the last ~13 kyrs (Dubois-Dauphin et al. 2017). Coral fragments were collected in the Sardinia Channel at 414 m water depth

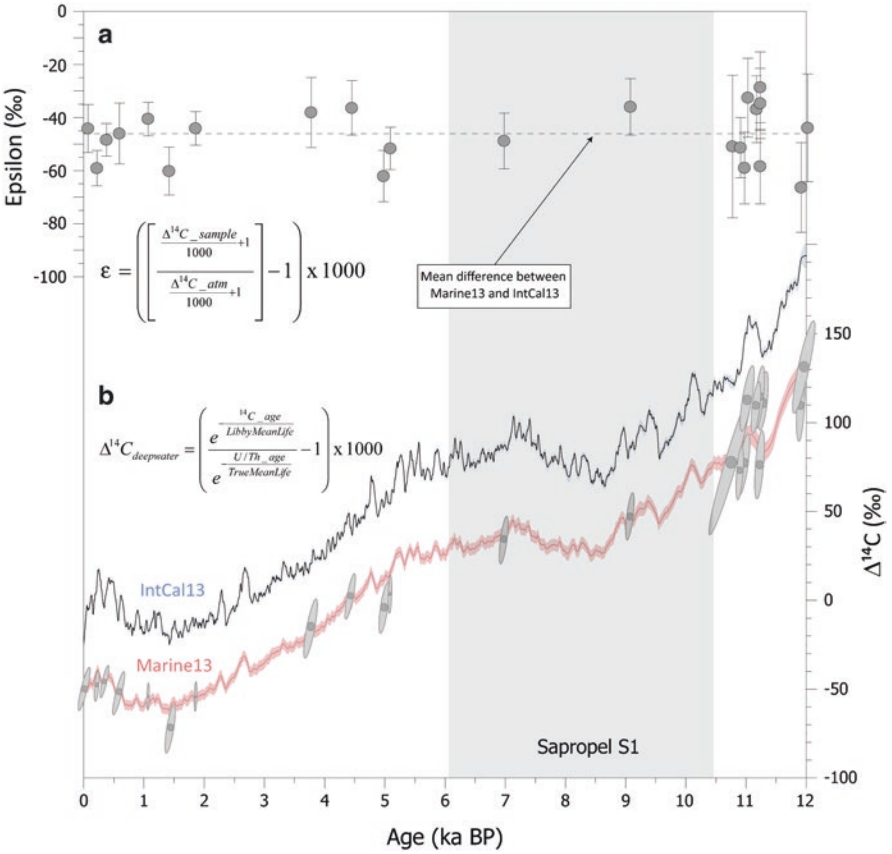

Fig. 11.2 (**a**) Mediterranean CWC $\Delta^{14}C$ record converted into epsilon values. Epsilon uncertainties (1σ) are calculated from the U/Th and $\Delta^{14}C$ errors. Dashed line is the mean difference between Marine 13 and IntCal atmospheric 13 $\Delta^{14}C$ curves. (**b**) Mediterranean CWC $\Delta^{14}C$ record plotted against Marine 13 and IntCal 13 atmospheric $\Delta^{14}C$ curves. Error ellipses represent 1σ correlated U/Th and $\Delta^{14}C$ errors (Data from McCulloch et al. 2010). Most of the coral $\Delta^{14}C$ values plot within error on the Marine 13 curve suggesting generally well ventilated intermediate and deep waters in the Mediterranean Sea. The grey shaded area indicates the sapropel S1 interval (~10.5-6 cal kyrs BP; De Lange et al. 2008)

(Taviani et al. 2017) and in the Alborán Sea between 280 and 442 m water depth (Fink et al. 2013) and analysed for Nd isotopes. Results reveal relatively constant εNd values through time for both locations, with the sole notable exception being a large shift at ~ 8.7 kyrs BP toward non-radiogenic εNd values in the Sardinian record (from −7.55 ± 0.2 at 10.170 kyrs BP to −8.66 ± 0.3 at 8.703 kyrs BP), indicative of a strong reduction of the LIW formation in the eastern Mediterranean basin during the sapropel S1 event (Dubois-Dauphin et al. 2017).

11.3.2 Cold-Water Coral Paleothermometers

So far, reliable seawater temperature reconstructions using the geochemistry of CWC have been difficult to achieve due to the strong physiological control of the coral organism on the elemental uptake and isotope fractionation during the skeleton formation or the impact of variables other than temperature on traditional paleothermometers. In particular, temperature-sensitive proxies, such as $\delta^{18}O$, Mg/Ca and Sr/Ca, commonly used in annually-banded aragonite tropical and temperate corals (e.g. Beck et al. 1992; Mitsuguchi et al. 1996; Montagna et al. 2007), suffer to varying degrees from the effects of the organism's physiology, which can complicate the interpretation of the geochemical signal (e.g. Robinson et al. 2014). Despite this limitation, there have been some attempts to use Sr/Ca as sub-surface water temperature proxy in CWC (e.g. Cohen et al. 2006; Raddatz et al. 2013). Cohen et al. (2006) calculated the temperature dependence of Sr/Ca ratios in a living specimen of the azooxanthellate coral *Lophelia pertusa* collected on the Tisler Reef in the submarine boarder between Norway and Sweden and concluded that only ~25% of the changes in Sr/Ca can be related to the temperature variation. The remaining signal is controlled by the seasonal variation in the saturation state of the coral's calcifying fluid, which drives the skeletal "precipitation efficiency". Similarly, Raddatz et al. (2013) observed a weak temperature dependence of Sr/Ca from specimens of *L. pertusa* live-collected in the North Atlantic and Mediterranean Sea.

First attempts to use $\delta^{18}O$ in CWC as a temperature proxy took advantage of the large isotopic fractionation observed in their aragonite skeleton at fine-scale resolution to derive the "lines technique" method (Smith et al. 2000). Both oxygen and carbon isotopes in CWC exhibit large micron-meter scale variability that can only be explained by biologically-mediated vital and/or kinetic effects (e.g. Adkins et al. 2003; Rollion-Bard et al. 2003; López Correa et al. 2010). $\delta^{18}O$ and $\delta^{13}C$ in corals (especially CWC) show strong linear correlations, with the intercepts of the $\delta^{18}O$-$\delta^{13}C$ trends being related with the ambient temperature (Smith et al. 2000; Lutringer et al. 2005). Accordingly, Smith and co-authors developed the "lines technique" method that enables deriving the value of $\delta^{18}O_{coral} - \delta^{18}O_{water}$ at apparent equilibrium (Grossman and Ku 1986), which is related to the seawater temperature where the coral grew. So far, the only study that applied the "lines technique" to Mediterranean CWC is the one performed by López Correa et al. (2010) on two *L. pertusa* specimens live-collected from the Santa Maria di Leuca coral province in the Ionian Sea. This method provided good estimates of the ambient seawater temperature. In particular, using the equation of Smith et al. (2000) that accounts for the correction of the seawater $\delta^{18}O$ composition, the reconstructed temperatures (14.20 and 13.61 °C) are within ~0.3 °C of the *in situ* temperature value (13.9 °C). However, although promising in correcting for the vital effects, the "lines technique" method requires a rather time-consuming sampling strategy at high-resolution (e.g. more than 10–15 sub-samples for each coral) to obtain a single temperature estimate and the knowledge of the past seawater $\delta^{18}O$ composition. Moreover, this method is based on the assumption that $\delta^{13}C_{coral}$ is equal to the $\delta^{13}C$ of the seawater DIC (i.e. $\delta^{13}C_{coral} - \delta^{13}C_{DIC} = 0‰$), which is not the case since the carbon isotopic fractionation value between inorganic aragonite and bicarbonate is ~2.7‰ (Romanek et al. 1992). The "lines technique" method therefore presents several caveats, strongly limiting its use as reliable paleothermometer.

Other efforts were focused on the application of "clumped isotopes" (Δ_{47}: Thiagarajan et al. 2011) and stable strontium isotopes ($\delta^{88/86}Sr$: Rüggeberg et al. 2008) in CWC. The clumped isotopes method is independent of the isotopic composition of the water, thus providing unique advantages compared to the other proxies. However, it requires the averaging of multiple replicates of homogeneous samples to obtain the necessary precision (<1°C) for deep-sea temperature reconstructions and recent studies suggest the presence of clumped isotope vital effects (Spooner et al. 2016). Rüggeberg et al. (2008) used stable strontium isotopes in *L. pertusa* and reported a precision of about ±1 °C and an apparent lack of physiological control on the fractionation of $\delta^{88/86}Sr$. However, subsequent studies on tropical and CWC based on an improved analytical method (isotope dilution TIMS vs. MC-ICP-MS) did not confirm the initial $\delta^{88/86}Sr$ *vs.* T positive relationship (Raddatz et al. 2013; Fruchter et al. 2016), undermining the reliability of this geochemical proxy.

A very promising coral paleothermometer has been recently developed through the analysis of the Li/Ca and Mg/Ca composition of scleractinian corals (Montagna et al. 2009a, 2014; Case et al. 2010; Hathorne et al. 2013; Raddatz et al. 2013). Montagna and co-authors conducted a widespread screening of the element/Ca ratios of several scleractinian coral species (*L. pertusa, Madrepora oculata, Flabellum impensum, Porites* sp. *Cladocora caespitosa, Acropora* sp.), from live-collected and cultured specimens covering a large temperature range (0.8–28 °C), from warm shallow-water tropical environments to the cold deep-waters at high-latitudes. The extensive coral collection also included specimens of *L. pertusa* collected in the Adriatic Sea, Santa Maria di Leuca coral province and the Strait of Sicily at ambient temperatures of 13.65 ± 0.1 °C. By normalising Li/Ca on Mg/Ca, the resulting multi-species coral Li/Mg ratios have been shown to be highly correlated with the ambient seawater temperature ($r^2 = 0.975$), following the empirical exponential relationship: Li/Mg (mmol/mol) = 5.41 exp (− 0.049*T) (Montagna et al. 2014) (Fig. 11.3). The new Li/Mg paleothermometer does not seem species-dependent and provides a precision of ±0.9 °C for the temperature reconstruction. Using Li/Mg, most of the biologically-mediated "vital effects" linked to Rayleigh fractionation are accounted for, as both elements (Li and Mg) are likely controlled by similar uptake mechanisms and comparable biological and physico-chemical factors during coral calcification (Montagna et al. 2014). Moreover, both elements have long residence times in the ocean, on the order of 1–10 Ma (Lécuyer 2016), therefore the seawater Li/Ca and Mg/Ca ratios are relatively constant through time during the late Quaternary and any changes in the metal/Ca of corals can be potentially attributed to variations in the environmental parameters. An additional advantage of the Li/Mg method compared to other paleothermometers stems from the fact that it requires a relatively easy analytical approach, consisting in measuring few mg of coral material by a basic quadrupole inductively coupled plasma mass spectrometry (ICP - QMS). This analytical instrument is commonly found in most geochemical laboratories and allows fast and low-cost multi-element analysis. Although few aspects of the Li/Mg paleothermometer still needs to be investigated, as for example the precise role of coral microstructures (COCs *vs.* fibres) or the skeletal growth rate in modifying the geochemical signal (Montagna et al. 2014), this proxy is now considered one of the most promising paleothermometer for surface and sub-surface water masses. Further development for an improved Li/Mg *vs.* T calibration should include the analysis of more live-collected field coral samples and specimens grown under temperature-controlled conditions in aquaria (e.g. Orejas et al., this volume) together with a careful micro-sampling strategy that considers the spatial distribution of COCs and fibres in the skeleton.

11.3.3 Boron Isotopes *vs.* Seawater pH

A very active area of research in paleoceanography in the past decade has been the study of boron isotopes (^{11}B and ^{10}B) in scleractinian corals for pH reconstruction (e.g. Vengosh et al. 1991; Hemming and Hanson 1992; Hönisch et al. 2004; Reynaud et al. 2004; Pagani et al. 2005; Pelejero

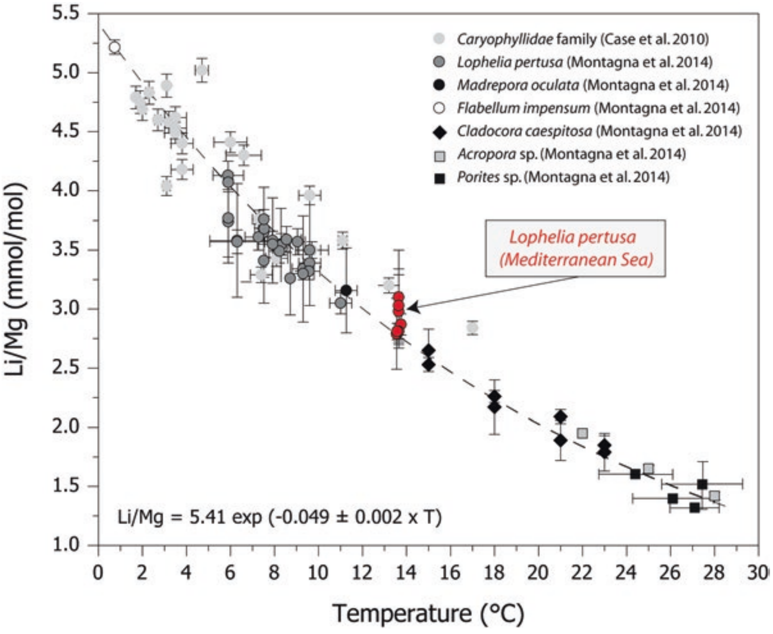

Fig. 11.3 Coral Li/Mg vs. seawater temperature. Symbols represent the Li/Mg composition of several tropical, temperate and CWC spanning a temperature range from 0.8 to 28 °C. The coral Li/Mg ratios are inversely correlated to the ambient seawater temperature and follow an exponential relationship [Li/Mg = 5.41 exp. (−0.049 ± 0.002 × T)]. The red dots indicate the Mediterranean CWC used for the calibration. (Figure modified from Montagna et al. 2014)

et al. 2005; Douville et al. 2010b; Krief et al. 2010; Anagnostou et al. 2012; Dissard et al. 2012; Lazareth et al. 2016; Stewart et al. 2016; Thil et al. 2016). Few studies have also evaluated the boron isotopic composition of Mediterranean corals, like the shallow-water species *C. caespitosa* (Trotter et al. 2011) and the azooxanthellate species *Caryophyllia smithii, L. pertusa* and *D. dianthus* (McCulloch et al. 2012b).

The boron isotopic composition of marine carbonates, which is commonly expressed in delta notation (in per mil, ‰) relative to the international standard NBS-951:

$$\delta^{11}\mathrm{B} = \left[\left({}^{11}\mathrm{B}/{}^{10}\mathrm{B}_{\mathrm{sample}} / {}^{11}\mathrm{B}/{}^{10}\mathrm{B}_{\mathrm{NBS-951}}\right) - 1\right] * 1000$$

has been shown to be a powerful tool for pH reconstruction of the ocean. The boron isotope systematics in biogenic carbonates is based on the pH-dependent speciation reaction between borate ion [$B(OH)_4^-$] and boric acid [$B(OH)_3$] and the different abundances of ^{10}B and ^{11}B in the two molecular species. The $\delta^{11}B$-pH proxy relies on basic principles (Hemming and Hanson 1992):

1. The boron isotopic composition of the ocean is known and homogeneous. The value of 39.61‰ determined by Foster et al. (2010) is now commonly used within the boron community.
2. It assumes that only the borate ions are incorporated into the carbonate lattice. This has been shown in initial $\delta^{11}B$ studies in corals (Vengosh et al. 1991; Hemming and Hanson 1992) and recently validated in aragonite through inorganic precipitation experiments (Noireaux et al. 2015).
3. It assumes that the isotopic fractionation (α_B) between borate ion and boric acid is accurately determined. Initially, a value of 1.0194 was obtained by Kakihana et al. (1977) from theoretical calculations based on vibrational frequency data. More recently, experimental measurements in seawater gave a significantly larger value of 1.0272 (Klochko et al. 2006), which is today widely accepted in the boron community.

The $\delta^{11}B$ can be analysed in corals using different analytical techniques, including secondary ion mass spectrometry (SIMS) (e.g. Blamart et al. 2007), positive or negative thermal ionisation mass spectrometry (PTIMS, NTIMS) (e.g. Hönisch et al. 2004; Trotter et al. 2011) and multi-collector inductively coupled plasma mass spectrometry (MC-ICP-MS) in solution (e.g. Foster 2008; Douville et al. 2010b) or coupled to a laser ablation system (e.g. Thil et al. 2016). The different analytical techniques present specific advantages and disadvantages, including sample size, time and cost of analysis, matrix effects, ionisation efficiency and memory effect that will not be discussed in the present paper (for details see review by Aggarwal and You 2016).

pH is then calculated from the coral $\delta^{11}B$ value using the following equation:

$$\mathrm{pH} = pK_{\mathrm{B}} - \log\left[\left(\delta^{11}\mathrm{B}_{\mathrm{sw}} - \delta^{11}\mathrm{B}_{\mathrm{coral}}\right) / \left(\alpha_{\mathrm{B}}{}^{*}\delta^{11}\mathrm{B}_{\mathrm{coral}} - \delta^{11}\mathrm{B}_{\mathrm{sw}} + 1000^{*}\left(\alpha_{\mathrm{B}} - 1\right)\right)\right]$$

where $\delta^{11}B_{sw}$ and $\delta^{11}B_{coral}$ represent the $\delta^{11}B$ in seawater and in the coral, respectively and pK_B is the dissociation constant of boric acid (8.587 at 25 °C and salinity 35; Dickson 1990). A temperature and pressure correction needs to be applied for coral samples living in cold and deep environments, like the CWC.

Although the theoretical foundation of the boron isotopes is well constrained, quantitative reconstructions of seawater pH based on $\delta^{11}B$ in scleractinian corals remain challenging (e.g. Trotter et al. 2011).

Figure 11.4a shows a compilation of $\delta^{11}B$ values obtained from the aragonite skeleton of several shallow-water symbiont-bearing coral species (white and grey symbols) and deep-water species (coloured symbols). Overall, the $\delta^{11}B$ values decrease with decreasing seawater pH following the boron isotope theory but all the values generally lie above the borate curve. The offset between the boron isotopic composition of the corals and the $\delta^{11}B$ of the borate curve is explained by a physiological control of the organism on the boron fractionation (e.g. Trotter et al. 2011). This biological control seems to be stronger for CWC species that present higher $\delta^{11}B$ values compared to tropical and temperate corals growing at similar pH conditions (McCulloch et al. 2012a). It is now well accepted that the $\delta^{11}B$ of the coral reflects the pH of the calcifying fluid (pH_{cf}) (Trotter et al. 2011) that is actively modified by mechanisms of up-regulation controlled by the Ca-ATPase pump (e.g. Allemand et al. 2004). Using a large suite of tropical, temperate and CWC, with few key corals collected in the Mediterranean Sea, Trotter et al. (2011) and McCulloch et al. (2012a,b) developed a method to calculate

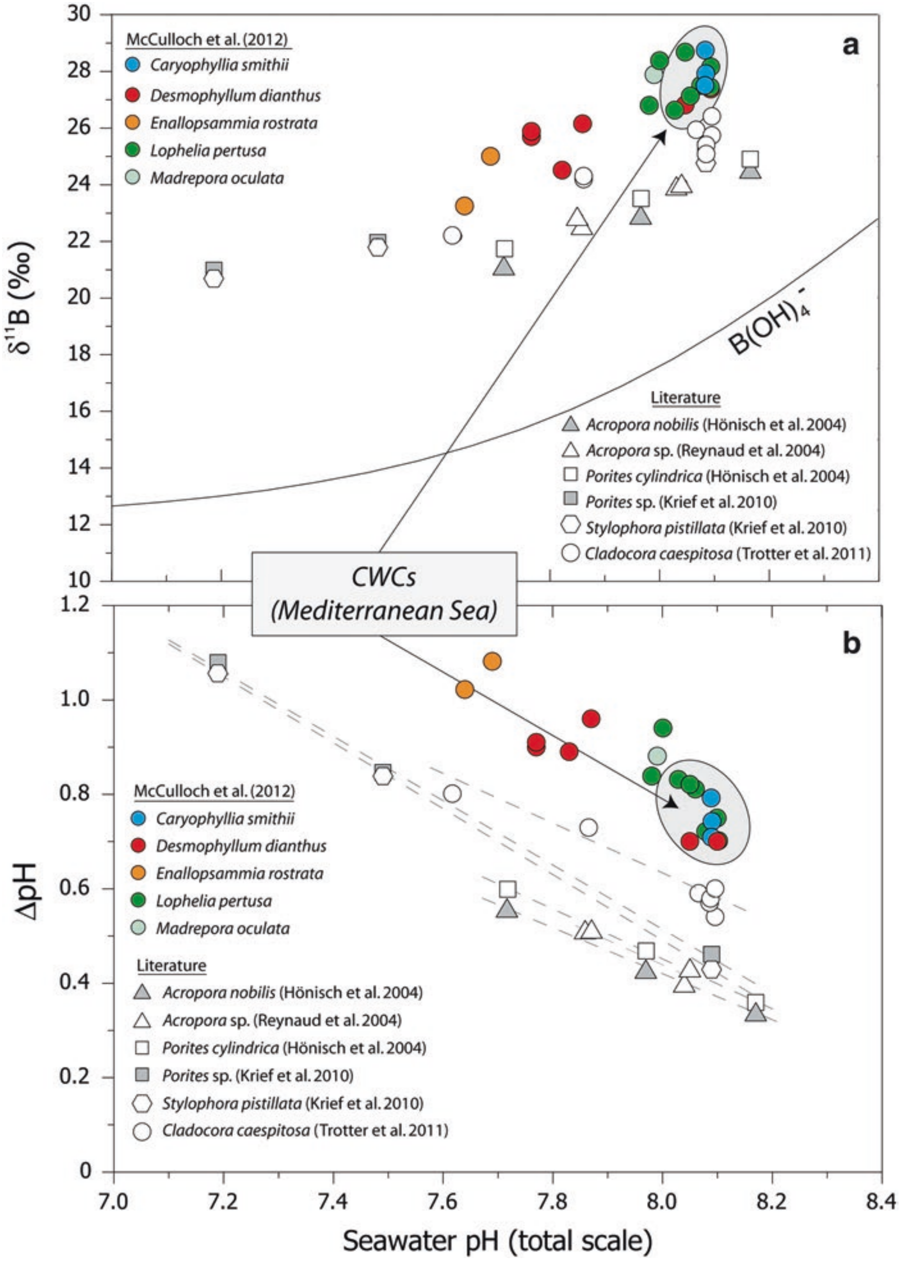

Fig. 11.4 (**a**) Coral $\delta^{11}B$ *vs.* seawater pH plotted with the $\delta^{11}B$ composition of the borate species as a function of seawater pH, assuming an isotopic fractionation between the boric acid and borate ion of 1.0272 (Klochko et al. 2006), T = 25 °C, salinity = 35 and depth = 5 m. Coloured and grey symbols represent CWC and tropical corals, respectively. CWC $\delta^{11}B$ values are systematically higher than those of tropical corals, suggesting greater pH up-regulation of the calcifying fluid. (**b**) ΔpH ($pH_{cf} - pH_{sw}$) *vs.* seawater pH. (Figure modified from McCulloch et al. 2012b)

the offsets in the pH_{cf} relative to ambient seawater pH ($\Delta pH = pH_{cf} - pH_{sw}$) (Fig. 11.4b). These offsets are linearly related to the ambient seawater pH with slopes varying between ~−0.5 and −0.7 depending on the species, meaning that pH changes in the calcifying space are approximately one-half of those in ambient seawater. This finding has a series of implications, including the possibility of using the boron isotopic composition of the coral skeleton as a probe into the processes controlling biomineralisation. Specifically, $\delta^{11}B$ values can be used to quantify pH up-regulation mechanisms for different coral species, eventually providing unique information on the resilience of corals to ocean acidification (McCulloch et al. 2012a). The higher $\delta^{11}B$-derived internal pH of the CWC compared to the tropical corals (i.e. higher ΔpH) can be explained by the requirement of corals living to challenging low temperature environment to sustain calcification (McCulloch et al. 2012a).

Combining $\delta^{11}B$ with coral B/Ca ratios as a proxy for the relative abundance of borate and carbonate ions in solution (Holcomb et al. 2016), the full carbonate chemistry of the site of calcification can be reconstructed, notably pH, DIC and aragonite saturation state. The quantification of these parameters is critical to understand the mechanisms used by the coral to promote calcification.

To date, only few attempts have been conducted to reconstruct intermediate-depth water pH using the boron isotopic composition of CWC (e.g. Gonzalez et al. 2012) due to the lack of proper species-specific calibrations. Such $\delta^{11}B$ *vs*. pH calibrations can be empirically derived through the analysis of boron isotopes from *in situ* live-collected specimens whose ambient seawater pH has been determined and/or from corals cultured at controlled pH conditions. However, reliable pH data for intermediate-deep waters are often not available or are based on pH database whose accuracy may be uncertain. First calibrations for CWC have been obtained through the $\delta^{11}B$ analysis of live *D. dianthus* specimens retrieved from the warm and high pH Mediterranean Sea and the colder and low pH regions of the North Atlantic, Pacific and Southern Ocean (Anagnostou et al. 2012; McCulloch et al. 2012b). Living at relatively high pH conditions, Mediterranean CWC serve as an end-member group for well-constrained empirical calibrations that can be used to extend pH reconstruction of sub-surface waters beyond the instrumental period.

In the future, efforts should be made to improve coral sampling methods for $\delta^{11}B$ by selecting specific micro-scale skeletal portions through micro-drilling sampling or laser ablation ICP-MS as recently reported by Stewart et al. (2016). This would generate improved calibrations and more reliable seawater pH reconstructions. Alternatively, bulk $\delta^{11}B$ values can be corrected for "vital effects" through a combination of elements or isotopes (e.g. $\delta^{18}O$ and $\delta^{13}C$) that act as tracers to quantify the biological component, following the example reported in Gonzalez et al. (2012) and Martin et al. (2016).

11.3.4 Coral P/Ca as a Seawater Nutrient Proxy

The reconstruction of seawater nutrient concentration in the past is critical to estimate changes in productivity and remineralisation patterns, nutrient inventory and water mass mixing and eventually the contribution of the biological pump to the levels of atmospheric CO_2. The search for a reliable nutrient proxy has been a major goal in paleoceanography and attempts have been mainly focused on the development of geochemical tracers that can provide information on the relative degree of nutrient utilisation in surface waters, including for example $\delta^{13}C$, $\delta^{15}N$ and $\delta^{30}Si$ (e.g. Sarnthein et al. 1988; De La Rocha 2003; Sherwood et al. 2011). Cd/Ca ratio in foraminifera and corals has been suggested to serve as a tracer for seawater phosphate (PO_4) concentration, one of the main bio-limiting macronutrients (Shen et al. 1987; Adkins et al. 1998; Boyle 1998). However, this proxy relies on the assumption that modern Cd/PO_4 relationship has remained the same as in the past oceans, which is difficult to assess. Moreover, recent seawater Cd/Ca values obtained within the GEOTRACES program indicate different Cd/PO_4 relationships for different ocean basins and depths (Xie et al. 2015), limiting the simple use of Cd/Ca ratio as a PO_4 tracer. So far, the only direct proxy yielding absolute phosphate concentration is the P/Ca ratio incorporated into the coral skeleton of scleractinian shallow- and deep-water corals (Montagna et al. 2006; LaVigne et al. 2010; Anagnostou et al. 2011; Godinot et al. 2011). A linear relationship between coral P/Ca and seawater dissolved inorganic phosphorus (DIP) has been found through the analysis of the aragonite skeleton of several scleractinian specimens living and cultured under different nutrient regimes. These studies produced the first calibrations and the first paleo-phosphorus reconstructions. In particular, Montagna and co-authors (2006) measured P/Ca in the septa of the CWC *D. dianthus* live-collected from the Mediterranean Sea, the Australian sector of the western Pacific Ocean and the Chilean fjords (Fig. 11.5). The P/Ca *vs*. DIP calibration was then used to quantify past changes of seawater PO_4 concentration in the Mediterranean Sea (Montagna et al. 2006). However, the same authors also identified coral portions with anomalously high P/Ca ratios related to high Mn/Ca values that suggest the presence of contamination. Further studies on the phosphorus speciation in inorganic and coral aragonite revealed small quantities of hydroxylapatite inclusions (Mason et al. 2011), which could potentially complicate the P/Ca interpretation. These high-P inclusions or any additional crystalline phases can be carefully avoided following an improved micro-sampling strategy that targets only the fibrous aragonite portions along the cross-section of the *D. dianthus* septum (Fig. 11.5b, c) (Montagna et al. 2009b). Compared to the centres of calcification or the outer septal surface

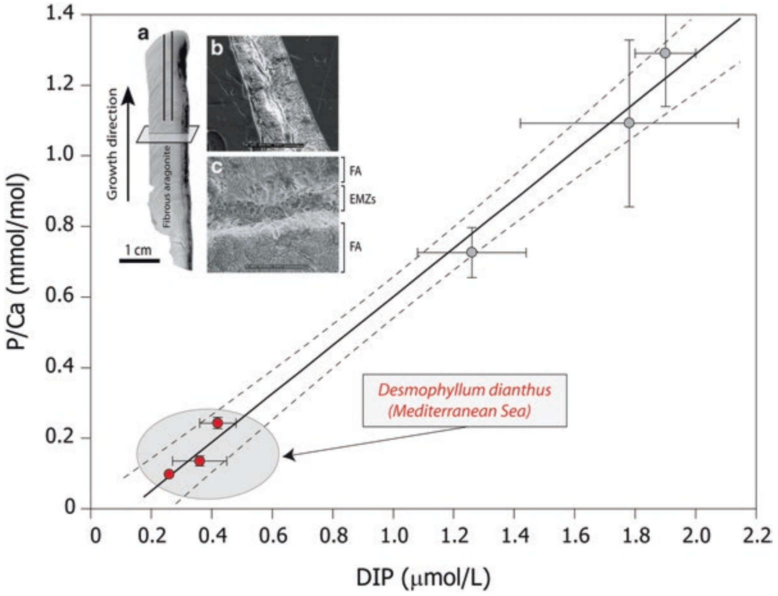

Fig. 11.5 P/Ca ratio measured in the CWC *D. dianthus vs*. seawater Dissolved Inorganic Phosphorus (DIP) concentration. Coral P/Ca is linearly correlated to DIP, providing a tool to reconstruct past changes of seawater phosphate. The analyses were conducted by laser ablation ICP-MS along the fibrous aragonite of the outer septal surface (**a**). Also shown the cross section of the septum (**b**), which is formed by fibrous aragonite and centres of calcification (**c**). (Figure modified from Montagna et al. 2006)

(Fig. 11.5a), the internal fibrous aragonite shows lower and less variable P/Ca values, yielding more accurate paleo-environmental reconstructions.

11.4 Conclusions and Future Perspectives

CWC are emerging as an important archive of environmental change, providing a wealth of new information on the chemical and physical history of intermediate-deep waters that are not available from other archives. The aragonite skeleton of CWC can be precisely dated by U/Th, ^{14}C, ^{210}Pb and ^{226}Ra techniques and incorporates geochemical proxies that reflect past environmental changes. The last two decades have witnessed an increasing number of studies dealing with the geochemistry of CWC, in particular the investigation of trace elements (B/Ca, Li/Mg, P/Ca, Sr/Ca, Ba/Ca, U/Ca), stable (δ^{11}B, δ^{13}C, δ^{18}O), radioactive (^{14}C, ^{238}U) and radiogenic (εNd) isotopes as proxies for seawater temperature, pH, carbonate ions concentration, nutrient content, ventilation and water mass dynamics. These studies have brought unprecedented information on environmental changes of the sub-surface waters at decadal to centennial-scale resolution (e.g. Adkins et al. 1998). In addition, coral fragments from coral-bearing sediment cores are particularly attractive archives, providing centennial-millennial records at near continuous sub-decadal resolution for the modern period and equivalent time windows into the LGM, deglaciation and Holocene.

However, one issue that is not fully resolved is the role of the coral physiology in controlling the geochemical signal and potentially biasing the paleoenvironmental reconstructions. Commonly known as "vital effect", the biological overprint affects some of the climate-related geochemical tracers and complicates their interpretation. A great effort has been made to correct for those biologically-induced modifications and obtain reliable coral proxies but our knowledge on the biomineralisation processes and geochemical signal incorporation is still limited.

Further investigations should be carried out to refine existing coral paleo-proxies through a better understanding of their limitations related to the coral physiology in order to fully exploit CWC as reliable archives of oceanic variability. This can be achieved by tightly coupling biology and geochemistry in an integrated view of the biomineralisation processes. For example, following Holcomb et al. (2014), studies should combine pH micro-sensors or pH-sensitive dyes with coral skeleton δ^{11}B and B/Ca measurements in CWC cultured under controlled pCO$_2$ conditions (Orejas et al., this volume). This unique combination can provide critical information on the pH up-regulation mechanisms of different coral species and on the δ^{11}B and B/Ca proxies.

The influence of the "vital effects" or the micro-structures on the coral geochemistry can be quantified using newly-developed nano-micro-sampling capabilities, such as NanoSIMS, synchrotron-based X-ray fluorescence or femto laser ICP-MS. Those analytical techniques can be used to either map fine-scale geochemical heterogeneities or selectively target specific coral micro-portions showing minimal biological overprint (e.g. fibrous aragonite) for proxy calibrations or paleoclimate reconstructions.

Further improvements should also be made in understanding the nature of the skeletal banding in CWC and their growth rates, a necessary requirement to obtain accurate multi-annual to decadal scale time-series (see Lartaud et al., this volume).

Finally, paleoclimate research in the Mediterranean Sea would benefit from new collections of fossil corals from key oceanographic locations, including the intermediate and deep-water formation areas in the western and eastern Mediterranean Sea and sites where mass exchange is particularly active, such as the Siculo-Tunisian and Gibraltar Straits. The geochemical study of those fossil specimens could provide invaluable information on the hydrological changes of the Levantine Intermediate Water or the western/eastern Mediterranean Deep Waters over the late Pleistocene. For instance, the reconstruction of past sub-surface changes in water mass circulation could help understanding the role of Mediterranean intermediate and deep circulation in the formation of the sapropel units or in pre-conditioning North Atlantic Deep Water.

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References

Adkins JF, Boyle EA (1997) Changing atmospheric $\Delta^{14}C$ and the record of deep water paleoventilation ages. Paleoceanography 12:337–344. https://doi.org/10.1029/97PA00379

Adkins JF, Cheng H, Boyle EA, et al (1998) Deep-sea coral evidence for rapid change in ventilation of the deep North Atlantic 15,400 years ago. Science 280:725–728

Adkins JF, Griffin S, Kashgarian M, et al (2002) Radiocarbon dating of deep-sea corals. Radiocarbon 44:567–580

Adkins JF, Boyle EA, Curry WB, et al (2003) Stable isotopes in deep-sea corals and a new mechanism for “vital effects”. Geochim Cosmochim Acta 67:1129–1143

Adkins JF, Henderson GM, Wang S-L, et al (2004) Growth rates of the deep-sea scleractinia *Desmophyllum cristagalli* and *Enallopsammia rostrata*. Earth Planet Sci Lett 227:481–490

Aggarwal SK, You C-F (2016) A review on the determination of isotope ratios of boron with mass spectrometry. Mass Spectrom Rev 9999:1–21

Allemand D, Ferrier-Pagès C, Furla P, et al (2004) Biomineralisation in reef-building corals: from molecular mechanisms to environmental control. Comptes Rendus Palevol 3:453–467

Anagnostou E, Sherrell RM, Gagnon A, et al (2011) Seawater nutrient and carbonate ion concentrations recorded as P/Ca, Ba/Ca, and U/Ca in the deep-sea coral *Desmophyllum dianthus*. Geochim Cosmochim Acta 75:2529–2543. https://doi.org/10.1016/j.gca.2011.02.019

Anagnostou E, Huang K-F, You C-F, et al (2012) Evaluation of boron isotope ratio as a pH proxy in the deep sea coral *Desmophyllum dianthus*: evidence of physiological pH adjustment. Earth Planet Sci Lett 349:251–260

Angeletti L, Canese S, Franchi F, et al (2015) The “chimney forest” of the deep Montenegrin margin, south-eastern Adriatic Sea. Mar Pet Geol 66:542–554. https://doi.org/10.1016/j.marpetgeo.2015.04.001

Antonioli F, Auriemma R, Anzidei M, et al (2014) Sergio Silenzi (1969–2012). Quat Int 332:1

Beck JW, Edwards RL, Ito E, et al (1992) Sea-surface temperature from coral skeletal strontium/calcium ratios. Science 257:644–648

Bethoux JP, Gentili B (1996) The Mediterranean Sea, coastal and deep-sea signatures of climatic and environmental changes. J Mar Syst 7:383–394

Blamart D, Rollion-Bard C, Meibom A, et al (2007) Correlation of boron isotopic composition with ultrastructure in the deep-sea coral *Lophelia pertusa* : implications for biomineralization and paleo-pH. Geochem Geophys Geosyst https://doi.org/10.1029/2007GC001686

Boyle E (1998) Oceanography: pumping iron makes thinner diatoms. Nature 393:733–734. https://doi.org/10.1038/31585

Case DH, Robinson LF, Auro ME, et al (2010) Environmental and biological controls on Mg and Li in deep-sea scleractinian corals. Earth Planet Sci Lett 300:215–225

Cheng H, Adkins J, Edwards RL, et al (2000) U-Th dating of deep-sea corals. Geochim Cosmochim Acta 64:2401–2416

Cohen AL, Gaetani GA, Lundälv T, et al (2006) Compositional variability in a cold-water scleractinian, *Lophelia pertusa*: New insights into “vital effects”. Geochem Geophys Geosyst https://doi.org/10.1029/2006GC001354

Copard K, Colin C, Douville E, et al (2010) Nd isotopes in deep-sea corals in the North-Eastern Atlantic. Quat Sci Rev 29:2499–2508. https://doi.org/10.1016/j.quascirev.2010.05.025

Corrège T (2006) Sea surface temperature and salinity reconstruction from coral geochemical tracers. Palaeogeogr Palaeoclimatol Palaeoecol 232:408–428. https://doi.org/10.1016/j.palaeo.2005.10.014

Cuif J-P, Dauphin Y (2005) The two-step mode of growth in the scleractinian coral skeletons from the micrometre to the overall scale. J Struct Biol 150:319–331

De La Rocha CL (2003) Silicon isotope fractionation by marine sponges and the reconstruction of the silicon isotope composition of ancient deep water. Geology 31:423–426

De Lange GJ, Thomson J, Reitz A, et al (2008) Synchronous basin-wide formation and redox-controlled preservation of a Mediterranean sapropel. Nat Geosci 1:606–610

Del Bianco F, Gasperini L, Angeletti L, et al (2015) Stratigraphic architecture of the Montenegro/N. Albania Continental Margin (Adriatic Sea—Central Mediterranean). Mar Geol 359:61–74

Dickson AG (1990) Thermodynamics of the dissociation of boric acid in synthetic seawater from 273.15 to 318.15 K. Deep-Sea Res Part 1 Oceanogr Res Pap 37:755–766

Dissard D, Douville E, Reynaud S, et al (2012) Light and temperature effect on $\delta^{11}B$ and B/Ca ratios of the zooxanthellate coral *Acropora* sp.: results from culturing experiments. Biogeosci Discuss 9:5969–6014

Douville E, Sallé E, Frank N, et al (2010a) Rapid and accurate U-Th dating of ancient carbonates using inductively coupled plasma-quadrupole mass spectrometry. Chem Geol 272:1–11

Douville E, Paterne M, Cabioch G, et al (2010b) Abrupt sea surface pH change at the end of the Younger Dryas in the central sub-equatorial

Pacific inferred from boron isotope abundance in corals (*Porites*). Biogeosciences 7:2445–2459

Dubois-Dauphin Q, Bonneau L, Colin C, et al (2016) South Atlantic intermediate water advances into the North-East Atlantic with reduced Atlantic meridional overturning circulation during the last glacial period. Geochem Geophys Geosyst https://doi.org/10.1002/2016GC006281

Dubois-Dauphin Q, Montagna P, Siani G, et al (2017) Hydrological variations of the intermediate water masses of the Western Mediterranean Sea during the past 20 ka inferred from neodymium isotopic composition in foraminifera and cold-water corals. Clim Past 13:17–37

Eltgroth SF, Adkins JF, Robinson LF, et al (2006) A deep-sea coral record of North Atlantic radiocarbon through the Younger Dryas: evidence for intermediate water/deepwater reorganization. Paleoceanography. https://doi.org/10.1029/2005PA001192

Emiliani C, Hudson JH, Shinn E, et al (1978) Oxygen and carbon isotopic growth record in a reef coral from the Florida keys and a deep-sea coral from Blake Plateau. Science 202:627–629

Fallon SJ, McCulloch MT, van Woesik R, et al (1999) Corals at their latitudinal limits: laser ablation trace element systematics in *Porites* from Shirigai Bay, Japan. Earth Planet Sci Lett 172:221–238. https://doi.org/10.1016/S0012-821X(99)00200-9

Fink HG, Wienberg C, Hebbeln D, et al (2012) Oxygen control on Holocene cold-water coral development in the Eastern Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96

Fink HG, Wienberg C, De Pol-Holz R, et al (2013) Cold-water coral growth in the Alboran Sea related to high productivity during the Late Pleistocene and Holocene. Mar Geol 339:71–82

Fink HG, Wienberg C, De Pol-Holz R, et al (2015) Spatio-temporal distribution patterns of Mediterranean cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) during the past 14,000 years. Deep-Sea Res Part 1 Oceanogr Res Pap 103:37–48

Flecha S, Pérez FF, García-Lafuente J, et al (2015) Trends of pH decrease in the Mediterranean Sea through high frequency observational data: indication of ocean acidification in the basin. Sci Rep 5:16770

Foster GL (2008) Seawater pH, pCO_2 and $[CO_3^{2-}]$ variations in the Caribbean Sea over the last 130 kyr: a boron isotope and B/Ca study of planktic foraminifera. Earth Planet Sci Lett 271:254–266

Foster GL, Pogge von Strandmann PAE, Rae JWB (2010) Boron and magnesium isotopic composition of seawater. Geochem Geophys Geosyst. https://doi.org/10.1029/2010GC003201

Frank N, Paterne M, Ayliffe L, et al (2004) Eastern North Atlantic deep-sea corals: tracing upper intermediate water D14C during the Holocene. Earth Planet Sci Lett 219:297–309

Fruchter N, Eisenhauer A, Dietzel M, et al (2016) $^{88}Sr/^{86}Sr$ fractionation in inorganic aragonite and in corals. Geochim Cosmochim Acta 178:268–280. https://doi.org/10.1016/j.gca.2016.01.039

Godinot C, Ferrier-Pages C, Montagna P, et al (2011) Tissue and skeletal changes in the scleractinian coral *Stylophora pistillata* Esper 1797 under phosphate enrichment. J Exp Mar Biol Ecol 409:200–207

Gonzalez C, Douville E, Hall-Spencer J, et al (2012) High acidification rate of Norwegian Sea revealed by boron isotopes in the deep-sea coral *Madrepora oculata*. AGU fall meeting abstract 1:1994

Grossman EL, Ku T-L (1986) Oxygen and carbon isotope fractionation in biogenic aragonite: temperature effects. Chem Geol Isot Geosci Sect 59:59–74

Hassoun A, Gemayel E, Krasakopoulou E, et al (2015) Acidification of the Mediterranean Sea from anthropogenic carbon penetration. Deep-Sea Res Part 1 Oceanogr Res Pap 102:1–15

Hathorne EC, Felis T, Suzuki A, et al (2013) Lithium in the aragonite skeletons of massive *Porites* corals: a new tool to reconstruct tropical sea surface temperatures. Paleoceanography 28:143–152

Hemming NG, Hanson GN (1992) Boron isotopic composition and concentration in modern marine carbonates. Geochim Cosmochim Acta 56:537–543

Hines SKV, Southon JR, Adkins JF (2015) A high-resolution record of Southern Ocean intermediate water radiocarbon over the past 30,000 years. Earth Planet Sci Lett 432:46–58

Holcomb M, Venn AA, Tambutté E, et al (2014) Coral calcifying fluid pH dictates response to ocean acidification. Sci Rep 4:5207. https://doi.org/10.1038/srep05207

Holcomb M, DeCarlo TM, Gaetani GA, et al (2016) Factors affecting B/Ca ratios in synthetic aragonite. Chem Geol 437:67–76

Hönisch B, Hemming NG, Grottoli AG, et al (2004) Assessing scleractinian corals as recorders for paleo-pH: empirical calibration and vital effects. Geochim Cosmochim Acta 68:3675–3685

Hughen KA, Baillie MGL, Bard E, et al (2004) Marine04 marine radiocarbon age calibration, 0-26 cal kyr BP. Radiocarbon 46:1059–1086

Kakihana H, Kotaka M, Satoh S, et al (1977) Fundamental studies on the ion-exchange separation of boron isotopes. Bull Chem Soc Jpn 50:158–163

Klochko K, Kaufman AJ, Yao W, et al (2006) Experimental measurement of boron isotope fractionation in seawater. Earth Planet Sci Lett 248:276–285

Krief S, Hendy EJ, Fine M, et al (2010) Physiological and isotopic responses of scleractinian corals to ocean acidification. Geochim Cosmochim Acta 74:4988–5001

LaVigne M, Matthews KA, Grottoli AG, et al (2010) Coral skeleton P/Ca proxy for seawater phosphate: multi-colony calibration with a contemporaneous seawater phosphate record. Geochim Cosmochim Acta 74:1282–1293. https://doi.org/10.1016/j.gca.2009.11.002

Lazareth C, Soares-Pereira C, Douville E, et al (2016) Intra-skeletal calcite in a live-collected Porites sp.: impact on environmental proxies and potential formation process. Geochim Cosmochim Acta 176:279–294

Lécuyer C (2016) Seawater residence times of some elements of geochemical interest and the salinity of the oceans. Bull Soc Géol Fr 187:245–260

López Correa M, Montagna P, Vendrell-Simón B, et al (2010) Stable isotopes ($\delta^{18}O$ and $\delta^{13}C$), trace and minor element compositions of Recent scleractinians and Last Glacial bivalves at the Santa Maria di Leuca deep-water coral province, Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:471–486

Lutringer A, Blamart D, Frank N, et al (2005) Paleotemperatures from deep-sea corals: scale effects. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 1081–1096

Malinverno E, Taviani M, Rosso A, et al (2010) Stratigraphic framework of the Apulian deep-water coral province, Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:345–359

Mangini A, Lomitschka M, Eichstädter R, et al (1998) Coral provides way to age deep water. Nature 392:347–348

Marcellin Yao K, Marcou O, Goyet C, et al (2016) Time variability of the North-Western Mediterranean Sea pH over 1995–2011. Mar Environ Res 116:51–60

Margreth S, Gennari G, Rüggeberg A, et al (2011) Growth and demise of cold-water coral ecosystems on mud volcanoes in the West Alboran Sea: the messages from the planktonic and benthic foraminifera. Mar Geol 282:26–39

Martin P, Goodkin NF, Stewart JA, et al (2016) Deep-sea coral $\delta^{13}C$: a tool to reconstruct the difference between seawater pH and $d^{11}B$-derived calcifying fluid pH. Geophys Res Lett 43:299–308. https://doi.org/10.1002/2015GL066494

Mason HE, Montagna P, Kubista L, et al (2011) Phosphate defects and apatite inclusions in coral skeletal aragonite revealed by solid-state NMR spectroscopy. Geochim Cosmochim Acta 75:7446–7457. https://doi.org/10.1016/j.gca.2011.10.002

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the Younger Dryas. Earth Planet Sci Lett 298:143–152

McCulloch M, Falter J, Trotter J, et al (2012a) Coral resilience to ocean acidification and global warming through pH up-regulation. Nat Clim Change 2:623–627

McCulloch M, Trotter J, Montagna P, et al (2012b) Resilience of cold-water scleractinian corals to ocean acidification: boron isotopic systematics of pH and saturation state up-regulation. Geochim Cosmochim Acta 87:21–34

Mitsuguchi T, Matsumoto E, Abe O, et al (1996) Mg/Ca thermometry in coral skeletons. Science 274:961–963

Montagna P, McCulloch M, Taviani M, et al (2005) High-resolution trace and minor element compositions in deep-water scleractinian corals (*Desmophyllum dianthus*) from the Mediterranean Sea and the Great Australian Bight. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 1109–1126

Montagna P, McCulloch M, Taviani M, et al (2006) Phosphorus in cold-water corals as a proxy for seawater nutrient chemistry. Science 312:1788–1791

Montagna P, McCulloch M, Mazzoli C, et al (2007) The non-tropical coral *Cladocora caespitosa* as the new climate archive for the Mediterranean: high-resolution (~ weekly) trace element systematics. Quat Sci Rev 26:441–462

Montagna P, McCulloch M, Mazzoli C, et al (2008a) High-resolution geochemical records from cold-water corals: proxies for paleoclimate and paleoenvironmental reconstructions and the role of coral physiology. CIESM Workshop Monogr 36:55–60

Montagna P, Silenzi S, Devoti S, et al (2008b) Climate reconstructions and monitoring in the Mediterranean Sea: a review on some recently discovered high-resolution marine archives. Rend Lincei 19:121–140

Montagna P, Lopez Correa M, Ruggeberg A, et al (2009a) Li/Mg ratios in shallow-and deep-sea coral exoskeletons as a new temperature proxy. In: AGU fall meeting abstracts, p 1286

Montagna P, McCulloch M, Taviani M, et al (2009b) An improved sampling method for coral P/Ca as a nutrient proxy. Geochim Cosmochim Acta 25:1888–1947

Montagna P, Taviani M, Silenzi S, et al (2010) Marine climate archives and geochemical proxies: a review and future investigations on the Mediterranean Sea. Mar Res CNR:809–822, ISSN: 2239-5172

Montagna P, McCulloch M, Douville E, et al (2014) Li/Mg systematics in scleractinian corals: calibration of the thermometer. Geochim Cosmochim Acta 132:288–310

Noireaux J, Mavromatis V, Gaillardet J, et al (2015) Crystallographic control on the boron isotope paleo-pH proxy. Earth Planet Sci Lett 430:398–407

Nothdurft L, Webb G (2007) Microstructure of common reef-building coral genera *Acropora*, *Pocillopora*, *Goniastrea* and *Porites*: constraints on spatial resolution in geochemical sampling. Facies 53:1–26

Pagani M, Lemarchand D, Spivack A, et al (2005) A critical evaluation of the boron isotope-pH proxy: the accuracy of ancient ocean pH estimates. Geochim Cosmochim Acta 69:953–961

Painter SC, Tsimplis MN (2003) Temperature and salinity trends in the upper waters of the Mediterranean Sea as determined from the MEDATLAS dataset. Cont Shelf Res 23:1507–1522

Palmiéri J, Orr JC, Dutay JC, et al (2015) Simulated anthropogenic CO_2 storage and acidification of the Mediterranean Sea. Biogeosciences 12:781–802

Pelejero C, Calvo E, McCulloch MT, et al (2005) Preindustrial to modern interdecadal variability in coral reef pH. Science 309:2204–2207

Raddatz J, Liebetrau V, Rüggeberg A, et al (2013) Stable Sr-isotope, Sr/Ca, Mg/Ca, Li/Ca and Mg/Li ratios in the scleractinian cold-water coral *Lophelia pertusa*. Chem Geol 352:143–152

Reimer PJ, Bard E, Bayliss A, et al (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55:1869–1887

Reynaud S, Hemming NG, Juillet-Leclerc A, et al (2004) Effect of pCO_2 and temperature on the boron isotopic composition of the zooxanthellate coral *Acropora* sp. Coral Reefs 23:539–546

Rixen M, Beckers J-M, Levitus S, et al (2005) The Western Mediterranean deep water: a proxy for climate change. Geophys Res Lett L12608: 1–4. https://doi.org/10.1029/2005GL022702

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Robinson LF, Adkins JF, Frank N, et al (2014) The geochemistry of deep-sea coral skeletons: a review of vital effects and applications for palaeoceanography. Deep-Sea Res Part 2 Top Stud Oceanogr 99:184–198

Rohling EJ, Marino G, Grant KM (2015) Mediterranean climate and oceanography, and the periodic development of anoxic events (sapropels). Earth-Sci Rev 143:62–97

Rollion-Bard C, Blamart D (2014) SIMS method and examples of applications in coral biomineralization. In: Gower LB (ed) Biomineralization sourcebook, characterization of biominerals and biomimetic materials. CRC Press, Boca Raton, pp 249–261

Rollion-Bard C, Blamart D, Cuif J-P, et al (2003) Microanalysis of C and O isotopes of azooxanthellate and zooxanthellate corals by ion microprobe. Coral Reefs 22:405–415. https://doi.org/10.1007/s00338-003-0347-9

Romanek CS, Grossman EL, Morse JW (1992) Carbon isotopic fractionation in synthetic aragonite and calcite: effects of temperature and precipitation rate. Geochim Cosmochim Acta 56:419–430

Rüggeberg A, Fietzke J, Liebetrau V, et al (2008) Stable strontium isotopes ($\delta^{88/86}$Sr) in cold-water corals — a new proxy for reconstruction of intermediate ocean water temperatures. Earth Planet Sci Lett 269:570–575

Sabatier P, Reyss J-L, Hall-Spencer JM, et al (2012) ^{210}Pb-^{226}Ra chronology reveals rapid growth rate of *Madrepora oculata* and *Lophelia pertusa* on world's largest cold-water coral reef. Biogeosciences 9:1253–1265. https://doi.org/10.5194/bg-9-1253-2012

Sarnthein M, Winn K, Duplessy J-C, et al (1988) Global variations of surface ocean productivity in low and mid latitudes: influence on CO_2 reservoirs of the deep ocean and atmosphere during the last 21,000 years. Paleoceanography 3:361–399. https://doi.org/10.1029/PA003i003p00361

Schneider A, Wallace DWR, Körtzinger A (2007) Alkalinity of the Mediterranean Sea. Geophys Res Lett 34:L15608:1–5. https://doi.org/10.1029/2006GL028842

Schröder-Ritzrau A, Freiwald A, Mangini A (2005) U/Th-dating of deep-water corals from the Eastern North Atlantic and the Western Mediterranean Sea. In: Freiwald A, Roberts JM (eds). Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 157–172

Schroeder K, Millot C, Bengara L, et al (2013) Long-term monitoring programme of the hydrological variability in the Mediterranean Sea: a first overview of the HYDROCHANGES network. Ocean Sci 9:301–324

Shen GT, Boyle EA, Lea DW (1987) Cadmium in corals as a tracer of historical upwelling and industrial fallout. Nature 328:794–796. https://doi.org/10.1038/328794a0

Sherwood OA, Lehmann MF, Schubert CJ, et al (2011) Nutrient regime shift in the Western North Atlantic indicated by compound-specific δ^{15}N of deep-sea gorgonian corals. Proc Natl Acad Sci U S A 108:1011–1015. https://doi.org/10.1073/pnas.1004904108

Shirai K, Kusakabe M, Nakai S, et al (2005) Deep-sea coral geochemistry: implication for the vital effect. Chem Geol 224:212–222

Silenzi S, Bard E, Montagna P, et al (2005) Isotopic and elemental records in a non-tropical coral (*Cladocora caespitosa*): discovery of a new high-resolution climate archive for the Mediterranean

Sea. Glob Planet Change 49:94–120. https://doi.org/10.1016/j.gloplacha.2005.05.005

Sinclair DJ, Kinsley LPJ, McCulloch MT (1998) High resolution analysis of trace elements in corals by laser ablation ICP-MS. Geochim Cosmochim Acta 62:1889–1901

Smith JE, Schwarcz HP, Risk MJ, et al (2000) Paleotemperatures from deep-sea corals: overcoming “vital effects”. PALAIOS 15:25–32. https://doi.org/10.2307/3515589

Spooner PT, Guo W, Robinson LF, et al (2016) Clumped isotope composition of cold-water corals: a role for vital effects? Geochim Cosmochim Acta 179:123–141

Stewart JA, Anagnostou E, Foster GL (2016) An improved boron isotope pH proxy calibration for the deep-sea coral *Desmophyllum dianthus* through sub-sampling of fibrous aragonite. Chem Geol 447:148–160

Stolarski J (2003) Three-dimensional micro- and nanostructural characteristics of the scleractinian coral skeleton: a biocalcification proxy - Acta Palaeontologica Polonica. Acta Palaeontol Pol 48:497–530

Stuiver M, Polach H (1977) Discussion reporting of ^{14}C data. Radiocarbon 19:355–363

Taviani M, Vertino A, Correa ML, et al (2011) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603

Taviani M, Angeletti L, Beuck L, et al (2016) Reprint of “On and off the beaten track: Megafaunal sessile life and Adriatic cascading processes”. Mar Geol 375:146–160. https://doi.org/10.1016/j.margeo.2015.10.003

Taviani M, Angeletti L, Canese S, et al (2017) The “Sardinian cold-water coral province” in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78. https://doi.org/10.1016/j.dsr2.2015.12.008

Tesi T, Asioli A, Minisini D, et al (2017) Large-scale response of the Eastern Mediterranean thermohaline circulation to African monsoon intensification during sapropel S1 formation. Quat Sci Rev 159:139–154

Thiagarajan N, Adkins J, Eiler J (2011) Carbonate clumped isotope thermometry of deep-sea corals and implications for vital effects. Geochim Cosmochim Acta 75:4416–4425

Thil F, Blamart D, Assailly C, et al (2016) Development of laser ablation multi-collector inductively coupled plasma mass spectrometry for boron isotopic measurement in marine biocarbonates: new improvements and application to a modern Porites coral. Rapid Commun Mass Spectrom 30:359–371. https://doi.org/10.1002/rcm.7448

Titschack J, Fink HG, Baum D, et al (2016) Mediterranean cold-water corals - an important regional carbonate factory? Depos Rec 2:74–96. https://doi.org/10.1002/dep2.14

Touratier F, Goyet C (2011) Impact of the Eastern Mediterranean Transient on the distribution of anthropogenic CO_2 and first estimate of acidification for the Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 58:1–15

Trotter J, Montagna P, McCulloch M, et al (2011) Quantifying the pH “vital effect”in the temperate zooxanthellate coral *Cladocora caespitosa*: validation of the boron seawater pH proxy. Earth Planet Sci Lett 303:163–173

Tsimplis MN, Baker TF (2000) Sea level drop in the Mediterranean Sea: an indicator of deep water salinity and temperature changes? Geophys Res Lett 27:1731–1734

van de Flierdt T, Robinson LF, Adkins JF (2010) Deep-sea coral aragonite as a recorder for the neodymium isotopic composition of seawater. Geochim Cosmochim Acta 74:6014–6032

Vengosh A, Kolodny Y, Starinsky A, et al (1991) Coprecipitation and isotopic fractionation of boron in modern biogenic carbonates. Geochim Cosmochim Acta 55:2901–2910

Xie RC, Galer SJG, Abouchami W, et al (2015) The cadmium–phosphate relationship in the Western South Atlantic — the importance of mode and intermediate waters on the global systematics. Mar Chem 177:110–123. https://doi.org/10.1016/j.marchem.2015.06.011

Cross References

Lartaud F, Mouchi V, Chapron L, et al (this volume) Growth patterns of Mediterranean calcifying cold-water corals

Maier C, Weinbauer MG, Gattuso JP (this volume) Fate of Mediterranean scleractinian cold-water corals as a result of global climate change. A synthesis

Movilla J (this volume) A case study: variability in the calcification response of Mediterranean cold-water corals to ocean acidification

Orejas C, Taviani M, Ambroso S, et al (this volume) Cold-water coral in aquaria: advances and challenges. A focus on the Mediterranean

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals

Vertino A, Corselli C (this volume) Did Quaternary climate fluctuations affect Mediterranean deep-sea coral communities?

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Wienberg C (this volume) A deglacial cold-water coral boom in the Alborán Sea: from coral mounds and species dominance

Drop Chapter Tomography of Cold-Water Corals-Bearing Cores

12

Lorenzo Angeletti, Matteo Bettuzzi, and Maria Pia Morigi

Abstract

X-ray Computed Tomography is a non-destructive technique to resolve internal structures and their three-dimensional visualisation. Computed Tomography presents a wide spectrum of application in earth sciences and proves useful to unravel the architecture of sedimentary cores, including those containing cold-water corals. In particular the application of Computed Tomography not only discloses the presence of corals in the core and facilitates taxonomic identification up to species-level, but elucidates also their three-dimensional distribution and taphonomic aspects. The advantages offered by Computed Tomography-scan are continuously growing and is becoming a standard method of analysis for cold-water coral-bearing cores studies.

Keywords

Computed Tomography · Cold-water corals · *Madrepora*-mounds · Cores · Mediterranean Sea

Introduction

X-ray Computed Tomography (CT) represents a quick, non-destructive and routinary method in the three-dimensional analysis of cold-water corals (CWC) and associated macrofauna inside sedimentary cores. It is also functional in assessing physical characteristics of the sedimentary matrix (e.g., density, porosity). Standard methods to analyse CWCs in cores contemplate their cutting by sawing and then splitting using a wire, followed by the study of resulting halves. If sawing is done at a frozen status, later de-freezing may, however, compromise fine sedimentary structures, whilst non-frozen cores may suffer by disturbance due to dragging large objects by the wire, such as coral fragments. The application of the non-destructive X-ray analysis is useful to document cores prior of splitting and provides a two-dimensional low-resolution image (e.g., Foubert et al. 2007). Being sensitive to the water content, this analysis may at times show a saturated signal that masks sedimentary features. In the case of cores embedding CWC, the images are often oversaturated veiling the real distribution of the coral remains (Fig. 12.1). Another pitfall is that taxonomic identification on X-ray images is very difficult, so that the major value of X-ray analysis is the assessment of CWC presence or absence. This "drop chapter" summarises CT-scan use to CWC-bearing cores and presents some new results of their application to *Madrepora*-mound off Linosa Island.

Computed Tomography (CT)

Originally developed for medical diagnosis, CT application soon expanded to a varieties of disciplines, from archaeology (e.g., Applbaum and Applbaum 2005; Stelzner et al. 2010) to earth sciences (e.g., Petrovic et al. 1982; Holler and Kögler 1990; Boespflug et al. 1995; Orsi and Anderson 1999; Cnudde and Boone 2013; Nabawy and David 2016). Regarding marine research, CT analysis is a relatively quick and efficient way for non-destructive and high-resolution identification of internal structures of sediment cores before splitting (Ashi 1997, Iturrino et al. 2004; Tanaka and Nakano 2009; Tanaka et al. 2011). This includes the recognition and analysis of CWCs inside cores (e.g., Rüggeberg et al. 2005; López-Correa et al. 2007; Titschack et al. 2009, 2015, 2016; van der Land et al. 2010, 2011; Douarin et al. 2014; Eisele et al. 2014; Victorero et al. 2016).

In particular, the density contrast between CWCs and the sedimentary matrix (i.e., mud, sand) allows reconstructing

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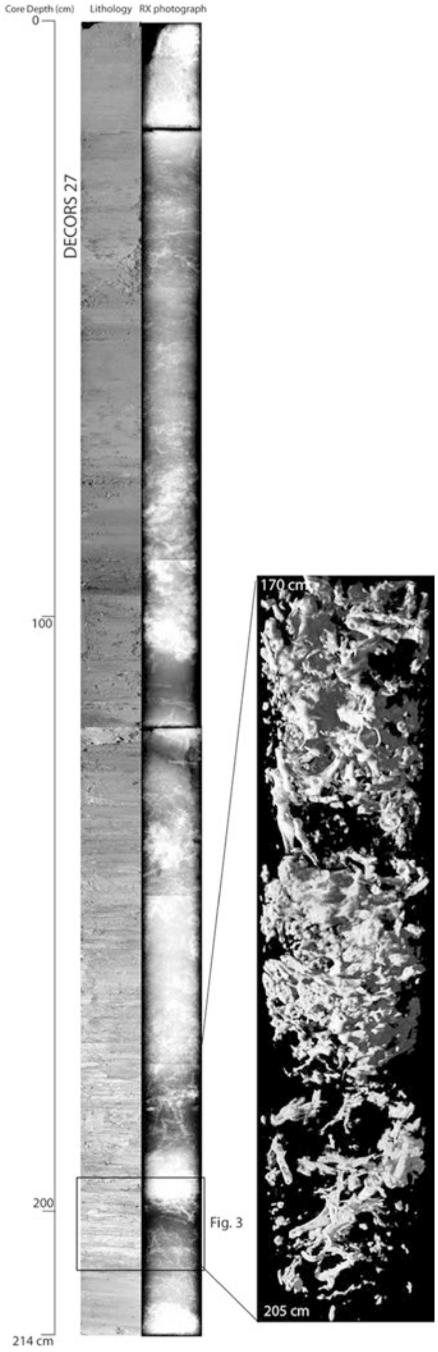

Fig. 12.1 Photograph, X-ray and Computed Tomography images from Decors 27 core from Strait of Sicily (© ISMAR-CNR Bologna)

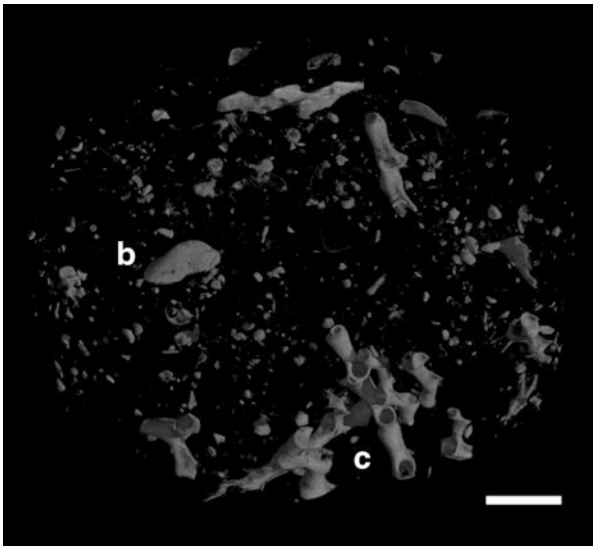

Fig. 12.2 3-D reconstruction from Computed Tomography along core Decors 27. It is clearly identifiable the coral (**c**) *Madrepora oculata* on the down right side and the bivalve (**b**) *Asperarca nodulosa.* Scale bar = 1 cm (© ISMAR-CNR Bologna)

their internal three-dimensional organisation, and is functional to decipher taphonomic aspects (Figs. 12.1 and 12.2). CT imaging offers the possibility to estimate the amount of corals in cores providing also information on their volume, the ratio with respect to matrix and some size parameters of coral fragments (e.g., Titschack et al. 2015, 2016). CT should provide a good approximation of the bulk density of the whole CWC-core with respect to other non-destructive analysis (e.g., MultiSensor Core Logger: Douarin et al. 2014). However, density measures obtained from CT have some limitations and, in general, tend to overestimate the density values with respect to wet bulk sediment (e.g., Tanaka et al. 2011; Titschack et al. 2015). Densities are sensitive to variations in the total content of the higher density material (coral skeletons), highlighting the proportion of fossil clasts *versus* matrix and a quick estimate of the fossil content prior core splitting (Douarin et al. 2014; Wienberg and Titschack 2017; and Fig. 12.3).

Another advantage offered by CT scanning is that its resolution is often good enough to allow taxonomic identification (even a low taxonomic level) before core opening (Fig. 12.2).

In addition, the technique of micro-CT scanning (Ritman 2004; Lenoir et al. 2007; Schönberg and Shields 2008) is now also applied to CWC studies and other marine carbonates from Northern Europe and the Mediterranean but is not discussed in this study (e.g., Beuck et al. 2007; Pirlet et al. 2010, 2012; Baum and Titschack 2016; Färber et al. 2016).

CT of Mediterranean Cold-Water Corals

Only a few papers discuss CWC-rich cores also including a CT analysis. These refer to the Roest, Traena and Stjernsund reefs off Norway (Titschack et al. 2015), the Mingulay reef (Douarin et al. 2014), the Propeller (Rüggeberg et al. 2005), Challenger (Foubert and Henriet 2009; Titschack et al. 2009) and Darwin Mound (Victorero et al. 2016), the Rockall Bank (van der Land et al. 2010, 2011) and the Banda Mound Province (Eisele et al. 2014) in the Atlantic, and, for the

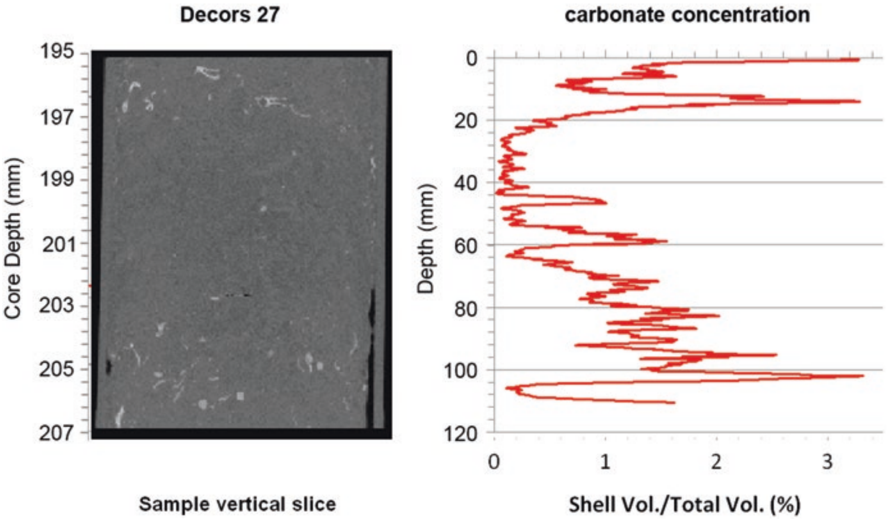

Fig. 12.3 Estimation of the ratio between mud and carbonate in the core. A threshold segmentation value of 2842/65535 grayvalue has been applied to each slice. The graph on the left represents the volume ratio between skeletonised particles (e.g., corals and shells) and the matrix (© ISMAR-CNR Bologna)

Mediterranean from the Melilla Coral Province, Urania Bank and Santa Maria di Leuca coral Province (Titschack et al. 2016).

Some CWC cores from Atlantic coral mounds have been analysed by means of CT-scans showing their usefulness in coral quantification (Foubert and Henriet 2009; Douarin et al. 2014; Titschack et al. 2015, 2016). CT has been proven to be useful in facies analysis and sedimentological descriptions, allowing the identification of layers and laminae in fine sediments, bioturbation and other sedimentary structures (e.g., Rüggeberg et al. 2005; van der Land et al. 2010; Titschack et al. 2016). CT imaging coupled with micro-CT scans allows the identification of early diagenetic processes (different stages of dissolution, moulds formation, porosity increasing, etc.) affecting corals (e.g., Pirlet et al. 2010, 2012). Furthermore, sedimentary, petrographic and diagenetic analyses on CWC-bearing cores have been successfully conducted using CT-scan images (e.g., van der Land et al. 2011; Titschack et al. 2016). CT-scans permit, also, taxonomic identification of skeletal parts (i.a., corals, molluscs, bryozoans) and allow to measure relative value of density of the matrix sediment (e.g., Eisele et al. 2014). Finally, as showed by Titschack et al. (2016) for the CWC-bearing cores from the Mediterranean Sea, CT-scans allow coral skeletons (bioclasts) volume quantification, their orientation and preservation patterns permitting to optimising sampling procedures for dating and identifying depositional units. Moreover, CT-scans have been proven to be a useful tool to disclose aggradation rates and carbonate accumulation rate of the CWCs (Titschack et al. 2016). A Mediterranean case-study is described here based upon two CWC-bearing cores (Decors 27 and 30, 214 and 150 cm long, respectively: Fig. 12.1) collected from dead and unburied *Madrepora*-dominated mounds off Linosa Island (Strait of Sicily) at ca. 350 m water depth. CT was performed at the Physics Department of the University of Bologna, using laboratory instruments designed to investigate archaeological, geological and historical objects. The Decors 27 and 30 cores have been scanned with a wide field of view system, designed for big objects. The CT system is equipped with an X-ray tube of maximum 200 kV and 7 mA with higher penetration capability with respect to a typical medical CT. The detector is a CCD camera coupled with a photographic lens to a 45 × 45 cm^2 wide scintillating screen of Cesium Iodide. The resolution achievable with such a detector is about 0.3 mm with the full field of view or 0.15 mm with the half field of view, which has been used for our samples. That permitted to obtain a higher resolution level compared to conventional medical CTs. Moreover, the specific adjustment of the scanning parameters like voltage, current, filtration and exposure time, without any dose constraints, as is required in the very strict scanning protocols of medical systems, allows to increase the image quality in terms of signal to noise ratio, increasing the global contrast, in addition to a higher spatial resolution with respect to a typical medical system. CT-scan image have been demonstrated helpful in coral-rich layer detection, clasts size measuring (coral skeletons) and their own orientation. However, standard methods, in CWC-rich core analysis, contemplate splitting of frost or non-frost cores, although both present some pitfalls. Typical cutting operations have no effect on sedimentary features, but commonly drag corals, or other particles, along the core. On the other hand, freezing is useful to prevent the displacement of skeletonised particles, but water frost-defrost generally alters or masks fine-scale structures.

Conclusions

The X-ray Computed Tomography is a powerful tool to resolve CWC in sedimentary cores. In fact, CT-scans facilitates identification and quantification of CWC presence, taxonomic assessment, as well as the three-dimensional reconstruction. CT-scans allow, thus far, the identification of sedimentary facies, layers useful for dating and geochemical analyses and, coupled with micro-CT, even for early diagenetic processes. CT-scans represent an excellent integration to different fields from sedimentology to palaeontology, petrography, geochemistry and dating, helpful in the understanding CWC growth and their evolution through time. This non-destructive approach is recommended to become a routine step to document CWC-bearing cores before cutting.

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References

Applbaum N, Applbaum YH (2005) The use of medical computed tomography (CT) imaging in the study of ceramic and clay archaeological artifacts from the ancient near east. In: Uda M, Demortier G, Nakai I (eds) X-rays for archaeology. Springer, Dordrecht, pp 231–245

Ashi J (1997) Computed tomography scan image analysis of sediments. In: Shipley TH, Ogawa Y, Blum P, Bahr J (eds) Proceedings of the ocean drilling program, scientific results 156, pp 151–159

Baum D, Titschack J (2016). Cavity and pore segmentation in 3D images with ambient occlusion. In: Bertini E, Elmqvist N, Wischgoll T (eds) Proceedings of the 18th EG/VGTC conference on visualization, Groningen, The Netherlands, pp 6–10

Beuck L, Vertino A, Stepina E, et al (2007) Skeletal response of *Lophelia pertusa* (Scleractinia) to bioeroding sponge infestation visualised with micro-computed tomography. Facies 53:157–176

Boespflug X, Long BFN, Occhietti S (1995) CAT-scan in marine stratigraphy: a quantitative approach. Mar Geol 122:281–301

Cnudde V, Boone MN (2013) High-resolution X-ray computed tomography in geosciences: a review of the current technology and applications. Earth-Sci Rev 123:1–17

Douarin M, Sinclair DJ, Elliot M, et al (2014) Changes in fossil assemblages in sediment cores from Mingulay Reef Complex (NE Atlantic): implications for coral reef build-up. Deep-Sea Res Part 2 Top Stud Oceanogr 99:286–296

Eisele M, Frank N, Wienberg C, et al (2014) Sedimentation patterns on a cold-water coral mound off Mauritania. Deep-Sea Res Part 2 Top Stud Oceanogr 99:316–326

Färber C, Titschack J, Schönberg CHL, et al (2016) Long-term macrobioerosion in the Mediterranean Sea assessed by micro-computed tomography. Biogeosciences 13:3461–3474

Foubert A, Henriet J-P (2009) Nature and Significance of the Recent Carbonate Mound Record. Lecture Notes in Earth Sciences. Springer, Berlin, Heidelberg 126: 1–298

Foubert A, Van Rooij D, Blamart D, et al (2007) X-ray imagery and physical core logging as a proxy of the content of sediment cores in cold-water coral mound provinces: a case study from Porcupine Seabight, SW of Ireland. Int J Earth Sci 96:141–158

Holler P, Kögler F-C (1990) Computed tomography: a nondestructive, high-resolution technique for investigation of sedimentary structures. Mar Geol 91:263–266

Iturrino GJ, Ketcham RA, Christiansen L, et al (2004) Data report: permeability, resistivity, and X-ray computed tomography measurements in samples from the PACMANUS hydrothermal system. In: FJAS B, Binns RA, Miller DJ, et al (eds) Proceedings of the ODP, scientific results, vol 193. Ocean Drilling Program, College Station, pp 1–14

Lenoir N, Bornert M, Desrues J, et al (2007) 3D digital image correlation applied to X-ray micro tomography images from triaxial compression tests on argillaceous rock. Strain 43:193–205

López-Correa M, Freiwald A, Demuth M (2007) Cold-water corals as climate archives in the ocean depths. Computer tomography of sediment cores provides outstanding insights for geologists. SOMATOM Sess 21:52–54

Nabawy BS, David C (2016) X-ray CT scanning imaging for the Nubia sandstone as a tool for characterizing its capillary properties. Geosci J 20(5):691–704

Orsi TH, Anderson AL (1999) Bulk density calibration for X-ray tomographic analyses of marine sediments. Geo-Mar Lett 19:270–274

Petrovic AM, Siebert JE, Rieke PE (1982) Soil bulk density analysis in three dimensions by computed tomographic scanning. Soil Sci Soc Am J 46:445–450

Pirlet H, Wehrmann LM, Brunner B, et al (2010) Diagenetic formation of gypsum and dolomite in a cold-water coral mound in the Porcupine Seabight, off Ireland. Sedimentology 57:786–805

Pirlet H, Wehrmann LM, Foubert A, et al (2012) Unique authigenic mineral assemblages reveal different diagenetic histories in two neighbouring cold-water coral mounds on Pen Duick Escarpment, Gulf of Cadiz. Sedimentology 59:578–604

Ritman EL (2004) Micro-computed tomography – current status and developments. Annu Rev Biomed Eng 6:185–208

Rüggeberg A, Dorschel B, Dullo WC, et al (2005) Sedimentary patterns in the vicinity of a carbonate mound in the Hovland Mound Province, northern Porcupine Seabight. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin, pp 87–112

Schönberg CHL, Shields G (2008) Micro-computed tomography for studies on *Entobia*: transparent substrate versus modern technology. In: Wisshak M, Tapanila L (eds) Current developments in bioerosion. Springer, Berlin, pp 147–164

Stelzner J, Ebinger-Rist N, Peek C, et al (2010) The application of 3D computed tomography with X-rays and neutrons to visualize archaeological objects in blocks of soil. Stud Conserv 55:95–106

Tanaka A, Nakano T (2009) Data report: three-dimensional observation and quantification of internal structure of sediment core from Challenger Mound area in the Porcupine Seabight off Western Ireland using a medical X-ray CT. In: Ferdelman TG, Kano A, Williams T, et al (eds) Proceedings of the IODP 307. Integrated Ocean Drilling Program Management International, Inc., Washington, DC

Tanaka A, Nakano T, Ikehara K (2011) X-ray computerized tomography analysis and density estimation using a sediment core from the Challenger Mound area in the Porcupine Seabight, off Western Ireland. Earth Planets Space 63:103–110

Titschack J, Thierens M, Dorschel B, et al (2009) Carbonate budget of a cold-water coral mound (Challenger Mound, IODP Exp. 307). Mar Geol 259:36–46

Titschack J, Baum D, De Pol-Holz R, et al (2015) Aggradation and carbonate accumulation of Holocene Norwegian cold-water coral reefs. Sedimentology 62:1873–1898

Titschack J, Fink HG, Baum D, et al (2016) Mediterranean cold-water corals – an important regional carbonate factory? Depos Rec 2(1):74–96

van der Land C, Mienis F, De Haas H, et al (2010) Diagenetic processes in carbonate mound sediments at the south-west Rockall Trough margin. Sedimentology 57:912–931

van der Land C, Mienis F, De Haas H, et al (2011) Paleo-redox fronts and their formation in carbonate mound sediments from the Rockall Trough. Mar Geol 284:86–95

Victorero L, Blamart D, Pons-Brachu E, et al (2016) Reconstruction of the formation history of the Darwin Mounds, N Rockall Trough: how the dynamics of a sandy contourite affected cold-water coral growth. Mar Geol 378:186–195

Wienberg C, Titschack J (2017) Framework-forming scleractinian cold-water corals through space and time: a late Quaternary North Atlantic perspective. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 699–732

Drop Chapter Changing Views About Mediterranean Cold-Water Corals

13

Marco Taviani

Abstract

Sedimentary deposits in southern Italy are renowned since the nineteenth century for their important legacy of deep-water benthic invertebrates, comprehensive of cold-water corals, which includes a number of extant taxa of Atlantic affinity. Interestingly, at the dawn of the biological exploration of the deep-sea and because of these fossils, it was proposed that the Mediterranean was one centre of origin of deep-water benthos that later migrated into the Atlantic. More recently in time, it was postulated that the cold-water corals fauna in the Mediterranean was in strong decline after having being prosperous at times in the Pleistocene. The advent of remotely operated vehicle exploration reversed this paradigm by revealing many sites of active coral life. The overall picture is, however, more complex since the Mediterranean cold-water corals indeed suffered times of strong demise in response to climatic reasons and still nowadays sectors of the basin have not fully recovered.

Keywords

Cold-water coral · Pleistocene · Recent · Mediterranean basin · Atlantic Ocean · Historical biology · Paleontology · Biogeography

Introduction

Today the widespread presence of live cold-water corals (CWC) in the Mediterranean Sea, also known as 'white corals', is an ascertained fact documented by a number of CWC provinces and other occurrences known especially in the central and western basins (Taviani et al. 2017). However, for long and well up a decade ago or so, this biological situation was circumstantially masked by the Mediterranean's unusually common fossil coral legacy resulting from the basin geodynamic evolution in the Cainozoic (Taviani et al. 2005a). The present text is meant to address this rather intriguing story by commenting upon an historical and a contemporary situation, respectively.

Seguenza or When Deep-Sea Forms Got Discovered First on Land Than Offshore

The Sicilian naturalist Giuseppe Seguenza was undoubtedly one of the most prestigious Mediterranean paleontologists of the nineteenth century (Bonfiglio 1991). His many scientific achievements encompassed the study of terranes in Southern Italy, which hosted numbers of benthic deep-water invertebrates, especially molluscs and corals (Seguenza 1864, 1873–1877, 1875, 1880). At those times, the exploration of the deep-sea was really as its beginning and quite little was known about the inhabitants of Atlantic and Mediterranean waters. Because the Pleistocene deposits of Calabria and Sicily contain many (morphologically-based) extant taxa (Fig. 13.1a–c), this paleontological material got in many cases to be known to Science (and some species even established) on fossil material almost contemporaneously when not before being found alive in the Atlantic or Mediterranean waters by earlier expeditions, such as those of the *Lightning*, *Porcupine* and *Washington* ships. This is especially true for molluscs (Taviani 1976; Di Geronimo 1991) but equally applies to scleractinian corals (*Lophelia, Madrepora, Desmophyllum, Caryophyllia* etc.) with many fossil species introduced by Seguenza, which are now attributed to living taxa (Zibrowius 1974, 1991; Vertino 2003, 2004; Vertino and Di Geronimo 2003). Indeed, Duncan (1870) already commented upon the situation of some CWC being collected alive in the eastern Atlantic and either only known as fossils

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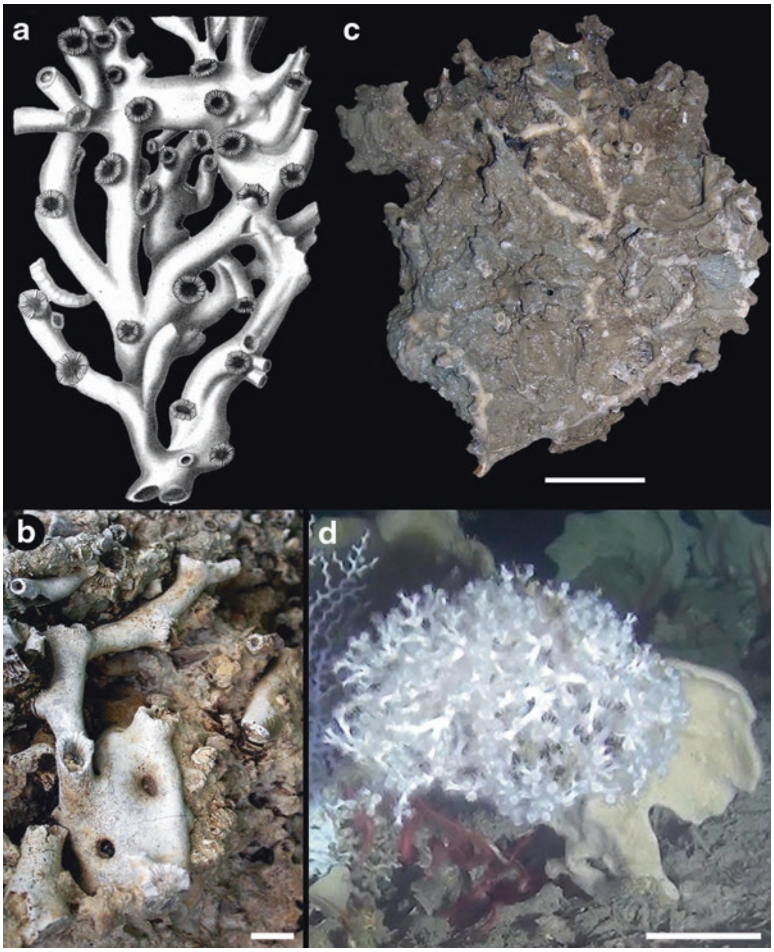

Fig. 13.1 (**a**) Fossil *Lophelia* (as *Lophohelia*) from Sicily reproduced in the plate 11 of the famous monograph *Disquisizioni paleontologiche intorno ai Corallarii fossili delle rocce terziarie del distretto di Messina*, published by Giuseppe Seguenza in 1864, (**b**) Pleistocene limestone embedding pieces of *Lophelia pertusa* from the Trapani creek outcrop, next to the town of Messina, one of Seguenza's classic localities cited in his 1864 monograph, bar = 1 cm (photo courtesy of A. Vertino), (**c**) Last glacial subfossil cold-water corals (prevalently *L. pertusa*) embedded in a muddy sediment, a common situation at many Mediterranean sites, bar = 5 cm (R/V *Urania*, Station ARCO-47, 43°10.82′ Lat. N – 15°09.10′ Long. E, 233 m), (**d**) Lush CWC reef imaged by the ROV in the Bari Canyon, showing healthy *L. pertusa* (right) with expanded polyps, bar = 10 cm (R/V *MinervaUno*, Station SIRIAD16-5, 43°17.65′ Lat. N – 17°07.94′ Long. E, 244 m). (Photographs: c, d: © ISMAR-CNR Bologna)

in Sicily or both fossil and live in the Mediterranean Sea (e.g., *Lophelia pertusa*). This bizarre situation (fossils known in the Mediterranean, living counterparts found in the east Atlantic) led Giuseppe Seguenza to develop the view that this deep-sea fauna (in his case-study molluscs) did originate in the Mediterranean to later spread into the adjacent Atlantic Ocean (Seguenza 1870). At any event, it was already identified in the nineteenth century a major biogeographic point: the Mediterranean CWC (with abundant fossils in outcrops and scant records in the sea) by large compares at specific level with northeastern Atlantic counterparts (Zibrowius 1980). Unwillingly and subtly, this fact possibly conspired to their later interpretation as animals doing better in cold waters whilst being troubled in warm situations.

Reversing the Paradigm

Coming to modern times, another paradoxical situation regards the submarine presence of CWC in the Mediterranean Sea and a radically-changed interpretation within a few decades. Because of a persistent paucity until a few years ago of biological investigation aimed at the Mediterranean deep-sea hard substrates, only some fragmentary CWC information was for long available to marine scientists. It mainly derived by pioneer French submersible expeditions and as by-catch products of marine geological sampling by means of chained heavy dredges, mostly by French and Italian surveys (revised in Taviani et al. 2005a, 2011a, 2017). In the years preceding the new millennium, the situation was such that only a few repositories contained substantial CWC Mediterranean material, and this was almost totally represented by loose dead material (Fig. 13.1b), often highly degraded, up to corals embedded into authigenic limestones (Selli 1970; Cita et al. 1979; Taviani and Colantoni 1979, 1984; Zibrowius 1981, 1987, 1991; Taviani et al. 2005a, 2011b, this volume). Probably, the largest of such collections was at the time hosted in the Laboratory of Marine Geology of CNR in Bologna. The extensive ^{14}C dating of those specimens, combined with scattered radiocarbon dates published by other scholars, demonstrated that the quasi-totality of dredged corals was late Pleistocene in age (Delibrias and Taviani 1985). Incidentally, a later confirmation of such ages came from the application of U-series dating (McCulloch et al. 2010). These dates supported earlier views about a dramatic CWC decline in the Mediterranean basin after having enjoyed better times in the Pleistocene (Blanc et al. 1959; Zibrowius 1980), and a paradigm was set on. At the turn of the millennium, an impressive jump in the interest for the deep-seabed, a wider use of marine technologies, and serendipitous findings in the Mediterranean opened the doors to challenge this view. How this happens is known: first the discovery of the Santa Maria di Leuca (SML) lush living CWC grounds in the northern Ionian Sea (Tursi et al. 2004; Taviani et al. 2005b) informed about the persistence of *Lophelia* and *Madrepora* in the Mediterranean. The later discovery of similar CWC grounds south of Malta (Schembri et al. 2007; Knittweis et al., this volume) provided unquestionable evidence that SML was not a sporadic CWC oasis, an exception, calling for a more accurate investigation and geographically spread survey to search live CWC. The breakthrough was M 70-1 expedition of R/V *Meteor* led in 2007 by André Freiwald, which made use of the working-class ROV (remotely operated vehicle) *Quest 4000* (Freiwald et al. 2009). Aptly to be described as epic in the Mediterranean deep-sea exploration, besides visiting and visually imaging the previously unseen CWC sites reported above, the mission took some risk in diving on sites characterised only by minor and uncertain clues about the actual presence of living coral, i.e. the Strait of Sicily other than south Malta (Zibrowius and Taviani 2005) and the southwestern Adriatic (Trincardi et al. 2007), respectively. On both locations, CWC were found to thrive (Freiwald et al. 2009), thus definitely reversing the paradigm of their basinal decline (Fig. 13.1d). Since then, this view has been reinforced by a growing number of new findings (summarised in Taviani et al. 2011a, 2017; Chimienti et al., this volume). Still, the situation is more complicated since areas in the Mediterranean seem almost deprived of substantial CWC growth at present, and this is especially true in the eastern basin (Taviani et al. 2011). It appears, in fact, that Mediterranean CWC resented climatic and oceanographic events that caused widespread demise, followed by complete or partial recovery in the Holocene, although not everywhere (Remia and Taviani 2005; McCulloch et al. 2010; Fink et al. 2012, 2015; Vertino et al. 2014, this volume).

Thus, the vision that is kept today about CWC viability in the Mediterranean needs necessarily to be more articulated. The Mediterranean Sea is neither a ‘Coral Cemetery’ as thought for a while, nor is a ‘Coral Sea’ in all its geographic extension. It surely maintains many situations optimal to CWC growth, but other areas are still not recovering their past prosperity, a lesson on how delicate and dynamic could be the life of CWC in the Mediterranean Sea, which is now threatened also by global warming, ocean acidification and anthropogenic disturbances.

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References

Blanc JJ, Pérès JM, Picard J (1959) Coraux profonds et thanatocoenoses quaternaires en Méditerranée. La topographie et la géologie des profondeurs océaniques. Coll Int CNRS 83:185–192

Bonfiglio L (ed) (1991) Celebrazioni del 1° Centenario in memoria di Giuseppe Seguenza, naturalista e paleontologo: Convegno di Paleontologia e Stratigrafia, Messina-Taormina 22–26 maggio 1989, Atti Accad Peloritana Pericolanti, Cl Sci Mat Fis Nat 67(1989) suppl 1

Cita MB, Fantini Sestini N, Salvatorini G, et al (1979) Late Neogene sediments and fossils from the Malta Escarpment and their geodynamic significance. Ann Géol Pays Hellen 1:273–283

Delibrias G, Taviani M (1985) Dating the death of Mediterranean deep-sea scleractinian corals. Mar Geol 62:175–180

Di Geronimo I (1991) Mollusca: specie nuove plio-quaternarie di G. Seguenza (1858–1881). In: Bonfiglio L (ed) Celebrazioni 1° centenario in memoria di G. Seguenza (Messina-Taormina, 22–26 Maggio, 1989), Atti Acc Peloritana Pericolanti Cl Sci Fis Mat Nat 67 (1989) suppl 1:137–254

Duncan PM (1870) A description of the Madreporaria dredged up during the expedition of H.M.S. Porcupine in 1869 and 1870. Part 1. Trans R Soc Lond 8:303–344

Fink HG, Wienberg C, Hebbeln D, et al (2012) Oxygen control on Holocene cold-water coral development in the eastern Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96

Fink HG, Wienberg C, De Pol-Holz R, et al (2015) Spatio-temporal distribution patterns of Mediterranean cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) during the past 14,000 years. Deep-Sea Res Part 1 Oceanogr Res Pap 103:37–48

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the Younger Dryas. Earth Planet Sci Lett 298:143–152

Remia A, Taviani M (2005) Shallow-buried Pleistocene *Madrepora*-dominated coral mounds on a muddy continental slope, Tuscan Archipelago, NE Tyrrhenian Sea. Facies 50:419–425

Schembri PJ, Dimech M, Camilleri M, et al (2007) Living deep water *Lophelia* and *Madrepora* corals in Maltese waters (Strait of Sicily, Mediterranean Sea). Cah Biol Mar 48:77–84

Seguenza G (1864) Disquisizioni paleontologiche intorno ai Corallarii fossili delle rocce terziarie del distretto di Messina. Mem R Acc Sci Torino (Ser 2) 21:399–560

Seguenza G (1870) Sull'antica distribuzione geografica di talune specie malacologiche viventi. Boll Malacol Ital 3:18 pp

Seguenza G (1873–1877) Studi stratigrafici sulla formazione pliocenica dell'Italia meridionale. Boll Reg Comit Geol Ital 4:29–45, 84–103, 131–153, 213–230, 280–301, 345–357 (1873); 8: 7–27, 91–99, 359–367 (1877)

Seguenza G (1875) Studi paleontologici sulla fauna malacologica dei sedimenti pliocenici depositatisi a grande profondità. Bull Soc Malacol It 1:99–124

Seguenza G (1880) La formazione terziaria nella provincia di Reggio (Calabria). Atti R Accad Lincei, Cl Sci Fis (Ser 3) Mem 6:1–446 pp

Selli R (1970) Campioni raccolti. Giorn Geol (Ser 2) 37:55–72

Taviani M (1976) Studio di una tanatocenosi pleistocenica dragata nel basso Adriatico. Thesis University of Bologna (unpublished), 145 pp

Taviani M, Colantoni P (1979) Thanatocoenoses würmiennes associées aux coraux blancs. Rapp Comm int Mer Médit 25/26:141–142

Taviani M, Colantoni P (1984) Paléobiocenoses profondes a scléractiniaires sur l'escarpement de Malte-Syracuse (Mer Méditerranée): leur structure, leur âge et leur signification. Rev Inst Fr Pétr 39:547–552

Taviani M, Freiwald A, Zibrowius H (2005a) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Taviani M, Remia A, Corselli C, et al (2005b) First geo-marine survey of living cold-water *Lophelia* reefs in the Ionian Sea (Mediterranean basin). Facies 50:409–417

Taviani M, Angeletti L, Antolini B, et al (2011a) Geo-biology of Mediterranean deep-water coral ecosystems. In: Brugnoli E, Cavaretta G, Mazzola S, et al (eds) Marine research at CNR, vol DTA/06-2011, p 705

Taviani M, Vertino A, López Correa M, et al (2011b) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78

Trincardi F, Foglini F, Verdicchio G, et al (2007) The impact of cascading currents on the Bari Canyon System, SW-Adriatic Margin (Central Mediterranean). Mar Geol 246:208–230

Tursi A, Mastrototaro F, Matarrese A, et al (2004) Biodiversity of the white coral reefs in the Ionian Sea (Central Mediterranean). Chem Ecol 20:107–116

Vertino A (2003) Sclerattiniari plio-pleistocenici e attuali del Mediterraneo (Sistematica, Biostratinomia e Paleoecologia). Ph D thesis, University of Messina (unpublished), 306 pp

Vertino A (2004) Esacoralli plio-pleistocenici del Mediterraneo (Sistematica, Biostratinomia, Paleoecologia). PaleoItalia Modena, 4 pp

Vertino A, Di Geronimo I (2003). How many *Caryophyllia* species lived in the Plio-Pleistocene Mediterranean? Seguenza's taxonomy revised. In: 9th international symposium on fossil Cnidaria and Porifera, 3–7 August Graz, Abstr

Vertino A, Stolarski J, Bosellini FR, et al (2014) Mediterranean corals through time: from Miocene to Present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 257–274

Zibrowius H (1974) *Caryophyllia sarsiae* n. sp. and other recent deep-water *Caryophyllia* (Scleractinia) previously referred to little-known fossil species (*C. arcuata, C. cylindracea*). J Mar Biol Assoc UK 54:769–784

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mém Inst Océanogr Monaco 11:284 pp

Zibrowius H (1981) Thanatocoenose pléistocène profonde à spongiaires et scléractiniaires dans la fosse Hellénique. In: Journées d'études sur la systématique évolutive et la biogéographie en Méditerranée. Cagliari, 13–14 octobre 1980. CIESM Monaco, 133–136

Zibrowius H (1987) Scléractiniaires et Polychètes Serpulidae des faunes bathyales actuelle et plio-pléistocène de Méditerranée. Doc Trav IGAL 11:255–257

Zibrowius H (1991) Les Scléractiniaires du Miocène au Pléistocène de Sicile et de Calabre de Giuseppe Seguenza (1864–1880) (Cnidaria: Anthozoa). Atti Accad Peloritana Pericolanti, Cl Sci Mat Fis Nat 67:159–179

Zibrowius H, Taviani M (2005) Remarkable sessile fauna associated with deep coral and other calcareous substrates in the Strait of Sicily, Mediterranean Sea. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 807–819

Cross References

Chimienti G, Bo M, Taviani M, et al (this volume). Occurrence and biogeography of Mediterranean cold-water corals

Knittweis L, Evans J, Aguilar R, et al (this volume) Recent discoveries of extensive cold-water coral assemblages in Maltese waters

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Part II

Present

14

Taxonomy, Genetics and Biodiversity of Mediterranean Deep-Sea Corals and Cold-Water Corals

Alvaro Altuna and Angelo Poliseno

Abstract

Within the Mediterranean basin there are 82 species of deep-sea corals belonging to six orders of the phylum Cnidaria (Antipatharia, Scleractinia, Zoantharia, Alcyonacea, Pennatulacea and Anthoathecata), with the Alcyonacea (40) and the Scleractinia (25) being the most speciose. Thirteen species have a pronounced habitat-building ability at depths >200 m. Remarkable sites characterised by rich coral frameworks and gardens have been found in biodiversity surveys during the last years, revealing that some species are more abundant than previously thought. However, in terms of species richness, the Mediterranean deep-sea coral fauna is less diverse when compared with the nearby Atlantic areas. This discrepancy is probably in part due to unfavourable environmental conditions of the deep Mediterranean Sea, and to differences in sampling efforts between both areas. In this respect, considerable efforts have been recently done in terms of deep-sea fauna inventories. Nevertheless, updates made to the Mediterranean inventory of deep-sea corals since the beginning of the twenty-first century are few except for the octocorals. Therefore, ten species were included to the Mediterranean inventory, among which two have been newly described. The species concerned belong to the orders Scleractinia (1), Pennatulacea (1) and Alcyonacea (8).

Keywords

Cnidaria · Cold-water corals · Mediterranean Sea · Taxonomy · Genetics · Biodiversity · Deep-sea

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14.1 Introduction

Corals pertain to different orders of the Phylum Cnidaria (Table 14.1), which includes diblastic solitary or colonial animals with primary radial or biradial symmetry and gross anatomical simplicity (Hyman 1940). Although their occurrence in the deep-sea is known since the eighteenth century (Roberts et al. 2006), their diversity and functionality in the deep-sea environments has been only recently explored thanks to the implementation of new research technologies. Given their vertical growth and due to their key-role in structuring the deep-sea environments, many corals provide substrate, food, shelter and nursery for other species (Rogers 1999; Baillon et al. 2012; De Clippele et al. 2015; Jiménez et al. 2016). Some species are habitat-builders able to structure communities that are widely distributed in European waters (Freiwald et al. 2004; Roberts et al. 2009; Mastrototaro et al. 2010; Bo et al. 2015). Once their importance was recognised, the scientific literature on these animals grew rapidly from the mid-1990s onwards (see Willison et al. 2001; Roberts et al. 2009; Roberts and Cairns 2014). Many studies include Mediterranean species (e.g., Zibrowius 2003; Taviani et al. 2005; Freiwald et al. 2009; Mastrototaro et al. 2010; Bo et al. 2014, 2015).

Three main groups of Mediterranean deep-sea corals can be distinguished according to their ability to form habitat: (i) those constructing frameworks on hard bottoms (white coral communities) capable of modeling the environment, as the scleractinians *Lophelia pertusa* and *Madrepora oculata* (see Zibrowius 2003; Taviani et al. 2005; Freiwald et al. 2009; Orejas et al. 2009; Mastrototaro et al. 2010; Gori et al. 2013); (ii) those forming "meadows" or "gardens" on hard bottoms (*Leiopathes glaberrima*, *Parantipathes larix*, *Viminella flagellum*) (see Giusti et al. 2012; Bo et al. 2014, 2015; Grinyó et al. 2016), and soft-bottoms (*Isidella elongata*, see Pérès and Picard 1964; Maynou and Cartes 2011; Cartes et al. 2013; Bo et al. 2015; Mastrototaro et al. 2017); and (iii) those of unequal abundance in hard and soft bottoms, that are

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Table 14.1 Mediterranean deep-sea corals

Phylum	Class	Subclass	Order	Suborder	N° sp.	A
Cnidaria	Anthozoa	Hexacorallia	Antipatharia		5	3
			Scleractinia		25	4
			Zoantharia	Macrocnemina	1	–
		Octocorallia	Alcyonacea	Alcyoniina*	7	–
				Calcaxonia	8	3
				Holaxonia	18	–
				Scleraxonia*	1	–
				Stolonifera*	6	–
			Pennatulacea		10	2
	Hydrozoa	Hydroidolina	Anthoathecata	Filifera	1	1
Total					82	13

(A) habitat-forming species at depths >200 m
(*) Taxa for which the taxonomic status is still controversial or not fully resolved; a suborder level is unacceptable for some authors

frequently associated to the communities structured by other organisms. Some of these species are poorly known and only rarely collected (see Mastrototaro et al. 2010; Bo et al. 2012a, 2014). The species in (i) and (ii) that live at certain depths are few and are commonly associated to the cold water coral (CWC) concept (see Freiwald et al. 2004; Roberts et al. 2006; Chimienti et al., this volume).

In this contribution, we provide information on the present state of knowledge of Mediterranean deep-sea corals, with special emphasis placed on their biodiversity, distribution, systematics and molecular taxonomy. We include a list of species with their depth ranges and bibliographic resources for taxonomic identification.

14.2 Some General Insights into the Anatomy and Systematics of the Deep-Sea Corals and Cold-Water Corals

14.2.1 Cold-Water Corals? Deep-Sea Corals?

Cairns (2007) suggested a definition of coral that reads as follows: "Corals: animals in the cnidarian classes Anthozoa and Hydrozoa that produce either calcium carbonate (aragonitic or calcitic) secretions resulting in a continuous skeleton or as numerous, usually microscopic, individual sclerites, or that have a black, horn-like, proteinaceous axis". For this author, deep-water corals are those living deeper than 50 m (see also WWF/IUCN 2004; Ramirez-Llodra et al. 2010; Yesson et al. 2012). This depth limit was proposed to separate deep/cold-water from shallow-water species, and reflects the tendency of zooxanthellate scleractinians and octocorals to occur in waters shallower than 50 m, unlike azooxanthellate species which occur typically deeper (>50 m) (Cairns 2007; Yesson et al. 2012). The terms deep-water corals, deep-sea corals and CWCs are commonly used indistinctly to refer to those corals living at certain depths (see Morgan 2005), although some authors do not concur (e.g., Freiwald et al. 2004). Some authors consider CWCs those cold-affinity species able to form structural habitat and commonly living deeper than 200 m depth (see Chimienti et al., this volume).

In this chapter we review the Mediterranean corals living deeper than 50 m (deep-sea corals), no matter whether they are capable of forming habitat deeper than 200 m depth. The Mediterranean deep waters are homothermic below 200–300 m depth, with temperatures ranging from 13 °C (western basin) to 15.5 °C (eastern basin) (Emig and Geistdoerfer 2004). This can be a reason why CWCs Mediterranean fauna is not as rich as in nearby Atlantic areas, as CWCs are largely restricted to temperatures between 4 °C and 12–13 °C (Freiwald et al. 2004; Roberts et al. 2006). In our review we include the coral species living in part of the circalittoral and in the bathyal zones. The former extends from the lower limit of occurrence of the photophilous algae to the lower limit of the sciaphilous algae; the bathyal starts in the lower limit of growth of the multicellular algae and comprises the continental slope and the area immediately below (Pérès and Picard 1964). In bathymetric terms, the circalittoral extends in the Mediterranean Sea from ~30–40 m depth to the shelf-break at ~100–110 m, and the bathyal from this lower limit to 3000 m (Pérès and Picard 1964; Emig and Geistdoerfer 2004). To our best knowledge, there are no corals living at abyssal depths (>3000 m, see Laubier and Emig 1993) in the Mediterranean Sea.

14.2.2 Anatomy and Systematics

The Mediterranean deep-sea corals and CWCs belong to the classes Anthozoa and Hydrozoa, and they are classified in six orders (Table 14.1). According to the previous definition of Cairns (2007), all the soft-bodied species included in the hexacorallian orders Actiniaria, Ceriantharia and Corallimorpharia are excluded. Additionally, the Hydrozoa are represented by a single family (Stylasteridae). Although several species belonging to these orders have similar external features, differences are significant in the anatomy of the polyps as shown in cross-section (see Häussermann et al. 2003a; Roberts et al. 2009), and by their skeletons. Cnidarian polyps typically have a hollow central body cavity (coelenteron) opening by the mouth, which is surrounded by a variable number of tentacles, and cnidae; the cnidome is the entire complement of the cnidae types in a given taxon (Bouillon et al. 2004). In the class Anthozoa, the mouth is followed by the actinopharynx, a tube-like structure which communicates with the gastrovascular cavity (see Roberts et al. 2009 and references therein). Its inner edge has one (Octocorallia) or more siphonoglyphs (Hexacorallia), which function is to conduct water into the body cavity (Hyman 1940). This cavity is divided into compartments by complex longitudinal structures called mesenteries (septa) that can be paired (Scleractinia, Zoantharia) or unpaired (Antipatharia, Octocorallia) (see Hyman 1940; Bayer et al. 1983; Häussermann et al. 2003a and references therein). The hydrozoan polyp lacks actinopharynx and mesenteries (see Bouillon et al. 2004). The type and nature of skeletal structures are essential to distinguish among the different groups of Mediterranean corals. The skeletons may be proteinaceous (Antipatharia, Zoantharia), calcareous (Scleractinia, Fig. 14.1), or mixed types even in a single species (many octocorals Fig. 14.2a). Mineralised skeleton can be continuous (Scleractinia, Fig. 14.1, Stylasteridae), or discontinuous in the form of calcareous sclerites of different shapes (Octocorallia, Fig. 14.2a–g); the sclerome is an inventory of all sclerites occurring in a given octocoral taxon. The analysis of the cnidomes of the deep-sea corals is limited, although there are ongoing studies on Mediterranean antipatharians (Bo 2008). Roberts et al. (2009) provided an identification key for the coral groups Antipatharia, Octocorallia, Scleractinia, Stylasteridae and Zoantharia based on characteristics of their mesenteries, tentacles and skeletons.

Discrepancy between morphological and molecular data are extended over the phylum. The phylogenetic reconstructions of many cnidarian taxa vary according to the morphological characters and molecular markers considered (Fig. 14.3). However, it is interesting to notice that one of the most recent phylogenetic studies of the phylum Cnidaria, based on genomes and transcriptomes (Fig. 14.3d), coincides with cladistic morphological analyses (Fig. 14.3a). Molecular studies are revolutionising Cnidarian systematics, therefore, changes in the classification as well as taxonomic revisions are expected in the near future.

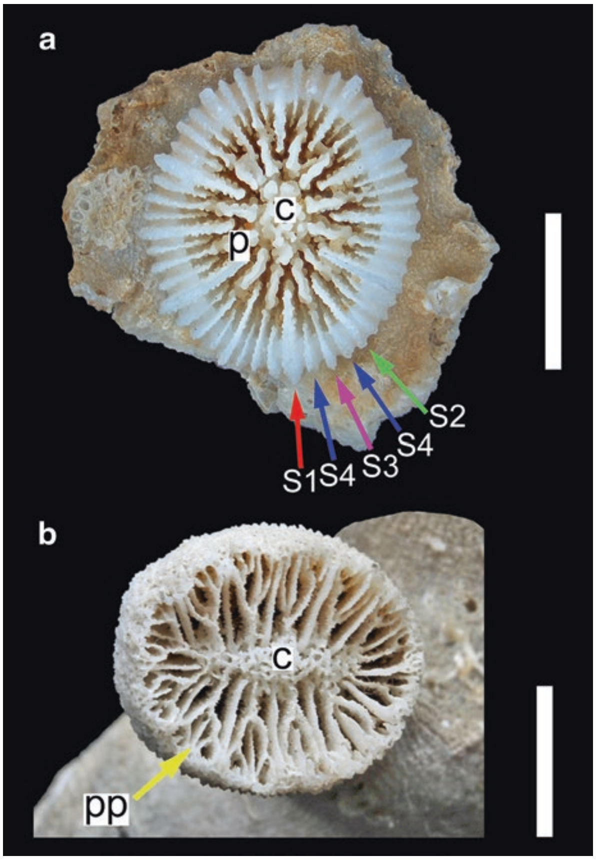

Fig. 14.1 Calicular structures in scleractinians. (**a**) *Caryophyllia inornata*, calicular view showing arrangement of septa (S1–S4), columella (c) and pali (p); Marseille, 60 m depth (specimen sent by H. Zibrowius). (**b**) *Dendrophyllia cornigera*, calicular view showing arrangement of septa according to Pourtalès plan, with septa fused forming triangles (pp, arrow); c, columella. The porosity of the corallum is characteristic of the Dendrophylliidae. Alborán Sea, depth unknown. Scale bar: **a** = 4 mm; **b** = 10 mm

14.3 The Mediterranean Deep-Sea Corals and Cold-Water Coral Groups

14.3.1 Class Anthozoa, Subclass Hexacorallia

Hexacorallians are solitary or colonial anthozoans having mostly hexamerous symmetry and simple tentacles rarely branched. The anatomy of their polyps is more complex and variable than that of octocorals, with one, two or exceptionally more siphonoglyphs and generally numerous mesenteries. Polyps do not exhibit polymorphism. The subclass includes six orders, with Antipatharia, Scleractinia and Zoantharia having representatives in the Mediterranean deep-sea coral fauna (Table 14.1). Häussermann et al. (2003a, b) published a general overview of the anatomy of the class Anthozoa and the subclass Hexacorallia, including

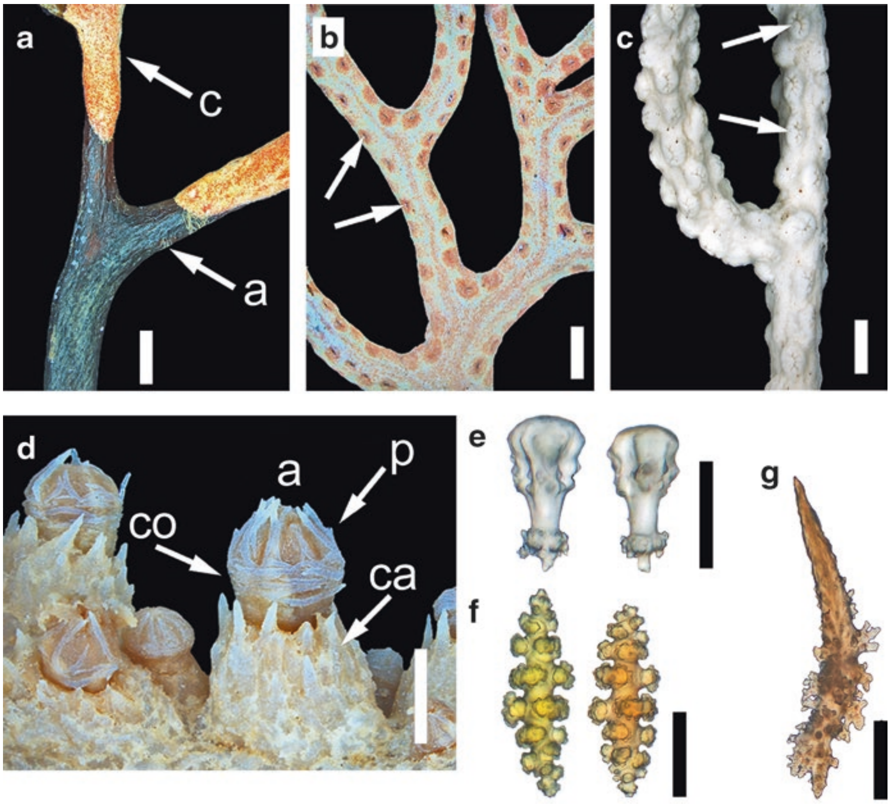

Fig. 14.2 Some morphological features of holaxonians. Gorgoniidae, (**a**) *Leptogorgia sarmentosa*. Part of a colony showing horny axis (a) and coenenchyme (c). Alborán Sea, depth unknown; (**b**) Another specimen showing slit-like apertures from polyps (arrows), same zone; (**c**) *Eunicella singularis*, polyps arrangement on stem (arrows). Alborán Sea, depth unknown. Plexauridae, (**d**) *Paramuricea clavata*, part of a branch showing polyps. Arrows show calyx with thornscales (ca), and the anthocodial sclerites in a collaret (co) (sclerites arranged in transversal rows) and points (p) arrangement; (a), anthocodia. Murcia, Spain, depth unknown (© National Museum of Natural Sciences, Madrid, MNCN 2.04/1054). (**e**) Balloon-clubs from specimen **c**. (**f**) Spindles from **b**. (**g**) Thornscale from **d**. Scale bar: **a**–**c** = 2 mm; **d** = 1 mm; **e**, **f** = 0.05 mm; **g** = 0.2 mm

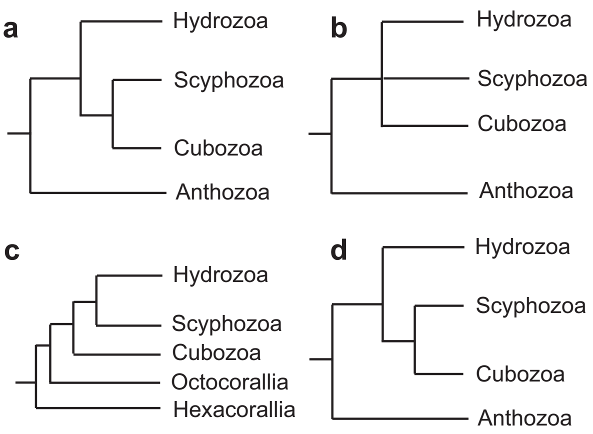

Fig. 14.3 Overview of the phylogenetic reconstructions of Cnidaria based on different morphological and molecular sources. (**a**) morphological cladistic analysis (Schuchert 1993); (**b**) phylogenetic reconstruction based on morphological characters, 18S rRNA and the mitochondrial 16S rRNA (Bridge et al. 1995); (**c**) molecular phylogeny based on complete mitochondrial genomes (Kayal et al. 2013) and (**d**) phylogenomics based on genomes and transcriptomes (Zapata et al. 2015)

a detailed glossary of anatomical terms covering all orders. Daly et al. (2003) provided a summary of the diagnostic morphological features for each hexacorallian order.

14.3.1.1 Order Antipatharia

The Order Antipatharia is a group of non-calcareous colonial cnidarians comprising about 247 species included in 7 families and 41 genera (Brugler et al. 2013). Also known as black corals, antipatharians are characterised by a colony consisting of a proteinaceous spiny rigid axis and numerous small six-tentacled polyps often no more than a few millimeters in diameter. These corals have six primary mesenteries, either zero, four or six secondary mesenteries, and a spiny skeletal axis (Opresko 2001; Daly et al. 2007). They are important slow-growing, frequently long-lived, habitat-forming animals. Black corals may have different types of colonies ranging from unbranched whip-like to densely ramified tree-like.

Antipatharians have been the subject of taxonomic difficulties until very recent times. The historical aspects and literature on the topic were reviewed by Opresko (1974) and

Brugler et al. (2013). Despite difficulties persist in some taxa, the systematics of these organisms was clarified mostly due to the revisions of Opresko (2001, 2002 and subsequent papers), with the families Antipathidae and Leiopathidae, still pending. Further changes are expected in the current systematic scheme when their revisions will be completed.

The habitat requirements of the Antipatharia were summarised by Wagner et al. (2012) and Bo and Bavestrello (this volume). Most antipatharians live attached to a hard substrate by means of a basal holdfast, but free-living colonies occur in soft-bottoms as well. They are important components of different Mediterranean CWC communities, including white corals, and typically form large 'sea forests' (Angeletti et al. 2014; Bo et al. 2014, 2015).

Taxonomy and Taxonomic Characters

The families were keyed out by Brugler et al. (2013). They are principally distinguishable by the internal and external anatomy of the polyps and their size, the growth form of the corallum, the size and shape of spines and the morphology and characteristics of the pinnules. These characters are also important at lower levels (genus and species). The spines of the skeleton are usually less than 0.5 mm tall and are commonly used to distinguish black corals from other tree-like anthozoans. Largely neglected in the literature as a taxonomic character, the cnidome could be a key element for species level identification (Bo 2008).

We refer to Brook (1889) for a detailed description of the anatomy of antipatharians, to Opresko et al. (2014) for a glossary with technical terms and morphological descriptions, and to Opresko (2001, 2002 and further papers) for taxonomic revisions with diagnoses of all families and genera, and description of type material and identification keys to genus level. In addition, Daly et al. (2007) and Brugler et al. (2013) provided diagnoses for each family, and Opresko and Försterra (2003) described the Mediterranean species.

Molecular Aspects

Phylogenetic analyses on the Order Antipatharia have been performed using both, nuclear and mitochondrial molecular markers. Brugler et al. (2013) explored the evolutionary history of the order using 18S and 28S rRNA, and mitochondrial intergenic regions (IGRs). These authors reported the presence of a novel group I intron within the COI gene, encoding for a putative homing-endonuclease, in six different antipatharian genera. Three families (Antipathidae, Aphanipathidae and Cladopathidae) comprise polyphyletic assemblages. The Antipathidae is the most speciose family, although it has been clearly defined as a taxonomic "dumping" ground due to its polyphyletic origin (Daly et al. 2007).

Concerning the mitochondrial genome of black corals, this has a size ranging from 17,000 to 20,000 bp with 14 protein coding genes and two ribosomal RNA subunits (rns and rnl). The longest IGRs seem to be those between trnW and Nad2 (igrW) and between Nad5 and Nad1 (igrN). To date the complete mitogenomes of only four species are available in the public repositories (Brugler and France 2007; Kayal et al. 2013), but none of them occur in the Mediterranean Sea.

Molecular analyses including Mediterranean species are scarce. *Antipathella subpinnata* and *Leiopathes glaberrima* have been placed, according to phylogenetic analyses, into families Myriopathidae and Leiopathidae, respectively (Lapian et al. 2007; Bo et al. 2012b; Brugler et al. 2013). This result agrees with the morphology-based taxonomy of these species (see Bo et al. 2008). One of the first studies performed on the Mediterranean species *L. glaberrima* has surprisingly reported the presence of a COI intron (Sinniger and Pawlowski 2009). *Leiopathes glaberrima* and *Antipathes dichotoma* have been included in the phylogenetic reconstructions by Brugler et al. (2013).

Mediterranean Species

The six Mediterranean species currently known belong to four families and four genera, Antipathidae (*A. dichotoma* and *Antipathes fragilis*), Leiopathidae (*L. glaberrima*), Myriopathidae (*A. subpinnata* and *Antipathella wollastoni*), and Schizopathidae (*Parantipathes larix*). Among these, five live at depths higher than 50 m, and one, *A. wollastoni*, is known only from a single record near the Gibraltar Strait at 35 m depth (Ocaña et al. 2007) and is therefore not considered a deep-sea species. Three are characteristic habitat-building species at depths higher than 200 m (CWCs) (*A. dichotoma*, *L. glaberrima*, *P. larix*).

The five deep-sea antipatharians were first described in the Mediterranean Sea, and except for *A. fragilis*, described by Gravier (1918), they are known in this area since the eighteenth century. Apart from *A. fragilis*, the types or neotypes of all species have been re-described in the last years, including SEM (Scanning Electron Microscope) images of pinnules and spines (see Opresko and Baron-Szabo 2001; Opresko 2001, 2003). Investigations on the cnidome of most Mediterranean species have been recently undertaken (see Table 14.2).

All Mediterranean antipatharians are hard-bottoms species and have mostly a bushy appearance (Fig. 14.4a–c, see also Bo et al. 2011, 2012a). *Leiopathes glaberrima* is probably the most easily distinguishable species, due to its large and irregularly branched corallum with colonies up to 2 m high, orange polyps and a black, smooth and brilliant axis with minute spines (Fig. 14.4c, see a redescription of the type in Opresko and Baron-Szabo 2001). *Parantipathes larix* is rather different, as it has monopodial to sparsely branched bottle-brush colonies up to 2 m in height and frequently purple in colour (Fig. 14.4d, see also Bo et al. 2014). Stem and branches are pinnulate, with six rows of simple pinnules on

Table 14.2 Deep-water corals (depth >50 m) known from the Mediterranean Sea

Species	A	B	C	D	E	F	Remarks	Species reference
Class Anthozoa								
Subclass Hexacorallia								
Order Antipatharia								
Family Antipathidae								
Antipathes dichotoma Pallas, 1766	c	h	90–645	x		x	Cnidome described by Bo et al. (2011), who summarised Mediterranean records including a distribution map	Opresko (2003) and Bo et al. (2011)
Antipathes fragilis Gravier, 1918	c	h	70–600			x	Last new antipatharian first described from the Mediterranean Sea, and last one added to the inventory	Gravier (1918)
Family Leiopathidae								
Leiopathes glaberrima (Esper, 1788)	c	h	120–800	x		x	Cnidome described by Bo et al. (2015)	Opresko and Baron-Szabo (2001) and Bo et al. (2015)
Family Myriopathidae								
Antipathella subpinnata (Ellis & Solander, 1786)	c	h	60–600			x	Cnidome described by Bo et al. (2008), who summarised Mediterranean records	Opresko (2001) and Bo et al. (2008)
Family Schizopathidae								
Parantipathes larix (Esper, 1790)	c	h	90–2200	x		x	Cnidome described by Bo et al. (2014)	Opresko and Baron-Szabo (2001) and Bo et al. (2014)
Order Scleractinia								Zibrowius (1980)
Family Caryophylliidae								
Anomocora fecunda (Pourtalès, 1871)	c	h	~200–300				Last deep-sea scleractinian added to the Mediterranean fauna inventory (Pardo et al. 2011; OCEANA 2014)	
Caryophyllia calveri Duncan, 1873	s	h	100–800					
Caryophyllia cyathus (Ellis & Solander, 1786)	s	h	65–300			x		
Caryophyllia inornata (Duncan, 1878)	s	h	0–443			x	Lower depth limit in the Gibraltar area (Álvarez-Pérez et al. 2005). Mostly occurring shallower than 50 m depth	
Caryophyllia smithii Stokes & Broderip, 1828	s	h, sb	~5–400+				Mostly occurring shallower than 50 m depth. Lower depth limit corresponds to the Alboran Sea	
Ceratotrochus magnaghii Cecchini, 1914	s	h	7–400		x	x	Shallow depth limit corresponds to submarine caves (Zibrowius 1980)	
Coenocyathus anthophyllites Milne Edwards & Haime, 1848	c	h	35–200			x		
Coenocyathus cylindricus Mine Edwards & Haime, 1848	c	h	65–600			?	Probably first described from the Mediterranean Sea (Zibrowius 1980)	
Desmophyllum dianthus (Esper, 1794)	s	h	30–1257	x			Shallow depth limit in the Gibraltar area (Álvarez-Pérez et al. 2005)	
Hoplangia durotrix Gosse, 1860	c	h	0–150				Mostly occurring shallower than 50 m depth	
Lophelia pertusa (L., 1758)	c	h	39–1100	x			Shallow depth limit in the Gibraltar area (Álvarez-Pérez et al. 2005)	
Paracyathus pulchellus (Philippi, 1842)	s	h	~7–220			x	Mostly occurring shallower than 50 m depth	
Pourtalosmilia anthophyllites (Ellis & Solander, 1786)	c	h	100+ (?)			?	Probably first described from the Mediterranean Sea (Zibrowius 1980). Scarce reliable depth data on live colonies available	
Thalamophyllia gasti (Döderlein, 1913)	c	h	13–610+			x	Shallow depth limit corresponds to submarine caves (Zibrowius 1980)	
Family Dendrophylliidae								
Balanophyllia cellulosa Duncan, 1873	s	sb	80–320					

(continued)

Table 14.2 (continued)

Species	A	B	C	D	E	F	Remarks	Species reference
Dendrophyllia cornigera (Lamarck, 1816)	c	h	72–733	x				
Dendrophyllia ramea (L., 1758)	c	h	30~240			x	Lower depth limit corresponds to the Menorca channel (Jiménez et al. 2016)	
Leptopsammia pruvoti Lacaze-Duthiers, 1897	s	h	~5–150			x	Mostly occurring shallower than 50 m depth	
Family Flabellidae								
Javania cailleti (Duchassaing & Michelotti, 1864)	s	h	400–660					
Monomyces pygmaea (Risso, 1826)	s	h	5–150			x	Mostly occurring shallower than 50 m depth	
Family Guyniidae								
Guynia annulata Duncan, 1872	s	h, sb	~5–300+			x	Shallow depth limit corresponds to submarine caves	
Family Stenocyathidae								
Stenocyathus vermiformis (Pourtalès, 1868)	s	h, sb	43–1350				Shallow depth limit in the Gibraltar area (Álvarez-Pérez et al. 2005)	
Family Oculinidae								
Madrepora oculata L., 1758	c	h	33–1100	x		x	Shallow depth limit in the Gibraltar area (Álvarez-Pérez et al. 2005)	
Family Turbinoliidae								
Sphenotrochus andrewianus Milne Edwards & Haime, 1848	s	sb	10–187				Lower depth limit corresponds to the Gibraltar area (Álvarez-Pérez et al. 2005). Mostly occurring shallower than 50 m depth	
Scleractinia Incertae Sedis								
Cladocora debilis Milne Edwards & Haime, 1849	c	sb	24–480					
Order Zoantharia								
Family Parazoanthidae								
Savalia savaglia (Bertoloni, 1819)	c	h	15–900			x	Last new deep-sea coral zoanthid described from the Mediterranean Sea	Lacaze-Duthiers (1864a) and Ocaña and Brito (2004)
Subclass Octocorallia								
Order Alcyonacea								
Suborder Alcyoniina								
Family Alcyoniidae								Weinberg (1977)
Alcyonium acaule Marion, 1878	c	h	10–125		*	x	Mostly occurring shallower than 50 m depth	Verseveldt (1964)
Alcyonium coralloides (Pallas, 1766)	c	h	0–135			x	Mostly occurring shallower than 50 m depth	
Alcyonium palmatum Pallas, 1766	c	sb	20–700			x		Verseveldt (1964)
Anthomastus sp.	c	h	400–500				As *Anthomastus* cf. *grandiflorus* (OCEANA 2014). Last deep-sea alcyonacean added to the Mediterranean fauna inventory. Only in the Alboran Sea	No description of this species available. See Fig. 14.6A–B
Family Nidaliidae								
Chironephthya mediterranea López-González, Grinyó & Gili, 2014	c	h	115–200		x	x	Last new deep-sea alcyonacean described from the Mediterranean Sea	López-González et al. (2014)
Nidalia studeri (von Koch, 1891)	c	h	100–329		x	x		López-González et al. (2012)
Family Paralcyoniidae								
Paralcyonium spinulosum (Delle Chiaje, 1822)	c	h	15–300+			x	Mostly occurring shallower than 50 m depth	Weinberg (1977)
Suborder Calcaxonia								
Family Dendrobrachiidae								

(continued)

Table 14.2 (continued)

Species	A	B	C	D	E	F	Remarks	Species reference
Dendrobrachia bonsai López-González & Cunha, 2010	c	h	200–1080				*D. fallax* Brook, 1889 records correspond to this species	López-González and Cunha (2010) and Sartoretto (2012)
Family Ellisellidae								Grasshoff (1972) and Weinberg and Grasshoff (2003)
Ellisella paraplexauroides Stiasny, 1936	c	h	15–200					Angiolillo et al. (2012)
Nicella granifera (Kölliker,1865)	c	h	~100–400+				Only in the Alboran Sea?	
Viminella flagellum (Johnson, 1863)	c	h	70–400+	x				
Family Isididae								
Acanella arbuscula (Johnson, 1862)	c	sb	300–800	?			Probably habitat-forming. Further studies needed	Saucier et al. (2017)
Acanella furcata Thomson, 1929	c	sb	190–1000	?	x	x	Probably habitat-forming. Further studies needed	Thomson (1929) and Saucier et al. (2017)
Isidella elongata (Esper, 1788)	c	sb	115–1656	x	*	x		Weinberg and Grasshoff (2003)
Family Primnoidae								
Callogorgia verticillata (Pallas, 1766)	c	h	90–1000	x		x		Carpine and Grasshoff (1975) and Weinberg and Grasshoff (2003)
Suborder Holaxonia								
Family Acanthogorgiidae								Grasshoff (1973)
Acanthogorgia armata Verrill, 1878	c	h	150–500+				Only in the Alboran Sea	
Acanthogorgia hirsuta Gray, 1857	c	h	100–924					Carpine and Grasshoff (1975)
Family Gorgoniidae								Carpine and Grasshoff (1975), Weinberg (1976), Grasshoff (1988, 1992) and Weinberg and Grasshoff (2003)
Eunicella cavolini (von Koch, 1887)	c	h	10–186+		x	x	Mostly occurring shallower than 50 m depth	
Eunicella filiformis (Studer, 1878)	c	sb	45–250				Only in the Alboran Sea	
Eunicella singularis (Esper, 1791)	c	h	10–100+		*	x	Two morphotypes have been described, one proper of deeper depths lacking zooxanthellae (Costantini et al. 2016). Mostly occurring shallower than 50 m depth	
Eunicella verrucosa (Pallas, 1766*)*	c	h	~5–200			x	Mostly occurring shallower than 50 m depth	
Filigorgia guineensis (Grasshoff, 1988)	c	sb	250–300				Only in the Alboran Sea	Ocaña et al. (2000a)
Leptogorgia sarmentosa (Esper, 1789)	c	h	~5–300			?	Probably first described from the Mediterranean Sea. Mostly occurring shallower than 50 m depth	
Family Plexauridae								Carpine and Grasshoff (1975), Grasshoff (1977) and Weinberg and Grasshoff (2003)
Bebryce mollis Philippi, 1842	c	h	100–250+			x		
Muriceides lepida Carpine & Grasshoff, 1975	c	h	80–718			x		
Paramuricea clavata (Risso, 1826)	c	h	35–110+		*	x	Mostly occurring at 50–60 m depth (Carpine and Grasshoff 1975)	

(continued)

Table 14.2 (continued)

Species	A	B	C	D	E	F	Remarks	Species reference
Paramuricea macrospina (Koch, 1882)	c	h	40–300+		x	x		
Placogorgia coronata Carpine & Grasshoff, 1975	c	h	~200–1000			x	Differentiation of *Paramuricea* and *Placogorgia* needs molecular evaluation	
Placogorgia massiliensis Carpine & Grasshoff, 1975	c	h	350–500			x		
Spinimuricea atlantica (Johnson, 1862)	c	h	50–96				Only in the Alboran Sea	
Spinimuricea klavereni (Carpine & Grasshoff, 1975)	c	h	50–80		x	x		
Swiftia pallida Madsen, 1970	c	h	100–600				*Swiftia* needs revision. Possible cryptic species	
Villogorgia bebrycoides (von Koch, 1887)	c	h	100–300+			x		
Suborden Scleraxonia								
Family Coralliidae								
Corallium rubrum (L., 1758)	c	h	3–800			x		Carpine and Grasshoff (1975) and Weinberg (1976)
Suborder Stolonifera								
Family Clavulariidae								
Clavularia carpediem Weinberg, 1986	c	h	40–200		x	x	Doubtful generic adscription. Mostly occurring shallower than 50 m depth	Weinberg (1986) and López-González (1993)
Clavularia marioni von Koch, 1891	c	h	70+			x	An extremely rare species. Doubtful generic adscription	Weinberg (1978)
Rolandia coralloides Lacaze-Duthiers, 1900	c	h	0–800 (?)			x	Mostly occurring shallower than 50 m depth	Ocaña et al. (2000b)
Sarcodictyon catenatum Forbes, 1847	c	h	0–100				Mostly occurring shallower than 50 m depth	Ocaña et al. (2000b)
Scleranthelia rugosa (Pourtalès, 1867)	c	h	200–714					Carpine (1964, as *Scleranthelia musiva* Studer, 1878)
Telestula septentrionalis Madsen, 1944	c	h	600–700				Description of the Mediterranean specimens needed	Madsen (1944)
Order Pennatulacea								Kükenthal (1915), Gili and Pagès (1987) and Williams (1995) (diagnoses of genera)
Family Funiculinidae								
Funiculina quadrangularis (Pallas, 1766)	c	sb	70–616	x		x		
Family Kophobelemnidae								
Kophobelemnon stelliferum (Müller, 1766)	c	sb	70–618	x			*K. leuckartii* Cecchini, 1917 is a synonym (Mastrototaro et al. 2013)	Mastrototaro et al. (2013)
Family Pennatulidae								
Pennatula aculeata Danielssen, 1860	c	sb	150–300					
Pennatula phosphorea L., 1758	c	sb	30–570					
Pennatula rubra (Ellis, 1761)	c	sb	20–200+			x		Abdelsalam (2014)
Pteroeides spinosum (Ellis, 1764)	c	sb	20–280			x		Abdelsalam (2014)
Family Protoptilidae								
Protoptilum carpenteri Kölliker, 1872	c	sb	240–451				Last sea-pen added to the Mediterranean fauna inventory	Mastrototaro et al. (2014)
Family Veretillidae								
Cavernularia pusilla (Philippi, 1835)	c	sb	14–200			x	Last new sea-pen described from the Mediterranean Sea	Abdelsalam (2014)

(continued)

Table 14.2 (continued)

Species	A	B	C	D	E	F	Remarks	Species reference
Veretillum cynomorium (Pallas, 1766)	c	sb	15–260			x	Shallow depth limit from Alboran Sea (Ocaña et al. 2000a)	
Family Virgulariidae								
Virgularia mirabilis (Müller, 1776)	c	sb	7–620				Shallow depth limit from Alboran Sea (Ocaña et al. 2000a)	
Class Hydrozoa								
Subclass Hydroidolina								
Order Anthoathecata								
Suborder Filifera								
Family Stylasteridae								
Errina aspera (L., 1767)	c	h	61–443	x		x	Last new stylasterid described from the Mediterranean Sea	Zibrowius and Cairns (1992)

(A) Coloniality: *s* solitary species, *c* colonial species
(B) Substrate: *h* hard-bottom species, *sb*, soft-bottom species
(C) Depth range (m)
(D) Habitat-forming species in the Mediterranean Sea at depths >200 m (see Chimienti et al., this volume)
(E) Mediterranean endemics (* Near-endemic, occurs also in nearby Atlantic waters)
(F) Species that was first described in the Mediterranean Sea. Species reference: papers in which Mediterranean material of the species concerned is described. Bibliographic references in cells corresponding to taxa higher than genus (family, order, etc.) means that most, if not all, species/genera in these taxa are described in the corresponding paper. For instance, all scleractinian corals (order Scleractinia) are described in Zibrowius (1980). In the Scleractinia, depth range refers to live specimens whenever this information was available

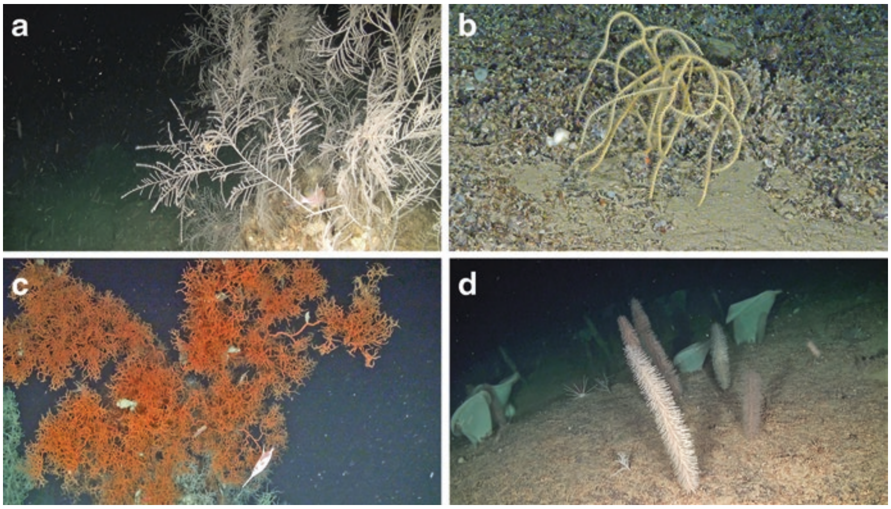

Fig. 14.4 (**a**) *Antipathella subpinnata*, Chella Bank, Alborán Sea off Spain, 330 m. (**b**) *Antipathes dichotoma*, Balearic Islands, 550 m. (**c**) *Leiopathes glaberrima*, Chella Bank, 400 m. (**d**) *Parantipathes larix*, Cabliers Bank, Alborán Sea, 420 m. (Photographs: © OCEANA)

the lower part of the corallum arranged in alternating groups along the sides of the stem (Opresko 2002). The type was thoroughly re-described by Opresko and Baron-Szabo (2001). According to these authors, further studies are needed in order to determine whether Mediterranean specimens with shorter pinnules are indeed *P. larix* or whether they represent a separate species. The morphological descriptions of *A. subpinnata* in the literature are frequent (see a review by Bo et al. 2008). A neotype was thoroughly described by Opresko (2001). The corallum reaches over 1 m in height, and is of a whitish colour underwater (see Bo et al. 2008). It consists of several elongate branches arising vertically and nearly parallel to each other, with branchlets along the stem and lower order branches mostly directed distally (Fig. 14.4a). *Antipathes dichotoma* was re-described by Opresko (2003) based on a specimen from Naples. According to this author, the corallum may reach 1 m in height or more, and the ramification is sparse. The branches are long and flexible disposed irregularly on all sides of the stem and lower order branches (Fig. 14.4b). Finally, *A. fragilis* is an obscure poor known species whose type was lost. The type was a fragment, so even the colony size is unknown. Colonies attributed to this species were recently observed at 600 m depth (Fabri and Pedel 2012).

Remarkable Sites and Distribution

The Mediterranean antipatharians occur on shoals and rocky cliffs (where they can constitute monospecific populations), on the shelf and at bathyal depths associated to white corals (developing mixed populations with other anthozoans), or sparse in the canyons (Bo et al. 2015). Bo et al. (2008, 2011, 2012a, 2014, 2015) and Ingrassia et al. (2015) described populations following these criteria.

Antipathella subpinnata, *A. dichotoma* and *L. glaberrima* are widely distributed in the Mediterranean Sea, and according to Bo et al. (2008) the former is probably the most commonly observed in this area. *Parantipathes larix* is considered uncommon (Bo et al. 2014). A distribution map of *A. dichotoma* with compilation of all records was given by Bo et al. (2011). In Vafidis (2010) and Chimienti et al. (this volume) comprehensive information on distribution as well as maps are included. Following these authors, all five species are known from the western basin, four are known from the Aegean Sea (*A. fragilis* not recorded), two from the Adriatic Sea (*A. subpinnata*, *L. glaberrima*) and two from the Ionian basin (*A. dichotoma*, *L. glaberrima*). All species (excepting *A. fragilis*) inhabit both shelf and slopes in the Mediterranean basin (Table 14.2). An exceptional record of *P. larix* at 2200 m was recently given by Fabri and Pedel (2012).

The bay of Naples is the type locality for three of the five Mediterranean deep-sea species that were first described from Naples in the eighteenth century (*A. fragilis*, *L. glaberrima*, *P. larix*). Opresko (2001, 2003) chose specimens collected in the bay for the description of neotypes of *A. dichotoma*, and *A. subpinnata*, whose types were lost. The bay is also the type locality of two species described by von Koch (1889) now considered not valid (*Antipathes aenea* and *Antipathes gracilis*). In addition, *L. glaberrima* is also the type species of the genus *Leiopathes*, *A. dichotoma* of the Order Antipatharia, *P. larix* of the genus *Parantipathes*, and *A. subpinnata* of the genus *Antipathella* (see Opresko 2001; Opresko and Baron-Szabo 2001). The fauna of Naples was described thoroughly in several papers (von Koch 1889; Gravier 1918; Opresko and Baron-Szabo 2001; Opresko 2003) and material from this area was used in the key-work of Brook (1889).

Due to the extended use of remotely operated vehicles (ROVs), exceptional antipatharian facies are being discovered mainly in the Italian waters of the western basin (Bo et al. 2014, 2015; Angeletti et al. 2014; Ingrassia et al. 2015), demonstrating that black corals are much more abundant than previously thought (see Bo et al. 2008, 2012b, 2015). Four of the Mediterranean species have been identified in Chella Bank (Alborán Sea off Spain), a site with a rich fauna. Antipatharians were recorded as deep as the 500–600 m interval (Fig.14.4a, c; OCEANA 2014). This is probably the area with the highest diversity known so far in the Spanish Mediterranean Sea. We refer to other chapters in this book for descriptions and locations of the newly discovered communities.

14.3.1.2 Order Scleractinia

Scleractinians are marine solitary or colonial cnidarians that account for 1482 extant species among which 615 are considered deep-sea corals (Cairns 2007). These corals are ecological important components as they shape the diversity of both shallow water environments and the deep-sea habitats.

Scleractinian polyps are similar to the model already described in the Subclass Hexacorallia. They have mesenteries arising in pairs and arranged in cycles. The external skeleton made of aragonite (corallum) has vertical partitions (septa) arising from the basal plate that form cycles and occur between the mesenteries (Fig. 14.1). Stony corals, including the Mediterranean species, have been deeply investigated through time. Studies on the anatomy of the skeleton and on the morphological features were performed by Vaughan and Wells (1943) and Wells (1956).

Recent papers on the microstructure and genetic diversity of these organisms contributed to shed light onto their systematics, and the taxonomy of numerous taxa was revised (Stolarski 2000; Stolarski and Roniewicz 2001; Budd et al. 2010). Molecular phylogenies and morphological studies are not necessarily congruent. The monophyly of the five "traditional" suborders (i.e. Astrocoeniina, Caryophylliina, Faviina, Fungiina and Dendrophylliina) based on morphology (Wells 1956) is not always supported by molecular studies (Budd et al. 2010). Therefore, different morphological characters are being tested to better explore the systematics of these groups (Budd and Stolarski 2009).

We refer to Stolarski and Roniewicz (2001) for a review of the evolutionary relationships and classification of the Scleractinia.

Taxonomy and Taxonomic Characters

Taxa discrimination is substantially based on different features of the skeleton (corallum) at three levels: macromorphology, micromorphology and microstructure (see Budd and Stolarski 2009; Budd et al. 2010). However, some features exhibit intraspecific variation, and the study of large series of specimens leads reductions in terms of valid species and complicated synonymies (Zibrowius 1984). Despite exhibiting convergence, most traditional macromorphological characters have been used to define genera and families (Kitahara et al. 2016) making their taxonomy even more complicated. Morphological variability includes: growth form in colonial species or shape of the corallum in solitary ones, coenosteal development, and size of the calyces. Calicinal structures also vary, as well as the number of septa and their width or exsertness, development of the columella, pali, symmetry of the radial structures, or the arrangement of septa according to Pourtalès plan in the dendrophylliids (septa fused forming triangles, see Fig. 14.1b, Table 14.3 and Cairns 2001). Zibrowius (1984) proposed the use of new characters for the azooxanthellate scleractinians taxonomy and reconsidered other characters such as the attachment structures, the spatial relationships of calicular elements, septal ornamentation and the type of asexual reproduction. Overall soft tissues and cnidome are not very useful for genus or species level identifications. However, Terrón-Sigler and López-González (2005) analysed the cnidome of two Mediterranean shallow-water *Balanophyllia*, showing its usefulness for taxonomic determinations among congeneric species. Little is so far known about the deep-sea species.

Vaughan and Wells (1943) keyed all scleractinian taxa until genus level, Kitahara et al. (2010a) worked on *Caryophyllia* species and provided identification keys, whereas Cairns and Kitahara (2012) explained and depicted all the morphological characters currently used for the description of the azooxanthellate species and keyed all genera. We refer to Zibrowius (1980) for descriptions, ecology, distribution and literature of all Mediterranean species.

Molecular Aspects

Genetic studies on Mediterranean deep-sea scleractinians are available only for a few species, although recent phylogenetic studies include some of them. For instance, molecular data of 12 Mediterranean species, seven of them included in the present chapter (*Caryophyllia inornata*, *Ceratotrochus magnaghii*, *Guynia annulata*, *Leptopsammia pruvoti*, *Monomyces pygmaea*, *Paracyatus pulchellus* and *Thalamophyllia gasti*), were considered for evolutionary studies (Romano and Cairns 2000). Additionally, Daly et al. (2003) and Le Goff-Vitry et al. (2004b) explored the use of mitochondrial 16S ribosomal RNA from some of these species for phylogenetic reconstructions within Hexacorallia and Scleractinia, respectively. The genetic structure of several Mediterranean populations of *L. pruvoti* was investigated by Goffredo et al. (2009), yet the molecular data available for other Mediterranean scleractinians concerns shallow-water species only. One of the most comprehensive phylogenetic analyses of the order was based on COI (see Kitahara et al. 2010b). In Kitahara's et al. study, more than 200 taxa representing both shallow and deep-sea species, from 25 scleractinian families, were analysed. However, among the taxa investigated, only two species occur in the Mediterranean Sea (*Madrepora oculata*, *Stenocyathus vermiformis*). The phylogenetic tree revealed that most of the families are polyphyletic. Subsequent analyses, based on partial mitochondrial 16S rRNA, performed on *Caryophyllia* and morphological similar caryophylliids, showed phylogenetic affinity between some *Dasmosmilia*, *Crispatotrochus* and *Caryophyllia* species (Kitahara et al. 2010a). Indeed the Mediterranean species *C. inornata* was placed in a group comprising three congeneric species and *Crispatotrochus rugosus*. The other Mediterranean species included in the dataset, *P. pulchellus*, was sister to *Polycyathus muellerae*, a shallow-water coral occurring also in the Mediterranean Sea. Although the majority of shallow-water scleractinian families are polyphyletic, Arrigoni et al. (2014) confirmed the monophyly of Dendrophylliidae using molecular phylogeny, micromorphology and skeleton microstructure. In their study, sequences of five Mediterranean species were included, two of which *Dendrophyllia cornigera* and *L. pruvoti* occur in deep waters, although the latter is of predominant shallow-water occurrence. Genetic studies on the Mediterranean *Desmophyllum dianthus* and *Lophelia pertusa* have been performed by Addamo et al. (2012, 2015), but see also Boavida et al. (this volume). Addamo et al. (2012) sequenced two nuclear (ITS and 28S rRNA) and two mitochondrial (16S rRNA and COI) markers of several deep-sea scleractinians, among which some were collected in the Mediterranean Sea. Although mostly from the North-eastern Atlantic, there are several molecular studies available on population genetics of *L. pertusa* (Le Goff-Vitry et al. 2004a; Le Goff-Vitry and Rogers 2005; Dahl 2013). Comparative analyses among complete mitochondrial genomes of Mediterranean and Norwegian *L. pertusa* populations were done by Flot et al. (2013). Regarding the mitochondrial DNA, few complete mitogenomes of Mediterranean deep-sea scleractinians were until now sequenced and published (i.e., *D. dianthus* by Addamo et al. 2016; *M. oculata* by Lin et al. 2012, and *L. pertusa* by Emblem et al. 2011).

Significant changes in the phylogenetic relationships are expected whenever more studies using different molecular markers become available. In the meantime, the current tendency in scleractinian taxonomy is to avoid a subordinal classification.

Mediterranean Species

Thirty deep-water scleractinians belonging to seven families, and an additional species of uncertain taxonomic ascription (*Cladocora debilis*, see Hoeksema and Cairns 2013), are known from the Mediterranean basin. Among these, five have only been collected dead, with a definitely fossil aspect or included in lithified sediment (*Caryophyllia ambrosia*, *C. atlantica*, *C. sarsiae*, *Schizocyathus fissilis*, *Trochocyathus mediterraneus*) (Zibrowius 1980; Pardo et al. 2011; Taviani et al. 2011; Vertino and Corselli, this volume) and therefore cannot be considered part of the extant fauna or definitely extinct. Only one species is endemic (*C. magnaghii*), and four are considered CWCs: *D. cornigera*, *D. dianthus*, *L. pertusa* and *M. oculata* (see Chimienti et al., this volume and

Table 14.3 Some morphological characteristics of the Mediterranean deep-sea Scleractinia

Species	Corallum shape	Colony form	Corallum attachment	Maximal GCD (mm)	Columella	Pali/paliform lobes	Septal cycles	Remarks
Family Caryophylliidae								
Anomocora fecunda	Colonial	Elongate and cylindrical	a	12	Trabecular	P2–P3	S1–S4	Budded corallites detach from parent
Caryophyllia inornata	Cylindrical/turbinate	–	a	12	Variable, fascicular	Absent/P3	S1–S5	Can form small pseudocolonies by fixation of juveniles on adults. S5 rarely complete
Caryophyllia calveri	Cylindrical/turbinate	–	a/f	15	Fascicular	P3	S1–S4	Septa arranged decamerally or hexamerally
Caryophyllia cyathus	Cylindrical/turbinate	–	a	30	Fascicular	P4	S1–S5	
Caryophyllia smithii	Cylindrical/trochoid	–	a/f	35	Fascicular/spongy	P3	S1–S5	S5 rarely complete
Ceratotrochus magnaghii	Cylindrical	–	a	8	Trabecular	Absent	S1–S4	
Coenocyathus cylindricus	Colonial	Phaceloid	a	11	Papillose	P3	S1–S4	Exceptionally, a few S5
Coenocyathus anthophyllites	Colonial	Phaceloid	a	9	Papillose	Absent	S1–S4	
Desmophyllum dianthus	Cylindrical/flared	–	a	80	Absent/a few rods	Absent	S1–S5	Corallum highly variable; GCD in Mediterranean specimens smaller
Hoplangia durotrix	Colonial	Incrusting/slightly ramified	a	6	Absent	Absent	S1–S4	Exceptionally, a few S5
Lophelia pertusa	Colonial	Dendroid	a	15	Absent/a few rods	Absent	Septa not arranged in regular systems	
Paracyathus pulchellus	Cylindrical/trochoid	–	a	20	Papillose	P1–P4	S1–S5	S5 rarely complete
Pourtalosmilia anthophyllites	Colonial	Bushy	a	11	Fascicular	(P2) P3	S1–S4	Exceptionally, a few S5
Thalamophyllia gasti	Colonial	Reptoid	a	6	Absent	Absent	S1–S3	
Family Dendrophylliidae								
Balanophyllia cellulosa	Trochoid	–	a/f	22	Spongy/fascicular	Absent	S1–S4	
Dendrophyllia cornigera	Colonial	Bushy	a	22	Spongy	Absent	S1–S4	
Dendrophyllia ramea	Colonial	Arborescent	a	16	Spongy/papillose	Absent	S1–S4	

(continued)

Table 14.3 (continued)

Species	Corallum shape	Colony form	Corallum attachment	Maximal GCD (mm)	Columella	Pali/ paliform lobes	Septal cycles	Remarks
Leptopsammia pruvoti	Turbinate/ cylindrical	–	a	17	Spongy	Absent	S1–S5	Septa not arranged according to Pourtalès plan in adult stage. S5 rarely complete
Family Flabellidae								
Javania cailleti	Ceratoid	–	a	40	Fusion of axial edges of S1–S2	Absent	S1–S4	Subfossil specimens up to 65 mm in GCD
Monomyces pygmaea	Cylindrical/ conical/ compressed	–	a	24	Papillose	Absent	S1–S4 (S5)	Attachment reinforced by rootlets
Family Guyniidae								
Guynia annulata	Cylindrical, scolecoid	–	a/f	1.4	A single ribbon	Absent	S1–S2	Septa octamerally arranged
Family Stenocyathidae								
Stenocyathus vermiformis	Cylindrical, vermiform	–	a/f	4	Absent/1–3 twisted ribbons	P2	S1–S3	
Family Oculinidae								
Madrepora oculata	Colonial	Dendroid	a	4	Absent/spongy	Absent	S1–S3	
Family Turbinoliidae								
Sphenotrochus andrewianus	Cuneiform	–	f	~6	Lamellar	Absent	S1–S3	
Scleractinia Incertae Sedis								
Cladocora debilis	Colonial		f	3	Papillose	(P1) P2	S1–S3	The colony lives attached in young stages

Px, Sx Pali and septa of cycle designated by numerical script, *a* corallum attached, *f* corallum free

For an explanation of the terminology we refer to Cairns and Kitahara (2012), and for full descriptions and iconography of the species we refer to Zibrowius (1980)

Table 14.2). No less than 11 of the extant species were first described from the Mediterranean Sea, most of them during the eighteenth and nineteenth centuries (Table 14.2).

Our knowledge of the scleractinian deep-water corals diversity could be considered satisfactory since the monograph of Zibrowius (1980). Thus, and despite new research undertaken in poorly studied deep-sea areas (e.g., Galil and Zibrowius 1992; Mastrototaro et al. 2010; Angeletti et al. 2014; Bo et al. 2011, 2012a, 2015), very little has been added in terms of biodiversity to Zibrowius' results, with only *Anomocora fecunda* newly recorded from the Alborán Sea (Pardo et al. 2011; OCEANA 2014). The latest new species discovered from the basin was also described in this paper (Zibrowius 1980, *T. mediterraneus*, only dead specimens known).

Caryophylliidae is the most diverse Mediterranean family, with 14 extant species distributed in 10 genera. Similar to other families, monophyly is not supported (Daly et al. 2007) and future taxonomic changes may apply whenever additional integrated morphological and molecular studies are undertaken. *Anomocora*, *Coenocyathus*, *Hoplangia*, *Lophelia*, *Pourtalosmilia* and *Thalamophyllia* include colonial corals. *Caryophyllia*, *Ceratotrochus*, *Desmophyllum* and *Paracyathus* are solitary. Apart from *Caryophyllia smithii* that may thrive on both hard- and soft-bottoms ("*Caryophyllia clavus*", see Zibrowius 1980), all extant *Caryophyllia* are, after the current knowledge, hard-bottom corals. Mediterranean caryophylliids can be distinguished by the external features of the skeleton (Fig. 14.1a, Table 14.3). As for the colonial species, calicular structures of *Coenocyathus* are similar to *Caryophyllia*, differing only from the fact that they form small phaceloid colonies. Both *Coenocyathus* species (*C. cylindricus*, *C. anthophyllites*) are uncommon and poorly known. *Lophelia pertusa* has analogous calicular structures than *D. dianthus*, but forms large dendroid colonies (Fig. 14.5d, f; see Addamo et al. 2016). The morphological affinity shown by these two genera was also detected under molecular analysis, therefore a taxonomic re-allocation of *L. pertusa* was recently proposed as *Desmophyllum pertusum* (Addamo et al. 2016; Boavida et al., this volume; Addamo, this volume).

Species of the family Dendrophylliidae have a porous wall and usually an arrangement of septa in Pourtalès plan (fusion o septa forming triangles) at least during some stages of the skeletal ontogeny (Cairns 2001) (Fig. 14.1b). Four Mediterranean species live in deep water, namely *Balanophyllia cellulosa*, *D. cornigera*, *Dendrophyllia ramea* and *L. pruvoti*. Both *Dendrophyllia* species, commonly known as yellow and pink corals respectively, are colonial, forming three-dimensional structures growing by extratentacular budding on hard bottoms (Figs. 14.1b and 14.5a–c). *Dendrophyllia ramea* forms arborescent colonies up to 1 m in height, while *D. cornigera* typically has a small and bushy colony with sparse irregular branching (Zibrowius 1980). According to Zibrowius (1980, 2003), these two species differ in geographical and depth distribution; *D. ramea* is abundant in the southern area of the western basin at 40–75 m depth, whereas *D. cornigera* has a larger occurrence (including the Aegean Sea) with a bathymetric distribution ranging from 80 to 600 m (see a distribution map in the chapter by Chimienti et al., in this volume). However, recent discoveries revealed the presence of *D. ramea* in deeper locations (between 125 and 170 m) off Cyprus in the Levantine Mediterranean (Orejas et al. 2017) and in the Menorca channel (~240 m, Jiménez et al. 2016). The corallum of *Balanophyllia* and *Leptopsammia* is solitary. They differ from each other principally for their septa arrangements according to Pourtalès plan in the adult (*Balanophyllia*), or in a normal insertion pattern (*Leptopsammia*). *Balanophyllia cellulosa* is an uncommon coral with a fragile skeleton that lives on soft-bottoms, while *L. pruvoti* is very abundant. It lives from rather shallow depths down to submarine canyons at 100–150 m (Zibrowius 1980).

Species of the family Flabellidae are epithecate solitary corals lacking costae but usually bearing chevron-shaped growth ridges that peak at major septa (Cairns 2000). This family includes two Mediterranean species occurring in deep-water, *Javania cailleti* and *M. pygmaea*, with the latter living mostly at shallow depths. Both are distinguished by their habitat and external morphology (Table 14.3). *Javania cailleti* is an uncommon bathyal coral living at 400–660 m depth that can grow up to 70 mm in height (Zibrowius 1980). The corallum has a long pedicel, a flared calyx with highly exsert septa, and a snow-white and porcelaneous wall. *Monomyces pygmaea* is smaller in size, up to 27 mm in height, and has a wall with horizontal ridges. The corallum is almost cylindrical, of brownish to pinkish colour, and its attachment is reinforced by rootlets. This coral has been found in the western basin and the Adriatic Sea down to 150 m depth (Zibrowius 1980).

Corals in the families Guyniidae and Stenocyathidae are of singular, somehow vermiform morphology, small calicular diameter and distinctive skeletal structure. Two species, *G. annulata* and *S. vermiformis*, are widely distributed in the Mediterranean Sea (Zibrowius 1980). Despite formerly included within the family Guyniidae, the singular skeletal features of *S. vermiformis* justified its recent inclusion in a different family (Stenocyathidae) (see Stolarski 2000). *Guynia annulata* inhabits in a broad bathymetric range from shallow waters to bathyal bottoms; *S. vermiformis* is more restricted to deep-circalittoral and bathyal communities, commonly associated to the white coral frameworks, although it may be free-living as well (Zibrowius 1980). Dead, although fresh-looking specimens of *S. fissilis* (Schizocyathidae), have been collected by Taviani et al. (2011) at ~1120 m depth in the Aegen Sea. Unless live speci-

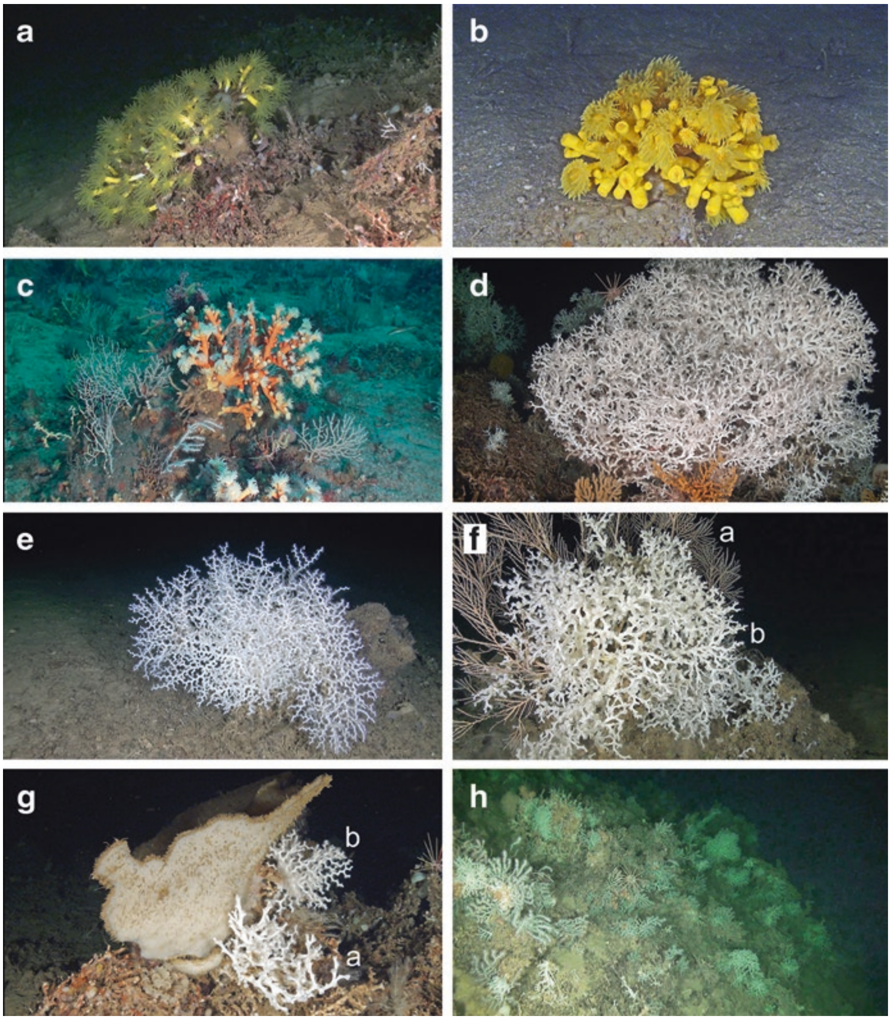

Fig. 14.5 (**a**) *Dendrophyllia cornigera* ("yellow coral") Catifas Bank, Alborán Sea, 400 m. (**b**) *D. cornigera*, off Calahonda, Málaga, 230 m. (**c**) *Dendrophyllia ramea*, Chella Bank, Alborán Sea, 100 m. (**d**) *Lophelia pertusa*, Cabliers Bank, Alborán Sea, 300 m. (**e**) *Madrepora oculata*, off Malta, 500 m. (**f**) *Callogorgia verticillata* (a) and *L. pertusa* (b), off Malta, 850 m. (**g**) *Lophelia pertusa* (a), *M. oculata* (b), Catifas Bank, 400 m. (**h**) White coral bank with *M. oculata* and numerous plexaurids, off Malta, 700 m. (Photographs: **a–d**, **g**: © OCEANA; **e**, **f**, **h**: OCEANA/© LIFE BaĦar for N2K)

mens are discovered, this species can not currently be included in the Mediterranean extant fauna inventory.

Madrepora oculata is the only deep-sea Mediterranean Oculinidae. It forms big-sized colonies whose branches may anastomose acting as substrate and providing refuge to many vagile and sessile organisms (Fig. 14.5e, h). This coral occurs throughout the Mediterranean basin, although is more commonly collected dead as often happens with *L. pertusa* (Zibrowius 1980).

The unique Mediterranean turbinoliid is *Sphenotrochus andrewianus*, a small solitary and unattached coral with a cuneiform corallum that is adapted to live in the interstices of coarse sands (see Cairns 1997).

Although was formerly assigned to the families Faviidae and to Caryophylliidae, the current taxonomic placement of *C. debilis* is still uncertain (see Hoeksema and Cairns 2013). It builds small colonies formed by extra-tentacular budding.

Overall, the number of solitary (14) and colonial (11) Mediterranean deep-sea scleractinians is similar. Differences are notable in terms of type of substrates, as most species inhabit only hard bottoms (19). Only three are typical of soft-bottoms (*B. cellulosa*, *C. debilis*, *S. andrewianus*), and three occur in both types of bottoms (*C. smithii*, *G. annulata*, *S. vermiformis*) (Table 14.2). Only one colonial species inhabits soft-bottoms (*C. debilis*). The scarce number of free-living Mediterranean scleractinians is worth mention (Table 14.3), particularly if compared with nearby Atlantic areas (see final Overview).

Remarkable Sites and Distribution

Vafidis (2010) reported the geographic distribution of scleractinians along five Mediterranean sectors. In this book there is also a chapter on the Mediterranean biogeographical distribution of CWCs (see Chimienti et al., this volume). With 25 known species, the highest diversity is in the western part of the basin, whereas with only ten species recorded the lowest diversity is in the Levantin basin. Given that some of these corals have a broad bathymetrical range (including shallow waters), they probably do not thrive in the deep waters of every sector. Concerning the species that are principally limited to the bathyal zone, the most widely distributed are *L. pertusa* and *M. oculata*, which occur in all five zones. On the contrary, *A. fecunda* (newly recorded after Vafidis' review), *B. cellulosa* and *J. cailleti* are uncommon and occur only in one sector.

Lophelia pertusa and *M. oculata* are of great importance in the deep-sea environments as they are structuring species in the so-called "white coral" communities (Pérès and Picard 1964; Zibrowius 2003; Freiwald et al. 2009) (Fig. 14.5h). Both species fall into the CWC concept according to their morphological features and depth distribution. They are scarce in the Mediterranean Sea (Taviani et al. 2005) and may be considered "relict species" from coldest phases (Taviani 2002; Taviani et al. 2011, this volume). Freiwald et al. (2009) pointed out the 14 known Mediterranean zones harbouring live white coral banks. We refer to other chapters in this volume for new information and distribution maps of these exceptional sites. One of these sites, the Cassidaigne canyon off Marseille, has been the subject of intensive research (see Fourt et al., this volume), even by direct observation as early as the late 1950s, and its fauna is one of the best documented (see Zibrowius 2003). Several species studied by Zibrowius (1980) (e.g., *M. oculata*, *C. debilis*, *C. calveri*, *C. cyathus*), were collected therein.

14.3.1.3 Order Zoantharia

This order mostly includes colonial species, many of which interact with other invertebrates establishing different kinds of associations. Almost all species are soft-bodied, have colonies frequently incrusted with sand and other particles, and lack a calcareous or proteinaceous skeleton with the exception of the genus *Savalia* which has a horny axis. Zoanthid polyps have two cycles of retractile tentacles, and their internal anatomy is distinctive, with mesenteries arranged in pairs some of which are incomplete (see Häussermann et al. 2003a).

Zoanthids are distributed worldwide and occur in a wide bathymetric range. Numerous new species will be probably described, as there might be an important cryptic diversification (see Sinniger et al. 2008, 2010, 2013), including the European seas, where a revision of its fauna is needed.

Taxonomy and Taxonomic Characters

Zoanthids have been traditionally identified based on the internal anatomy of the polyps, their external morphology, and sometimes also with the aid of the cnidome. For instance, separation between suborders Macrocnemina and Brachycnemina is based on the presence/absence of perfect (macrocnemic) and imperfect (brachycnemic) mesenteries (see Daly et al. 2007). The body plan is relatively simple and many species frequently show remarkable intra-specific plasticity (Alves Santos et al. 2015 and references therein); thus, species delimitation using external morphological characters is often difficult. The utility of cnidome (cnidae types and size ranges) for species discrimination among zoanthids needs further investigations (see Sinniger and Häussermann 2009).

Molecular Aspects

Molecular analyses using mitochondrial 16S ribosomal RNA and COI have introduced significant changes in the systematics of the order, contributing therefore to the description of newly proposed genera and species mostly from the Indo-Pacific (Sinniger et al. 2010, 2013). In addition, the use of molecular markers was exploited for the differentiation of morphologically cryptic species (Kise and Reimer 2016), taxonomic revisions (Risi and Macdonald 2015) and the assessment of species diversity from different geographic areas (e.g., Reimer et al. 2008). The current descriptions of new species in the order are hardly conceived without molecular comparative analyses.

Molecular analyses on the unique Mediterranean species (*Savalia savaglia*) have been done by Sinniger et al. (2007). Analyses performed on Atlantic individuals of this species showed no significant differences (Altuna et al. 2010).

Mediterranean Species

As shown by its colony structure and depth range, *S. savaglia* (Parazoanthidae) is the only Mediterranean deep-water coral of the order Zoantharia. A description of the species including internal anatomy was given by Lacaze-Duthiers (1864a), Carlgren (1895) and Ocaña and Brito (2004). Ocaña and Brito (2004) studied the cnidome of individuals from two Mediterranean localities. The species is recognised by its big-sized yellow, orange or whitish colonies commonly ramified in a plane having a horny axis, and soft fleshy polyps. These are up to 5 mm wide and 6 mm high (preserved material) and have up to 27 tentacles arranged in two cycles (Ocaña and Brito 2004). The systematics of this species has been problematic, principally due to the axis composition which resembles that of antipatharians. Nevertheless, the anatomy of the polyps, the absence of spines, and the cnidome indicate that this species belongs to Zoantharia (see Carlgren 1895; Roche and Tixier-Durivault 1951).

Savalia savaglia, called "false black coral", is a long-lived species and probably a slow-growing organism (see Druffel et al. 1995), which colonies create elevated and complex tertiary structures (Cerrano et al. 2010) that may be used as substrate by other organisms (Lacaze-Duthiers 1864a; Zibrowius 1985a). Cerrano et al. (2010) observed that the presence of *S. savalia* was associated with a significantly increased availability of substrates and enhanced biodiversity. *Savalia savaglia* commonly shares the habitat with the sea fan *Paramuricea clavata* and can cause necrosis covering progressively its axis (Zibrowius 1985b).

The capability of forming monospecific facies of hundreds of colonies have led to consider *S. savaglia* as habitat-forming and a vulnerable species. This species is protected in some of the Mediterranean countries, as was included in the convention for the conservation of European wildlife and natural habitats held in Bern in 1979, and more recently in the SPA/BD Protocol of the Barcelona Convention 1995 (Otero et al. 2017; Otero and Marin, this volume).

Remarkable Sites and Distribution

The false black coral has been considered a Mediterranean endemic species restricted to the western basin, the Adriatic Sea and the Aegean Sea (see Vafidis 2010). However, colonies were recently identified in some Atlantic sites (Altuna et al. 2010).

Within the Mediterranean basin, *S. savaglia* has a bathymetric range of 15–900 m (Giusti et al. 2015). Its occurrence is better documented from the western basin where is currently overall uncommon (Zibrowius 1985a, b; Cerrano et al. 2010; Giusti et al. 2015). Despite its scarceness, exceptional populations have been discovered in the Adriatic Sea with hundreds of colonies forming monospecific facies (Giusti et al. 2015). Mediterranean records from the Iberian Peninsula are few and include the Alborán Sea (Pardo et al. 2011). Since it is easily recognisable (due to its morphology and size that can exceed one meter in height), the scarcity of records in shallow waters seems to reflect its relative rareness or restriction to deeper depths. This coral may occur elsewhere in the Mediterranean Sea under favorable environmental conditions and protected from human impacts.

14.3.2 Class Anthozoa, Subclass Octocorallia

Octocorals are solitary or colonial anthozoans with octomerous symmetry and varied morphologies, mostly living in deep waters (Cairns 2007; Yesson et al. 2012; Pérez et al. 2016). Polyps have eight tentacles with lateral extensions or pinnules (pinnule-less species have been described in the Indo-Pacific Ocean, Alderslade and McFadden 2007), eight perfect mesenteries and a single ventral siphonoglyph. Polymorphism occurs in some groups.

All Mediterranean deep-sea octocorals are colonial and mostly present calcareous components (sclerites, Fig. 14.2e–g) embedded in the tissues, which provide solidity to the colony. They are included in two orders, Alcyonacea and Pennatulacea whose species have remarkably different morphologies (Figs. 14.6, 14.7, 14.8, 14.9 and 14.10). Pennatulaceans are almost exclusively adapted to soft-bottoms.

We refer to Hyman (1940), Bayer (1956), Fabricius and Alderslade (2001) and Weinberg and Ocaña (2003), for studies on the anatomy and morphological characteristics of the different orders, families and genera. A glossary including the morphological and anatomical terms applied to the subclass Octocorallia, and a comprehensive illustration with the different sclerite types were compiled by Bayer et al. (1983).

14.3.2.1 Order Alcyonacea

The order Alcyonacea constitutes a group of almost exclusively colonial octocorals including approximately 30 families of soft corals and sea fans (Daly et al. 2007). They are morphologically heterogeneous as shown by their colony forms that may include creeping colonies and fleshy masses lacking a skeletal axis, whip-like, fan-like, and tree-like structures profusely branched and axis of various nature (Figs. 14.2a–c, 14.6, 14.7 and 14.8). Some species are habitat-forming CWCs and can structure single- or multi-species assemblages (Yesson et al. 2012; Grinyó et al. 2016; Gori et al., this volume).

Five sub-ordinal divisions of the Alcyonacea include Mediterranean species. Although they are not fully supported by molecular data (some are polyphyletic groups, see

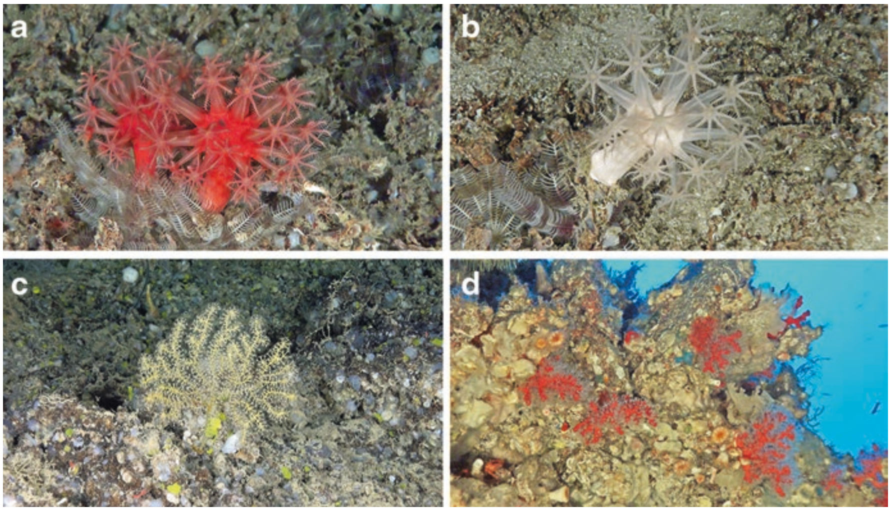

Fig. 14.6 (**a**, **b**) *Anthomastus* sp., Cabliers Bank, Alborán Sea, 350–400 m. (**c**) *Acanthogorgia* sp., off Malta, 745 m. (**d**) *Corallium rubrum*, Chella Bank, Alborán Sea, 150 m. (Photographs: **a**, **b**, **d**: © OCEANA; **c**: © OCEANA/© LIFE BaĦar for N2K)

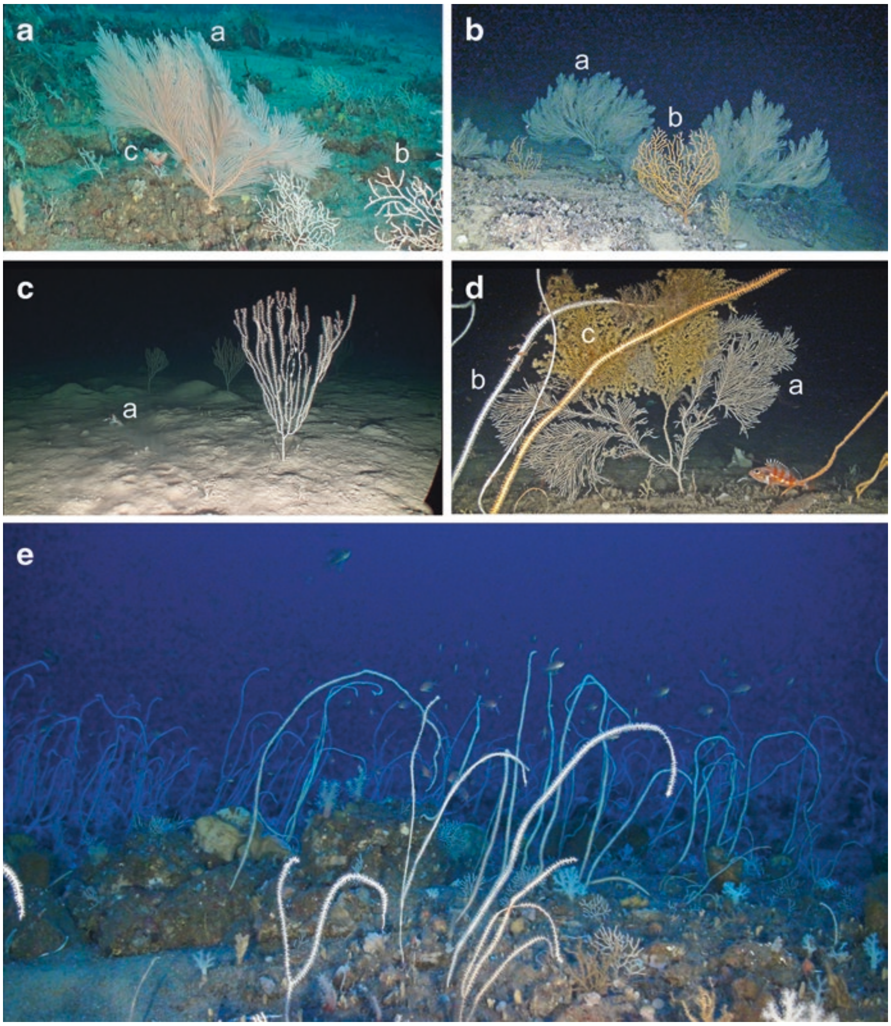

Fig. 14.7 (**a**) *Callogorgia verticillata* (a), *Eunicella* sp. (b) and *Alcyonium* sp. (c), Chella Bank, Alborán Sea, 110 m. (**b**) *C. verticillata* (a) and a plexaurid (b), probably *Placogorgia*, Balearic Islands, 600 m. (**c**) *Isidella elongata*, Balearic Islands, 460 m. Note *Nephrops* (a) on the left. (**d**) *C. verticillata* (a) and *Viminella flagellum* (b), Chella Bank, 330 m. Note epizoic zoanthid on the former (c). (**e**) A *V. flagellum* garden, with several other coral species, Chella Bank, 130 m. (Photographs: © OCEANA)

McFadden et al. 2006), they are still adopted for taxonomic simplicity (Daly et al. 2007). Based on morphology, Mediterranean alcyonarians fit into these sub-ordinal groups, except perhaps for one stoloniferan (*Rolandia coralloides*), which has strong affinity with Alcyoniina (Ocaña et al. 2000b). Some authors, however, disagree and do not recognise a "suborder" status for some of these groups. These divisions are: (i) Alcyoniina, whose colonies have polyps arising from a massive, lobate, coenenchymatous mass; (ii) Holaxonia with usually tree-like colonies with a horny axis formed by scleroproteinaceous layers around a hollow central core (Fig. 14.2a); (iii) Scleraxonia, that have an axial structure made up of loose to more or less firmly cemented sclerites by a horny material, which may even acquire a stony consistency; (iv) Calcaxonia including species that have a solid axis lacking a central hollow core, and nonscleritic calcareous (calcite or aragonite) material and (v) Stolonifera with simple polyps arising from reticulating ribbon-like or membranous stolons creeping upon the substrate, or forming branching colonies that arise from the stolon with a primary polyp producing secondary polyps from its wall.

Taxonomy and Taxonomic Characters

Identification of alcyonaceans is frequently difficult due to their plasticity, and the large variability of the taxonomic characters used to distinguish them. The characters useful for other cnidarians such as the internal anatomy and cnidome are often too uniform and of little help for most octocorals. Bayer (1961) divided the characters used for octocoral classification into those pertaining the colony as a whole (size and shape, pattern of branching, distribution of polyps, dimorphism), and those related to the skeletal elements (axis structure, sclerites). Taxonomic separation into families is traditionally done by considering the growth form of the colony, the structure of the axis (if present), and its composition; identification at genus and species levels is mostly based on the shape, size and distribution of the sclerites in the different portions of the colony (Daly et al. 2007). In some cases, occurrence of certain sclerites is crucial for

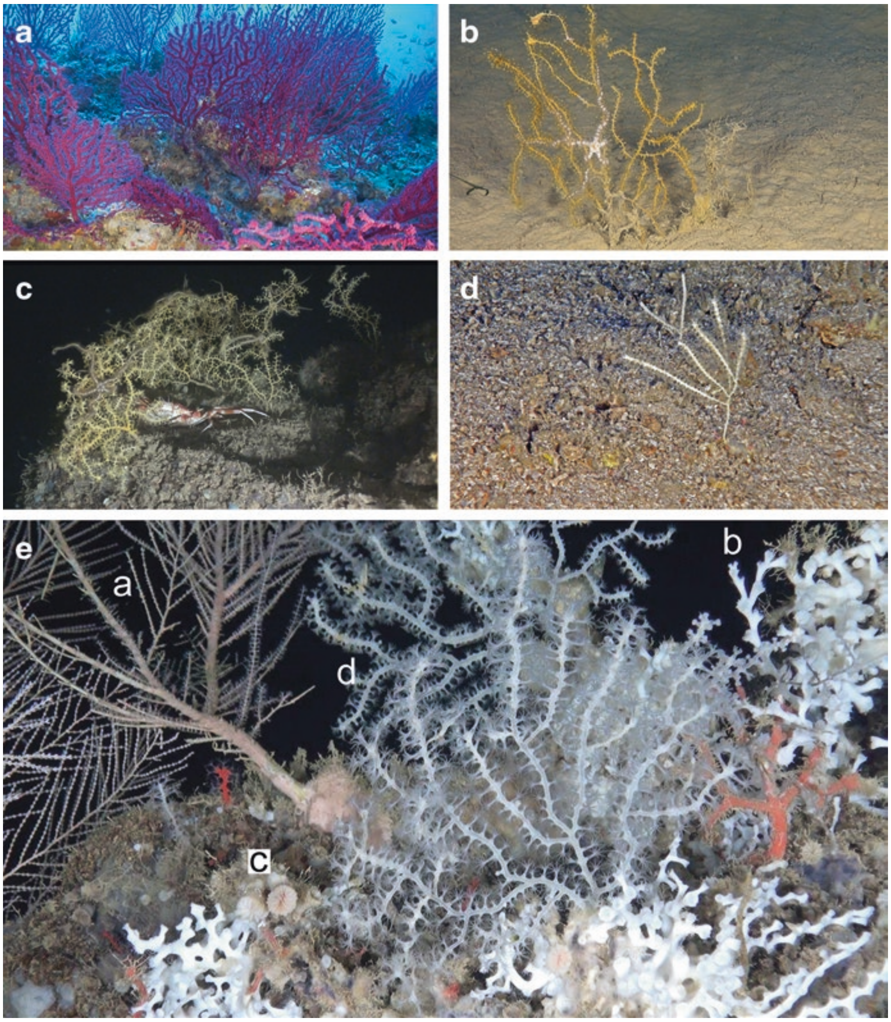

Fig. 14.8 (**a**) *Paramuricea clavata*, Balearic Islands, 75 m depth. (**b**) *Paramuricea macrospina*, off Malta, 300 m depth. Note epibiont brittle star. (**c**) *Placogorgia* sp., Chella Bank, Alborán Sea off Spain, 460 m. (**d**) *Swiftia pallida*, Chella Bank, 255 m. (**e**) Close-up image of a CWC community, with *Callogorgia verticillata* (a), *Lophelia pertusa* (b), solitary scleractinians (c, *Desmophyllum*?) and plexaurids (d, *Muriceides*?), off Malta, 895 m. (Photographs: **a**, **c**, **d**: © OCEANA; **b**, **e**: OCEANA/© LIFE BaĦar for N2K)

genus-level identification (*Bebryce*, *Ellisella*, *Eunicella*, *Leptogorgia*) (Fig. 14.2e–g).

An identification key to the Mediterranean gorgonians and descriptions of all the species were given by Carpine and Grasshoff (1975). Additional descriptions were provided by Grasshoff (1972, 1973, 1977, 1992), Weinberg (1976), and Weinberg and Grasshoff (2003). Circalittoral Mediterranean Alcyoniina and Stolonifera were revised by Weinberg (1977, 1978). Except for sea-pens (Pennatulacea), Bayer (1981) published a key for the identification of the octocoral genera occurring worldwide.

Molecular Aspects

The phylogenetic relationships of the Mediterranean alcyonaceans are poorly known, and the studies so far conducted are principally based on shallow water colonies of well-known species. According to the sequences so far available on GenBank, less than 50% of the Mediterranean species have been considered for molecular-based studies. Among these, the majority pertain to shallow-water species. Except for *Paramuricea macrospina*, most of the deep-sea endemics or near endemics were until now under-investigated. An exception is represented by *Corallium rubrum*, whose ecology, reproduction and genetics were largely explored in the last decades due to its commercial importance in jewelry (see Tsounis et al. 2010; Jiménez and Orejas 2017). Population-level studies have been performed aiming to investigate the structure and relationships at different bathymetric and spatial scales (e.g., Ledoux et al. 2010; Costantini et al. 2013; Bramanti et al., this volume and references therein). The transcriptome of the red coral has been recently published, broadening therefore our knowledge on population and adaptive genetics (Pratlong et al. 2015). The complete mitogenome of *C. rubrum* was sequenced by Uda et al. (2013) along with other precious corals. The Mediterranean species showed a different gene arrangement compared to some congenerics and high phylogenetic affinity with a species of *Paracorallium*. These data confirm that a taxonomic revision within Corallidae is required.

Mediterranean specimens of *Alcyonium* spp. were analysed for population genetics (McFadden 1999), phylogenetic reconstructions (McFadden et al. 2001), hybdridisation

(McFadden and Hutchinson 2004) and DNA-barcoding (McFadden et al. 2011).

The genetic structure of *Paramuricea clavata*, *Eunicella cavolini* and *E. singularis* was investigated by Valente et al. (2010), Mokhtar-Jamaï et al. (2011), Costantini et al. (2016) and Masmoudi et al. (2016). Costantini et al. (2016) utilised Mediterranean colonies of *E. cavolini*, *E. singularis* and *Eunicella verrucosa* for tracing the phylogenetic relationships among *Eunicella* species. Recently, two mitochondrial markers (mtMutS and COI) were used for phylogenetic comparisons among a newly described Mediterranean CWC species (*Chironephthya mediterranea*) and members of the genera *Chironephthya* and *Siphonogorgia* (López-González et al. 2014). The molecular data showed a strong affinity between the Atlantic and Mediterranean forms as already highlighted for other anthozoans. In this regard, Poliseno et al. (2017) recovered *Paramuricea* polyphletic and the phylogenetic tree inferred showed clear divergence between the two Mediterranean endemic gorgonians *P. clavata* and *P. macrospina*. The molecular dating and biogeographic analyses performed on a set of Atlanto-Mediterranean *Paramuricea* highlighted the role of geological events such as the Messinian Salinity Crisis for the speciation and evolution of the genus in the Mediterranean basin.

Mediterranean Species

Vafidis et al. (1994) analysed the Mediterranean alcyonacean fauna reporting details on the bibliography, the biogeography and diversity of these organisms. Subsequently, Vafidis (2010) reviewed the previous inventory and listed 41 Mediterranean alcyonarian species from shallow to deep waters. After excluding the shallow water species and adding the new records, the deep-water fauna consists of 40 alcyonarians. Three are habitat-building bathyal species at depths higher than 200 m (CWCs) (Table 14.2). At least 24 species were first described from the Mediterranean Sea, and seven were already known in the eighteenth century (Table 14.2). Most are hard-bottom species and only six are adapted to live on soft-bottoms (Table 14.2). Calcaxonia, Holaxonia and Scleraxonia (the so-called gorgonians or sea fans), are perhaps the most "popular" habitat-forming alcyonaceans (Figs. 14.7 and 14.8). Attribution of a given Mediterranean species to any of the different suborders, families or genera is, with some exceptions, not difficult due to their morphological differences. However, species identification is frequently challenging.

The Mediterranean Alcyoniina are included in three families (Alcyoniidae, Nidaliidae, Paralcyoniidae) differing in colony structure. Paralcyoniidae is the only family characterised by the capability of its species to retract the polyparium into the base. Among the seven Alcyoniina inventoried, four were first described in the Mediterranean basin (*Alcyonium acaule*, *A. coralloides*, *A. palmatum*, *Paralcyonium spinulosum*). Weinberg (1977) revised these species, by depicting large series of sclerites and by showing differences in the colony structures and sclerome. Mediterranean *Alcyonium* was also investigated by Verseveldt (1964), who clarified the differences between *A. acaule* and *A. palmatum*. *Alcyonium palmatum* is a typical sessile species occurring in muddy circalittoral communities; it settles on pebbles, shells and other similar substrates (Pérès and Picard 1964), while *A. coralloides* commonly overgrows on holaxonians such as *Eunicella*, *Leptogorgia* and *Paramuricea* (Carpine and Grasshoff 1975; Weinberg 1975, 1977). *Anthomastus* sp. is a dimorphic mushroom-shaped coral with a short stalk lacking polyps and a globose capitulum with large autozooids and small siphonozooids (Fig. 14.6a, b). *Nidalia studeri*, for long time considered an obscure species, has been recently re-described using material collected in the Menorca channel (López-González et al. 2012). This species has a stalk devoid of polyps and a capitulum with polyps, reminding *Anthomastus*, but it lacks siphonozooids, and the anthocodial sclerites are arranged in a collaret ('crown') and points (Fig. 14.2d) (López-González et al. 2012). In the collaret, the sclerites are arranged transversely in a ring below the tentacles; the points are eight rows of sclerites placed in chevron in the distal part of the anthocodia (see Bayer et al. 1983, plate 2). The newly described *Chironepthya mediterranea* was also collected in this channel (López-González et al. 2014). *Daniela koreni* (Nephtheidae) is another obscure species in need of evaluation that was collected by von Koch (1891) from the bay of Naples at 100 m depth. A population probably pertaining this species has been observed by López-González et al. (2012) at the same depth off Menorca and could be added to the Mediterranean inventory whenever new studies become available.

Among calcaxonians there are eigth Mediterranean species included into four families with different structure of the axis and morphology of sclerites. The three Mediterranean alcyonaceans considered CWCs are calcaxonians (*Callogorgia verticillata*, *Isidella elongata*, *Viminella flagellum*). Family Isididae is exceptional in having a jointed axis in which calcareous internodes are alternated with horny nodes made of gorgonin. There are three Mediterranean species in two genera, *Acanella arbuscula*, *A. furcata* and *I. elongata* that inhabit bathyal compact muds and are anchored to the substrate by a root-like base (Fig. 14.7c). *Acanella furcata*, described by Thomson (1929) and for a long time considered a synonym of *I. elongata* (see Carpine and Grasshoff 1975), has been resurrected by Saucier et al. (2017). *Isidella elongata* has been categorised as "critically endangered" in the UICN red list (see Otero et al. 2017; Otero and Marin, this volume). The species in the family Primnoidae have scale-like sclerites covering the axis and the polyps. In the wall of the polyps, they are usually arranged in rows. *Callogorgia verticillata* has big-sized white pinnate colonies with polyps arranged in pairs or whorls (Fig. 14.7a, b, d). Ellisellidae comprises three species in three genera (*Ellisella*, *Nicella* and *Viminella*) having colonies with a strongly calcified axis and small sclerites (see Grasshoff 1972; Carpine and Grasshoff 1975; Bayer and Grasshoff 1994) (Fig. 14.7d, e). Apart from the sclerites, differences in the colony shape of the three genera are marked (see Bayer and Grasshoff 1994). Colonies of *Viminella* are mostly flagelliform (Fig. 14.7e) while *Ellisella* and *Nicella* have ramified colonies. *Ellisella* has several long whip-like branches; *Nicella* repeatedly branch forming usually flabellate colonies with short end-branches. The geographic distribution in the Mediterranea Sea of *Ellisella paraplexauroides* is due to Angiolillo et al. (2012). Additionally, the distribution of *V. flagellum* was mapped by Giusti et al. (2012). Finally, Dendrobrachiidae comprises a single small-sized species recently described by López-González and Cunha (2010, *Dendrobrachia bonsai*). The enigmatic genus *Dendrobrachia* has a troubling taxonomic history due to its proteinaceous spiny axis and the lack of sclerites.

Holaxonians are the most diverse among Mediterranen deep-water alcyonaceans. They include 18 species in three families, Acanthogorgiidae, Gorgoniidae and Plexauridae. Several species are densely ramified in a plane or form tree-like colonies, although no one is considered a Mediterranean CWC. Usually, little information on the differentiation among the three families is given by the external structure of the axis, or the colony shape and branching pattern. Nevertheless, cross sections of the axis show significant differences in the structure. The Mediterranean holaxonian families are more easily recognisable by the types of sclerites and their arrangement in the polyps (see Carpine and Grasshoff 1975) (Fig. 14.2e–g).

In the Acanthogorgiidae species, polyps are not retractile, forming prominent calyces (Fig. 14.6c). Their armature is very characteristic, with numerous thin and long sclerites arranged in eight rows in chevron in the polyp wall, and long and thin strongly projecting spines at the base of the tentacles (see Grasshoff 1973; Bayer et al. 1983). There are two Mediterranean species: *Acanthogorgia armata* and *A. hirsuta* that can be distinguished by differences in the coenenchymal sclerites.

The Gorgoniidae comprises some of the most abundant and widely distributed Mediterranean species included in three genera, *Eunicella*, *Filigorgia* and *Leptogorgia* (Fig. 14.2a–c, e, f). These genera can be distinguished by their sclerome and colony habitus, with species ramified in a plane (e.g., *E. verrucosa*), bushy (e.g., *Leptogorgia sarmentosa*), or filiform (e.g., *Filigorgia guineensis*). Species descriptions including SEM images of the sclerome are available (see Carpine and Grasshoff 1975; Weinberg 1976; Grasshoff 1988, 1992; López-González 1993). The majority of the Mediterranean gorgoniids have a thick coenenchyme that is rich in small sclerites, principally spindles with whorls of tubercles (*Leptogorgia*, *Filigorgia*, see Carpine and Grasshoff 1975, Fig. 14.2f) and balloon clubs (*Eunicella*, Fig. 14.2e). The occurrence of balloon clubs help to quickly identify the species to genus level. Surface mounds, more or less prominent, into which the anthocodia fully retract are usually present in the Mediterranean gorgoniids. In *Leptogorgia*, retraction of the polyps commonly leaves a slit-like aperture in the coenenchyme (Fig.14.2b). Species of *Eunicella* and *Leptogorgia* are distinguished from their congeners by the morphology of the colony, colour, and sclerome. The colour and pattern of ramification are certainly variable in *Leptogorgia* colonies from the Alborán Sea, especially in individuals near the Strait of Gibraltar. If more than one species occurs, or these variants pertain to the widely distributed *L. sarmentosa*, should be further explored. *Eunicella* is the Mediterranean alcyonarian genus with the highest diversity. Six species are known and mostly occur at depths shallower than 50 m. Five species may be also found deeper than this limit (Table 14.2). Within gorgoniids there are two free-living species, *Eunicella filiformis* and *F. guineensis* (Grasshoff 1988, 1992; Ocaña et al. 2000a), considered a unique feature among Mediterranean alcyonarians.

Family Plexauridae is polyphyletic (Wirshing et al. 2005). It comprises seven genera and ten species of predominant deep-water occurrence (Table 14.2) that commonly have prominent calyces (Fig. 14.2d). The shape of the sclerites and their occurrence and arrangement in different parts of the colony (coenenchyme, calyces and anthocodiae) are important taxonomic features (Grasshoff 1977). Among the Mediterranean species the sclerites of the anthocodia are neatly arranged into a collaret and points (Fig. 14.2d). Sclerites are frequently big-sized and include characteristic forms that in some cases allow to promptly identify colonies to genus level (Carpine and Grasshoff 1975; Grasshoff 1977) (Fig. 14.2g). Species identification in some genera is a challenge as morphological characters like colony and sclerome are often highly variable. DNA analyses do not always show significant variations between different morphotypes, and in some cases intra- and inter-specific diversity may overlap. Genera like *Swiftia* need a taxonomic revision (Fig. 14.8d).

Mediterranean plexaurids occur mainly in deep waters forming moderately-sized colonies. By contrast, *P. clavata* may form robust colonies that can reach heights higher than 1 m (Weinberg 1976) (Fig. 14.8a). Branching pattern is variable, with some species having densely ramified colonies (*P. clavata*) and others with only few branches (*Spinimuricea* spp., *Swiftia pallida*). *Paramuricea clavata* is a key species in certain circalittoral communities and it has been recorded down to 110 m depth (Carpine and Grasshoff 1975). Other Mediterranean plexaurids (e.g., *Bebryce mollis*, *Muriceides* *lepida*, *Placogorgia coronata*, *P. massiliensis*, *Spinimuricea atlantica*, *S. klavereni*, *Villogorgia bebrycoides*) are poorly known as only rarely collected, and their role in the benthic communities is still understudied. In this respect, recent studies have shown that some species such as *B. mollis* may be abundant in the shelf edge and upper slope of the Menorca channel (Grinyó et al. 2016), a site with a high species richness of gorgonians. *Paramuricea clavata* and *P. macrospina* are known to provide substrata to several vagile and sessile animals of different phyla (Carpine and Grasshoff 1975). Scleraxonians in the Mediterranean Sea are limited to a single species. This is the eurybathic, slow-growing, and widely distributed *C. rubrum* know as the precious red coral (Fig. 14.6d). *Corallium rubrum* is characterised by its usually red to pink colour in both, axis and cortex and by its sclerome, with the lack of double clubs in the cortex (see Carpine and Grasshoff 1975; Bayer et al. 1983). The Corallidae have a continuous massive calcitic axis and loose sclerites in the polyps and coenenchyme. The axis may undergo fossilisation as shown by the coral remains and fossil records of species and genera (*Pleurocorallium*) now absent in the Mediterranean Sea. The majority of these fossils were identified in Mediterranean deposits of the Upper Miocene and Pleistocene (see Vertino et al. 2010). *Corallium rubrum* is distributed at unusual depths (600–800 m) in the Strait of Sicily as shown by Costantini et al. (2010) that detected a possible genetic isolation between deep and shallow populations. A monograph on this coral is due to Lacaze-Duthiers (1864b). Carpine and Grasshoff (1975) and Weinberg (1976) re-described the species and reviewed the taxonomic literature.

The six Mediterranean deep-water Stolonifera pertain five genera of the family Clavulariidae (*Clavularia*, *Rolandia*, *Sarcodyction*, *Scleranthelia*, *Telestula*). They are inconspicuous species with polyps arising from ribbons or thin membranes that cover the substrate (see Madsen 1944; Weinberg 1978, 1986; Ocaña et al. 2000b). Dead remains of another one, *Scyphopodium ingolfi* have been recently collected (Taviani et al. 2011). However, it is yet to be proven whether live colonies of this species occur in the Mediterranean Sea. The circalittoral species were revised by Weinberg (1978), who provided detailed descriptions and depicted long series of sclerites. Ocaña et al. (2000b) have solved long-lasting nomenclatural problems in *R.* and *Sarcodyction*, suggesting the possibility of moving *Rolandia coralloides* to the Alcyoniina. *Telestula septentrionalis* is characterised by its branching colonies arising from a band-like stolon and sclerome (Madsen 1944). The remaining species are differentiated principally by the shape and arrangement of the sclerites. The North-eastern Atlantic and Mediterranean species attributed to the genus *Clavularia* differ from the type species *Clavularia viridis*, and their generic position needs further evaluation.

Remarkable Sites and Distribution

Several species such as *B. mollis*, *E. cavolini*, *Clavularia marioni*, *N. studeri*, *P. spinulosum*, *P. macrospina* and *V. bebrycoides* were first described from the bay of Naples. Others were originally described as new species from this bay but later disregarded. These include *Gorgonia profunda* (= *E. verrucosa*), *Primnoa ellisii* (= *C. verticillata*) or *Evagora rosea*, tentatively ascribed to *R. coralloides* by Ocaña et al. (2000b).

Except for *Anthomastus*, known only from the Alborán Sea (OCEANA 2014), Alcyoniidae and Paralcyoniidae species are widely distributed in the Mediterranean basin including the Marmara Sea (Topçu and Öztürk 2015). On the contrary, *C. mediterranea* and *N. studeri* (Nidaliidae) are uncommon, occurring only deeper than 100 m in the western basin. The habitat-forming (CWC) *C. verticillata* and *I. elongata* are the most widely distributed calcaxonians in the Mediterranean Sea (see Vafidis 2010). Distribution maps of both and *V. flagellum* are given by Chimienti et al., in this volume. *Dendrobrachia bonsai*, is certainly uncommon, and is known from the Strait of Sicily, Corsica and the Alborán Sea (López-González and Cunha 2010; Sartoretto 2012). Among holaxonians, *A. hirsuta* (Acanthogorgiidae) has been largely considered the unique Mediterranean species of the genus occurring only in the western and Ionian basins (Vafidis 2010), yet *A. armata* is also known from the Alborán Sea (Ocaña et al. 2000a; Pardo et al. 2011). Most gorgoniids are widely distributed in the Mediterranean basin with the exception of the Levantine basin. The depth range of some species (e.g., *E. cavolini*, *E. verrucosa*, *L. sarmentosa*) is also wide, occurring from shallow waters to the bathyal. *Eunicella filiformis* and *E. guineensis* occur only in the Alborán Sea (Ocaña et al. 2000a). According to Vafidis (2010) all plexaurids are present in the western basin, whereas none is known from the Levantine basin. *Paramuricea clavata* and *P. macrospina* are the most widely distributed. *Corallium rubrum*, is known in all basins, although in several areas some populations are declining due to over-exploitation (e.g., Bruckner 2009, Tsounis et al. 2010).The distribution of stoloniferans was revised by Vafidis (2010). The highest species richness occurs in the western basin, with five out of six deep-water species known only therein. Data from other Mediterranean areas are scarce. The rarest species is *T. septentrionalis*, whose exclusive bathyal occurrence is reported from a single record in the Ligurian Sea (Morri et al. 2008).

14.3.2.2 Order Pennatulacea

Pennatulaceans, commonly known as sea-pens or sea-feathers, include 14 worldwide families and ~200 species occurring from shallow to deep waters where they are more diversified (Williams 1995, 2011; Daly et al. 2007). Taxonomic revision of several families is still needed and significant changes may apply.

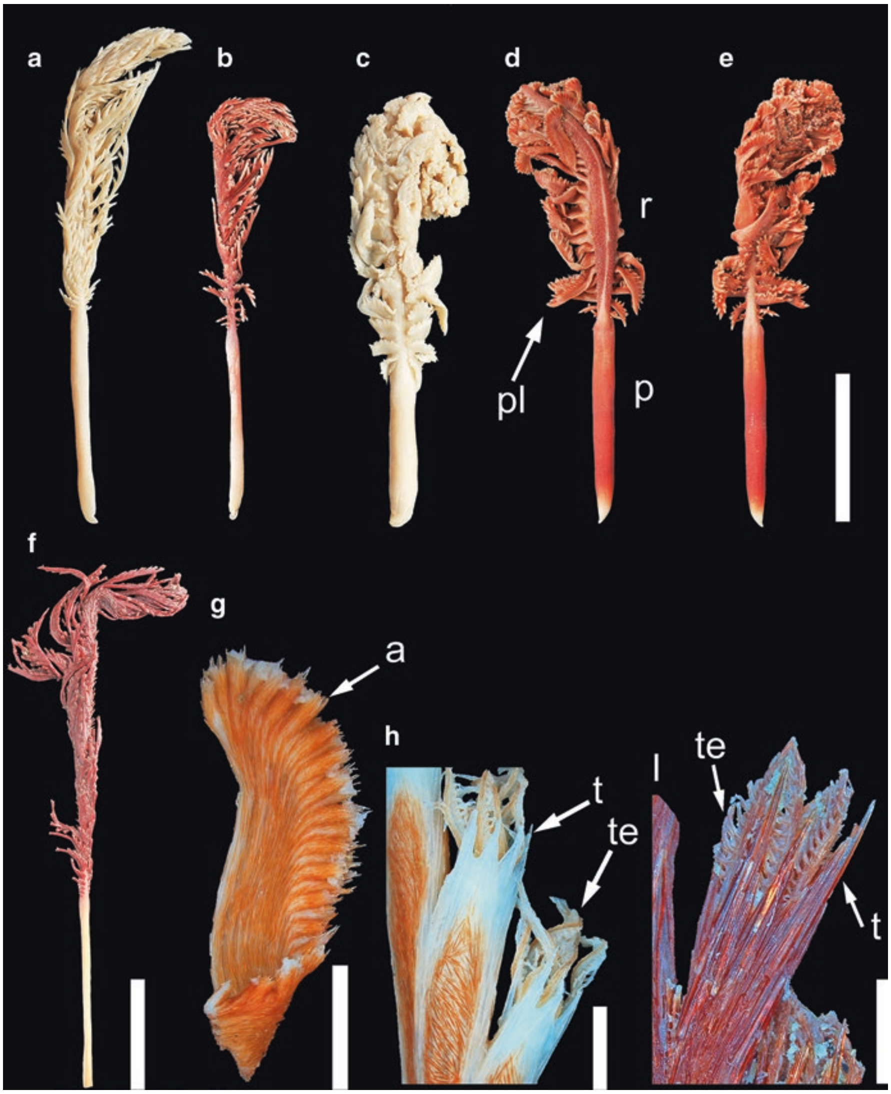

Fig. 14.9 *Pennatula* species from the Mediterranean Sea. (**a**, **b**) *P. phosphorea*, showing two colour varieties; MEDITS 2015 Balearic Islands, 99 m and 138 m depth respectively. (**c**) *P. rubra*, cream specimen; MEDITS 2015 Balearic Islands, 99 m depth. (**d**, **e**) *P. rubra*, red specimens, dorsal and ventral views showing peduncle (p), raquis (r) and polyp leaves (pl); MEDITS 2015, Alborán Sea off Malaga, 71 m depth. (**f**) *P. aculeata*, Bay of Biscay specimen, 773 m depth. (**g**) A polyp leave from *P. rubra* removed from colony; arrow (a) shows autozooid. (**h**) Two autozooids from *P. phosphorea*; arrows show teeth from calyx (t) and tentacles (te). (**i**) Autozooid from *P. aculeata*; arrows show tentacles (te) and teeth from calyx (t). Scale bar: **a**–**f** = 30 mm; **g** = 5 mm; **h**, **i** = 1 mm

Sea-pens have a very distinctive morphology that reflects adaptation to the different kinds of sediments. Their colony structure is the most complex within the Octocorallia, making these animals a morphological distinct and discrete taxonomic entity. Colonies typically comprise an axial or primary polyp (oozooid) differentiated into a muscular, fleshy, basal peduncle that anchors the animal into the sediments, and a distal rachis with numerous secondary polyps that are budded from it (Figs. 14.9 and 14.10). Usually the colony has an internal, thin, axial rod round or quadrangular in cross-section. Secondary polyps were traditionally divided into three types according to their morphology (principally different grades of reduction of the tentacles), which have varied functions within the colony. Autozooids capture and digest food and provide nourishment and protection to the gametes. Siphonozooids produce inhalant currents inflating the colony. Mesozooids have an exhalant function deflating the colony.

We refer to Kükenthal and Broch (1911), Kükenthal (1915), and Williams (1995) for thorough accounts of the order. Williams (1999) compiled and analysed all the literature on sea-pens, including geographic and subject indexes. His work includes also the Mediterranean fauna.

Taxonomy and Taxonomic Characters

Families and genera are distinguished on the basis of: (i) colony shape; (ii) arrangement of the secondary polyps in the rachis and their morphology (including presence-absence of calyces in the autozooids and their shapes, Fig. 14.9h, i); (iii) presence or absence of sclerites in the colony or in different parts of it, and (iv) sclerites morphology (Williams 1995; Daly et al. 2007). Williams (1995) provided information on the distribution and diversity of nominal species, including identification keys for families and genera, and diagnoses of all genera. Diagnoses of families were provided by Kükenthal (1915) and Hickson (1916).

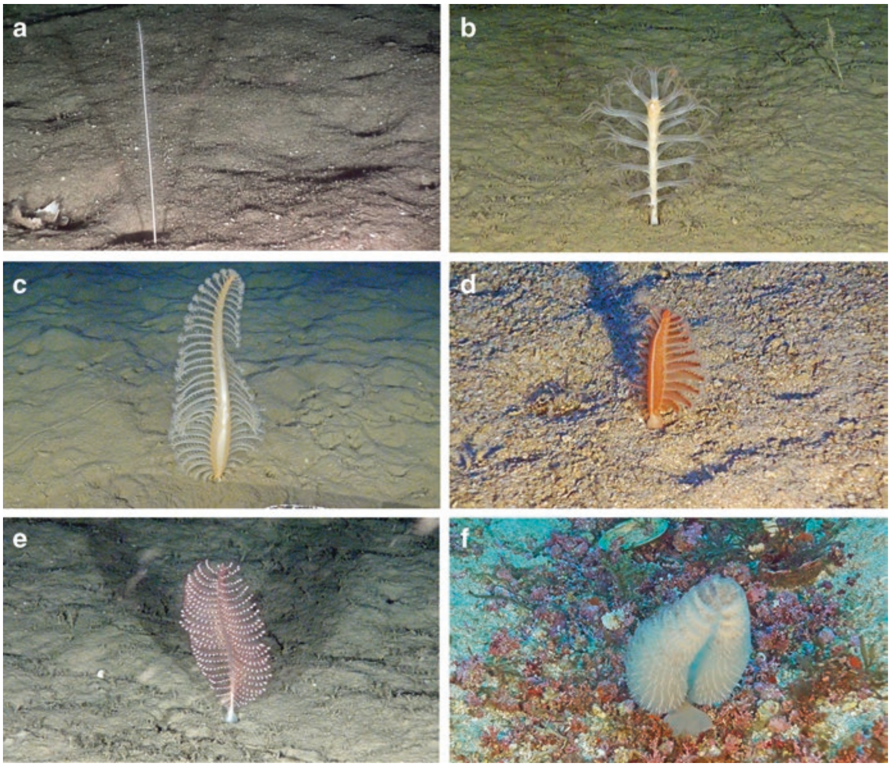

Fig. 14.10 (**a**) *Funiculina quadrangularis*, Chella Bank, Alborán Sea off Spain, 230 m. (**b**) *Kophobelemnon stelliferum*, Chella Bank, 600 m. (**c**) *Pennatula rubra*, Balearic Islands, 200 m. (**d**) *P. rubra*, Chella Bank, 125 m. (**e**) *Pennatula phosphorea*; compare this image of an inflated colony *in situ*, with contracted specimen in Fig. 14.9a, b. (**f**) *Pteroeides spinosum*, Sicily, 80 m. (Photographs: © OCEANA)

The world species were keyed by Kükenthal (1915) and those occurring off the Spanish North-western Mediterranean Sea by Gili and Pagès (1987).

Molecular Aspects

The systematics and molecular phylogeny of deep-sea pennatulaceans were recently investigated by Dolan et al. (2013) using six different markers. MtMutS was confirmed the most suitable marker for lower level phylogenetic studies as formerly shown by France and Hoover (2001) and van der Ham et al. (2009). Although four species occurring in the Mediterranean Sea were analysed (*Funiculina quadrangularis*, *Pennatula aculeata*, *P. phosphorea* and *Virgularia mirabilis*), none of the colonies studied was of Mediterranean origin. This highlights once again the lack of molecular data for specimens collected in the Mediterranean Sea. The genetic structure of *F. quadrangularis* from Scotland as well as other European areas was studied by Wright et al. (2014).

The systematics of the order established by Kükenthal and Broch (1911) and Kükenthal (1915), mostly based on external features of the colony, has been proven to be inadequate at sub-ordinal, familial and sub-familial levels (Williams 1995; Dolan et al. 2013). Some of the families including Mediterranean deep-water species (Kophobelemnidae, Pennatulidae and Protoptilidae) are polyphyletic.

Mediterranean Species

Ten deep-sea pennatulaceans, included in six families, have been recorded from the Mediterranean Sea. Two have habitat-building ability at depths higher than 200 m (CWC), *F. quadrangularis* and *Kophobelemnonm stelliferum* (Tables 14.2 and 14.4). Five were first described from the Mediterranean Sea, four of them in the eighteenth century, and eight were already known by the early twentieth century (Kükenthal and Broch 1911): *Cavernularia pusilla*, *F. quadrangularis*, *K. stelliferum*, *Pennatula rubra*, *P. phosphorea*, *Pteroeides spinosum*, *V. mirabilis*, *Veretillum cynomorium*. Further records include *P. aculeata* (Thomson 1927) and *Protoptilum carpenteri* (Mastrototaro et al. 2014, 2017).

Distinction among Mediterranean species is not difficult, as their colonies show peculiar external features with marked differences between the families and most of the genera (see Kükenthal and Broch 1911; Kükenthal 1915) (Table 14.4). Within the ten deep-sea Mediterranean species, half have isolated autozooids arising directly from the rachis (*C. pusilla*, *V. cynomorium*, *F. quadrangularis*, *K. stelliferum*, *P. carpenteri*), whereas the others have autozooids grouped in leaves arranged alternately in two opposite rows (*P. aculeata*, *P. rubra*, *P. phosphorea*, *P. spinosum*, *V. mirabilis*) (Fig. 14.9). *Cavernularia pusilla* and *V. cynomorium* are radially symmetrical while *F. quadrangularis*, *K. stelliferum* and *P. carpenteri* are more or less bilateral. In *P. aculeata*, *P. rubra*, *P. phosphorea* and *P. spinosum* the polyp leaves are

Table 14.4 Some external features of the Mediterranean deep-sea pennatulaceans. Sizing refers to Mediterranean specimens (mainly according to Gili and Pagès 1987) and do not refer to maximal sizes

Species	Colony shape/size in cm	Symmetry	Autozooids fusion/leaves	N° autozooids on each leaf	Sclerites in the tentacles of the autozooids	Calyces in autozooids/n° terminal teeth	Mesozooids	Siphonozooids	Remarks
Family Funiculinidae									
Funiculina quadrangularis	Thin, long, whip-like/145 (P)	Bilateral	Free	–	Absent	Yes, spiculiferous/8	Absent	Sparsely distributed between autozooids	Occurrence of three-flanged sclerites
Family Kophobelemnidae									
Kophobelemnon stelliferum	Clavate/22 (P)	Bilateral	Free	–	Yes	Absent	Absent	Numerous all over the rachis	Occurrence of three-flanged sclerites
Family Pennatulidae									
Pennatula aculeata	Feather-like/24 (P)	Bilateral	Fused/ leaves	~15	Yes	Yes, spiculiferous/8	Abundant in the dorsal side of rachis, big-sized	Numerous in the dorsal and ventral sides of rachis	Occurrence of three-flanged sclerites
Pennatula phosphorea	Feather-like/17 (P)	Bilateral	Fused/ leaves	~10	Yes	Yes, spiculiferous/8	Absent?	Numerous in the dorsal and ventral sides of rachis	Occurrence of three-flanged sclerites
Pennatula rubra	Feather-like/20 (P)	Bilateral	Fused/ leaves	~50	Absent	Yes, spiculiferous/4	Abundant in the dorsal side of rachis; one on the base of the leaves	Numerous in the dorsal and ventral sides of rachis	Occurrence of three-flanged sclerites
Pteroeides spinosum	Feather-like/12 (P)	Bilateral	Fused/ leaves	~100	Absent	Yes, fleshy	Absent	Only in a proximal zone of each polyp leaf	
Family Protoptilidae									
Protoptilum carpenteri	Long, slender/45 (P)	Bilateral	Free	–	Yes	Yes, spiculiferous/ teeth no evident	Absent	Numerous all over the rachis	Occurrence of three-flanged sclerites
Family Veretillidae									
Cavernularia pusilla	Cylindrical to slightly clavate/~8 (P)	Radial	Free	–	Absent	Absent	Absent	Numerous all over the rachis	Autozooids fully retractile into rachis
Veretillum cynomorium	Cylindrical/50 (L)	Radial	Free	–	Absent	Absent	Absent	Numerous all over the rachis	Autozooids fully retractile into rachis
Family Virgulariidae									
Virgularia mirabilis	Feather-like/35 (P)	Bilateral	Fused/ leaves	~16	Absent	Yes, fleshy	Absent	Only in a single row at the foot of each leaf	Colonies without sclerites

In some species, the size changes notably between live (L) and preserved (P) specimens. We refer to Kükenthal (1915) and Gili and Pagès (1987) for a full description and iconography of the species well-developed and big-sized, giving a feather-like appearance to the colony (Figs. 14.9 and 14.10), while in *V. mirabilis* they are short and the feather appearance is less pronounced.

Species identification among North-eastern Atlantic and Mediterranean *Pennatula* has been problematic. However, the three Mediterranean species can be differentiated by the number of autozooids on each leaf and their orientation (see Chimienti et al. 2015), occurrence of mesozooids associated to the base of the leaves, number of teeth in the calyces, and presence of sclerites in the tentacles of the autozooids (Fig. 14.9, Table 14.4). Several *P. phosphorea* morphotypes were formerly described based on their colour differences (see Kükenthal 1915). Cream-coloured specimens of *P. phosphorea* and *P. rubra* co-occur at the same stations in the Alborán Sea off Spain (Fig. 14.9a–e). Hence, chromatic variation in these species is of little value for taxonomic determinations.

Kükenthal and Broch (1911) and Kükenthal (1915) provided descriptions of the Mediterranean species. Further taxonomic and biological information on the Adriatic and North-western Mediterranean (off Catalonia) species were published by Pax and Müller (1962), and Gili and Pagès (1987), respectively. *Protoptilum carpenteri* was thoroughly described by Mastrototaro et al. (2014), whereas *C. pusilla*, *P. rubra* and *P. spinosum* were re-described by Abdelsalam (2014) by considering shallow-water colonies collected off Egypt. The sea-pen sizes vary dramatically when colonies are inflated, with remarkable differences among species (Figs. 14.9 and 14.10). For example, colonies of *V. cynomorium* measuring 50 cm in height are only 20 cm when preserved (López-González 1993). *Funiculina quadrangularis* is certainly the Mediterranean pennatulacean with the largest colony. Pax and Müller (1962) found Adriatic specimens with colonies that may reach up to 145 cm in height (Fig. 14.10a). *Cavernularia pusilla* is the smallest, reaching ~6.0 cm in height when contracted (see Table 14.4). Overall, Mediterranean sea-pens do not reach sizes as high as those described from northern Europe such as for instance *P. phosphorea* (40 cm) or *F. quadrangularis* (200 cm) (see Hughes 1998). Mediterranean small-sized specimens of *K. stelliferum* collected by Mastrototaro et al. (2013) were attributed to possible "dwarfism" due to local hydrological conditions.

Protoptilum carpenteri is the unique species living only deeper than 200 m depth. All others live in both coastal and deep off-shore areas (*C. pusilla*, *F. quadrangularis*, *K. stelliferum*, *P. aculeata*, *P. phosphorea*, *P. rubra, P. spinosum*, *V. cynomorium*, *V. mirabilis*) (Table 14.2). *Funiculina quadrangularis*, *K. stelliferum* and *P. aculeata* are, however, of predominantly bathyal occurrence. Except for *P. aculeata*, an uncommon species, Mediterranean Pennatulidae are mainly platform-inhabiting sea pens. Population assessments are uncommon and difficult, similarly studies on population density may be sometimes underestimated due to the ability of some species to withdraw below the sediments surface. This capability has been noticed in *K. stelliferum*, *V. mirabilis*, *P. phosphorea* and *P. aculeata* (Langton et al. 1990; Hughes 1998; De Clippele et al. 2015). *In situ* observations on withdrawal behavior of *V. mirabilis* were reported in Mediterranean waters at 100 m depth (Ambroso et al. 2013).

Funiculina quadrangularis and *P. phosphorea* are near-cosmopolitan, a unique feature among the Mediterranean octocorals. Concerning *P. phosphorea*, several morphotypes and subspecies, in need of genetic corroborations, have been described worldwide. Additionally, *F. quadrangularis* and *P. carpenteri* have rather wide bathymetric ranges, an uncommon feature among octocorals. *Funiculina quadrangularis* is very sensitive to bottom fishing activities, as it shares habitat with important commercial crustaceans in the Mediterranean Sea. Facies of this species have almost completely disappeared from the Mediterranean Sea (Sardà et al. 2004) so that it has been categorised as "vulnerable" in the UICN red list (Otero et al. 2017; Otero and Marin, this volume).

Remarkable Sites and Distribution

The most widely distributed species is *F. quadrangularis*, followed by *V. cynomorium*, *P. phosphorea* and *P. spinosum* (Vafidis 2010). *Pennatula phosphorea* and *P. rubra* are widespread and abundant along the Mediterranean shelf, occurring from the Sea of Marmara (Topçu and Öztürk 2015) to the Alborán Sea (López-González 1993). On the contrary, *P. aculeata* is a North Atlantic species known in the Mediterranean basin only from a few records along the French coast (Thomson 1927) and in the Alborán Sea (Ocaña et al. 2000a) (Fig. 14.9f). *Protoptilum carpenteri* is known in the Ionian Sea and the Balearic Islands (Mastrototaro et al. 2014, 2017). *Cavernularia pusilla* is also uncommon; in deep-waters occurs in the western basin and the Aegean Sea. *Kophobelemnon stelliferum* is locally abundant in the western basin (Pardo et al. 2011; Bo et al. 2012a (as *K. leuckartii*); Mastrototaro et al. 2013), the Ionian basin (Vafidis et al. 1994) and the Sea of Marmara (Topçu and Öztürk 2015, as *K. leuckartii*). The highest species richness occurs in the western basin with ten species known after updating Vafidis (2010). Distribution maps of the deep-sea habitat forming species *F. quadrangularis* and *K. stelliferum* are provided in other chapters of this book (see Chimienti et al., this volume).

14.3.3 Class Hydrozoa, Subclass Hydroidolina

Hydrozoa is a group of mostly colonial cnidarians, frequently polymorphic, with sessile polyps and free-living medusae. They have tetramerous or polymerous radial symmetry, and lack stomodeum (actynopharynx) (Hyman 1940). Polyps do not have mesenteries, and the gastrovascular cavity is undivided. Medusae, if present, are budded from the polyps and have a velum. The subclass Hydroidolina includes three orders, among which only the Anthoathecata includes Mediterranean CWCs as defined herein. However, some species in the order Leptothecata lacking calcareous skeletons, as *Lytocarpia* spp., *Nemertesia* spp. and others, may attain large sizes and be important as habitat-forming species. We refer to Bouillon et al. (2006) for a full account of the class, and to Bouillon et al. (2004) for the Mediterranean species.

14.3.3.1 Order Anthoathecata

This order comprises hydroids without a perisarcal theca covering the hydranth body, and having medusae with gonads confined on manubrium; medusae lack statocysts (Bouillon et al. 2006). They are divided into two suborders, Filifera (hydranths with filiform tentacles) and Capitata (hydranths mostly with capitate tentacles). Only Stylasteridae (Filifera) is represented in the Mediterranean by a unique species (*Errina aspera*, see Fig. 19.1 in Chimienti et al., this volume). Stylasterids frequently form a white or pigmented fan-shaped, erect and rigid corallum of calcium carbonate, although encrusting species occur as well. Polyps are polymorphic, and include gastrozooids, dactylozooids and gonophores, with the latter developed inside typical cup-like structures known as ampullae. Stylasteridae are azooxanthellate and are typically deep-sea organisms. It is a speciose family with about 320 extant species (Cairns and Schuchert 2010).

Taxonomy and Taxonomic Characters

The calcareous skeleton of stylasterids and its different components (e.g., cyclosystems, gastropores, dactylopores, ampullae, gastrostyles, etc.) are commonly used in systematics to discriminate the different genera and species (see Zibrowius and Cairns 1992).

A paper on stylasterids anatomy is due to Moseley (1879), while Cairns (2011) provided a detailed anatomical glossary of the family. An identification key of the North-eastern Atlantic and Mediterranean genera, including descriptions and SEM images of all species, was given by Zibrowius and Cairns (1992).

Molecular Aspects

A first morphology-based phylogenetic study of the stylasterid genera was based on the skeletal features (Cairns 1984, 2011). These characters are also useful for species identification. Genetic studies on stylasterids are limited compared to other groups of hydroids in which, due to variability in taxonomic characters, scientists are searching alternative identification schemes. A relatively recent phylogenetic study based on nuclear rRNA genes is now available (Lindner et al. 2008) and further studies are ongoing (see e.g., Cairns 2015). To date, there are no data published on *E. aspera*.

Mediterranean Species

Despite the abundance of anthoathecate hydroids in the Mediterranean Sea with 142 species so far known (Boero and Bouillon 1993), only *E. aspera* is a CWC. This hydrocoral was first discovered in the Mediterranean Sea and re-described by Zibrowius and Cairns (1992), who gave a comprehensive account with a review of the literature, ecology and SEM images. *Errina aspera* forms white and porous calcareous colonies that grow up to ~20 cm and can ramify either in a plane or building bush-like colonies with cylindrical branches tapering to pointed tips (see Zibrowius and Cairns 1992; Salvati et al. 2010; see Fig. 19.1 in Chimienti et al., this volume).

In the North-east Atlantic there are 19 species and three subspecies (Zibrowius and Cairns 1992), a considerable amount if compared with the Mediterranean basin. A possible explanation to the lack of diversity within the Mediterranean Sea might be the definitely insular distribution of stylasterids, which are mainly found off small volcanic oceanic islands, archipelagos and seamounts (Cairns 1992). In this respect, no stylasterids were recorded from "Erathostenes" Seamount in the Eastern Mediterranean basin (see Galil and Zibrowius 1992).

Prosobranch gastropods of the genus *Pedicularia* are obligate symbionts of stylasterids. Hence, their occurrence in the deep-sea or in the fossil record is considered an evidence for the existence of stylasterids. Indeed, *E. aspera* is regularly found with traces of *Pedicularia* throughout its geographical range (Zibrowius and Cairns 1992; Salvati et al. 2010).

Remarkable Sites and Distribution

Errina aspera is not widely distributed in the Mediterranean Sea and its presence is limited to the Straits of Messina and Gibraltar (Zibrowius and Cairns 1992; Giacobbe 2001; Giacobbe et al. 2007; Salvati et al. 2010; Chimienti et al., this volume). Both areas can be considered of special interest by the exceptional occurrence of this species, its abundance and the environmental conditions. There are strong currents that seem to be important for the occurrence of this species and its growth. A thorough study of the Messina population, occurring at 83–230 m depth, has been undertaken by Salvati et al. (2010). In the Gibraltar area the same species occurs at 61–443 m depth (Álvarez-Pérez et al. 2005).

14.4 Overview

14.4.1 Overall Biodiversity

The study of the Mediterranean deep-sea coral fauna started long time ago and at least 47 of the species considered herein were first described from the Mediterranean basin (Table 14.2). The presence of important research laboratories, some of them founded in the nineteenth century (e.g., Stazione Zoologica "Anton Dohrn" di Napoli), was essential for the exploration of the Mediterranean fauna and its diversity. The biodiversity of these organisms in the Mediterranean is unequal, with the western basin being better explored than others. Overall, the western basin displays the highest diversity in terms of species richness. The expected biodiversity of the Mediterranean deep-sea corals and CWCs is difficult to predict. Our knowledge is restricted to few sites, mostly from the western basin, and the unexplored areas are numerous. Despite numerous recent expeditions to new promising locales, very little has been added to the inventories over the last years. In this context, further studies are needed, especially on the deep-water hard-bottom communities around canyons and seamounts, and the white coral frameworks. The Mediterranean fauna includes 82 species, among which 68 are colonial (83%), and 14 solitary (17%). All the solitary species are scleractinians. Thirteen deep-sea corals are considered CWCs by their habitat-building ability at bathyal depths (16%).

The use of ROVs is allowing the discovery of exceptional sites and near-pristine CWC communities (e.g., Bo et al. 2015). CWCs that were considered until now very rare or nearly extinct were repeatedly found and the geographic distribution and bathymetric ranges of other species were recently reconsidered (see Mastrototaro et al. 2010; Bo et al. 2012a, 2015; Giusti et al. 2015; Chimienti et al., this volume). Despite all these efforts, there are no new records since the early twentieth century for Antipatharia, the eighteenth century for Stylasteridae, and since the early nineteenth century for Zoantharia (Table 14.2). As for scleractinians, only *Anomocora fecunda* (Pardo et al. 2011) and dead colonies of *Schyzocyathus fissilis* (Taviani et al. 2011) have been discovered since Zibrowius (1980). Octocorals are an exception to some extent (see Table 14.2). New findings within pennatulaceans are restricted to *Protoptilum carpenteri*, that was recorded for the first time by Mastrototaro et al. (2015). As for Alcyonacea, new species or records are more common since the late twentieth century. For instance, new species were described by Carpine and Grasshoff (1975, *Placogorgia coronata*, *P. massiliensis*, *Spinimuricea klavereni*), Weinberg (1986, *Clavularia carpediem*), López-González and Cunha (2010, *Dendrobrachia bonsai*), and López-González et al. (2014, *Chironephthya mediterranea*). New records, even of previously unrecorded genera, are *Acanella arbuscula*, *Acanthogorgia armata*, *Anthomastus* sp., *Filigorgia guineensis*, *Nicella granifera* and *Telestula septentrionalis*. Most of these new records correspond to the Alborán Sea and have been done during the twenty-first century.

Despite having an average depth of 2500 m, with a maximum of 5121 m and the bathyal domain covering 60% of its surface (WWF/IUCN 2004), no Mediterranean corals have been collected as deep as in the nearby Atlantic areas. Only nine species have been recorded deeper than 1000 m depth (9%) and ten, among which the majority is represented by alcyonaceans (seven species), live only deeper than 200 m depth (Table 14.2). This represents the 17.5% of all deep-sea Mediterranean alcyonaceans so far inventoried (40 species). Comparisons with Atlantic areas as the Bay of Biscay (see Altuna 2015) gives opposite results, as 77% of the 73 deep-sea alcyonacea inventoried live only deeper than 200 m depth.

Although biased by the differences in sampling efforts, the Mediterranean deep-sea fauna diversity is lower if compared with the North-east Atlantic one. In this respect, Grasshoff (1989) concluded that none of several characteristic Atlantic bathyal species of antipatharians, "gorgonians" and sea-pens cross the Gibraltar strait and live in the Mediterranean Sea. Species, genera or families typically observed in bathyal zones off the Iberian Peninsula, the Iberian-Moroccan gulf and/or North-western Africa are absent from the Mediterranean Sea. This is remarkable in some taxa, as for instance, the Calcaxonia. Some chrysogorgiids are abundant in the Gulf of Cadiz (*Radicipes challengeri*), but members of the family are absent from the Mediterranean Sea. Families Primnoidae (five genera and seven species known off the Atlantic coast of the Iberian Peninsula) and Isididae (five genera and six species) are represented by three genera and four species in the Mediterranean Sea. Similar examples have been reported in several taxa namely, Antipatharia, Octocorallia, Scleractinia and Stylasteridae.

Concerning the order Scleractinia, Zibrowius (1980) considered the Mediterranean deep-sea fauna poor if compared with the Atlantic areas at the same latitudes. In this respect, 30 species have been identified from a single seamount off North-western Spain (Galicia Bank, unpublished) at a depth interval ranging from 614 to 1764 m. Thirty species are a considerable amount if compared with the only nine species collected in the whole Mediterranean basin at depths greater than 600 m mostly inhabiting hard bottoms (Table 14.2). On the contrary, in the Galicia bank there is a similar number of species that inhabit hard- (16 species) and soft-bottoms (14 species). These differences are partially explained by the absence in the Mediterranean Sea of corals that prefer soft-bottoms such as the scleractinian genera *Deltocyathus*, *Eguchipsammia*, *Flabellum*, *Fungiacyathus*, *Premocyathus* or *Stephanocyathus*, as well as the lack of some free-living *Caryophyllia* species. We do not known in our present state of knowledge if the absence of these species is due to a lack of studies in certain environments, or if they actually do not inhabit the Mediterranean Sea. Reductions of species diversity compared to the nearby Atlantic areas are not compensated by a substantial increase in the Mediterranean endemics, as these are ~14% of the total deep-sea coral fauna (including near-endemic species). There are no endemic species restricted to depths greater than 200 m (Table 14.2).

The reasons explaining such a difference in species richness between Mediterranean and nearby Atlantic faunas are surely varied and have been discussed in other chapters of this book. Apart from scleractinians (see chapters from the "Past" section in this volume), the fossil records of deep-sea corals are scarce and extremely rare. However, some fossil remains showed that several species and/or genera occurred in the Mediterranean Sea during the Pliocene (5.33–2.58 Ma) and Pleistocene (2.58–0.01 Ma) as documented for *Enallopsammia*, *Flabellum*, *Fungiacyathus* and *Stephanocyathus* (Zibrowius and Placella 1982; Di Geronimo et al. 2005; Vertino et al. 2014). Fossils of stylasterids in Europe and in the Mediterranean basin are rare (Zibrowius and Cairns 1992). Nevertheless, a rich and exceptional upper bathyal hard ground fauna including stylasterids was discovered in Carboneras (Almería, South-eastern Spain) (Barrier et al. 1991). This unique place, dated back to the Late Miocene, included well-preserved fossils of at least eight genera (*Calyptopora*, *Conopora*, *Crypthelia*, *Distichopora*, *Lepidopora*, *Pliobothrus*, *Stenohelia*, and *Stylaster*) and 14 species. Interestingly, none of these genera occur now in the Mediterranean as *E. aspera* is the only stylasterid described from the whole basin. Finally, fossils of two species of *Keratoisis* (Isididae), a typical bathyal octocoral genus now absent from the Mediterranean Sea, were found in Late Miocene, Pliocene and Late Pleistocene deposits from several Mediterranean areas (Grasshoff 1980; Barrier et al. 1991; Taviani et al. 2011).

14.4.2 Future Perspectives

Perspectives on the study and conservation of Mediterranean deep-sea corals and CWCs are overall optimistic. Scientists are now aware of their importance, and our knowledge on the subject is rapidly increasing thank to technological advances. One of the most important challenges will be to find a balance between resources exploitation and conservation (see Otero and Marin, this volume), aiming to better protect the environments and their biodiversity. Local communities and industries will compromise the financial benefits that marine resources can ensure. However, they should be aware that they could also be guaranteed by policies of conservation and protection of the species and their habitats. Several species are habitat-forming and can be often exploited by other organisms due to their commercial interest, refuge, nurseries or feeding purposes (see D'Onghia, this volume; Otero and Marin, this volume; Rueda et al., this volume). Deep-sea corals and CWCs are mostly slow-growing organisms (see Bramanti et al., this volume; Lartaud et al., this volume), some of them can even represent the most long-lived organisms on the planet, but can be irreversibly damaged by rough fishing practices (Bo et al. 2015; Otero and Marin, this volume). This said, understanding the importance of these organisms, their biodiversity, and community structure is paramount. Moreover, the management of concrete conservation and protection strategies is not properly doable if our knowledge is altered or scarce. For this reason, inventories and studies on the CWCs communities are of great importance, especially in the areas that are constantly subject to human impacts like the Mediterranean Sea. Although necessary to monitorise future changes in the biota due to different factors, comprehensive biodiversity investigations of the Mediterranean deep-sea corals are at the present state complicated and poor. The work to be done is notable and it requires additional sampling efforts from under-investigated and unknown areas as well as the revision of large museum collections and (re)description of species under modern standards. Re-descriptions of type material, or the selection of neotypes for those species whose types were lost, is essential. An example on this respect is the recovery of good species such as *Nidalia studeri* or *Daniela koreni* described by von Koch (1891) (see López-González et al. 2012) that were later forgotten. The material of the latter discovered by López-González et al. (2012) is pending re-description, and once cleared it could confirm the exceptional occurrence of the family Nephtheidae in the Mediterranean Sea. These cases are surely not unique, especially among octocorals, and the study of old collections using new comparative material will probably induce changes in the inventories of the Mediterranean coral fauna so far known (see for instance the examples of *Acanella furcata* and *A. arbuscula*, Saucier et al. 2017). It is however surprising that, despite relevant discoveries of new areas with rich CWCs communities, the additions of new species and records is limited as already discussed. Whether this is due to a poor Mediterranean deep-sea fauna compared with the nearby Atlantic areas, or to a lack of sampling, will be cleared in the forthcoming years whenever new studies using molecular tools, and morphological descriptions of forgotten species will become available.

The use of molecular tools and the sequencing of DNA traits has revolutioned the systematics of cnidarians, contributing sometimes to better investigate the relationships between different species rich taxa. Nevertheless, in some groups, among which significant Mediterranean taxa of the family Plexauridae, the molecular markers used failed to discriminate morphological puzzling species of genera such as *Paramuricea* and *Swiftia*, or among and within genera like *Placogorgia* and *Paramuricea*. Although cryptic biodiversity can be suspected in some taxa, we do not always have tools to detect it. Finally, and given that many Mediterranean species were first described long time ago and that their types went lost or are currently useless for genetic analyses, the challenge to link newly collected material to museum specimens is obvious. In future a better knowledge of the Mediterranean deep-sea coral fauna will require cooperation between experts in different scientific disciplines.

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References

Abdelsalam KM (2014) Faunistic study of benthic Pennatulacea (Cndaria, Octocorallia) from the northern coast of Egypt. Egypt J Aquat Res 40:261–268

Addamo AM, Reimer JD, Taviani M, et al (2012) *Desmophyllum dianthus* (Esper, 1794) in the Scleractinian phylogeny and its intraspecific diversity. PLoS One 7:e50215. https://doi.org/10.1371/journal.pone.0050215

Addamo AM, García-Jiménez R, Taviani M, et al (2015) Development of microsatellite markers in the deep-sea cup coral *Desmophyllum dianthus* by 454 sequencing and cross-species amplifications in Scleractinia order. J Hered 106:322–330

Addamo AM, Vertino A, Stolarski J, et al (2016) Merging scleractinian genera: the overwhelming genetic similarity between solitary *Desmophyllum* and colonial *Lophelia*. BMC Evol Biol 16:108

Alderslade P, McFadden C (2007) Pinnule-less polyps: a new genus and new species of Indo-Pacific Clavulariidae and validation of the soft coral genus *Acrossota* and the family Acrossotidae (Coelenterata: Octocorallia). Zootaxa 1400:27–44

Altuna A (2015) Cnidarios bentónicos (Cnidaria) del Golfo de Vizcaya y zonas próximas (Atlántico NE) (42° N a 48°30′N y 13° W). Lista de especies, batimetría y anotaciones. Available via http://www.fauna-iberica.mncn.csic.es/faunaib/altuna9.pdf. Accessed 15 Aug 2016

Altuna A, Sinniger F, Aldrey JM (2010) Occurrence of *Savalia savaglia* (Anthozoa: Zoantharia) in the Ría de Arousa (Galicia, North-Western Spain, North-Eastern Atlantic). Mar Biodivers Rec 3:e1

Álvarez-Pérez G, Busquets P, de Mol B, et al (2005) Deep-water coral occurrences in the Strait of Gibraltar. In: Freiwald A, Roberts JM (eds) Cold water corals and ecosystems. Springer, Heidelberg, Berlin, pp 207–221

Alves Santos ME, Kitahara MV, Lindner A, et al (2015) Overview of the order Zoantharia (Cnidaria: Anthozoa) in Brazil. Mar Biodivers. https://doi.org/10.1007/s12526-015-0396-7

Ambroso S, Dominguez-Carrió C, Grinyó J, et al (2013) In situ observations on withdrawal behaviour of the sea pen *Virgularia mirabilis*. Oceanarium. https://doi.org/10.1007/s12526-013-0172-5

Angeletti L, Taviani M, Canese S, et al (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Mediterr Mar Sci 15:263–273

Angiolillo M, Bo M, Bavestrello G, et al (2012) Record of *Ellisella paraplexauroides* (Anthozoa: Alcyonacea: Ellisellidae) in Italian waters (Mediterranean Sea). Mar Biodivers Rec 5:e4

Arrigoni R, Kitano YK, Stolarski J, et al (2014) A phylogeny reconstruction of the Dendrophylliidae (Cnidaria, Scleractinia) based on molecular and micromorphological criteria, and its ecological implications. Zool Scr 43:661–688

Baillon S, Hamel JF, Wareham VE, et al (2012) Deep cold-water corals as nurseries for fish larvae. Front Ecol Environ 10:351–356

Barrier P, Zibrowius H, Lozouet P, et al (1991) Une faune de fond dur du bathyal supérieur dans le Miocene terminal des cordillères bétiques (Carboneras, SE Espagne). Mesogée 51:3–13

Bayer FM (1956) Octocorallia. In: Moore RC (ed), Treatise on invertebrate paleontology. Pt F (Coelenterata). The University of Kansas Press, Lawrence, pp F166–F231

Bayer FM (1961) The shallow-water Octocorallia of the West Indian region. A manual for marine biologists. Stud Fauna Curaçao 12:1–373

Bayer FM (1981) Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnoses of new taxa. Proc Biol Soc Wash 94:901–947

Bayer FM, Grasshoff M (1994) The genus group taxa of the family Ellisellidae, with clarification of the genera established by J. E. Gray. Senckenb Biol 74:21–45

Bayer FM, Grasshoff M, Verseveldt J (eds) (1983) Illustrated trilingual glossary of morphological and anatomical terms applied to Octocorallia. Brill EJ, Backhuys W, Leiden, 75 p

Bo M (2008) Taxonomy and ecology of antipatharians. Dissertation, Universita Politecnica delle Marche, 212 p

Bo M, Tazioli S, Spanò N, et al (2008) *Antipathella subpinnata* (Antipatharia, Myriopathidae) in Italian seas. Ital J Zool 75:185–195

Bo M, Bavestrello G, Canese S, et al (2011) Coral assemblage off the Calabrian Coast (South Italy) with new observations on living colonies of *Antipathes dichotoma*. Ital J Zool 78:231–242

Bo M, Canese S, Spaggiari C, et al (2012a) Deep coral oases in the south Tyrrhenian Sea. PLoS One 7:e49870. https://doi.org/10.1371/journal.pone.0049870

Bo M, Lavorato A, Di Camillo CG, et al (2012b) Black coral assemblages from Machalilla National Park (Ecuador). Pac Sci 66:63–81

Bo M, Canese S, Bavestrello G (2014) Discovering Mediterranean black coral forests: *Parantipathes larix* (Anthozoa: Hexacorallia) in the Tuscan Archipelago, Italy. Ital J Zool 81:112–121

Bo M, Bavestrello G, Angiolillo M, et al (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS One 10:e0119393. https://doi.org/10.1371/journal.pone.0119393

Boero F, Bouillon J (1993) Zoogeography and life cycle patterns of Mediterranean hydromedusae (Cnidaria). Biol J Linn Soc 48:239–266

Bouillon J, Medel MD, Pagès F, et al (2004) Fauna of the Mediterranean hydrozoa. Sci Mar 68:5–438

Bouillon J, Gravili C, Pagès F, et al (2006) An introduction to hydrozoa. Mém Mus Natl Hist Nat, Paris 194:1–591

Bridge D, Cunningham CW, DeSalle R, et al (1995) Class-level relationships in the phylum Cnidaria: molecular and morphological evidence. Mol Biol Evol 12:679–689

Brook G (1889) Report on the Antipatharia. In: Thomson CW, Murray J (eds) Report on the scientific results of the voyage of the H.M.S. Challenger, vol 32. Royal Stationery Office, London

Bruckner AW (2009) Rate and extent of decline in *Corallium* (pink and red coral) populations: existing data meet the requirements for a CITES Appendix II listing. Mar Ecol Prog Ser 397:319–332

Brugler MR, France SC (2007) The complete mitochondrial genome of the black coral *Chrysopathes formosa* (Cnidaria:Anthozoa:Antipatharia) supports classification of antipatharians within the subclass Hexacorallia. Mol Phylogenet Evol 42:776–788

Brugler MR, Opresko DM, France SC (2013) The evolutionary history of the order Antipatharia (Cnidaria: Anthozoa: Hexacorallia) as inferred from mitochondrial and nuclear DNA: implications for black coral taxonomy and systematic. Zool J Linnean Soc 169:312–361

Budd A, Stolarski J (2009) Searching for new morphological characters in the systematic of scleractinian reef corals: comparison of septal teeth and granules between Atlantic and Pacific Mussidae. Acta Zool 90:142–165

Budd A, Romano SL, Smith ND, et al (2010) Rethinking the phylogeny of scleractinian corals: a review of morphological and molecular data. Integr Comp Biol 50:411–427

Cairns SD (1984) A generic revision of the Stylasteridae (Coelenterata: Hydrozoa). Part 2. Phylogenetic analysis. Bull Mar Sci 35:38–53

Cairns SD (1992) Worldwide distribution of the Stylasteridae (Cnidaria: Hydrozoa). Sci Mar 56:125–130

Cairns SD (1997) A generic revision and phylogenetic analysis of the Turbinoliidae (Cnidaria: Scleractinia). Smithson Contrib Zool 591:1–55

Cairns SD (2000) A revision of the shallow-water azooxanthellate Scleractinia of the western Atlantic. Stud Nat Hist Caribbean Region 75:1–231

Cairns SD (2001) A generic revision and phylogenetic analysis of the Dendrophylliidae. Smithson Contrib Zool 615:1–75

Cairns SD (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. Bull Mar Sci 81:311–322

Cairns SD (2011) Global diversity of the Stylasteridae (Cnidaria: Hydrozoa: Athecatae). PLoS One 6(7):e21670. https://doi.org/10.1371/journal.pone.0021670

Cairns SD (2015) Stylasteridae (Cnidaria: Hydrozoa: Anthoathecata) of the New Caledonian Region. Mém Mus Natl Hist Nat, Paris 207:1–361

Cairns SD, Kitahara MV (2012) An illustrated key to the genera and subgenera of the recent azooxanthellate Scleractinia (Cnidaria, Anthozoa), with an attached glossary. Zookeys 227:1–47

Cairns S, Schuchert P (2010) Stylasteridae Gray, 1847. Available via WoRMS. http://www.marinespecies.org/aphia.php?p=taxdetails&id=22805. Accessed 30 Aug 2016

Carlgren O (1895) Ueber die Gattung *Gerardia* Lac.-Duth. Öfvers Kongl Vetensk Akad Förh 5:319–334

Carpine C (1964) Un octocoralliaire nouveau pour la Méditerranée: *Scleranthelia musiva* Studer, 1878. Bull Inst Océanogr Monaco 65:1–10

Carpine C, Grasshoff M (1975) Les gorgonaires de la Méditerranée. Bull Inst Océanogr Monaco 71:1–140

Cartes JE, Lo Iacono C, Mamouridis V, et al (2013) Geomorphological, trophic and human influences on the bamboo coral *Isidella elongata* assemblages in the deep Mediterranean: to what extent does *Isidella* form habitat for fish and invertebrates? Deep-Sea Res Part 1 Oceanogr Res Pap 76:52–65

Cerrano C, Danovaro R, Gambi C, et al (2010) Gold coral (*Savalia savaglia*) and gorgonian forests enhance benthic biodiversity and ecosystem functioning in the mesophotic zone. Biodivers Conserv 19:153–167

Chimienti G, Maiorano P, Mastrototaro F (2015) *Pennatula rubra* facies in the Ionian Sea (Central Mediterranean). Biol Mar Mediterr 22:76–80

Costantini F, Taviani M, Remia A, et al (2010) Deep-water *Corallium rubrum* (L., 1758) from the Mediterranean Sea: preliminary genetic characterisation. Mar Ecol 31:261–269

Costantini F, Carlesi L, Abbiati M (2013) Quantifying spatial genetic structuring in mesophotic populations of the precious coral *Corallium rubrum*. PLoS One 8:e61546. https://doi.org/10.1371/journal.pone.0061546

Costantini F, Gori A, Lopez-González P, et al (2016) Limited genetic connectivity between gorgonian morphotypes along a depth gradient. PLoS One 11:e0160678. https://doi.org/10.1371/journal.pone.0160678

Dahl M (2013) Conservation genetics of *Lophelia pertusa*. Dissertation, University of Gothenburg

Daly M, Fautin DG, Cappola VA (2003) Systematics of the Hexacorallia (Cnidaria: Anthozoa). Zool J Linnean Soc 139:419–437

Daly M, Brugler MR, Cartwright P, et al (2007) The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. Zootaxa 1668:127–182

De Clippele LH, Buhl-Mortensen P, Buhl-Mortensen L (2015) Fauna associated with cold water gorgonians and sea pens. Cont Shelf Res 195:67–78

Di Geronimo I, Messina C, Rosso A, et al (2005) Enhanced biodiversity in the deep: early Pleistocene coral communities from southern Italy. In: Freiwald A, Roberts JM (eds) Cold water corals and ecosystems. Springer, Heidelberg, Berlin pp 61–86

Dolan E, Tyler PA, Yesson C, et al (2013) Phylogeny and systematics of deep-sea sea pens (Anthozoa: Octocorallia: Pennatulacea). Mol Phylogenet Evol 69:610–618

Druffel ERM, Griffin S, Witter A, et al (1995) *Gerardia*: bristlecone pine of the deep-sea? Geochim Cosmochim Acta 59:5031–5036

Emblem S, Karlsen BO, Evertsen J, et al (2011) Mitogenome rearrangement in the cold-water scleractinian coral *Lophelia pertusa* (Cnidaria, Anthozoa) involves a long-term evolving group I intron. Mol Phylogenet Evol 61:495–503

Emig C, Geistdoerfer P (2004) The Mediterranean deep-sea fauna: historical evolution, bathymetric variations and geographical changes. Carnets Géol 4:1–10

Fabri MC, Pedel L (2012) Habitats particuliers du bathyal et de l'abyssal/SRM MO, 10 p. https://doi.org/10.13155/34118

Fabricius K, Alderslade P (2001) Soft corals and sea fans. A comprehensive guide to the tropical shallow-water genera of the Central-West Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science, Townsville, 264 p

Flot JF, Dahl M, André C (2013) *Lophelia pertusa* corals from the Ionian and Barents seas share identical nuclear ITS2 and near-identical mitochondrial genome sequences. BMC Res Notes 6:144

France SC, Hoover LL (2001) Analysis of variation in mitochondrial DNA sequences (ND3, ND4L, MSH) among Octocorallia (= Alcyonaria) (Cnidaria: Anthozoa). Bull Biol Soc Wash 10:110–118

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs. UNEP-WCMC, Cambridge, 86 p

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Galil B, Zibrowius H (1992) First benthos samples from Eratosthenes Seamount, Eastern Mediterranean. Senckenb Mar 28:111–121

Giacobbe S (2001) Distribuzione areale e batimetrica della facies a *Errina aspera* L. (Hydrozoa, Stylasteridae) nello Stretto di Messina. Biol Mar Mediterr 8:246–251

Giacobbe S, Laria G, Spanò N (2007) Hard bottom assemblages in the strait of Messina: distribution of *Errina aspera* L.(Hydrozoa: Stylasteridae). Rapp Comm Int Mer Médit 38:485

Gili JM, Pagès F (1987) Pennatuláceos (Cnidaria, Anthoza) recolectados en la plataforma continental catalana (Mediterráneo occidental). Misc Zool 11:25–39

Giusti M, Bo M, Bavestrello G, et al (2012) Record of *Viminella flagellum* (Alcyonacea: Ellisellidae) in Italian waters (Mediterranean Sea). Mar Biodivers Rec 5:e34

Giusti M, Cerrano C, Angiolillo M, et al (2015) An updated overview of the geographic and bathymetric distribution of *Savalia savaglia*. Mediterr Mar Sci 16:128–135

Goffredo S, Di Ceglie S, Zaccanti F (2009) Genetic differentiation of the temperate-subtropical stony coral *Leptopsammia pruvoti* in the Mediterranean Sea. Isr J Ecol Evol 55:99–115

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Grasshoff M (1972) Die Gorgonaria des östlichen Nordatlantik und des Mittelmeeres. I. Die Familie Ellisellidae (Cnidaria: Anthozoa). "Meteor" Forsch-Ergebn (D) 10:73–87

Grasshoff M (1973) Die Gorgonaria des östlichen Nordatlantik und des Mittelmeeres. II. Die Gattung *Acanthogorgia* (Cnidaria: Anthozoa). "Meteor" Forsch-Ergebn (D) 13:1–10

Grasshoff M (1977) Die Gorgonaria des östlichen Nordatlantik und des Mittelmeeres. III. Die Familie Paramuriceidae (Cnidaria: Anthozoa). "Meteor" Forsch-Ergebn (D) 27:5–76

Grasshoff M (1980) Isididae aus dem Pliozän und Pleistozän von Sizilien (Cnidaria : Octocorallia). Senckenb Lethaea 60:435–447

Grasshoff M (1988) The genus *Leptogorgia* (Octocorallia: Gorgoniidae) in West Africa. Atlantide Rep 14:91–147

Grasshoff M (1989) Die Meerenge von Gibraltar als Faunen-Barriere: Die Gorgonaria, Pennatularia und Antipatharia der Balgim-Expedition (Cnidaria: Anthozoa). Senckenb Marit 20:201–223

Grasshoff M (1992) Die Flachwasser-Gorgonarien von Europa und Westafrika (Cnidaria, Anthozoa). Cour Forschungsinst Senckenb 149:1–135

Gravier C (1918) Note sur les Antipathaires du Golfe de Naples. Pubbl Staz Zool Napoli 2:223–239

Grinyó J, Gori A, Ambroso S, et al (2016) Diversity, distribution and population size structure of deep Mediterranean gorgonian assemblages (Menorca Channel, Western Mediterranean Sea). Progr Oceanogr 145:42–56

Häussermann V, Försterra G, Weinberg S, et al (2003a) Klasse Anthozoa (Blumentiere). In: Hofrichter R (ed) Das Mittelmeer. Fauna, Flora, Ökologie, II/1. Spektrum Akademischer Verlag, Heidelberg, pp 410–411

Häussermann V, Försterra G, Opresko D, et al (2003b) Unterklasse Hexacorallia Haeckel, 1866. In: Hofrichter R (ed) Das Mittelmeer. Fauna, Flora, Ökologie, II/1. Spektrum Akademischer Verlag, Heidelberg, pp 444–449

Hickson SJ (1916) The Pennatulacea of the Siboga expedition, with a general survey of the order. Siboga Expeditie Monogr 14:1–265

Hoeksema B, Cairns S (2013) *Cladocora* Ehrenberg, 1834. Available via WORMS. http://www.marinespecies.org/aphia.php?p=taxdetails&id=22805. Accessed 30 Nov 2016

Hughes DJ (1998) Sea pens and burrowing megafauna (volume III). An overview of dynamics and sensitivity characteristics for conservation management of marine SACs. Scottish Association for Marine Science, Oban

Hyman LH (1940) The invertebrates: protozoa through Ctenophora. McGraw HillBook Company, New York, London

Ingrassia M, Macelloni L, Bosman A, et al (2015) Black coral (Anthozoa, Antipatharia) forest near the western Pontine Islands (Tyrrhenian Sea). Mar Biodivers 16:285─290

Jiménez C, Orejas C (2017) The builders of the oceans – part II: corals from the past to the present (the stone from the sea). In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: The Ecology of Benthic Biodiversity Hotspots. Springer, Cham, pp 657–698 https://doi.org/10.1007/978-3-319-17001-5_56-1

Jiménez C, Achilleos K, Abu Alhaija R, et al (2016) Living in close quarters: epibionts on *Dendrophyllia ramea* deep-water corals (Cyprus and Menorca channel). Rapp Comm Int Mer Médit 41:466

Kayal E, Roure B, Philippe H, et al (2013) Cnidarian phylogenetics relationships as revealed by mitogenomics. BMC Evol Biol. https://doi.org/10.1186/1471-2148-13-5

Kise H, Reimer JD (2016) Unexpected diversity and a new species of *Epizoanthus* (Anthozoa, Hexacorallia) attached to eunicid worm tubes from the Pacific Ocean. ZooKeys 562:49–71

Kitahara MV, Cairns SD, Miller DJ (2010a) Monophyletic origin of *Caryophyllia* (Scleractina, Caryophylliidae), with decription of six new species. Syst Biodivers 8:91–118

Kitahara MV, Cairns SD, Stolarski J, et al (2010b) A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. PLoS One 5:e11490. https://doi.org/10.1371/journal.pone.0011490

Kitahara MV, Fukami H, Benzoni F, et al (2016) The new systematics of Scleractinia: integrating molecular and morphological evidence. In: Goffredo S, Dubinsky Z (eds) The Cnidaria, past, present and future. Springer, Heidelberg, pp 41–59

Kükenthal W (1915) Pennatularia. Das Tierreich 43:1–132

Kükenthal W, Broch H (1911) Pennatulacea. Wiss Ergebn Dt Tiefsee-Exped 'Valdivia' 1889–1899, 13:113–576

Lacaze-Duthiers H (1864a) Mémoire sur les Antipathaires (Gen. Gerardia, L.D). Ann Sci Nat B 2:169–239

Lacaze-Duthiers H (1864b) Histoire naturelle du corail. J. B. Baillière et Fils, Paris

Langton RW, Langton EW, Theroux RB et al (1990) Distribution, behavior and abundance of sea pens, *Pennatula aculeata*, in the Gulf of Maine. Mar Biol 107:463–469

Lapian HFN, Barucca M, Bavestrello G, et al (2007) A systematic study of some black coral species (Antipatharia, Hexacorallia) based on rDNA internal transcribed spacers sequences. Mar Biol 151:785–792

Laubier L, Emig CC (1993) La faune benthique profonde de Méditerranée. In: Della Croce FR (ed) Symposium Mediterranean Seas 2000. Istituto di Scienze Ambientale Marine, Genova, pp 396–424

Le Goff-Vitry MC, Rogers AD (2005) Molecular ecology of *Lophelia pertusa* in the NE Atlantic. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin pp 653–662

Le Goff-Vitry MC, Pybus OG, Rogers AD (2004a) Genetic structure of the deep-sea coral *Lophelia pertusa* in the North East Atlantic revealed by microsatellites and ITS sequences. Mol Ecol 13:537–549

Le Goff-Vitry MC, Rogers AD, Baglow D (2004b) A deep-sea slant on the molecular phylogeny of the Scleractinia. Mol Phylogenet Evol 30:167–177

Ledoux JB, Mokhtar-Jamaï K, Roby C, et al (2010) Genetic survey of shallow populations of the Mediterranean red coral [*Corallium rubrum* (Linnaeus, 1758)]: new insights into evolutionary processes shaping nuclear diversity and implications for conservation. Mol Ecol 19:675–690

Lin MF, Kitahara MV, Tachikawa H, et al (2012) Novel organization of the mitochondrial genome in the deep-sea coral, *Madrepora oculata* (Hexacorallia, Scleractinia, Oculinidae) and its taxonomic implications. Mol Phylogenet Evol 65:323–328

Lindner A, Cairns SD, Cunningham CW (2008) From offshore to onshore: multiple origins of shallow-water corals from deep-sea ancestors. PLoS One 3:e2429. https://doi.org/10.1371/journal.pone.0002429

López-González PJ (1993) Taxonomía y zoogeografía de los antozoos del Estrecho de Gibraltar y áreas próximas. Dissertation, University of Seville

López-González PJ, Cunha MR (2010) Two new species of *Dendrobrachia* Brook, 1889 (Cnidaria: Octocorallia: Dendrobrachiidae) from the north-eastern Atlantic and western Mediterranean. Sci Mar 74:423–434

López-González P, Grinyó J, Gili JM (2012) Rediscovery of *Cereopsis studeri* Koch, 1891, a forgotten Mediterranean soft coral species, and its inclusion in the genus *Nidalia* Gray, 1835 (Octocorallia, Alcyonacea, Nidaliidae). Mar Biol Res 8:594–604

López-González P, Grinyó J, Gili JM (2014) *Chironephthya mediterranea* n.sp. (Octocorallia, Alcyonacea, Nidaliidae), the first species of the genus discovered in the Mediterranean Sea. Mar Biodiver. https://doi.org/10.1007/s12526-014-0269-5

Madsen FJ (1944) Octocorallia. Danish Ingolf-Exped 5:1–65

Masmoudi MB, Chaoui L, Topçu NE, et al (2016) Contrasted levels of genetic diversity in a benthic Mediterranean octocoral: consequences of different demographic histories? Ecol Evol 6:8665–8678

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

Mastrototaro F, Maiorano P, Vertino A, et al (2013) A facies of *Kophobelemnon* (Cnidaria, Octocorallia) from Santa Maria di Leuca coral province (Mediterranean Sea). Mar Ecol 34:313–320

Mastrototaro F, Chimienti G, Capezzuto F, et al (2014) First record of *Protoptilum carpenteri* (Cnidaria: Octocorallia: Pennatulacea) in the Mediterranean Sea. Ital J Zool 82:61–68

Mastrototaro F, Chimienti G, Acosta J, et al (2017) *Isidella elongata* (Cnidaria: Alcyonacea) facies in the western Mediterranean Sea: visual surveys and descriptions of its ecological role. Eur Zool J 84:209–225

Maynou F, Cartes JE (2011) Effects of trawling on fish and invertebrates from deep-sea coral facies of *Isidella elongata* in the western Mediterranean. J Mar Biol Assoc UK:1–7

McFadden CS (1999) Genetic and taxonomic relationships among Northeastern Atlantic and Mediterranean populations of the soft coral *Alcyonium coralloides*. Mar Biol 133:171–184

McFadden CS, Hutchinson MB (2004) Molecular evidence for the hybrid origin of species in the soft coral genus *Alcyonium* (Cnidaria. Anthozoa: Octocorallia). Mol Ecol 13:1495–1505

McFadden CS, Donahue R, Hadland K, et al (2001) A molecular phylogenetic analysis of reproductive trait evolution in the soft coral genus *Alcyonium*. Evolution 55:54–67

McFadden CS, France SC, Sánchez JA, et al (2006) A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences. Mol Phylogenet Evol 41:513–527

McFadden CS, Benayahu Y, Pante E, et al (2011) Limitations of mitochondrial gene barcoding in Octocorallia. Mol Ecol Resour 11:19–31

Mokhtar-Jamaï K, Pascual M, Ledoux JB, et al (2011) From global to local genetic structuring in the red gorgonian *Paramuricea clavata*: the interplay between oceanographic conditions and limited larval dispersal. Mol Ecol 2:3291–3305

Morgan LE (2005) What are deep-sea corals? J Mar Educ 21:1–4

Morri C, Esposito F, Pessani D (2008) Anthozoa. Biol Mar Mediterr 15:92–101

Moseley HN (1879) On the structure of the Stylasteridae, a family of the hydroid stony corals. Phil Trans R Soc London 169:425–503

Ocaña O, Brito A (2004) A review of the Gerardiidae (Anthozoa: Zoantharia) from the Macaronesian Islands and the Mediterranean Sea with the description of a new species. Rev Acad Canar Cienc 15:159–189

Ocaña A, Sánchez Tocino L, López-González PJ (2000a) Consideraciones faunísticas y biogeográficas de los antozoos (Cnidaria: Anthozoa) de la costa de Granada (Mar de Alborán). Zool Baetica 11:51–65

Ocaña O, López-González PJ, Núñez J, et al (2000b) A survey of the genera *Sarcodictyon* Forbes, 1847, and *Rolandia* Lacaze-Duthiers, 1900 (Anthozoa: Octocorallia) in the North-Eastern Atlantic and the Mediterranean. Zool Meded, Leiden 73:413–426

Ocaña O, Opresko DM, Brito A (2007) First record of the black coral *Antipathella wollastoni* (Anthozoa: Antipatharia) outside of Macaronesian waters. Rev Acad Canar Cienc 18:125–138

OCEANA (2014) Informe de síntesis para proceder a la elaboración del borrador del Plan de Gestión del LIC "Sur de Almería-Seco de los Olivos": Seco de los Olivos. Proyecto LIFE + INDEMARES (LIFE07/NAT/E/00732). OCEANA–Instituto Español de Oceanografía, Madrid

Opresko D (1974) A study of the classification of the Antipatharia (Coelenterata: Anthozoa), with redescriptions of eleven species. Dissertation, University of Miami

Opresko D (2001) Revision of the Antipatharia (Cnidaria: Anthozoa). Part I. Establishment of a new family, Myriopathidae. Zool Meded Leiden 75:147–174

Opresko D (2002) Revision of the Antipatharia (Cnidaria: Anthozoa). Part II Schizopathidae Zool Meded Leiden 76:411–442

Opresko D (2003) Redescription of *Antipathes dichotoma* Pallas, 1766 (Cnidaria: Anthozoa: Antipatharia). Zool Meded Leiden 77:481–493

Opresko D, Baron-Szabo R (2001) Re-descriptions of the antipatharian corals described by E.J.C. Esper with selected English translations of the original German text (Cnidaria, Anthozoa, Antipatharia). Senckenb Biol 81:1–2

Opresko D, Försterra G (2003) Ordnung Antipatharia. In: Hofrichter R (ed) Das Mittelmeer. Fauna, Flora, Ökologie, II/1. Spektrum Akademischer Verlag, Heidelberg, pp 506–509

Opresko D, Tracey D, Mackay E (2014) Antipatharia (black corals) for the New Zealand region. N Z Aquat Environ Biodivers Rep 131:1–20

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Prog Ser 397:37–51

Orejas C, Gori A, Jiménez C, et al (2017) First *in situ* documentation of a population of the coral *Dendrophyllia ramea* off Cyprus (Levantine Sea) and evidence of human impacts. Galaxea J Coral Reef Stud 19:15–16

Otero MM, Numa C, Bo M, et al (2017) Overview of the conservation status of Mediterranean anthozoans. In: IUCN. Málaga, Spain, 73 p

Pardo E, Aguilar R, García S, et al (2011) Documentación de arrecifes de corales de agua fría en el Mediterráneo occidental (Mar de Alborán). Chronica Nat 1:20–34

Pax F, Müller I (1962) Die Anthozoen fauna der Adria. Fauna Flora Adriat 3:1–343

Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la mer Méditerranée. Recl Trav Stn Mar Endoume 47:3–137

Pérez CD, de Moura Neves B, Cordeiro RT, et al (2016) Diversity and distribution of Octocorallia. In: Goffredo S, Dubinsky Z (eds) The Cnidaria, past, present and future. Springer, Heidelberg, pp 109–123

Poliseno A, Altuna A, Cerrano C, et al (2017) Historical biogeography and mitogenomics of two endemic Mediterranean gorgonians (Holaxonia, Plexauridae). Org Divers Evol 17:365–373. https://doi.org/10.1007/s13127-017-0322-x

Pratlong M, Haguenauer A, Chabrol O (2015) The red coral (*Corallium rubrum*) transcriptome: a new resource for population genetics and local adaptation studies. Mol Ecol Resour 15:1205–1215

Ramirez-Llodra E, Brandt A, Danovaro R, et al (2010) Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences 7:2851–2899

Reimer JD, Sinniger F, Hickman CP Jr (2008) Zoanthid diversity (Anthozoa: Hexacorallia) in the Galapagos Islands: a molecular examination. Coral Reefs 27:641–654

Risi MM, Macdonald AHH (2015) Possible synonymies of *Zoanthus* (Anthozoa: Hexacorallia) species on the east coast of South Africa with Pacific congeners. Syst Biodivers 13:93–103

Roberts JM, Cairns SD (2014) Cold water corals in a changing ocean. Curr Opin Environ Sustain 7:118–126

Roberts JM, Wheeler A, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystem. Science 312:543–547

Roberts JM, Wheeler A, Freiwald A, et al (2009) Cold-water corals. Cambridge University Press, Cambridge, New York, p 334

Roche J, Tixier-Durivault A (1951) Rapports des Gerardiides avec les Zoanthides et les Antipathaires. Bull Mus Natl Hist Nat Paris 23:402–409

Rogers AD (1999) The biology of *Lophelia pertusa* (Linnaeus, 1758) and other deep-water reef-forming corals and impacts from human activities. Int Rev Hydrobiol 84:315–406

Romano SL, Cairns SD (2000) Molecular hypotheses for the evolution of scleractinian corals. Bull Mar Sci 67:1043–1068

Salvati E, Angiolillo M, Bo M, et al (2010) The population of *Errina aspera* (Hydrozoa: Stylasteridae) of the Messina Strait (Mediterranean Sea). J Mar Biol Assoc UK 90:1331–1336

Sardà F, Calafat A, Flexas MM, et al (2004) An introduction to Mediterranean deep-sea biology. Sci Mar 68:7–38

Sartoretto S (2012) New records of *Dendrobrachia bonsai* (Octocorallia: Gorgonacea: Dendrobrachiidae) in the western Mediterranean Sea. Mar Biodivers Rec 5:e7

Saucier EH, Sajjadi A, France SC (2017) A taxonomic review of the genus *Acanella* (Cnidaria: Octocorallia: Isididae) in the North Atlantic Ocean, with descriptions of two new species. Zootaxa 4323:359–390

Schuchert P (1993) Phylogenetic analysis of the Cnidaria. Z Zool Syst Evol Forsch 31:161–173

Sinniger F, Häussermann V (2009) Zoanthids (Cnidaria: Hexacorallia: Zoantharia) from shallow waters of the southern Chilean fjord region, with descriptions of a new genus and two new species. Org Divers Evol 9:23–36

Sinniger F, Pawlowski J (2009) The partial mitochondrial genome of *Leiopathes glaberrima* (Hexacorallia: Antipatharia) and the first report of the presence of an intron in COI in black corals. Galaxea J Coral Reef Stud 11:21–26

Sinniger F, Chevaldonné P, Pawlowski J (2007) Mitochondrial genome of *Savalia savaglia* (Cnidaria, Hexacorallia) and early metazoan phylogeny. J Mol Evol 64:196–203

Sinniger F, Reimer JD, Pawlowski J (2008) Potential of DNA sequences to identify zoanthids (Cnidaria: Zoantharia). Zool Sci 25:1253–1260

Sinniger F, Reimer JD, Pawlowski J (2010) The Parazoanthidae (Hexacorallia: Zoantharia) DNA taxonomy: description of two new genera. Mar Biol 40:57–70

Sinniger F, Ocaña OV, Baco AR (2013) Diversity of zoanthids (Anthozoa: Hexacorallia) on Hawaiian seamounts: description of the Hawaiian gold coral and additional zoanthids. PLoS One 8:e52607. https://doi.org/10.1371/journal.pone.0052607

Stolarski J (2000) Origin and phylogeny of Guyniidae (Scleractinia) in the light of microstructural data. Lethaia 33:13–38

Stolarski J, Roniewicz E (2001) Towards a new synthesis of evolutionary relationships and classification of Scleractinia. J Palaeont 75:1090–1108

Taviani M (2002) The Mediterranean benthos from Late Miocene up to present: ten million years of dramatic climatic and geological vicissitudes. Biol Mar Mediterr 9:445–463

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin, pp 137–156

Taviani M, Vertino A, López Correa M, et al (2011) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603

Terrón-Sigler A, López-González PJ (2005) Cnidae variability in *Balanophyllia europaea* and *B. regia* (Scleractinia: Dendrophylliidae) in the NE Atlantic and Mediterranean Sea. Sci Mar 69:75–86

Thomson JA (1927) Alcyonaires provenant des campagnes scientifiques du Prince Albert Ier de Monaco. Rés Camp Sci Monaco 73:1–77

Thomson JA (1929) Alcyonaires des environs de Monaco et de localités diverses. Bull Inst Océanogr Monaco 534:1–10

Topçu EN, Öztürk B (2015) Composition and abundance of octocorals in the Sea of Marmara, where the Mediterranean meets the Black Sea. Sci Mar 79:125–135

Tsounis G, Rossi S, Grigg R, et al (2010) The exploitation and conservation of precious corals, vol 48. CRC Press, Boca Raton

Uda K, Komeda Y, Fujita T, et al (2013) Complete mitochondrial genomes of the Japanese pink coral (*Corallium elatius*) and the Mediterranean red coral (*Corallium rubrum*): a reevaluation of the phylogeny of the family Coralliidae based on molecular data. Comp Biochem Physiol D-Genomics Proteomics 8:209–219

Vafidis D (2010) Anthozoans (Table S13). In: Coll M, Piroddi C, Steenbeek J et al. (eds) The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PLoS One 5:e11842. https://doi.org/10.1371/journal.pone.0011842

Vafidis D, Koukouras A, Voultsiadou-Koukoura E (1994) Octocoral fauna of the Aegean Sea with a check list of the Mediterranean species: new information, faunal comparisons. Ann Inst Océanogr, Paris 70:217–229

Valente M, Maltagliati F, Cupido R, et al (2010) Absence of genetic structure in the gorgonian *Paramuricea clavata* (Cnidaria, Octocorallia) from the NW Mediterranean, as inferred by the COI gene. Biol Mar Mediterr 17:78–79

Van der Ham JL, Brugler MR, France SC (2009) Exploring the utility of an indel-rich, mitochondrial intergenic region as a molecular barcode for bamboo corals (Octocorallia: Isididae). Mar Genomics 2:183–192

Vaughan TW, Wells JW (1943) Revision of the suborders, families, and genera of the Scleractinia. Geol Soc Am Spec Pap 44:1–361

Verseveldt J (1964) Notes on Mediterranean *Alcyonium* species (Coelenterata: Octocorallia). Zool Meded, Leiden 39:153–167

Vertino A, Zibrowius H, Rocca M, et al (2010) Fossil Corallidae in the Mediterranean basin. NOAA Tech Memo CRCP 13:94–98

Vertino A, Stolarski J, Bosellini FR, et al (2014) Mediterranean corals through time: from Miocene to present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Heidelberg, pp 257–274

von Koch G (1889) Die Antipathiden des Golfes von Neapel. Mitt Zool Stat Neapel 9:187–204

von Koch G (1891) Die Alcyonacea des Golfes von Neapel. Mitt Zool Stat Neapel 9:652–676

Wagner D, Luck DG, Toonen RJ (2012) The biology and ecology of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). Adv Mar Biol 63:67–132

Weinberg S (1975) Contribution à la connaissance de *Parerythropodium coralloides* (Pallas) (Octocorallia, Alcyonacea). Beaufortia 23:53–73

Weinberg S (1976) Revision of the common Octocorallia of the Mediterranean circalittoral. 1. Gorgonacea. Beaufortia 24:63–104

Weinberg S (1977) Revision of the common Octocorallia of the Mediterranean circalittoral. 2. Alcyonacea. Beaufortia 25:131–166

Weinberg S (1978) Revision of the common Octocorallia of the Mediterranean circalittoral. 3. Stolonifera. Beaufortia 27:139–176

Weinberg S (1986) Mediterranean Octocorallia: description of *Clavularia carpediem* n. sp. and synonymy of *Clavularia crassa* and *C. ochracea*, on etho-ecological grounds. Bijdr Dierk 56:232–246

Weinberg S, Grasshoff M (2003) Gorgonien. In: Hofrichter R (ed) Das Mittelmeer. Fauna, Flora, Ökologie, II/1. Spektrum Akademischer Verlag, Heidelberg, pp 428–443

Weinberg S, Ocaña O (2003) Unterklasse Octocorallia Haeckel, 1866. In: Hofrichter R (ed) Das Mittelmeer. Fauna, Flora, Ökologie, II/1. Spektrum Akademischer Verlag, Heidelberg, pp 412–414

Wells JW (1956) Scleractinia. In: Moore RC (ed), Treatise on Invertebrate Paleontology. Pt F (Coelenterata). The University of Kansas Press, Lawrence, Kansas, pp F328–F444

Williams GC (1995) Living genera of sea pens (Coelenterata: Octocorallia: Pennatulacea): illustrated key and synopses. Zool J Linnean Soc 113:93–140

Williams GC (1999) Index Pennatulacea. Annotated bibliography and indexes of the sea pens of the world 1469–1999. Proc Calif Acad Sci 51:19–103

Williams GC (2011) The global diversity of sea pens (Cnidaria: Octocorallia: Pennatulacea). PLoS One 6:e22747. https://doi.org/10.1371/journal.pone0022747

Willison JHM, Hall J, Gass SE, et al (2001) Proceedings of the first international symposium on deep-sea corals. Ecology Action Center, Halifax

Wirshing HH, Messing CG, Douady CJ, et al (2005) Molecular evidence for multiple lineages in the gorgonian family Plexauridae (Anthozoa: Octocorallia). Mar Biol 147:497–508

Wright EP, Kemp K, Rogers AD, et al (2014) Genetic structure of the tall sea pen *Funiculina quadrangularis* in NW Scottish sea lochs. Mar Ecol 36:659–667

WWF/IUCN (2004) The Mediterranean deep-sea ecosystems: an overview of their diversity, structure, functioning and anthropogenic impacts, with a proposal for conservation. IUCN, Málaga and WWF, Rome, 65 pp

Yesson C, Taylor ML, Tittensor DP, et al (2012) Global habitat suitability of cold-water octocorals. J Biogeogr 39:1278–1292

Zapata F, Goetz FE, Smith SA, et al (2015) Phylogenomic analyses support traditional relationships within Cnidaria. PLoS One 10(10):e0139068. https://doi.org/10.1371/journal.pone.0139068

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mém Inst Océanogr, Monaco 11:1–107

Zibrowius H (1984) Taxonomy in ahermatypic scleractinian corals. Palaeontogr Am 54:80–85

Zibrowius H (1985a) *Gerardia savaglia* (Cnidaria: Anthozoa: Zoantharia) nouvel hôte de *Balssia gasti* (Crustacea: Decapoda: Pontoniinae). Rapp P-V Réun Comm Int Explor Sci Mer Méditerr 29:349–350

Zibrowius H (1985b) Comportement agressif du Zoanthaire *Geradia savaglia* contre le Gorgonaire *Paramuricea clavata* (Cnidaria: Anthozoa). Rapp P-V Réun. Comm Int Explor Sci Mer Méditerr 29:351–353

Zibrowius H (2003) The "white coral community", canyon and seamount faunas of the deep Mediterranan Sea. RAC/SPA – Regional Activity Centre for Specially Protected Areas, Tunis

Zibrowius H, Cairns SD (1992) Revision of the Northeast Atlantic and Mediterranean Stylasteridae (Cnidaria: Hydrozoa). Mém Mus Natl Hist Nat, Paris, (A) 153:1–136

Zibrowius H, Placella B (1982) First record of the genus *Fungiacyathus* (Cnidaria, Scleractinia) from the Mediterranean area: Pliocene of Masseria Concarone (NT.), southern Italy. Boll Soc Paleontol Ital 20:143–146

Cross References

Addamo AM (this volume) *Desmophyllum dianthus* genetics and more

Bo M, Bavestrello G (this volume) Mediterranean black coral communities

Boavida J, Becheler R, Addamo A, et al (this volume) Past, present and future connectivity of Mediterranean cold-water corals: patterns, drivers and fate in a technically and environmentally changing world

Bramanti L, Santangelo G, Benedetti MC, et al (this volume) Demography and conservation of deep corals: the study of population structure and dynamics

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

D'Onghia G (this volume) Cold-water coral as shelter, feeding and life-history critical habitats for fish species: ecological interactions and fishing impact

Fourt M, Goujard A, Chevaldonné P (this volume) Working with visual methods, comparison among the French deep-sea canyons

Gori A, Grinyó J, Dominguez-Carrió C, et al (this volume) Gorgonian and black coral assemblages in deep coastal bottoms and continental shelves of the Mediterranean Sea

Lartaud F, Mouchi V, Chapron L, et al (this volume) Growth patterns of Mediterranean calcifying cold-water corals

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals

Vertino A, Corselli C (this volume) Did Quaternary climate fluctuations affect Mediterranean deep-sea coral communities?

15

Habitat Mapping of Cold-Water Corals in the Mediterranean Sea

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Abstract

Habitat mapping is increasingly considered as a reliable and efficient methodology to explore and represent the complexity and extent of benthic communities. Providing a full-coverage spatial perspective of habitat heterogeneity is becoming an essential tool in science-based management of natural resources, specifically regarding vulnerable marine ecosystems such as cold-water corals. Here we present two case studies, where we revisit known cold-water coral areas of the Mediterranean Sea and where we apply original habitat mapping techniques. The areas correspond to the Chella Bank, in the Alborán Sea, and the Santa Maria de Leuca cold-water coral province, in the Ionian Sea. The Chella Bank is one of a series of volcanic banks and knolls located in the western Mediterranean that have been described as geologic features hosting vulnerable marine ecosystems. The cold-water coral province off Santa Maria de Leuca represents one of the largest known occurrences of living reef-forming cold-water coral species (i.e. *Lophelia pertusa* and *Madrepora oculata*) in the Mediterranean Sea, where corals grow on the exposed summits and flanks of mound-like structures (up to 300 m wide and 25 m high) associated with mass wasting events. Both cases adopt a holistic and integrated study of the environmental characteristics (geology and oceanography) of the observed benthic habitats and aim to map their extent using supervised automated classifications. Multibeam swath bathymetry, the derived acoustic backscatter, sidescan sonar, video footage gathered with a remotely operated vehicle, photo stills from underwater drop camera, and CTD casts where available, have been used together to identify the geological and oceanographic processes that most likely are responsible for the distribution of the observed cold-water corals and associated benthic communities.

Keywords

Habitat mapping · Cold-water corals · Geomorphology · Benthic habitats · Mediterranean Sea

15.1 Introduction

Mapping the distribution of benthic habitats using robust and objective methodologies can support science-based monitoring, management and protection of natural marine resources, specifically for deep-sea vulnerable marine ecosystems (VMEs), whose dynamics are not entirely understood (European Parliament 2008; Farmer et al. 2012; Golon 2014; Grehan et al. 2017). Habitat mapping aims to describe the distribution of seafloor habitats by exploring the interactions between geological, ecological and oceanographic processes, allowing point data to be extended to full-coverage maps. Under this perspective, the application of geo-acoustic full-coverage mapping, supported by groundtruthing information and water column measurements, gives additional information to ecological studies by providing a realistic view on the ecosystem structure and on its multi-scale spatial variability. The application of classical hull-mounted multi

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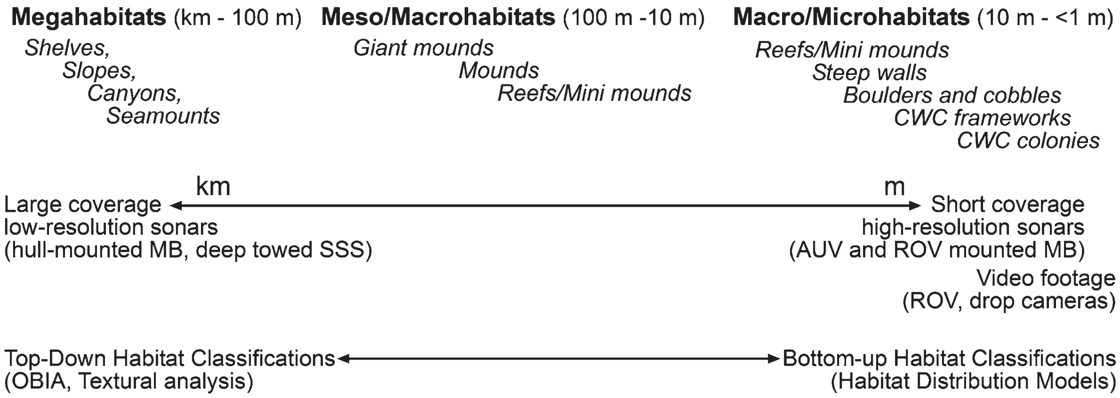

Fig. 15.1 Schematic illustration displaying the different spatial scales of the physical habitats associated with CWC ecosystems (*sensu* Green et al. 1999), the relative survey techniques (geo-acoustic and video) applied in their exploration and the most adopted habitat mapping approaches. Although both top-down and bottom-up classifications are mostly associated with broad and fine spatial scales respectively, these approaches can be applied over the full range of scales

beam (MB) systems and the increasing use of the most developed autonomous underwater vehicles (AUV) represent the base for mapping and monitoring strategies of marine environments at different spatial resolutions (Ramirez-Llodra et al. 2010; Wynn et al. 2014; Angeletti et al., this volume), spanning from large geo-habitats (e.g.: continental shelves, submarine canyons, seamounts, scale of hundreds of meters to few kilometres) to small species assemblages (sub-metrical scale) (Fig. 15.1).

As the distribution of species can be influenced by seabed morphology (through substrate type and rugosity, fine-scale effects of currents, distribution of food supply) MB swath bathymetry can provide digital terrain models (DTM) of the submarine landscape at resolutions which allow for the differentiation of physical boundaries between different benthic habitats. Surrogates derived from DTMs (such as slope, aspect, bathymetric position index, rugosity) can then be used as proxies to explain ecological patterns (Guinan et al. 2000; Savini et al. 2014; Robert et al. 2016; Bargain et al. 2017; Lastras et al., this volume; Angeletti et al., this volume). This is specifically true for those environments displaying a strong three dimensional (3D) complexity, as in the case of Mediterranean coralligenous build-ups (Lo Iacono et al. 2018a) or framework forming scleractinian cold-water corals (CWCs) (Freiwald et al. 2002; Savini and Corselli 2010; Lo Iacono et al. 2014; Glogowski et al. 2015). Stony CWCs can occur as isolated colonies or patchily distributed aggregations among a variety of different substrates, which can only be captured by maps with sub-metrical resolutions (Davies et al. 2017). Under suitable environmental conditions alternating with less favourable conditions in a cyclical pattern over time, CWCs are able to form reefs and mounds with a complex 3D structure. Mounds can reach a few hundreds of metres in height and can be several kilometres wide (see a comprehensive list of references in Roberts et al. 2009; Lo Iacono et al. 2018a).

Seafloor acoustic backscatter (BS) is sensitive to the textural properties (hardness and roughness) of the seafloor (Ferrini and Flood 2006; Lo Iacono et al. 2008; Brown et al. 2011; Pierdomenico et al. 2016). Acoustic BS can be used to differentiate sedimentary facies associated with specific habitats (Masson et al. 2003), to map seagrass distribution (Tonielli et al. 2016), to discern different degrees of bioturbation as controlled by volume scattering (Urgelés et al. 2002) or to distinguish living CWC colonies from coral rubble (Huvenne et al. 2016). Nonetheless, despite full coverage acoustic mapping being a key requirement, reliable maps of benthic habitats need to be validated through ground-truth data (such as video, still photos or seafloor samples). Over recent years, further information from oceanographic data (bottom currents, wave regimes, tidal cycle, chemical properties of the water column etc..) are increasingly being integrated with seafloor data to assess the interactions between geological and oceanographic processes as driving mechanisms for habitat distribution (Fabri et al. 2016), specifically for passive filter-feeding organisms, which rely on food-rich bottom currents (Roberts et al. 2009 and references therein). Habitat mapping techniques are progressively refined from subjective interpretations of habitat distributions to more objective and time-saving approaches based on complex image analysis algorithms and statistical approaches, either unsupervised or supervised.

Habitat mapping and seafloor classification techniques can be broadly separated into two main approaches: top-down and bottom-up approaches (Brown et al. 2011; Angeletti et al., this volume). Top-down habitat classifications based on acoustic maps generally obtained through MB hull-mounted echo-sounders, have the advantage of covering large areas, addressing the heterogeneity of geologic features (mega-habitats *sensu* Green et al. 1999) as the main driving control in habitat distribution (LaFrance et al. 2014; Ismail et al. 2015). On the other hand, bottom-up approaches define habitat boundaries based on the biological/ecological variability observed through punctual observations, and extrapolate/predict them on a broader scale by building statistical relationships between biotic (e.g.: macrofaunal assemblages) and abiotic (geomorphology, sedimentary settings, water depth, water column etc.) characteristics of the environment (Fig. 15.1) (Davies et al. 2008; LaFrance et al. 2014; Robert et al. 2015).

The ecosystems formed by CWCs, including stony corals, soft corals, black corals and gorgonians, are considered among the most endangered in the ocean (Freiwald et al. 2004; UNGA 2006; Roberts et al. 2009; Otero and Marin, this volume). Despite being aware of their relevant role in maintaining high levels of biodiversity in marine ecosystems, the existence of these sensitive habitats is being seriously compromised by anthropogenic activities, such as commercial bottom trawling and ocean acidification (Reed 2002; Söffker et al. 2011; Baillon et al. 2012; Maier et al., this volume; Movilla, this volume; Otero and Marin, this volume). Their vulnerability to such massive impacts is making scientific and political communities aware of the need for their conservation in several Exclusive Economic Zones (EEZ) around the world. Thus, specific studies and dedicated measures to preserve natural resources are urgently needed, as well as detailed and statistically robust mapping methodologies, and continued monitoring of the protected areas. Over the last few years, several studies have unveiled the existence of living CWC communities in the Mediterranean Sea (among others Taviani et al. 2005a; Schembri et al. 2007; Trincardi et al. 2007; Orejas et al. 2009; Vertino et al. 2010; Mastrototaro et al. 2010, 2017; Lo Iacono et al. 2012b; Cartes et al. 2013; Gori et al. 2013; Fabri et al. 2014; Mytilineou et al. 2014; Taviani et al. 2017; Evans et al. 2016; Fanelli et al. 2016; Grinyó et al. 2016; Aymà et al., this volume; Knittweis et al., this volume; Orejas et al., this volume). Nonetheless, the scientific understanding of the dynamics and distribution patterns of CWC communities in the Mediterranean is still far from complete. Despite the increasing availability of echosounders (hull mounted MB, AUV mounted MB, SSS) and high-definition visual tools (ROV and deep-towed cameras) within the European research fleets, relatively few studies adopted habitat mapping approaches on CWC fields, trying to describe and quantify their extent and spatial patterns in a coherent way (Vertino et al. 2010; Lo Iacono et al. 2012b, 2014; de Juan et al. 2013; Fabri et al. 2014). Few habitat mapping studies have used automated classification techniques, either attempting top-down (De Mol et al. 2012; Savini et al. 2014) or bottom-up approaches (Coiras et al. 2010; Vertino et al. 2010; Giusti et al. 2014; Lauria et al. 2015; Boavida et al. 2016; Fabri et al. 2016; Lo Iacono et al. 2018b). This is partly due to the lack of seafloor maps (MB and BS) whose spatial resolution is high enough to allow the distinction of the morphological and acoustic patterns associated with CWC communities, from mound to colony scale.

Here we present two case studies of habitat mapping of Mediterranean areas containing CWC assemblages and associated species: the Chella Bank in the Alborán Sea (western Mediterranean) and the Santa Maria de Leuca (SML) CWC province in the Ionian Sea (central Mediterranean). The areas are characterised and classified adopting similar approaches, although at different spatial scales. Both regions have already been described and recognised by national and international organisations as physiographic features associated to a high level of biodiversity, with the occurrence of endangered VMEs, including CWC (de Juan and Lleonart 2010; OCEANA 2011, 2014; OCEANA and IEO 2014).

15.2 CASE STUDY 1 – The Chella Bank, Alborán Sea

This case study revisits and implements previous observations on the geomorphic features and benthic habitats of the Chella Bank, also named as “Seco de los Olivos”, in the NE Alborán Sea, and expands on those by integrating the published high-resolution swath bathymetry, BS data, and original video images and water column data (Fig. 15.2). The Alborán Sea is located in the SW Mediterranean and displays several clusters of seamounts and volcanic banks hosting VMEs (Milliman et al. 1972; Lo Iacono et al. 2008; Munòz et al. 2008; Oceana and IEO 2014; Palonimo et al. 2015; Hebbeln, this volume; Wienberg, this volume; Palomino et al., this volume). Amongst those, the Chella Bank is located in the northeastern sector of this basin within a depth range of 70–700 m and is composed of middle Miocene to Pleistocene volcanic rocks (Duggen et al. 2004) (Fig. 15.2). The Chella bank displays a sub-circular shape. It contains three main geomorphic features: a central sub-horizontal flat top surrounded by two linear ridges at its western and eastern sides (Coiras et al. 2010; Lo Iacono et al. 2012a), covering a total surface of up to 100 km^2 (Fig. 15.2). Previous studies in the area described the Chella Bank as a seamount hosting suitable habitats for CWCs, such as framework building corals and coral gardens (Lo Iacono et al. 2012a; OCEANA and IEO 2014). Data for this study comprise a high resolution bathymetric grid (10 m pixel size) acquired by the Instituto Español de Oceanografia (IEO) using a Simrad EM300 hull-mounted MB echosounder (30 kHz, for further details see Coiras et al. 2010; Lo Iacono et al. 2012a), a corresponding BS mosaic (5 m pixel size) and videos/photos collected to ground-truth the seafloor. The original videos/photos were acquired using a SeaTronic DTS6000 frame equipped with the HR camera Kongsberg OE 14-208 and a small Mariscope-SPY ROV equipped with standard resolution cameras. Eleven CTD casts were

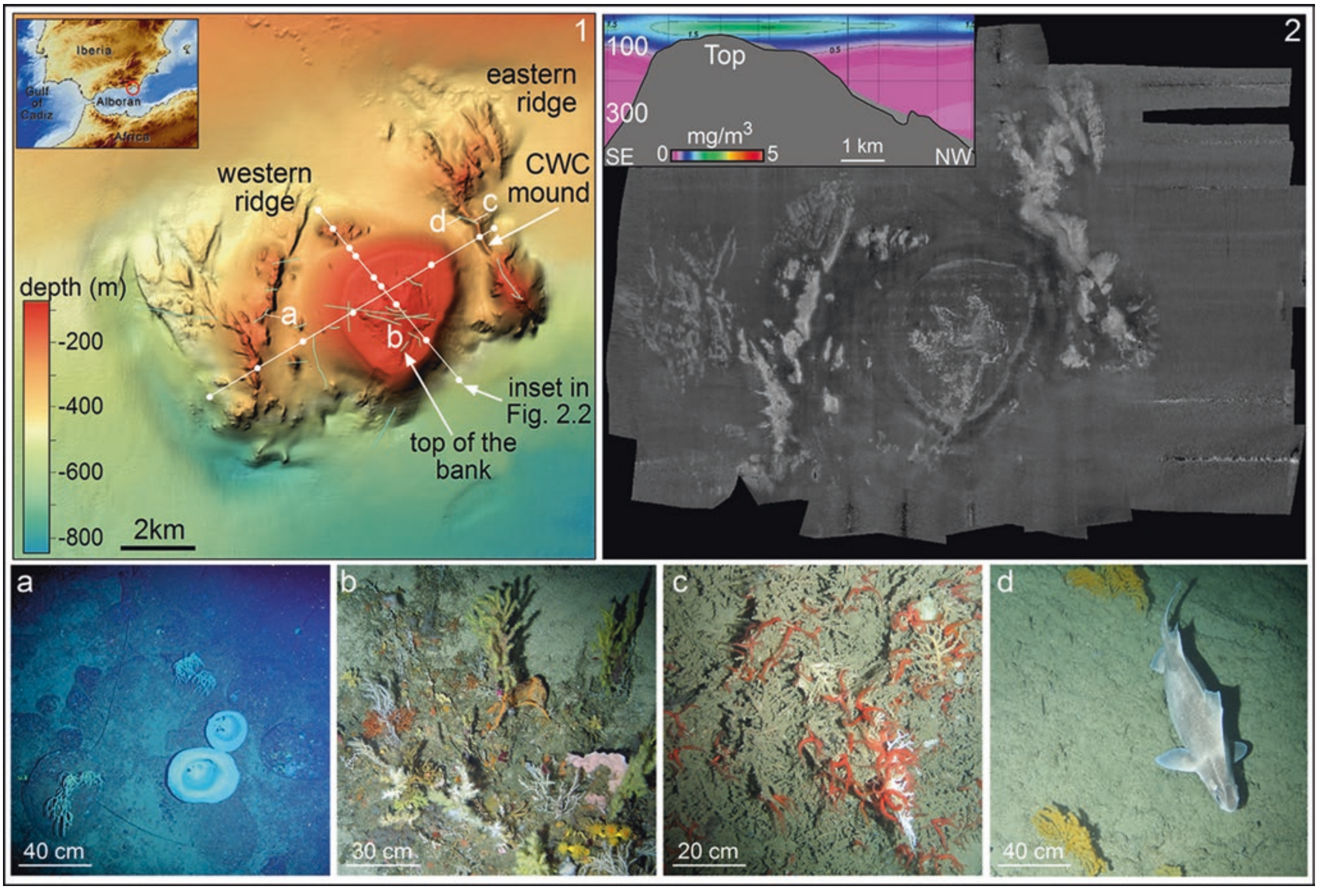

Fig. 15.2 (**1**) MB bathymetric map of the Chella Bank. The white lines indicate the CTD transects carried out in the area, with dots indicating the locations where the casts were acquired. The NW-SE oriented transect is displayed in (**2**); *a*, *b*, *c* and *d* indicate the locations where the digital stills showed in the figure were taken. Blue lines indicate the ROV and digital camera transects used to ground-truth the area. The inset shows the location of the study area in the red circle. (**2**) Backscatter mosaic acquired in the area. Light tones correspond to high BS values. The inset shows the chlorophyll fluorescence values acquired through the CTD casts along the NW-SE transect displayed in 1 (vertical black lines indicate the locations where the casts were acquired), vertical scale in m. (**a**) volcanic boulders and blocks with the glass sponge *Asconema setubalense*, the black coral *Antipathes dichotoma* and a small *Dendrophyllia cornigera* (class 5 in automatic classification); (**b**) coral garden including CWCs (class 1 in automatic classification); (**c**) dense and partly oxidised frameworks of dead *Lophelia pertusa* draped by fine grained sediments, with dense aggregations of *Ophiothrix sp.* observed on top of the CWC mound of the Chella Bank; (**d**) CWC frameworks and coral rubble with spotted gorgonians *Acanthogorgia hirsuta* observed along the flank of the CWC mound of the Chella Bank. The shark is an *Oxynotus centrina*. In this last photo, the estimated inclination of the seafloor is between 14° and 18°

acquired on the Chella Bank with a Seabird SBE9 along two transects crossing the centre of the Bank (Fig. 15.2-1). Turbidity, salinity, temperature, fluorescence and oxygen were recorded along the water column for each station. Video footage and CTD casts were acquired during the EVENT-SHELF and EVENT-DEEP Cruises, in the frame of the EVENT Spanish National Project (CGl200612861-C02-02, CTM2003.QJJ46-ElMAR).

15.2.1 Conservation Value of the Chella Bank

The Chella Bank is one of the marine areas in Spanish waters designated as Sites of Community Importance (SCI) and Special Areas of Conservation (SAC) under the EU Habitats Directive. Evidence gathering was carried out in the frame of the EU-LIFE INDEMARES Project (OCEANA 2014; OCEANA and IEO 2014). Some of the species observed in this area belong to the list of endangered species recognised by different national and international conventions. The most relevant conventions which have been taken into consideration are: the Bonn Convention (Convention on the Conservation of Migratory Species of Wild Animals), the EU Habitats Directive (92/43/CEE), the Barcelona Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean, the Mediterranean Red List of endangered species produced by the International Union for Conservation of Nature (IUCN) and the Spanish law 42/2007 for conservation of Natural Patrimony and Biodiversity. Most of the vulnerable and endangered species belong to the Phyllum Cnidaria, which include CWC species such as *Antipathes dichotoma, Antipathella subpinnata, Savalia sav-*

aglia (false black coral), *Leiopathes glaberrima, Parantipathes larix*, *Lophelia pertusa, Madrepora oculata, Dendrophyllia cornigera, Dendrophyllia ramea, Eunicella verrucosa, Leptogorgia sarmentosa, Paramuricea clavata, Callogorgia verticillata.* The Habitat 1170 (Reefs – Annex I), identified based on the EU Habitats Directive (92/43/CEE), occurs on the Chella Bank. Based on video observations, CWC communities show a poor conservation status but with achievable actions towards their recovery and preservation of a good environmental status (OCEANA and IEO 2014). The Chella Bank has also been recognised as an area with relevant occurrence of cetaceans, such as *Balaenoptera acutorostrata*, *Delphinus delphis*, *Stenella coeruleoalba* and *Globicephala melas*, which are also described as endangered species in Annex IV of the EU Habitats Directive (OCEANA 2014; OCEANA and IEO 2014).

15.2.2 The Chella Bank and Its Habitats

The western ridge of the Chella Bank extends for around 16 km^2 and covers a depth range of 160–620 m. (Fig. 15.2). The ridge stretches in N-S direction in the southern half and bifurcates towards the north in a Northwest and a Northeast direction (Fig. 15.2) (Lo Iacono et al. 2012a). The walls display an average slope of 8°, with maximum values of 17°. Available data reveal the complex geological nature of peaks and crests along the ridge, which consist of hard and massive volcanic bedrock and volcanic breccias (Fig. 15.2a). More detailed information on the geology and geomorphology of the western ridge is available in Lo Iacono et al. (2012a). Original videos reveal that peaks and crests correspond to habitats mostly dominated by the hat-shaped glass sponge *Asconema setubalense*, accompanied by scattered stony cup corals (*D. cornigera*), black corals (*Anthipates sp.*; *Anthipates dichotoma*), gorgonians (*Acanthogorgia hirsuta*), grey encrusting sponges (*Hamacantha falcula*) and sponges (*Pachastrella monilifera*; *Petrosia* sp.). Sedimentary bottoms are mainly composed of muds mixed with fine sands, dominated by different species of echinoids (*Spatangus purpureus*, *Cidaris cidaris*, *Echinus acutus*), with scattered sea pens (*Kophobelemnon stelliferum)* and bamboo corals (*Isidella elongata*). Coarse sand regions are randomly characterised by 40–50 cm long asymmetric ripples, suggesting the occurrence of unidirectional currents in the area (Lo Iacono et al. 2012a).

The eastern ridge of the Chella Bank covers a depth range of 100–480 m along a NW-SE trend and consists of two main banks connected by a linear, slightly sinuous 2 km long and 400 m wide structure, 300 m deep and up to 60 m high (Fig. 15.2) (Lo Iacono et al. 2012a). The southern bank is a 200 m high sub-conical massif with slopes from 15° to 20°. Based on video images, the southern bank consists of basaltic slabs, in some cases showing typical disjunctions. The northern bank develops over a depth range of 150–350 m and presents four main NW-SE trending ridges and a single NE-SW oriented ridge (Lo Iacono et al. 2012a). Based on their morphology and on previous studies, these ridges are most likely composed of volcanic rocks (Lo Iacono et al. 2012a; OCEANA and IEO 2014). Available video footage along the southern bank of the eastern ridge suggests a low species richness and diversity along this sector, which is apparently dominated by scattered specimens of the glass sponge *A. setubalense*. Contrasting with the geological nature and with the dominant benthic communities of the two banks, original videos and photo stills along the 2 km long sinuous feature connecting them has unveiled the biogenic origin of this relief. Both the top and the flanks of this relief showed the presence of subfossil CWC frameworks (mainly *L. pertusa* and *D. cornigera*). The top, at around 300 m deep, showed dense frameworks of dead *L. pertusa* draped by a fine sediment veneer and intensely colonised by the brittlestar *Ophiothrix sp.* Occasionally, scattered living colonies of *M. oculata, D. cornigera*, *A. hirsuta*, and the sponge *P. monilifera* were registered. The flank displays a smooth morphology, consisting of dead *L. pertusa* frameworks and fine sediments showing an apparent stratification, spotted coral rubble and bioclastic debris. Scattered specimens of the gorgonian *A. hirsuta* and the black coral *P. larix* were registered along the flank. Based on the available data, also including seismic records crossing the area and imaging its internal structure (Lo Iacono et al. 2011), the sinuous feature along the Chella eastern ridge most probably corresponds to a CWC mound, up to 60 m tall. Similar cold-water carbonate bioconstructions have already been described in the same basin, south of the Chella Bank (Cabliers CWC mound: Lo Iacono et al. 2016, 2018a; East Melilla CWC Mounds: Fink et al. 2013, Wienberg, this volume; West Melilla CWC Mounds: Lo Iacono et al. 2014).

The top of the Chella Bank displays a sub-circular shape and covers a total surface of 7.6 km^2 (Fig. 15.2). The area is composed of an irregular central sector showing a rough seafloor and a surrounding flat and sub-horizontal sector (Fig. 15.2). The irregular central sector ranges from 76 to 118 m in depth and rises up from 5 up to 40 m above the surrounding bank top (Lo Iacono et al. 2012a). The BS image of this sector presents an alternation of high BS stripes correlated to rocky outcrops in the video images, and low BS facies where bioclastic coarse sandy sediments were observed.

The area surrounding the rough central sector presents a smooth, low reflective sub-horizontal seafloor, with depths ranging from 130 to 115 m. In this area, the predominant seafloor substrate corresponds to coarse sands and gravels, entirely composed of bioclasts (Fig. 15.2) (Lo Iacono et al. 2012a). Analysis of the composition of the sands revealed the presence of planktonic foraminifera, shells, molluscs (especially bivalves), echinoid spines and bryozoan remains (Lo Iacono et al. 2012a).

Original video tracks along the rough rocky outcrops also revealed extensive fields of cemented bioclastic sediments mainly consisting of gravels and coarse sands. Based on composition and depth of rocky outcrops, they likely correspond to relict coastal deposits formed during previous sea level stages, and now provide substrate for a wide variety of gorgonians typically found along the Mediterranean shelf edge and upper slope environments (Grinyó et al. 2016). Gorgonian species observed included *C. verticillata, Viminella flagellum, Swiftia pallida, P. clavata, Eunicella cavolinii, E. verrucosa, Muriceides lepida* and *Ellisella paraplexauroides*. These gorgonian species form dense coral gardens that cover vast extents of the top of the Chella Bank. Among these gorgonian species, we also observed numerous colonies of the CWC *D. cornigera*, the recently described soft coral *Chironephthya mediterranea* (López-González et al. 2014), an undetermined species of the genus *Alcyonium*, several large desmosponge species such as *P. monilifera*, *Aplysina cavernicola*, *Poecillastra compressa*, *Phakellia ventilabrum*, the bryozoans *Pentapora facialis,* and the polychaete *Salmacina disteri*. Some gorgonian species presented substrate for large individuals of the epiphyte *Astrospartus mediterraneu*s. Video tracks also showed that part of this habitat has been seriously damaged by long-line fishing activities.

Processing of the acquired CTD casts shows increased values of turbidity and fluorescence in the surface waters overlying at the top of the Chella Bank (Fig. 15.2). The observed increased values could arise from the interaction between the topography of the Bank and the circulation of the highly productive surface waters, already described in the Alborán Sea (Uitz et al. 2012; Oguz et al. 2014). The acceleration of food-rich bottom currents, when interacting with the rough local topography, most likely represents the driving mechanism controlling the occurrence of the observed extensive fields of CWC communities. Accelerated currents can increase the supply of particulate food and induce the recruitment and growth of passive suspension feeders, able to exploit suspended particles as a potential food source (Gili and Coma 1998).

15.2.3 Automatic Classification of Benthic Habitats on the Chella Bank

The automated classification of the Chella Bank environment was based on a combination of MB and BS data, together with still photos and videos for ground-truthing. Input data to the classification process consisted of:

- Bathymetry grid (10 m pixel), smoothed with a 3 × 3 mean filter
- Slope map, calculated from the above smoothed bathymetry (using ArcGIS)
- Benthic Positioning Index map, calculated from the smoothed bathymetry, using an annulus kernel with inner radius of 8 pixels and outer radius of 21 pixels (using the freely available Benthic Terrain Modeller 3.0 toolbox (Wright et al. 2012).
- Backscatter grid (10 m pixel), smoothed with a 5 × 5 mean filter
- Grey-Level Co-Occurrence Matrix (GLCM) Dissimilarity as defined by Haralick (1979), calculated in 21 × 21 pixel moving windows, with an inter-pixel distance of 8, averaged over 4 directions and with backscatter reduced to 64 grey levels (in-house developed Matlab routine).
- GLCM Entropy (Haralick 1979), calculated in 21 × 21 pixel moving windows, with inter-pixel distance of 8, averaged over 4 directions and with backscatter reduced to 64 grey levels (Matlab).

Video and photography data were classified into the following dominant habitat types: (1) Rocky outcrops with coral gardens and gorgonian fields; (2) bioclastic coarse sands and gravels with dominance of echinoids; (3) volcanic ridges with dominance of the glass sponge *Asconema setubalense* and anthipatarians; (4) sub-outcropping volcanic ridges draped by mud, with spotted glass sponge *A. setubalense*; (5) fine bioclastic sediments; (6) CWC framework.

The ROV video tracks were split into 200 m long sections which, together with a series of point observations from the drop-camera, were selected as ground-truthing points. Every other 200 m section was discarded to limit the 'spatial autocorrelation' between samples. Twenty percent of the leftover sections/points of each class were randomly selected as test samples to evaluate the classification. The other 80% were used to create "training areas".

A Maximum Likelihood Classifier (MLC) algorithm was used in ArcGIS to produce a full-coverage map for the rest of the Chella area. The result is presented in Fig. 15.3.

The automated classification was able to identify and map out all six recognised substrate types. Our test dataset indicated a very good performance: only one of the test samples in the bioclastic sand class (2) was classified as fine sediments (5). Nonetheless, it is clear from Fig. 15.3 that the noise in the MB and BS data also creates a number of misclassification patterns (generally recognisable because they are oriented NS or EW). Moreover, the system showed a low performance in isolating the distribution of the CWC framework, which was erroneously found along the southern flank of the seamount. The automated habitat classification already produced in the same region by Coiras et al. (2010) came to broadly similar results, although limited to 3 instead of 6 classes. Coiras et al. 2010 used a linear classifier predicting the main habitat distribution on the Chella Bank employing a Matlab's classification routine for the three habitat classes

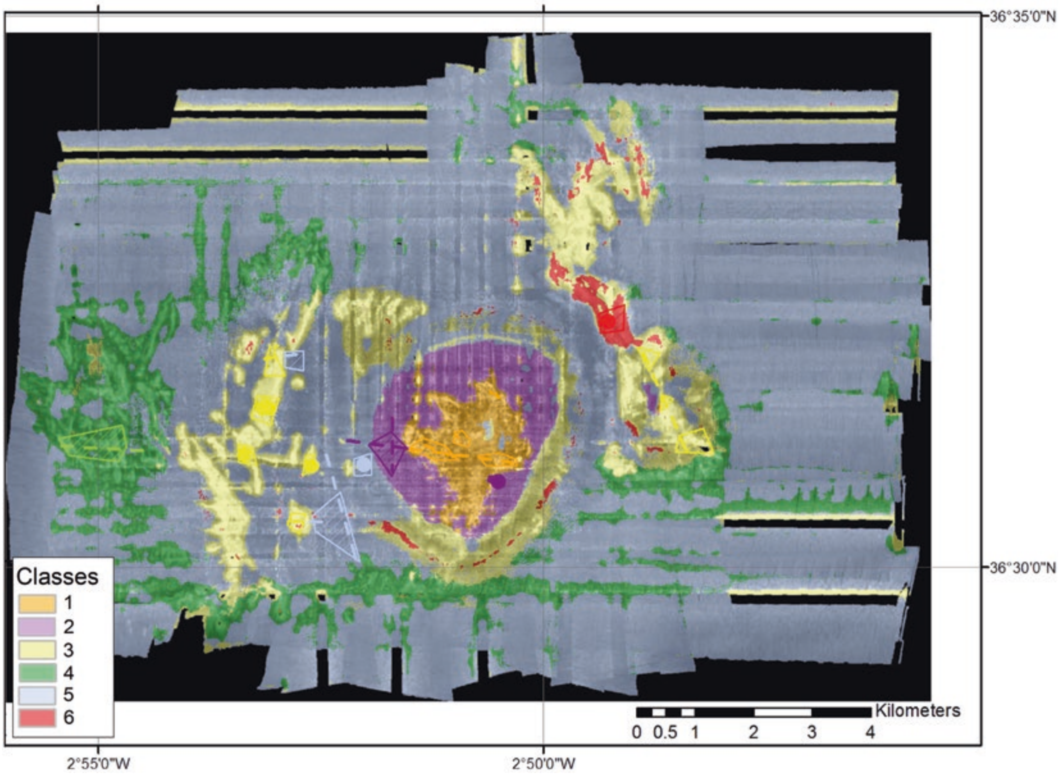

Fig. 15.3 Supervised automated classification of the benthic habitats on the Chella Bank. Class 1: Coral gardens, found on top of the Bank; Class 2: bioclastic coarse sands and gravels, mainly found along the outer sector of the top; Class 3: Volcanic ridges with dominance of the glass sponge *Asconema setubalense* and antipatharians; Class 4: sub-outcropping volcanic rocks draped by muddy veneers, with spotted glass sponge *Asconema setubalense*; Class 5: bioclastic fine sediments; Class 6: dead CWC framework. See the text for a comprehensive description of each class. Dots and lines represent the ground-truthing data (still photos and ROV tracks respectively). Different colours correspond to the different assigned classes. Polygons represent the areas selected for the training and the control of the classification system

(flat seafloor with CWCs, hard substrates with sponges, sandy deposits) (for more details see Coiras et al. 2010). Despite a smaller number of adopted classes, results in Coiras et al. 2010 mainly coincide with what this study independently presents, giving confidence in the objective and repeatable aspect of our classification.

15.3 CASE STUDY 2 – The Santa Maria de Leuca CWC Province, Ionian Sea

The CWC province off SML represents one of the largest known occurrences of living scleractinian CWCs in the Mediterranean Sea, where dense aggregations of coral topped mounds are distributed over more than 800 km^2 on the northern Ionian margin, between 500 and 1000 m in depth (Savini et al. 2016; Chimienti et al., this volume). The extent of SML CWC habitats has been estimated recently at multiple spatial scales (Savini et al. 2014) and is summarised here. A more exhaustive explanation on the control that local geomorphic processes have in determining CWC distribution and extent across the whole surveyed area is provided, where corals are spread on different geological features, including the summits of positive features associated to mass wasting geomorphologies. The province is located offshore the southern limit of the Apulian Peninsula, on the north-eastern Ionian margin, along the Apulian plateau (Fig. 15.4). The plateau is an antiform formed by a 6 km thick Mesozoic carbonate platform, overlaid by a thin Plio-Quaternary sedimentary succession which slightly thickens eastward (Argnani et al. 2001). It is crosscut by a NNW-SSE normal fault network, which forms prominent fault scarps and promontories towards the west. Late Pleistocene mass-wasting deposits dominate instead the central/eastern sector of the surveyed plateau, shaping the seafloor in a number of landslide related landforms (headscarps, longitudinal and transverse lineations, extensional and pressure ridges, sediment blocks, as described in Savini et al. 2016) (Fig. 15.4). As documented by the occurrence of sediment drifting (Taviani et al. 2005b; Savini and Corselli 2010), the benthic environment is also impacted by bottom currents, generated by a core of cold (12.92 °C), less saline (38.64 psu), and oxygenated water of Adriatic origin that moves in geostrophic balance along isobaths of 600–1000 m (Budillon et al. 2010).

Data for this study have been collected over the past 10 years (Corselli 2010; Savini et al. 2014) and are com-

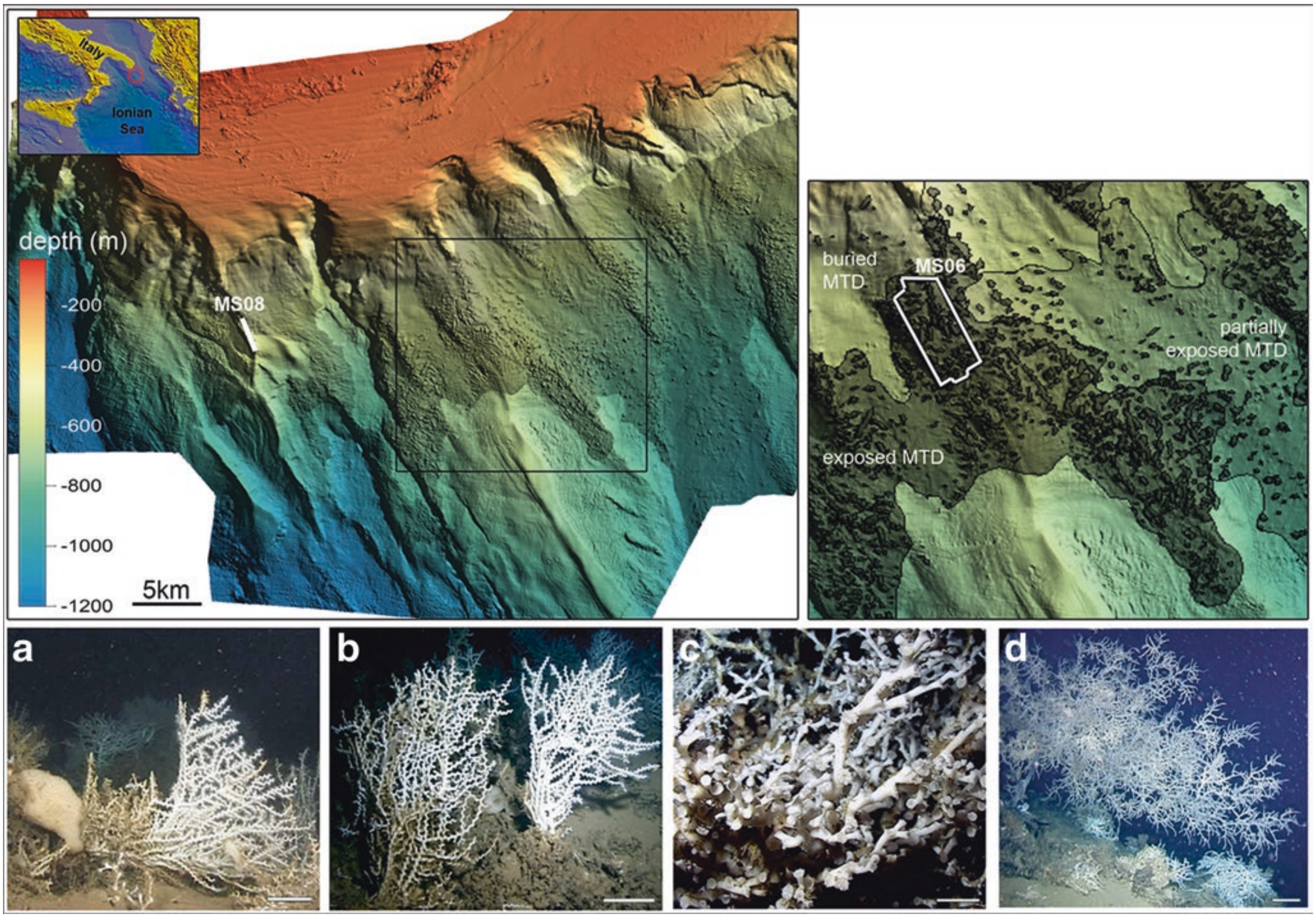

Fig. 15.4 Distribution of coral-topped mounds in the northern Ionian Sea (SML CWC province). **Top-left panel**: MB bathymetric map showing the location of MTDs (semi-transparent gray polygon). **Top-right panel**: a detail of the multibeam bathymetric map (see the black inset in the top-left panel for location) showing the distribution of sediment blocks (black polygons) within the exposed, partially exposed and buried MTDs. The white polygon indicates the location of the SSS mosaic of Fig. 15.5. **Bottom panels** include 4 representative Pluto-ROV seafloor images of coral-dominated macro-habitats: (**a**) live colony of *Madrepora oculata* and the sponge *Poecillastra compressa* (adapted from Vertino et al. 2010 and Savini et al. 2016); (**b**) live planar colonies of *Madrepora oculata* (adapted from Savini et al. 2016); (**c**) detail of a live *Lophelia pertusa* colony, some tiny branches of *Madrepora oculata* are visible on the upper left corner (adapted from Savini et al. 2016); (**d**) large colony of the antipatharian *Leiopathes glaberrima* colonising, together with scleractinians, dead coral frameworks and hardground crusts interspersed with mud (adapted from Savini et al. 2016). Scale bar: 10 cm (**a**–**c**), 3 cm (**d**)

prised of a MB dataset (30 m pixel size) acquired through a hull-mounted Reson SeaBat 8160 (50 KHz), a Klein 3000 SSS backscatter mosaic for certain selected sites (1 m pixel size) and videos/photos collected for ground-truthing using the Modus Gas Shipack deep-sea module (Etiope et al. 2010) equipped with cameras, or an observation class ROV – Pluto (Vertino et al. 2010) equipped with a HR camera. CTD casts were acquired on the margin with a Seabird SBE9 along four transects crossing the whole province from N to S, identifying the core of the Adriatic Deep Water (ADW) flow, associated with the CWC distribution (Budillon et al. 2010). Most of the data have been analysed in recent literature (Freiwald et al. 2009; Corselli 2010; Savini et al. 2014; Bargain et al. 2017), although for seafloor mapping data, published results are still fragmented and not presented in comparable forms.

15.3.1 Conservation Value of the SML CWC Province

D'Onghia et al. (2017) presented recently a comprehensive resume of conservation value and incidence of anthropogenic impacts on CWC habitats of the SML province. The province is included among the selected areas of conservation interest in the open Mediterranean Sea, which includes the deep-sea (Specially Protected Areas of Mediterranean Importance – SPAMIs) (UNEP-MAP RAC/SPA, UNEP-MAP-RAC/SPA 2009, UNEP-MAP-RAC/SPA 2010, UNEP-MAP-RAC/SPA 2011; de Juan et al. 2012). Based on criteria of rarity, importance for life history stages of species, importance for threatened and endangered species/habitats, vulnerability, biological diversity and naturalness, the SML CWC province is considered a "Vulnerable habitat" (de Juan and Lleonart 2010). In addition, this Mediterranean CWC area is also included among the proposed priority conservation areas suggested by several conservation initiatives (e.g. UNEP MAP EBSA; CIESM/Mediterranean Marine Peace Parks; Oceana/MedNet) (Oceana 2011; Micheli et al. 2013). Taking into account the documented impact of trawling and, to a lesser extent, of other types of fishing gear on the deep-sea coral community, the General Fisheries Commission for the Mediterranean (GFCM) created in January 2006 the new legal category of "Fisheries Restricted Area" (FRA) at the SML CWC province (D'Onghia et al. 2012; Otero and Marin, this volume). Towed dredges and bottom trawl nets have been prohibited in the FRA, which covers a part of the SML CWC province. Members are required to call the attention of the appropriate authorities in order to protect this FRA from the impacts of any activity jeopardising the conservation of this spectacular submerged landscape (GFCM-RAC/SPA GFCM-RAC/S 2007), dotted by more than 1000 sub-conical and elongated coral-topped mounds, located in water depths of 500–900 m. Unauthorised operations likely take place within the FRA, even if trawling is formally illegal. Indeed, recent explorations have provided images of trawl marks and solid waste along the coral community (Freiwald et al. 2009; Vertino et al. 2010; Savini et al. 2014; D'Onghia et al. 2017), indicating that trawlers sometimes operate inside the northern limit of the FRA (Indennidate et al. 2010).

15.3.2 The SML CWC Topped Mounds and Other Coral Facies

The SML CWC province was first mapped in 2004 (Savini and Corselli 2010) and since then has become the focus of a series of oceanographic expeditions examining the overall biodiversity of CWC habitats (D'Onghia et al. 2010; Rosso et al. 2010; Mastrototaro et al. 2010; Vertino et al. 2010; D'Onghia, this volume) and the geological-stratigraphic framework in which corals grow (Malinverno et al. 2010). The majority of research activities were carried out exploring some representative coral-topped mounds (Savini et al. 2016), located in water depths of 500–900 m, originally formed as sediment blocks (originating from by late Pleistocene Mass-Transport Deposits – MTDs) that likely offered widespread suitable substrate for coral colonisation during the last deglaciation (i.e.: 13.4–11.4 cal kyr BP, according to the oldest dated coral fragment reported in Malinverno et al. (2010) and Fink et al. (2012)). Coral-topped mounds are sub-circular to elongated, 200 m wide in average, from few meters to 25 m high and densely aggregated at places (i.e. more than 5 mounds per km^2 – Fig. 16.2 in Savini et al. 2016). Analysis of sediment cores collected at the top of sampled coral-topped mounds, revealed a temporary extinction during the Early to Mid Holocene (from 11.4 to 5.9 cal kyr BP), at the time of the sapropel S1 event, during which the deep eastern Mediterranean basin turned anoxic (Fink et al. 2012). Nonetheless present-day oceanographic conditions (Manca et al. 2006; Budillon et al. 2010) coupled with an on-going uplift (Carminati and Doglioni 2012) of the margin (which reduced the accommodation space promoting low sedimentation rate in most part of the exposed MTDs) represent the most important geo-environmental controls that allow scleractinian corals to thrive on the upper and north-eastern slopes of a huge number of exposed and partially exposed sediment blocks (Vertino et al. 2010; Rosso et al. 2010; Savini et al. 2014, 2016).

Nevertheless other settings seem to offer suitable areas for coral growth on the margin. Freiwald et al. (2009) reported the occurrence of small-scale bioconstructions on the sub-vertical and overhanging walls of a main canyon system, located to the west. Savini and Corselli (2010) also published mosaics of high frequency SSS data acquired along an erosive and gently-sloping surface forming the western flank of a prominent ridge that typifies the south-central sector of the surveyed area, where coral colonies, along with hardground facies, are patchily distributed as described in Rosso et al. (2010), without creating prominent geomorphological features (i.e. mounds detectable on standard hull-mounted multibeam bathymetry). An additional location to the west of the coral occurrences has been also documented in Malinverno et al. (2010) and Savini et al. (2014), associated to a series of narrow ridges and fault scarps, where corals form extensive framework at their top, here assuming a mound shape and producing typical hyperboles on seismic data.

Detailed investigations on the overall biodiversity and mapping activities were carried out only at those locations in which reef-forming species contributed in generating coral-topped mounds and identified respectively 222 species (Mastrototaro et al. 2010) and a total of 13 distinct macro-habitats (*sensu* Green et al. 1999). These include *Lophelia pertusa* and *Madrepora oculata* coral frameworks, that prevail on the summits and on the eastern mound flanks, and hardground crusts and boulders colonised by the antipatharian species *Leiopathes glaberrima* (Vertino et al. 2010). A fine scale macro-habitat characterisation and mapping is still missing from the other areas.

15.3.3 Supervised Automatic Classification of SML Coral Facies

Exploration by means of a 100–500 kHz SSS (Klein 3000) was performed in an operating range of 300 m at four main sites located between 400 and 700 m water depth. As described in Savini et al. (2014), quantitative textural measurements were computed on the obtained SSS mosaics using co-occurrence matrices (Haralick 1973; Reed and Hussong

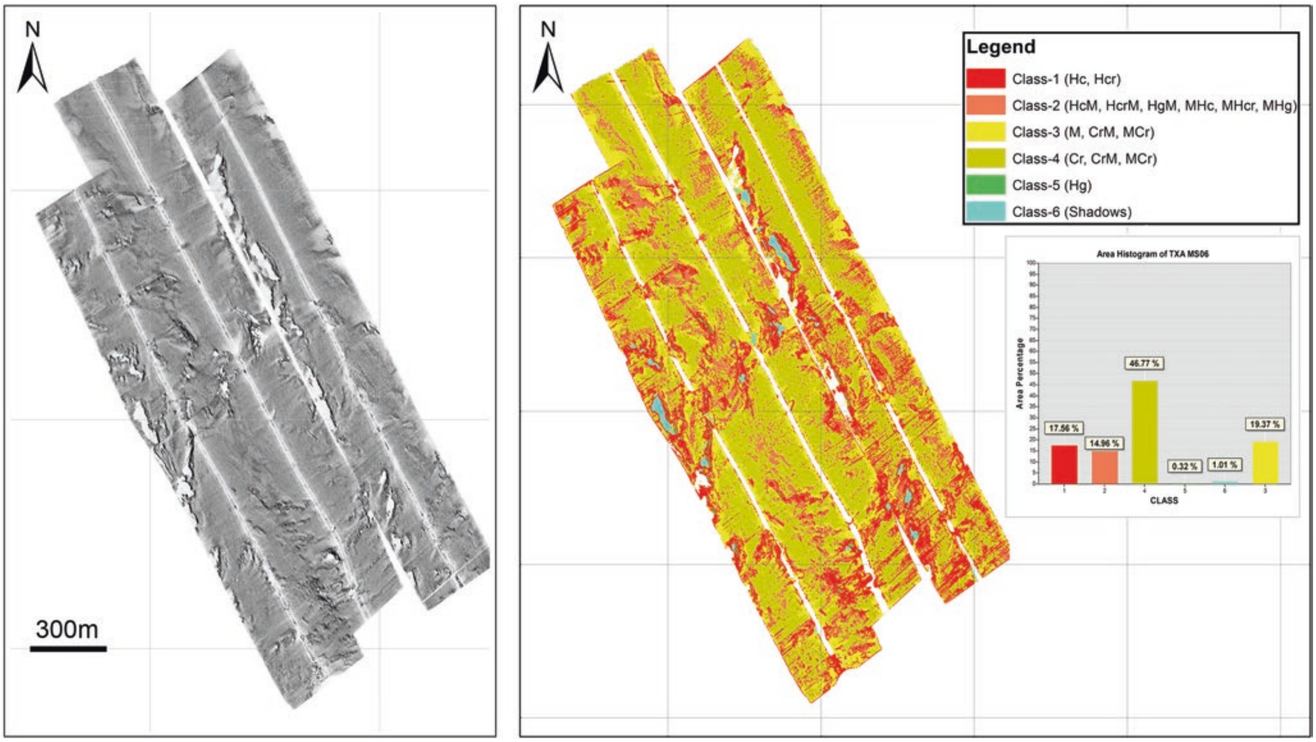

Fig. 15.5 The SSS mosaic (**left** – see Fig. 15.4 for location) and the obtained classification map (**right**) representing the distribution of the six acoustic classes at MS06 site. Acronyms in brackets within the legend represent macrohabitats associated to each class: (Hc) coral framework; (Hcr) coral rudstone; (HcM) corals and mud; (HcrM) coral rudstone and mud; (HgM) mudstone and mud; (MHc) mud and corals; (MHcr) mud and coral rudstone; (MHg) mud and mudstone; (M) mud; (CrM) coral rubble and mud; (MCr) mud and coral rubble; (Cr) coral rubble; (Hg) Mudstone. (Detailed explanation are provided in Savini et al. 2014)

1989; Gao et al. 1998; Huvenne et al. 2002; Savini 2004), using a similar approach as described previously for the Chella Bank (see Savini et al. 2014 for further details) with accuracy assessment performed according to Pontius and Millones (2011). Relying on the ground-truthing information obtained from sediment samples and visual investigations, a number of training areas were selected to represent six distinct acoustic classes, defined by coupling expert interpretation with results from the textural analysis (see Fig. 4 in Savini et al. 2014). A Maximum Likelihood Classification algorithm (according to Gibson and Power 2000) was subsequently applied to generate a full-coverage classification map for each mosaic. Each class was then converted into polygons (following integration of the classification maps in ArcGIS™) in order to quantify the total coverage for each of the defined acoustic facies, as indicated in Fig. 7 of Savini et al. (2014).

As it was outside the scope of the Savini et al. (2014) study, details regarding the spatial distribution of acoustic facies at the different locations were not reported. We therefore illustrate in Figs. 15.5 and 15.6 how the performed supervised automatic classification, showed the fine scale habitat distribution over two distinct areas (namely MS06 and MS08 as indicated in Fig. 15.4). The first area (Fig. 15.5) represents coral-topped mounds located in the central sector of the provided DTM, at MS06 site (see Savini et al. 2014 for further details). To the west, the second area is located at the top of a ridge (MS08), which enhances the step-like morphology of the margin towards the west.

At the MS06 site coral macrohabitats, with significant abundance of living coral frameworks (namely coral frameworks/rudstone described in Savini et al. 2014 and grouped in classes 1 and 2), dominate the mound's tops and the north-eastern flanks. The western mound's flanks are instead typified by a mosaic of coral rubble, coral rudstone fragments (from pebbles to boulders), dismantled hardground crusts (resulting in clustered to isolated elements highly colonised by solitary corals) and mud, with a high lateral variability in their distribution. Small scale parallel surface deformations originated by sediment thrusted south-westward are also visible in inter-mounds areas, where sedimentary facies dominated by coral rubble or buried (at place partially) rubble (occasionally hosting sparse coral colonies) were observed in recoded videos (Vertino et al. 2010), generating coral macrohabitats grouped in class 2. Worthy of attention on the western mound's flanks is the exclusive occurrence of “Antipatharian Facies” described by Vertino et al. (2010) and Rosso et al. (2010), consistently characterised by meter-sized specimens of the black coral species *L. glaberrima* on

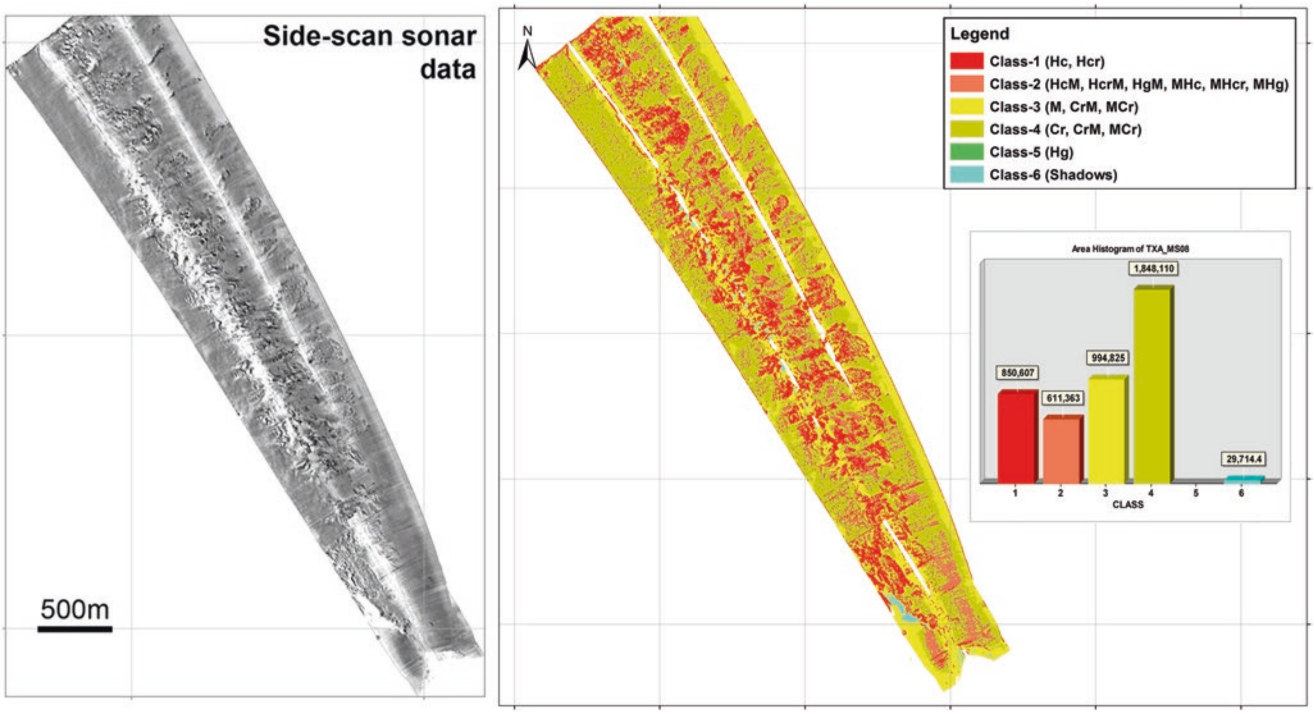

Fig. 15.6 The SSS mosaic (**left** – see Fig. 15.4 for location) and the obtained classification map (**right**) representing the distribution of the six acoustic classes at MS08 site. Acronyms in brackets within the legend represent macrohabitats associated to each class: (Hc) coral framework; (Hcr) coral rudstone; (HcM) corals and mud; (HcrM) coral rudstone and mud; (HgM) mudstone and mud; (MHc) mud and corals; (MHcr) mud and coral rudstone; (MHg) mud and mudstone; (M) mud; (CrM) coral rubble and mud; (MCr) mud and coral rubble; (Cr) coral rubble; (Hg) Mudstone. (Detailed explanation are provided in Savini et al. 2014)

a mixed seafloor. Distinctions between scleractinian dominated facies and Antipatharian facies could not be achieved based on the side scan sonar mosaic, although the latter were consistently observed in those facies grouped under class 2.

At MS08, corals still formed mounds, although their origin is not related to mound-like sediment blocks displaced by failure events. Mounds are located at the top of a ridge, where evidence from core samples, coupled with observations from shallow geophysics, testified to the presence of a widespread erosional surface, leading to the emergence of stiff/hardened substrata, constituted by older sediments dated to the early to middle Pleistocene (Malinverno et al. 2010), which likely offered suitable substratum for coral growth. Few data from videos and samples are available to comprehensively describe the variety of coral facies and especially their distribution pattern in this area. Nonetheless based on the acoustic patterns recognized in classes 1 and 2 (coral dominated facies), the overall growth structure of coral facies appears more homogenous over the gross mound morphology, where coalescing coral reefs (as interpreted based on their acoustic response and video images) gave rise to CWC mounds (displaying a well defined mounded 3D structure with sub-circular bases – Fig. 15.5), reaching dimensions of up to few meters in height and from 100 to 200 m in diameter. The mechanisms promoting the formation of coral mounds in this area still remain largely unexplored and unquantified. Future systematic research is thus needed to overcome the limitations of previous studies investigating how interactions between hydrography, topography and present-day sedimentary processes influence the assembly and structural complexity of the reef-forming species present over the whole SML CWC province.

15.4 Conclusions

The distribution patterns and spatial complexity of CWC communities and associated habitats have been revisited and described at two representative sites of the Mediterranean basin through previously published geophysical data (MB bathymetric data and associated BS, SSS), interpreted with new water column data (CTDs) and new ground-truth data (video, photos and seafloor samples), and finally mapped and classified through the application of (supervised) automatic classification routines. Our interpretations confirm that seafloor complexity, most likely together with physical/chemical properties of the water column are two factors of crucial importance in driving the distribution and development of CWC communities.

The produced habitat maps provide quantitative information on estimated CWC extent and represent examples of scientific products useful in supporting marine spatial planning, monitoring or recovery. Nonetheless, very few studies provide a spatial context to CWC habitats in the Mediterranean Sea and more (geophysical and visual) data from less explored areas are required to better define their distribution and relate them to environmental drivers.

An important strategic goal in habitat mapping regards the definition of protocols and standardised methodologies to produce normalised classification schemes and datasets, specifically regarding VMEs such as CWCs, which urgently require specific monitoring and protection actions coordinated at a basin scale and over a long time span.

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References

Argnani A, Frugoni F, Cosi R, et al (2001) Tectonics and seismicity of the Apulian Ridge south of Salento peninsula Southern Italy. Ann Geofis 44:527–540

Baillon S, Hamel JF, Wareham VE, et al (2012) Deep cold-water corals as nurseries for fish larvae. Front Ecol Environ 10:351–356

Bargain A, Marchese F, Savini A, et al (2017) Santa Maria di Leuca province (Mediterranean Sea): identification of suitable mounds for cold-water coral settlement using geomorphometric proxies and maxent methods. Front Mar Sci 4:338. https://doi.org/10.3389/fmars.2017.00338

Boavida J, Assis J, Silva I, et al (2016) Overlooked habitat of a vulnerable gorgonian revealed in the Mediterranean and Eastern Atlantic by ecological niche modelling. Sci Rep 6:36460. https://doi.org/10.1038/srep36460

Budillon G, Lo Bue N, Siena S, et al (2010) Hydrographic characteristics of water masses in the northern Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:441–457

Brown CJ, Todd BJ, Kostylev VE, et al (2011) Image-based classification of multibeam sonar backscatter data for objective surficial sediment mapping of Georges Bank, Canada. Cont Shelf Res 31:110–119

Carminati E, Doglioni C (2012) Alps vs. Apennines: the paradigm of a tectonically asymmetric Earth. Earth Sci Rev 112:67–96

Cartes JE, Lo Iacono C, Mamouridis V, et al (2013) Geomorphological, trophic and human influences on the bamboo coral *Isidella elongata* assemblages in the deep Mediterranean: to what extent does *Isidella* form habitat for fish and invertebrates? Deep-Sea Res Part 1 Oceanogr Res Pap 76:52–65

Coiras E, Lo Iacono C, Gràcia E, et al (2010) Automatic segmentation of multi-beam data for predictive mapping of benthic habitats. Geosci Remote Sens Lett 4:809–813. https://doi.org/10.1109/JSTARS.2011.2123874

Corselli C (2010) Introduction: cold-water coral communities in the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:345–359

Davies AJ, Wisshak M, Orr JC, et al (2008) Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). Deep-Sea Res Part 1 Oceanogr Res Pap 55–8:1048–1062

Davies JS, Guillaumont B, Tempera F, et al (2017) A cold-water coral biota classification scheme for ecosystem-based management of the deep sea. Deep-Sea Res Part 2 Top Stud Oceanogr 145:102–109

D'Onghia G, Maiorano P, Sion L, et al (2010) Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:397–411

D'Onghia G, Maiorano P, Carlucci R, et al (2012) Comparing deep-sea fish Fauna between coral and non-coral "megahabitats" in the Santa Maria di Leuca cold-water coral province (Mediterranean Sea). PLoS One 7:e44509. https://doi.org/10.1371/journal.pone.0044509

D'Onghia G, Calculli C, Capezzuto F, et al (2017) Anthropogenic impact in the Santa Maria di Leuca cold-water coral province (Mediterranean Sea): observations and conservation straits. Deep-Sea Res Part 2 Top Stud Oceanogr 145:87–101. https://doi.org/10.1016/j.dsr2.2016.02.012

De Mol B, Amblas D, Calafat A, et al (2012) Cold-water coral colonization of Alboran Sea Knolls, Western Mediterranean Sea. In: Harris P, Baker E (eds) Seafloor geomorphology as benthic habitat: GeoHab Atlas of seafloor geomorphic features and benthic habitats. Elsevier, Amsterdam, Boston, pp 819–829

de Juan S, Lleonart J (2010) A conceptual framework for the protection of vulnerable habitats impacted by fishing activities in the Mediterranean high seas. Ocean Coast Manag 53:717–723

de Juan S, Moranta J, Hinz H, et al (2012) A regional network of sustainable managed areas as the way forward for the implementation of an Ecosystem-Based Fisheries Management in the Mediterranean. Ocean Coast Manag 65:51–58

de Juan S, Lo Iacono C, Demestre M (2013) Benthic habitat characterisation of soft-bottom continental shelves: integration of acoustic surveys, benthic samples and trawling disturbance intensity. Estuar Coast Shelf Sci 117:199–209

Duggen S, Hoernle K, van de Bogaard H (2004) Magmatic evolution of the Alboran region: the role of subduction in forming the western Mediterranean and causing the Messinian Salinity Crisis. Earth Planet Sci Lett 218:91–108

Etiope G, Savini A, Lo Bue N, et al (2010) Deep sea survey for the detection of methane at the "Santa Maria di Leuca" cold-water coral mounds (Ionian Sea, South Italy). Deep-Sea Res Part 2 Top Stud Oceanogr 57:431–440

European Parliament, Council of the European Union (2008) Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for Community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of the European Union L 164/19

Evans J, Aguilar R, Alvarez H, et al (2016) Recent evidence that the deep sea around Malta is a biodiversity hotspot. Rapp Comm Int Mer Méditerr 41:2016

Fabri MC, Pedel N, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207

Fabri MC, Bargain A, Pairaud I, et al (2016) Cold-water coral ecosystems in Cassidaigne Canyon: an assessment of their environmental living conditions. Deep-Sea Res Part 2 Top Stud Oceanogr 137:436–453. https://doi.org/10.1016/j.dsr2.2016.06.006

Fanelli E, Delbono I, Vivaldi R, et al (2016) Cold-water coral *Madrepora oculata* in the eastern Ligurian Sea (NW Mediterranean): historical and recent findings. Aquat Conserv 27:965–975. https://doi.org/10.1002/aqc.2751

Farmer A, Mee L, Langmead O, et al (2012) The ecosystem approach in marine management. EU FP7 KNOWSEAS Project. ISBN: 0-9529089-5-6

Ferrini VL, Flood RD (2006) The effects of fine-scale surface roughness and grain size on 300 kHz multibeam backscatter intensity in sandy marine sedimentary environments. Mar Geol 228:153–172

Fink HG, Wienberg C, Hebbeln D, et al (2012) Oxygen control on Holocene cold-water coral development in the eastern Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96

Fink HG, Wienberg C, De Pol-Holz R, et al (2013) Cold-water coral growth in the Alboran Sea related to high productivity during the Late Pleistocene and Holocene. Mar Geol 339:71–82

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs. UNEP-WCMC, Cambridge, 86 pp

Freiwald A, Beuck L, Rüggerberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:36–52

Freiwald A, Huhnerbach V, Lindberg B, et al (2002) The Sula Reef Complex, Norwegian Shelf. Facies 47:179–200

Gao D, Hurst SD, Karson JA, et al (1998) Computer-aided interpretation of side-looking sonar images from the eastern intersection of the Mid-Atlantic Ridge with the Kane transform. J Geophys Res 103:20997–21014

GFCM-RAC/S (2007) Report of the transversal workshop on marine protected areas (MPAs), Salammbô, Tunisia, p 34

Gibson PJ, Power CH (2000) Introductory remote sensing: digital image processing and applications. Routledge, London

Gili JM, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol Evol 13:316–321

Giusti D, Innocenti C, Canese S (2014) Predicting suitable habitat for the gold coral *Savalia savaglia* (Bertoloni, 1819) (Cnidaria, Zoantharia) in the South Tyrrhenian Sea. Cont Shelf Res 81:19–28

Glogowski S, Dullo WC, Feldens P, et al (2015) The Eugen Seibold coral mounds offshore western Morocco: oceanographic and bathymetric boundary conditions of a newly discovered cold-water coral province. Geo-Mar Lett 35:257–269

Golon J (2014) OSPAR convention (Convention for the Protection of the Marine Environment of the North-East Atlantic) and OSPAR Commission

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of coldwater coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 9:19053–19084

Green HG, Yoklavich MM, Starr RM, et al (1999) A classification scheme for deep seafloor habitats. Oceanol Acta 22:663–678

Grehan AJ, Arnaud-haond S, D'onghia G, et al (2017) Towards ecosystem based management and monitoring of the deep Mediterranean, North-East Atlantic and Beyond. Deep-Sea Res Part 2 Top Stud Oceanogr 145:1–7. https://doi.org/10.1016/j.dsr2.2017.09.014

Grinyó J, Gori A, Ambroso S, et al (2016) Diversity, distribution and population size structure of deep Mediterranean gorgonian assemblages (Menorca Channel, Western Mediterranean Sea). Progr Oceanogr 145:42–56

Guinan J, Grehan AJ, Dolan MFJ, et al (2000) Quantifying relationships between video observations of cold-water coral cover and seafloor features in Rockall Trough, west of Ireland. Mar Ecol Progr Ser 375:125–138

Haralick RM (1973) Textural features for image classification. IEEE Trans Syst Man Cybern SMC-3:610–621

Haralick R (1979) Statistical and structural approaches to texture. IEEE Trans Syst Man Cybern 67:786–804

Huvenne VAI, Blondel P, Henriet JP (2002) Textural analyses of sidescan sonar imagery from two mound provinces in the Porcupine Seabight. Mar Geol 189:323–341

Huvenne VAI, Bett B, Masson D, et al (2016) Effectiveness of a deep-sea cold-water coral Marine Protected Area, following eight years of fisheries closure. Biol Conserv 200:60–69

Indennidate A, Carlucci R, Maiorano P, et al (2010) Fishing effort and catch composition on the boundaries of Santa Maria di Leuca deep-water coral bank. Biol Mar Mediterr 17:340–341

Ismail K, Huvenne V, Masson D (2015) Objective automated classification technique for marine landscape mapping in submarine canyons. Mar Geol 362:17–32

LaFrance M, King JW, Oakley BA, et al (2014) A comparison of top-down and bottom-up approaches to benthic habitat mapping to inform offshore wind energy development. Cont Shelf Res 83:24–44

Lauria V, Gristina M, Attrill MJ, et al (2015) Predictive habitat suitability models to aid conservation of elasmobranch diversity in the Central Mediterranean Sea. Sci Rep 5:13245. https://doi.org/10.1038/srep13245

Lo Iacono C, Gràcia E, Diez S, et al (2008) Seafloor characterization and backscatter variability of the Almería Margin (Alboran Sea, SW Mediterranean) based on high-resolution acoustic data. Mar Geol 250:1–18

Lo Iacono C, Gracia E, Bartolomé R, et al (2011) Geo-acoustic characterization and habitat distribution in the Chella Bank (Eastern Alboran Sea – SW Mediterranean). In: Abstract of the GeoHab marine geological and biological habitat mapping conference. Helsinki, 3–6 May 2011

Lo Iacono C, Gràcia E, Bartolomé R, et al (2012a) The habitats of the Chella Bank. Eastern Alboran Sea (Western Mediterranean). In: Harris P, Baker E (eds) Seafloor geomorphology as benthic habitat: GeoHab Atlas of seafloor geomorphic features and benthic habitats. Elsevier, Amsterdam, pp 681–687

Lo Iacono C, Orejas C, Gori A, et al (2012b) The habitats of the Cap de Creus continental shelf and Cap de Creus Canyon, northwestern Mediterranean. In: Harris P, Baker E (eds) Seafloor geomorphology as Benthic habitat: GeoHab Atlas of seafloor geomorphic features and benthic habitats. Elsevier, Amsterdam, pp 457–464

Lo Iacono C, Gracia E, Ranero C, et al (2014) The West Melilla cold water coral mounds, Eastern Alboran Sea: morphological characterization and environmental context. Deep-Sea Res Part 2 Top Stud Oceanogr 99:316–326

Lo Iacono C, Huvenne VAI, Gonzalez LV, et al (2016) Living reefs and CWC mounds in the Alboran Sea (Western Mediterranean). Holocene evolution and present-day conditions. 6th ISDSC, 11–16 September, Boston, USA

Lo Iacono C, Savini A, Basso D (2018a) Cold-water carbonate bioconstructions In: Micallef A, Krastel S, Savini A (eds) Submarine geomorphology. Springer Geology, Cham, pp 425–455

Lo Iacono C, Robert K, Villanueva Gonzalez R, et al (2018b) Predicting cold-water coral distribution in the Cap de Creus Canyon (NW Mediterranean): implications for marine conservation planning. Progr Oceanogr 169:169–180

López-González PJ, Grinyó J, Gili JM (2014) *Chironephthya mediterranea* n. sp. (Octocorallia, Alcyonacea, Nidaliidae), the first species of the genus discovered in the Mediterranean Sea. Mar Biodiver. https://doi.org/10.1007/s12526-014-0269-5

Malinverno E, Taviani M, Rosso A, et al (2010) Stratigraphic framework of the Apulian deep-water coral province, Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:345–359

Manca BB, Ibello V, Pacciaroni M, et al (2006) Ventilation of the deep waters in the Adriatic and Ionian Seas following changes in the thermohaline circulation of the Eastern Mediterranean. Clim Res 31:239–256

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57: 412–430

Mastrototaro F, Chimienti G, Acosta J, et al (2017) *Isidella elongata* (Cnidaria: Alcyonacea) facies in the western Mediterranean Sea: visual surveys and descriptions of its ecological role. Eur Zool J 8:209–225

Masson DG, Bett BJ, Billett DSM, et al (2003) The origin of deep-water, coral-topped mounds in the northern Rockall Trough, Northeast Atlantic. Mar Geol 194:159–180

Micheli F, Levin N, Giakoumi S, et al (2013) Setting priorities for regional conservation planning in the Mediterranean Sea. PLoS One 8:e59038

Milliman JD, Weiler Y, Stanley DJ (1972) Morphology and carbonate sedimentation on Shallow Banks in the Alboran Sea. In: Stanley DJ (ed) The Mediterranean Sea: a natural sedimentation laboratory. Dowden, Huthcinson and Ross, Stroudsburg, pp 241–259

Mytilineou C, Smith CJ, Anastasopoulou A, et al (2014) New cold-water coral occurrences in the Eastern Ionian Sea: results from experimental longline fishing. Deep-Sea Res Part 2 Top Stud Oceanogr 99:146–157

Muñoz A, Ballesteros M, Montoya I, et al (2008) Alborán Basin, southern Spain – Part I: Geomorphology. Mar Pet Geol 25:59–73

Oceana (2011) Oceana MedNet, MPA proposal for the Mediterranean Sea. 100 reasons to reach 10%. Oceana, Madrid, p 96

Oceana (2014) Scientific information to describe Mediterranean areas meeting scientific criteria for EBSAs. Oceana, Madrid, p 143

Oceana, IEO (2014) Informe de síntesis para proceder a la elaboración del borrador del Plan de Gestión del LIC "Sur de Almería-Seco de los Olivos": Seco de los Olivos. Proyecto LIFE + INDEMARES (LIFE07/NAT/E/00732). OCEANA – Instituto Español de Oceanografía. Coordinación: Fundación Biodiversidad, Madrid, 123 pp

Oguz T, Macias D, Garcia-Lafuente J, et al (2014) Fueling plankton production by a meandering frontal jet: a case study for the alboran sea (Western Mediterranean). PLoS One 9:e111482

Orejas C, Gori A, Lo Iacono C, et al (2009) Distribution of the deep corals *Madrepora oculata*, *Lophelia pertusa*, *Dendrophyllia cornigera*, and quantification of anthropogenic impact in the Cap de Creus Canyon (North Western Mediterranean). Mar Ecol Progr Ser 397:37–51

Palonimo D, Alonso B, Lo Iacono C, et al (2015) Seamounts and seamount-like structures of the Alborán Sea. In: Würtz M, Rovere M (eds) Atlas of the Mediterranean seamounts and seamount-like structures. IUCN, Gland/Málaga, p 276

Pierdomenico M, Martorelli E, Dominguez-Carrió C, et al (2016) Seafloor characterization and benthic megafaunal distribution of an active submarine canyon and surrounding sectors: the case of Gioia Canyon (Southern Tyrrhenian Sea). J Mar Syst 157:101–117

Pontius RG, Millones M (2011) Death to Kappa: birth of quantity disagreement and allocation disagreement for accuracy assessment. Int J Remote Sens 32:4407–4429

Ramirez-Llodra E, Brandt A, Danovaro R, et al (2010) Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences 7:2851–2899

Reed TB, Hussong D (1989) Digital image processing techniques for enhancement and classification of SeaMARC II side-scan sonar imagery. J Geophys Res 94(B6):7469–7490

Reed J (2002) Deepwater Oculina Coral Reefs of Florida: biology, impacts and management. Hydrobiologia 471:43–55

Robert K, Jones D, Tyler P, et al (2015) Finding the hotspots within a biodiversity hotspot: fine-scale biological predictions within a submarine canyon using high-resolution acoustic mapping techniques. Mar Ecol 36:1256–1276

Robert K, Jones D, Roberts M, et al (2016) Improving predictive mapping of deep-water habitats: considering multiple model outputs and ensemble techniques. Deep-Sea Res Part 1 Oceanogr Res Pap 113:80–89

Roberts JM, Wheeler AJ, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334. https://doi.org/10.1017/CBO9780511581588

Rosso A, Vertino A, Di Geronimo I, et al (2010) Hard versus soft-bottom thanatofacies from the Santa Maria di Leuca deep-water coral mound province, recent Mediterranean. Deep-Sea Res Part 2 Top Stud Oceanogr 57:360–379

Savini A (2004) Analysis of Marine Acoustic Geophysical data and their management in GIS applications. PhD thesis, University of Milano-Bicocca

Savini A, Corselli C (2010) High resolution bathymetry and acoustic geophysical data from Santa Maria di Leuca cold water coral province (northern Ionian Sea–Apulian continental slope). Deep-Sea Res Part 2 Top Stud Oceanogr 57:326–344

Savini A, Marchese F, Verdicchio G, et al (2016) Submarine slide topography and the distribution of vulnerable marine ecosystems: a case study in the Ionian Sea (Eastern Mediterranean). In: Lamarche G, Mountjoy J, Bull S, et al (eds) Submarine mass movements and their consequences: 7th international symposium. Springer, Cham, pp 163–170

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. Plos One 9:e87108. https://doi.org/10.1371/journal.pone.0087108

Schembri PJ, Dimech M, Camilleri M, et al (2007) Living deep-water Lophelia and Madrepora corals in Maltese waters (Strait of Siciliy, Mediterranean Sea). Cah Biol Mar 48:77–83

Söffker M, Sloman KA, Hall-Spencer JM (2011) In situ observations of fish associated with coral reefs off Ireland. Deep-Sea Res Part 1 Oceanogr Res Pap 58:818–825

Taviani M, Freiwald A, Zibrowius H (2005a) Deep-coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Deep-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Taviani M, Remia A, Corselli C, et al (2005b) First geo-marine survey of living cold-water Lophelia reefs in the Ionian Sea (Mediterranean basin). Facies 50:409–417

Taviani M, Angeletti L, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78. https://doi.org/10.1016/j.dsr2.2015.12.008

Tonielli R, Innangi S, Budillon F, et al (2016) Distribution of *Posidonia oceanica* (L.) Delile meadows around Lampedusa Island (Strait of Sicily, Italy). J Maps 12:249–260. https://doi.org/10.6084/m9.figshare.3443966.v1

Trincardi F, Foglini F, Verdicchio G, et al (2007) The impact of cascading currents on the Bari Canyon System, SW-Adriatic Margin (Central Mediterranean). Mar Geol 246:208–230

Uitz J, Stramski D, Gentili B, et al (2012) Estimates of phytoplankton class-specific and total primary production in the Mediterranean Sea from satellite ocean color observations. Glob Biogeochem Cycles 26:GB2024. https://doi.org/10.1029/2011GB004055

UNEP-MAP-RAC/SPA (2009) Synthesis of National Overviews on vulnerability and impacts of climate change on marine and coastal biological diversity in the Mediterranean region. Pavasovic A, Cebrian D, Limam A, et al (eds), RAC/SPA, Tunis, p 76

UNEP-MAP-RAC/SPA (2010) The Mediterranean Sea biodiversity: state of the ecosystems, pressures, impacts and future priorities. Bazairi H, Ben Haj S, Boero F, et al (eds) RAC/SPA, Tunis, p 100

UNEP-MAP-RAC/SPA (2011) In: Scovazzi T (ed) Note on the establishment of marine protected areas beyond national jurisdiction or in areas where the limits of national sovereignty or jurisdiction have not yet been defined in the Mediterranean Sea. RAC/SPA, Tunis, p 54

UNGA (2006) Resolution 61/105. Sustainable Fisheries, Including through the 1995 Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 Relating to the Conservation and Management of Straddling Fish Stocks and highly Migratory Fish Stocks, and Related Instruments, United Nations, p 21

Urgelés R, Locat J, Schmitt T, et al (2002) The July 1996 flood deposit in the Saguenay Fjord, Quebec, Canada: implications for sources of spatial and temporal backscatter variations. Mar Geol 184:41–60

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Mound Province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396

Wynn RB, Huvenne VAI, Le Bas TP, et al (2014) Autonomous Underwater Vehicles (AUVs): their past, present and future contributions to the advancement of marine geoscience. Mar Geol 352:451–468

Wright DJ, Pendleton M, Boulware J, et al (2012) ArcGISBenthic Terrain Modeler (BTM), v. 3.0, Environmental Systems Research Institute, NOAA Coastal Services Center, Massachusetts Office of Coastal Zone Management. Available online at: http://esriurl.com/5754

Cross References

Angeletti L, Bargain A, Campiani E, et al (this volume) Cold-water coral habitat mapping in the Mediterranean Sea: methodologies and perspectives

Aymà A, Aguzzi J, Canals M, et al (this volume) Occurrence of living cold-water corals at large depths within submarine canyons of the northwestern Mediterranean Sea

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

D'Onghia G (this volume) Cold-water coral as shelter, feeding and life-history critical habitats for fish species: ecological interactions and fishing impact

Hebbeln D (this volume) Highly variable submarine landscapes in the Alborán Sea created by cold-water corals

Knittweis L, Evans J, Aguilar R, et al (this volume) Recent discoveries of extensive cold-water coral assemblages in Maltese waters

Lastras G, Sanchez-Vidal A, Canals M (this volume) A cold-water coral habitat in La Fonera submarine canyon, northwestern Mediterranean Sea

Maier C, Weinbauer MG, Gattuso JP (this volume) Fate of Mediterranean scleractinian cold-water corals as a result of global climate change. A synthesis

Movilla J (this volume) A case study: variability in the calcification response of Mediterranean cold-water corals to ocean acidification

Orejas C, Jiménez C, Gori A, et al (this volume) Corals of Aphrodite: *Dendrophyllia ramea* populations of Cyprus

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Palomino D, Rueda JL, Vázquez JT, et al (this volume) Cold-water corals in fluid venting submarine structures

Wienberg C (this volume) A deglacial cold-water coral boom in the Alborán Sea: from coral mounds and species dominance

Cold-Water Coral Habitat Mapping in the Mediterranean Sea: Methodologies and Perspectives

16

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Abstract

The marine scientific community developed new habitat mapping procedures that proved to be effective to map seafloor habitats in a holistic manner, thus refining our knowledge of benthic sea life. Several works on this topic focused on cold-water coral habitats at the global scale, with focus on the Atlantic Ocean while, only a few studies applied these methods to the Mediterranean Sea. The prime objective of this chapter is to comment the methodologies used to describe cold-water coral habitats and map their extension; secondly we discuss statistical models to outline the most suitable areas for cold-water coral settlement (habitat suitability models). Furthermore, recent technological developments in habitat mapping procedures provide geophysical data and seafloor images of higher resolution than ever before, while multi-frequency systems supply new hyperspectral images of the seabed. This new type of data could be crucial for a better characterisation of such Mediterranean cnidarian habitats. Here we reviewed the procedures for the Mediterranean cold-water coral habitat mapping applied so far, describing two case studies in the Southern Adriatic Sea and discussing caveats and future perspectives.

Keywords

Cold-water corals · Habitat mapping · Geophysical data · Mediterranean Sea

16.1 Introduction

Reliable description and classification of seafloor habitats and their resident benthic life are needed for assessing management and conservation measures, especially the impact of growing anthropogenic pressures. Considering how little of the global seafloor has been mapped in comparison with terrestrial environments (Sandwell et al. 2006), there is an urgent need to collect and integrate spatial information related to the distribution of marine biotic and abiotic components to effectively build benthic habitat maps (Kostylev et al. 2001; Robert et al. 2016).

Habitat mapping defies a simple and univocal definition (e.g. Morris 2003; Mitchell 2005; Greene et al. 2007; MESH 2008a, b; Tillin et al. 2008; Costello 2009; Brown et al. 2011). A pragmatic definition was provided in 2008 as part of the MESH (Mapping European Seabed Habitats) project; “Plotting the distribution and extent of habitats to create a map with complete coverage of the seabed showing distinct boundaries separating adjacent habitats”. Despite the lack of a standard definition, there is a consensus that a habitat can be identified only through an integrated approach that measures, analyses and considers in full the physical, biological, chemical and oceanographic aspects characterising that specific area on different spatial scales. To this end, different approaches and methods have been proposed (e.g. Greene et al. 1999; Diaz et al. 2004; MESH 2008a, b; Brown et al. 2011; Lecours et al. 2015 and references therein). Acoustic technologies (multibeam echosounder, side scan sonar, etc.) are used to acquire remote-sensing data of the seabed at a large scale, while bottom samples, video footage and photography provide information at fine scale. Hence, there is a

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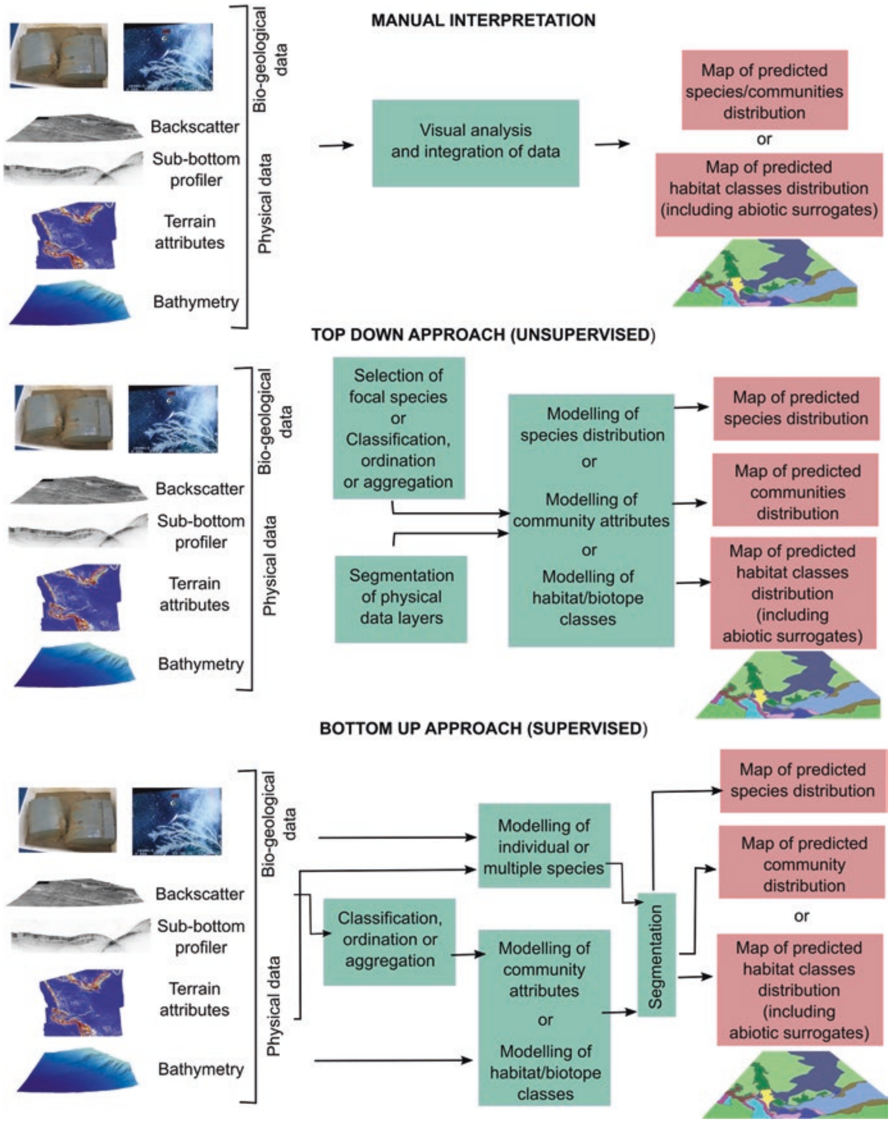
Fig. 16.1 Schematic overview of the complementary approaches usually applied for habitat mapping. (Modified from Brown et al. 2011)



large mismatch between the large and the very fine scale and a major challenge in benthic habitat mapping is a consistent integration of these two types of information (Brown et al. 2011). Several strategies are used to obtain habitat maps going from top-down to bottom-up approaches (Brown et al. 2011) (Fig. 16.1).

There is a growing application of habitat mapping to the exploration of cold-water coral (CWC) grounds, mainly focused upon the Atlantic Ocean (Davies et al. 2008; Dolan et al. 2008; Guinan et al. 2009a, b; Tong et al. 2012, 2013; García-Alegre et al. 2014; Ross et al. 2017) and the Mediterranean Sea (Lo Iacono et al. 2008, this volume; Savini and Corselli 2010; Vertino et al. 2010, 2014; Savini et al. 2014). The main concepts and operations related to CWC habitats mapping are presented by Lo Iacono et al., (this volume), with examples from the Ionian and Alborán seas. This chapter provides further discussion on this topic by examining critically the various methodologies applied to CWC habitat mapping in the Mediterranean, and commenting upon caveats and future perspectives. Our discussion will consider two case studies from the Southern Adriatic Sea, the Bari Canyon and the Montenegro slope (Fig. 16.2). Geophysical information on these sites is reported in Trincardi et al. (2007, 2014), Foglini et al. (2016a), and Angeletti et al. (2015a), while CWC presence is discussed by Freiwald et al. (2009), Angeletti et al. (2014), and Taviani et al. (2011, 2016).

16.2 Large Scale Data

16.2.1 Bathymetric Data

The influence of seafloor bathymetry and morphology on the submarine environment, including oceanographic and sedimentary patterns and type of biota, is well documented for

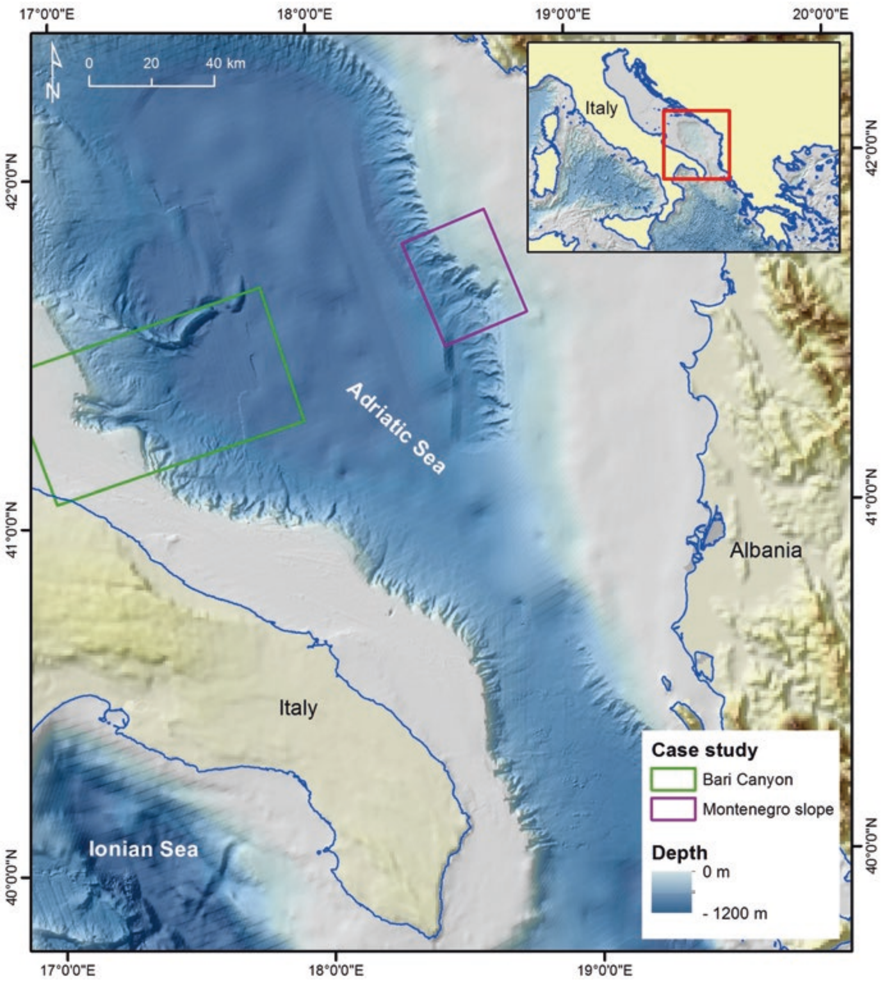


Fig. 16.2 Bathymetry of the Southern Adriatic Sea (EMODnet repository: http://www.emodnet.eu/) and geographic setting of the case studies shown in this chapter: Bari Canyon and Montenegro continental slope

the Mediterranean Sea (Genin et al. 1986; Fredericksen et al. 1992; Canals et al. 2006; De Geest et al. 2008; Trincardi et al. 2014; Bonaldo et al. 2016; Foglini et al. 2016a; Rebesco and Taviani, this volume, with references). CWCs are generally thriving on hard substrates at depths between ca. 200 and 1000 m, characterised by strong bottom currents (e.g. Roberts et al. 2009). Thus, seafloor bathymetry and morphology are fundamental aspects to consider for identifying CWC sites and need to be included in habitat mapping and model predictions (Mortensen and Buhl-Mortensen 2004; Harris and Baker 2011; Lo Iacono et al. 2014, this volume; Robert et al. 2016; Fabri et al. 2017). Multibeam Echosounders (MBES) provide bathymetry and morphology data with continuous coverage and high-resolution (Roberts et al. 2005; Durán-Muñoz et al. 2009; Correa et al. 2013; Savini et al. 2014; Lo Iacono et al., this volume).

16.2.1.1 Terrain Morphometric Attributes

Seafloor morphology can be described quantitatively (geomorphometry: Lecours et al. 2016) through a number of metrics that can be calculated from the Digital Elevation Model (DEM), including slope, aspect, curvature, Bathymetric Position Index, Ruggedness, Terrain Surface Texture, Vector Ruggedness Measure, and many others. Geographic Information System (GIS) software usually offers tools to perform this task, unfortunately often using different algorithms for the same metric. Available software include GRASS, SAGA, Spatial Analyst toolset of ArcGIS, Benthic Terrain Modeller (Wright et al. 2012), ArcGeomorphometry (Rigol-Sanchez et al. 2015), BSG seabed mapping toolbox (De Clippele et al. 2016), TASSE (Terrain Attribute Selection for Spatial Ecology: Lecours et al. 2015, 2017) and other software (Wood 2009).

The slope is the first derivative of the bathymetric DEM and indicates the steepness of the terrain in degrees or in percentage, while the aspect identifies the slope orientation with respect to the north and it is expressed in clockwise degrees from 0 to 360 relative to North. Jointly, slope and aspect have been used as an approximation of topographic exposure to bottom current regimes (Davies et al. 2008; Edinger et al. 2011). The curvature (plan and profile) is the second derivative and describes concavity and convexity of the slope, which influences the acceleration or deceleration of the currents and thus provides information on erosional and depositional processes. The Bathymetric Position Index (BPI) describes the relative elevation of an area with respect to its surroundings, thus identifying topographic highs, often related to bedrock outcrop and/or hard substrates (Wright et al. 2012). Ruggedness, Terrain Surface Texture, Vector Ruggedness Measure are all measures of the terrain roughness and can thus be used as a proxy for sediment and substrate type (Dunn and Halpin 2009). All of these measures can be calculated at different spatial scales, thus describing seafloor morphology at several scales (Wilson et al. 2007). They have been widely used in CWC habitat mapping and suitability models (e.g. Davies et al. 2008; Arantes et al. 2009; Davies and Guinotte 2011; Buhl-Mortensen et al. 2012; Fabri et al. 2014, 2017; Robert et al. 2016; Bargain et al. 2017; Lo Iacono et al., this volume).

Slope, terrain roughness, BPI, and, to a lesser extent, aspect and curvature, appear to be the best indices to morphologically describe suitable habitats for Mediterranean CWCs (Cau et al. 2017; Fabri et al. 2017; Bargain et al. 2017, 2018). For instance, Bargain et al. (2018) found that these derivatives, each one calculated at a specific scale, are the best indices to predict the most suitable surfaces for CWC presence in the Bari Canyon, Southern Adriatic Sea (Freiwald et al. 2009; Angeletti et al. 2014; Taviani et al. 2016). Using TASSE, we calculated the following morphometric attributes of this site (Fig. 16.3): relative difference to mean value (a relative position index, similar to BPI); local standard deviation (a measure of roughness); eastness and northness (similar to aspect); local mean; slope (computed as per Horn 1981).

16.2.2 Backscatter Data

Backscatter data is a measure of the acoustic reflectivity of the seafloor and is related to substrate composition and attributes (Jackson and Briggs 1992). Backscatter is influenced also by incident angle, seafloor morphology (both at large and small scale, such as rugosity) and volume heterogeneity. Both MBES and side-scan sonar (SSS) systems can acquire this type of data (Fig. 16.4a, b), although these systems have different conditions of acquisition and thus produce different results. This configuration results in a high sensitivity of SSS images to fine scale morphology (e.g. sand waves, cables, wrecks, moorings and outcropping rocks: Lurton and Lamarche 2015; Lamarche et al. 2016 and references therein).

Backscatter data offer qualitative information on type of substrate (Hughes Clarke et al. 1996), a crucial element for habitat mapping. High-intensity backscatter values are usually associated with hard substrates (cropping bedrock, overconsolidated sediments, hardgrounds, bio-constructions, gravelly beds), while low intensity values are typically related to soft sediments, such as mud, clay, or fine sand (Hughes Clarke et al. 1997; Lurton and Lamarche 2015). By giving qualitative indication on the type and quality of the seafloor, backscatter data could then provide predictive information on resident biological communities or their activity (Urgelés et al. 2002; De Falco et al. 2010), including CWC colonies, reefs or mounds (Fosså et al. 2005; Lo Iacono et al. 2008; Huvenne et al. 2005, 2016a, b). However, some ambiguities on a direct correspondence between acoustic facies and benthic habitats still persist due to some subtle variations within the habitat itself that are scale- and resolution-dependent (Lurton and Lamarche 2015).

Despite some limitations, acoustic backscatter has been widely used for benthic habitat mapping, and several works have exploited seafloor acoustic backscatter for mapping CWC habitat (e.g. Fosså et al. 2005; Roberts et al. 2009, 2014), in particular in the Mediterranean Sea (Lo Iacono et al. 2008, this volume; Savini and Corselli 2010; Vertino et al. 2010, this volume; Savini et al. 2014; Lastras et al. 2016). CWCs usually grow on hard substrates, which is generally characterised by higher backscatter intensity compared to softer bottom types (Lo Iacono et al. 2008; Savini and Corselli 2010). Patches of CWCs also tend to display typical backscatter patterns (e.g. cauliflower-like pattern: Fosså et al. 2005), which give information on coral coverage, whether it is alive or dead (Roberts et al. 2009), morphology and potential burial under sediment.

16.2.3 Sub-bottom Profiles

Sub-bottom profiles are displays of the acoustic reflectivity of the sediment layers below the seafloor, obtained through the use of sub-bottom profilers or seismic sources. Sub-bottom profiles have proven useful for the identification of CWC mounds and for the three-dimensional characterisation of CWC bioconstructions (e.g. Masson et al. 2004; Fosså et al. 2005; Roberts et al. 2005; Wheeler et al. 2005; Correa et al. 2012; Somoza et al. 2014). In the Mediterranean Basin, they have been used in the Tuscan Archipelago (Remia and Taviani 2005), Almería Margin (Lo Iacono et al. 2008), Santa Maria di Leuca (Taviani et al. 2005; Malinverno et al. 2010; Savini and Corselli 2010) and Southern Adriatic Sea (Taviani et al. 2016). A typical seismic signature of CWC colonies is acoustically transparent hyperbole on the seafloor (Savini and Corselli 2010; Taviani et al. 2016). While sub-bottom profiles are a good tool to detect CWCs, especially on a seafloor characterised by coral mounds, the technique is less useful on canyon walls as the signal is noisy due to diffraction hyperboles caused by the high acclivity (e.g. Bari Canyon: Trincardi et al. 2007).

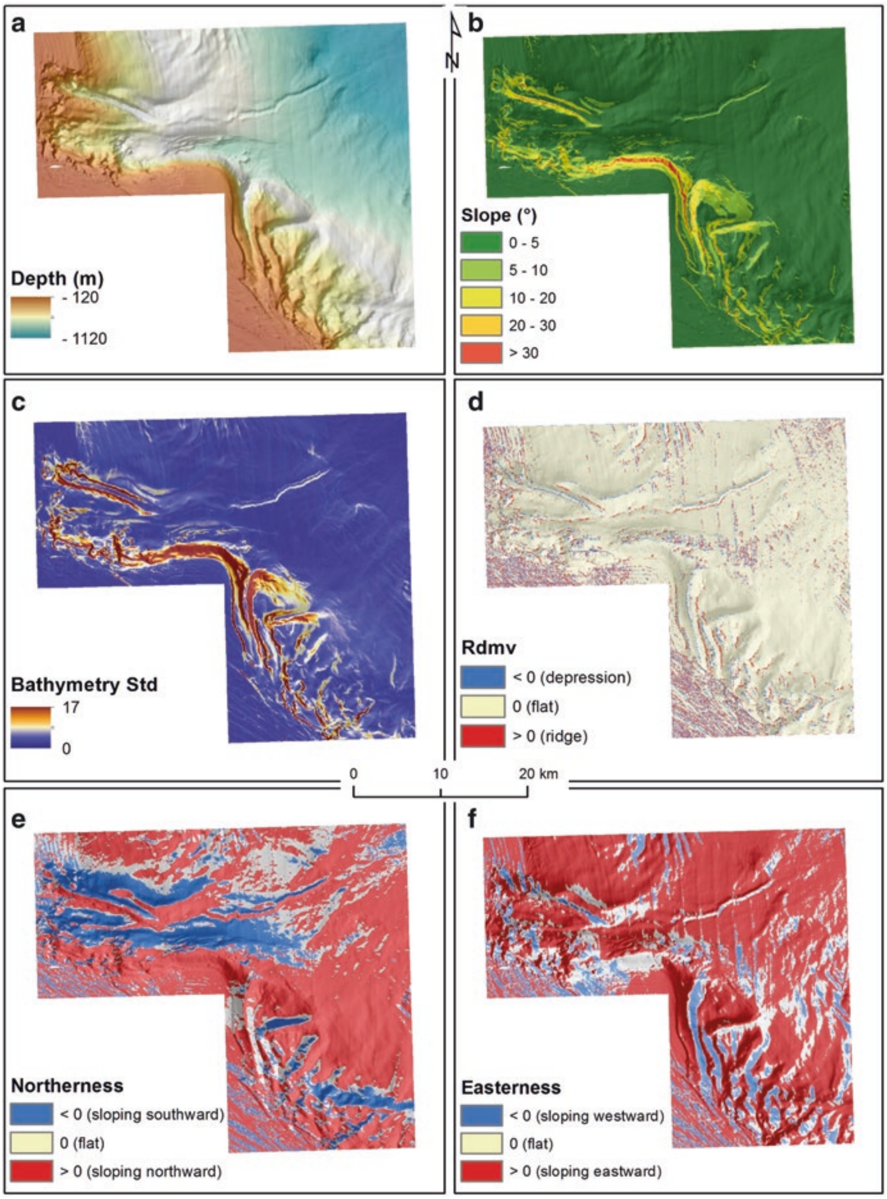


Fig. 16.3 Terrain attributes calculated for Bari Canyon through TASSE toolset (Lecours et al. 2015): (**a**) bathymetric DEM, source for the derivatives; (**b**) slope; (**c**) local standard deviation of the bathymetry (measure of rugosity); (**d**) relative difference to mean value (rdmv; measure of relative position); (**e**) northerness and (**f**) easterness (measure of slope orientation). (© ISMAR-CNR Bologna)

16.3 Small Scale Data

The scale of acoustic data is often too large to accurately identify the seafloor type and morphology. The acquisition of small scale data (direct observations of the seafloor) then becomes fundamental to validate habitat maps resulting from acoustic data analyses (ground-truthing). Video footage or photography of the seafloor are usually acquired through cameras mounted on autonomous underwater vehicles (AUVs), remotely operated vehicles (ROVs) or manned submersibles, and are usually mandatory to describe megabenthic communities such as CWCs (e.g. Orejas et al. 2009; Vertino et al. 2010; Gori et al. 2013; Angeletti et al. 2014; Taviani et al. 2016, 2017). Other types of ground-truth include bottom sampling through grab, box-corer, robotic arm, or push corer, which provide information on macro- and micro-benthic epifaunal and infaunal components, and is also propitious to assess textural and compositional properties.

16.3.1 Video Processing

Processing footage of photography acquired from AUV or ROV-mounted cameras into useful ground-truth data also requires the analysis of the vehicle's navigation, and its synchronisation with the footage. There are several software packages specifically developed for handling underwater georeferenced scientific video, such as ADELIE (a GIS-based software developed by IFREMER) and OFOP (Ocean

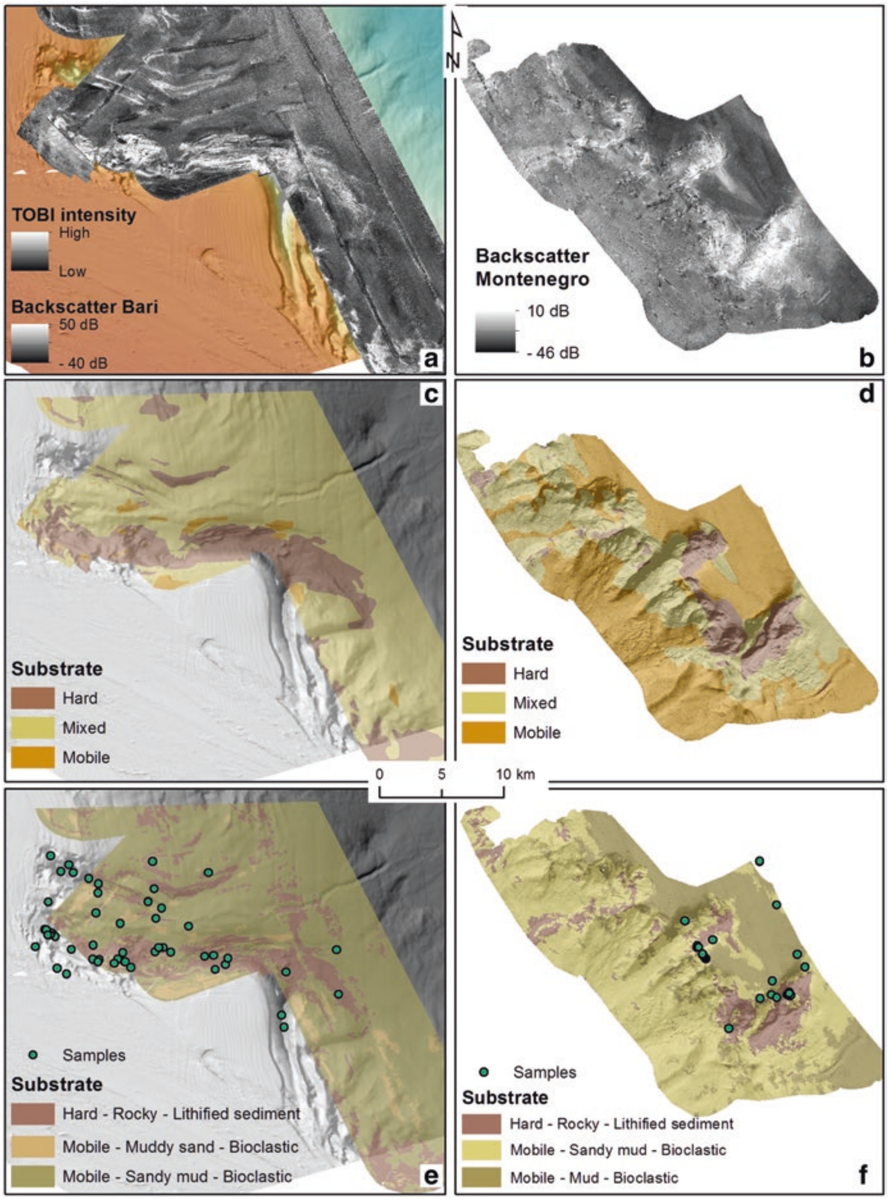


Fig. 16.4 Backscatter data available for Bari Canyon (**a**) – MBES backscatter and SSS TOBI imagery – and Montenegro slope (**b**, **c**) and (**d**) visual interpretation of the backscatter for the two sites; automatic classification of backscatter images through RSOBIA validated with seabed samples, for Bari Canyon (**e**) and Montenegro datasets (**f**). Obviously, the resulting maps only emphasises mobile sediment as recorded by a very limited number of grabs, disregarding rocky substrate and bedrocks at places overwhelming the actual geology of the margins. (© ISMAR-CNR Bologna)

Floor Observation Protocol: Huetten and Greinert 2008; Ludvigsen 2010). The synchronisation of video with navigation allows georeferencing and capturing video-frames, creating video summaries along the survey path. Subsequently, the analysis of still photographs can be represented through a classification of the AUV or ROV track according to substrate and benthic component. As for the Mediterranean Sea, this methodology has been applied to the Santa Maria di Leuca CWC province by Vertino et al. (2010). Here we present a second case study focused on the Bari Canyon and Montenegro slope. We identify CWC habitats at fine scale using ROV video observation and classification of ROV tracklines according to CoCoNet classification scheme (Figs. 16.5 and 16.6) (Foglini et al. 2014; Angeletti et al. 2015b, 2016; Grande et al. 2015; Boero et al. 2016).

While ROV video classifications provide "punctual" information, a continuous spatial coverage can be obtained by operating a georeferenced collage of the video still frames, effectively creating a photo-mosaic (Ludvigsen and Soreide 2006). For this purpose, it is necessary that the underwater vehicle navigates at a constant altitude from the seafloor. Several softwares are able to process images to produce photo-mosaics, among them ADELIE OTUS (implemented by IFREMER) and the freeware LAPMv2 (Marcon 2016). Photo-mosaics allow one to map objects, such as species or communities, manually (Wheeler et al. 2005; Roberts et al. 2009) or automatically (Lim et al. 2017) over a continuous area. Largely applied to CWC habitat mapping in the Atlantic Ocean (e.g. Porcupine Seabight, NE Atlantic: Wheeler et al. 2005; Roberts et al. 2009; Lim et al. 2017), the

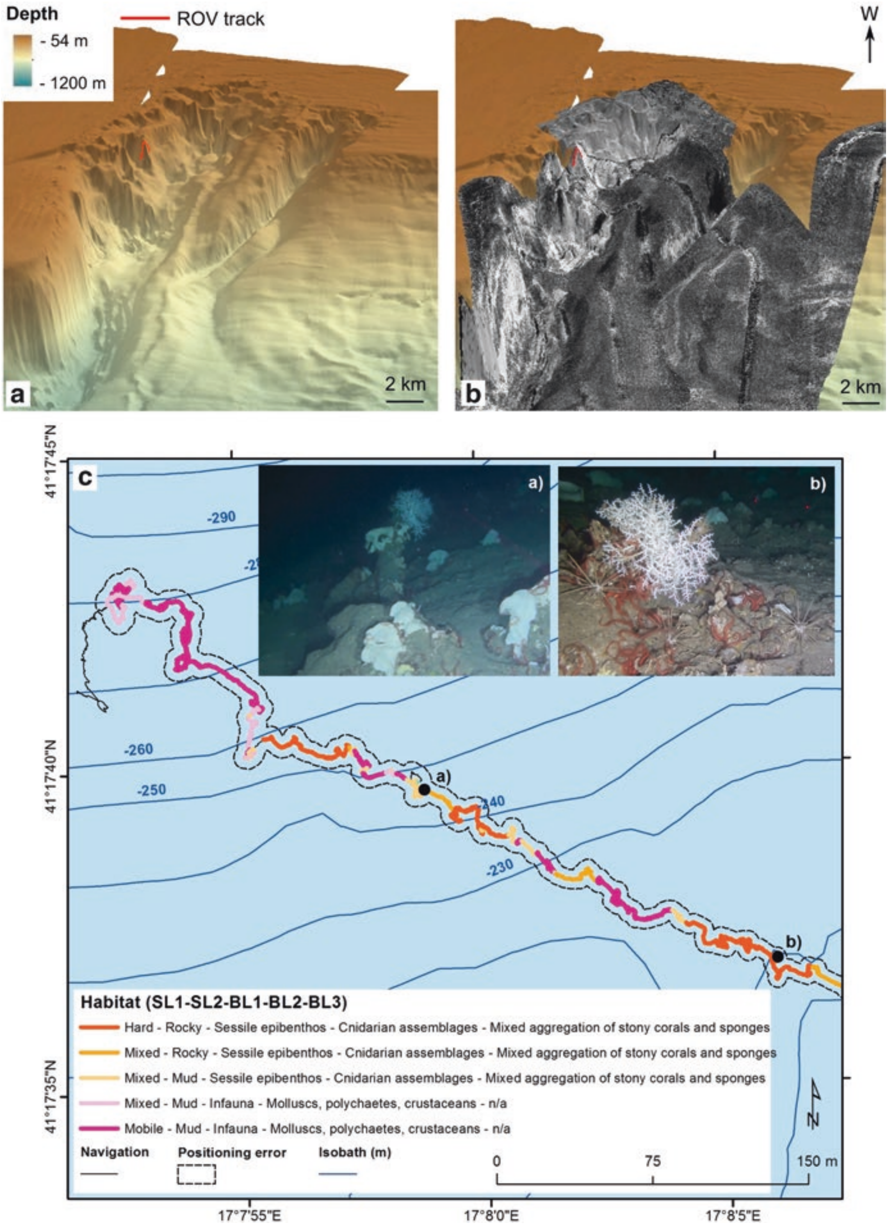


Fig. 16.5 (**a**) 3D view of Bari Canyon bathymetry (vertical exaggeration 10×) and (**b**) backscatter data draped on it (vertical exaggeration 10×) with localisation of the ROV track (© ISMAR-CNR Bologna). (**c**) Detail on the ROV track mapped according to CoCoNet classification scheme for the substrate (levels 1 and 2) and biological component (levels 1, 2 and 3) and georeferenced video still frames along the track showing (**a**) mixed substrate with emerging rocks and hardgrounds from muddy sediments with mixed aggregation dominated by big fan-shaped sponges such as *Pachastrella monilifera* and stony corals (*Madrepora oculata*: in background) and (**b**) rocky substrate with mixed aggregation of stony corals (*M. oculata* in foreground) and sponges (*P. monilifera* in background) (Photographs: a, b: © ISMAR-CNR Bologna)

only published example for Mediterranean CWCs is the photo-mosaic at Santa Maria di Leuca produced by Vertino et al. (2010).

16.4 Cold-Water Coral Habitat Mapping

The usual approach to map the distribution of CWC habitat in the Mediterranean Sea is through an expert's interpretation of acoustic data, coupled with photographs of the seafloor and bottom samples (Lo Iacono et al. 2008, 2012a, b; Savini and Corselli 2010; Vertino et al. 2010). In our case study, the benthoscape (*sensu* Zajac et al. 2003; Brown et al. 2012; Lacharité et al. 2017: the integration of geomorphological and substrate interpretation resulting in an abiotic surrogate (or marine landscape)) map has been produced by integrating the geomorphological (Fig. 16.7) and substrate maps, obtained through manual interpretation of bathymetry and backscatter data according to the classification scheme of the European Project "Towards COast to COast NETworks of marine protected areas (from the shore to the high and deep-sea) coupled with sea-based wind energy potential" – CoCoNet (Fig. 16.4a–d: Foglini et al. 2014; Angeletti et al. 2015b, 2016; Grande et al. 2015) (Fig. 16.8). The benthic habitat map shows the distribution of CWC habitat in the study area (Fig. 16.9), resulting from the addition of its biological component as derived from ROV images and bottom samples (Angeletti et al. 2014, 2015a, b; Taviani et al. 2016).

The main issue of the above approaches is that they are subjective and time-consuming. A number of more automatic

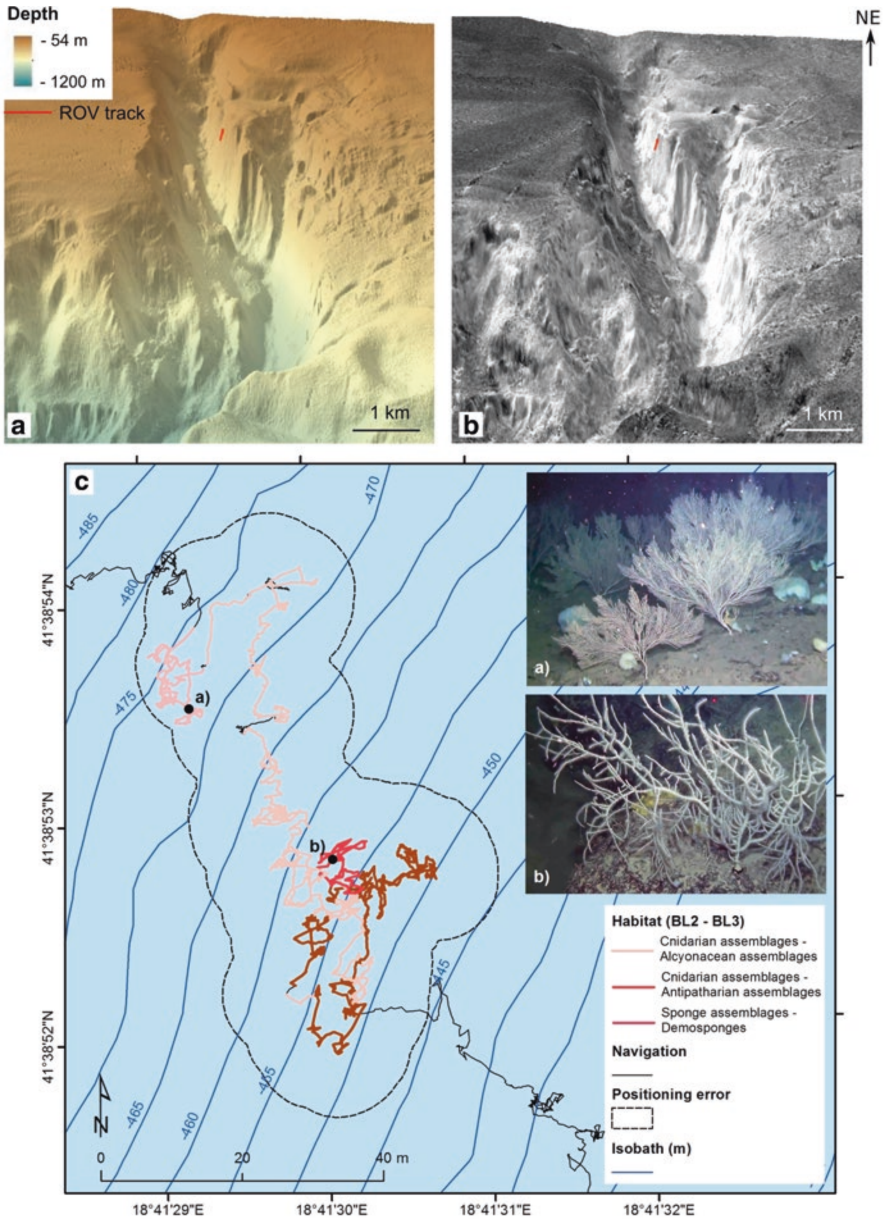


Fig. 16.6 (**a**) 3D view of Montenegro continental slope bathymetry (vertical exaggeration 10×) and (**b**) backscatter data draped on it (vertical exaggeration 10×) with localisation of the ROV track (© ISMAR-CNR Bologna). (**c**) Detail on the ROV track mapped according to CoCoNet classification scheme for the biological component (levels 2 and 3) and georeferenced video still frames along the track showing (**a**) Alcyonacean assemblages typified by monospecific forest of *Callogorgia verticillata* (Angeletti et al. 2014) and (**b**) Antipatharian assemblages characterised by *Leiopathes glaberrima* and *Antipathes dichotoma* (Angeletti et al. 2014)

approaches have been devised over the years. They can usually be categorised as either top-down or bottom-up (Brown et al. 2011).

16.4.1 Top-Down Approach

Benthic habitat mapping top-down approaches are methods that classify input data with no supervision, based solely on the patterns and variation in the input data. Then, ground-truth data may be used to identify the seascape, substrate (abiotic surrogates), species or communities characterising the classes (Fig. 16.1). Geomorphology (expressed by bathymetry and its derivatives) and seafloor backscatter can be both automatically classified (e.g. Lecours et al. 2016 with references therein).

The input data for these methodologies can be bathymetry, its derivatives, or backscatter data, or often a combination of them. Top-down approaches using backscatter data have been developed based both on signal (e.g. Angular Range Analysis: Fonseca et al. 2009; Anderson et al. 2008) and on mosaic characteristics (e.g. Image texture analysis, TexAn: Blondel 1996; Principal Component Analysis: McGonigle et al. 2009; Neural Network: Marsh and Brown 2009). Backscatter image analysis is the most common method for substrate and/or habitat classification because it describes large-scale patterns of seafloor substrate and benthic habitats better than backscatter signal analysis and can

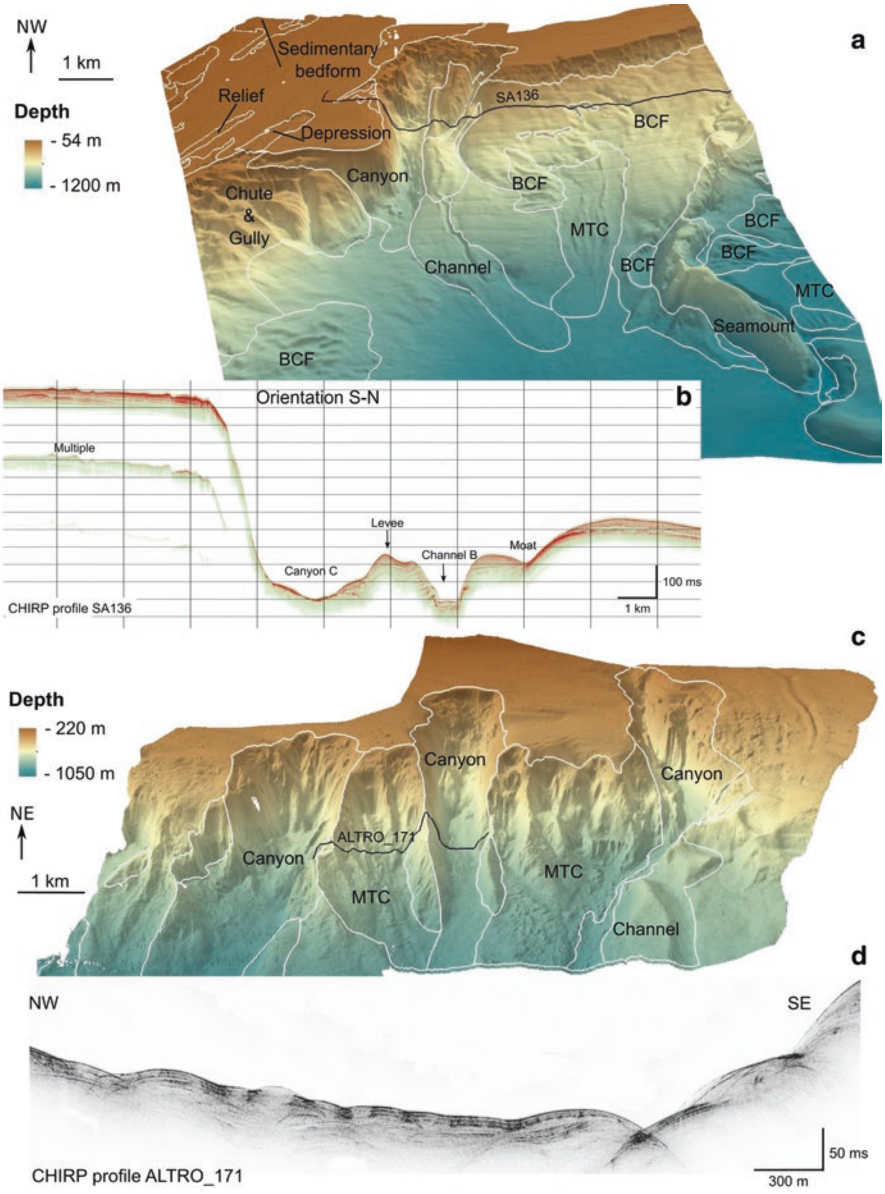


Fig. 16.7 Manual geomorphological interpretation for Bari Canyon (**a**) and Montenegro continental margin (**c**) aided by CHIRP sub-bottom profiles (**b**). The shown geomorphological interpretation reflects the level 2 of CoCoNet classification scheme (Foglini et al. 2014; Angeletti et al. 2015b, 2016; Grande et al. 2015). (© ISMAR-CNR Bologna)

be performed with several GIS software (Lamarche et al. 2016 and references therein). Such analysis typically consists in segmenting the sonar image based on the local spectral and spatial characteristics. The clusters are then grouped into homogeneous subsets through a process called classification, based on user-specified combinations and can be unsupervised or supervised.

Using the freeware RSOBIA (Remote Sensing OBIA: Le Bas 2016), we have segmented the TOBI image of the Bari Canyon and the backscatter image of the Montenegro dataset using an Object-Based Image Analysis (OBIA: Blaschke 2010) (Fig. 16.4e, f). In this process, the segmentation is based on the shape of the clusters and on their spatial correlation (not only on their thematic similarity; Lamarche et al. 2016). The resulting OBIA segmentation was ground-truthed using the sediment samples falling within each segment. Once sampling is extended to consider all lithotypes and sediment types making up the considered margins, this OBIA exercise would be able to discriminate potentially CWC-suitable substrates (Fig. 16.4e, f).

16.4.2 Bottom-Up Approach

Bottom-up, or supervised, approaches to habitat mapping consist in using the ground-truthing data (images and bottom samples) to train the segmentation of the environmental data (bathymetry and backscatter). In the following sections, two methodologies applied for CWC habitat mapping in the Mediterranean Sea are discussed: (i) automatic classification (supervised pixel-based image analysis of backscatter), and (ii) CWC habitat suitability models.

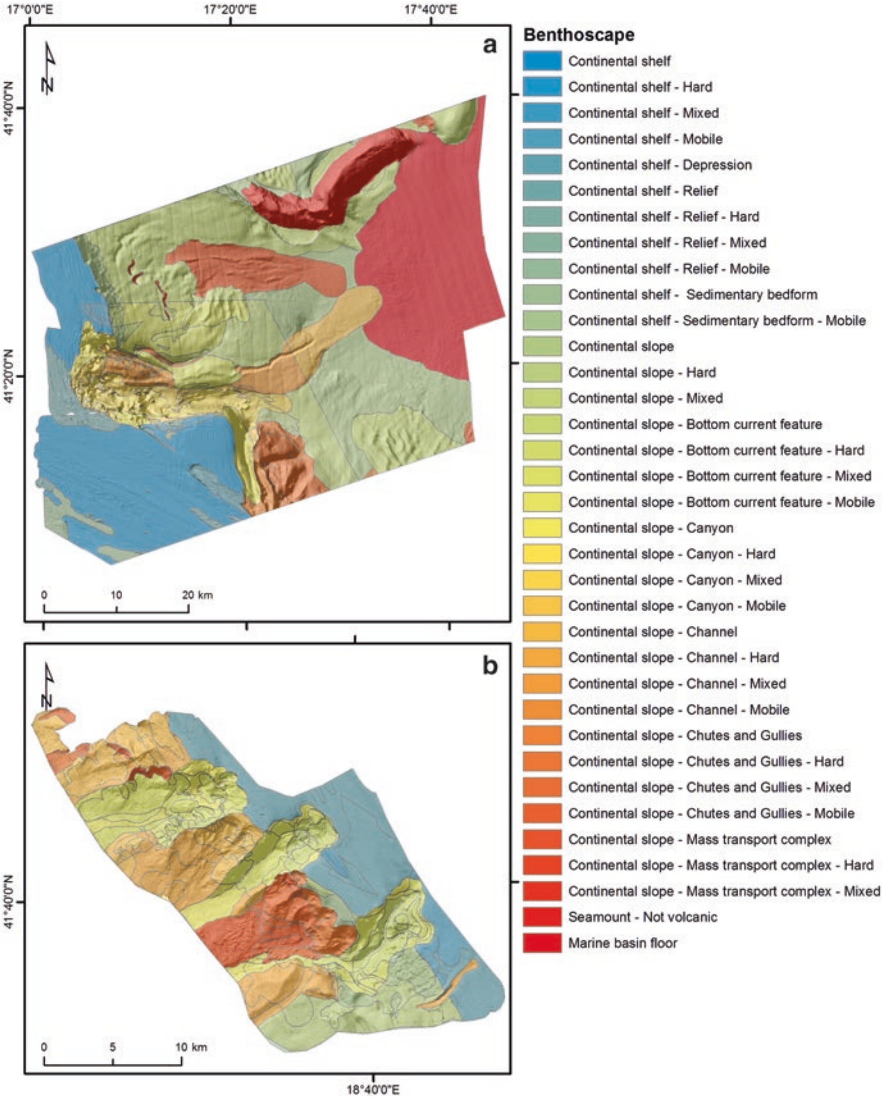


Fig. 16.8 Benthoscape of the sites of Bari Canyon (**a**) and Montenegro slope (**b**) obtained with the combination of geomorphological and backscatter manual interpretation, following CoCoNet classification scheme. (© ISMAR-CNR Bologna)

16.4.2.1 Automatic Classification

Supervised pixel-based image analysis is an automatic classification method applied to characterise CWC habitats and their distribution. Maximum Likehood classification, Iso Cluster and Textural analysis (using Grey Level Co-occurrence Matrices) are algorithms developed to carry out supervised pixel-based image classifications and have been applied in Mediterranean CWC sites (Savini et al. 2014; Lo Iacono et al., this volume).

Maximum Likehood and Iso Cluster algorithms were used to segment bathymetry and its derivatives to identify the seafloor morphologies that are likely to support CWCs. Textural analysis was used to quantify and identify backscatter image textures and patterns. This analysis was instructed using training zones chosen by experts (seafloor areas where substrate type and biological assemblages are known thanks to ground-truth data), in order to classify the nature of substrate and benthic habitat (Blondel 1996).

16.4.2.2 Habitat Suitability Models

The automatic classifications depicted so far allows for a description of the physical and biological components of CWC habitat as well as mapping their spatial distribution and variations within a surveyed area. However, such statistical analyses can also be used to predict the areas that are prone to host this habitat. This procedure is called Habitat Suitability Modelling (HSM) and is achieved through different methods, such as Ecological-Niche Factor Analysis (ENFA: developed by Hirzel et al. 2002), Maximum Entropy modelling (Davies and Guinotte 2011; Yesson et al. 2012; Anderson et al. 2016) and Generalised Linear Models (Woodby et al. 2009; Rengstorf et al. 2014). Most of the CWC habitat suitability models developed to date were in the Atlantic Ocean (e.g. Leverette and Metaxas 2005; Davies et al. 2008; Dolan et al. 2008; Guinan et al. 2009a, b; Robert et al. 2014, 2016), or at a global scale (Bryan and Metaxas 2007; Tittensor et al. 2009; Yesson et al. 2012). Recent HSM

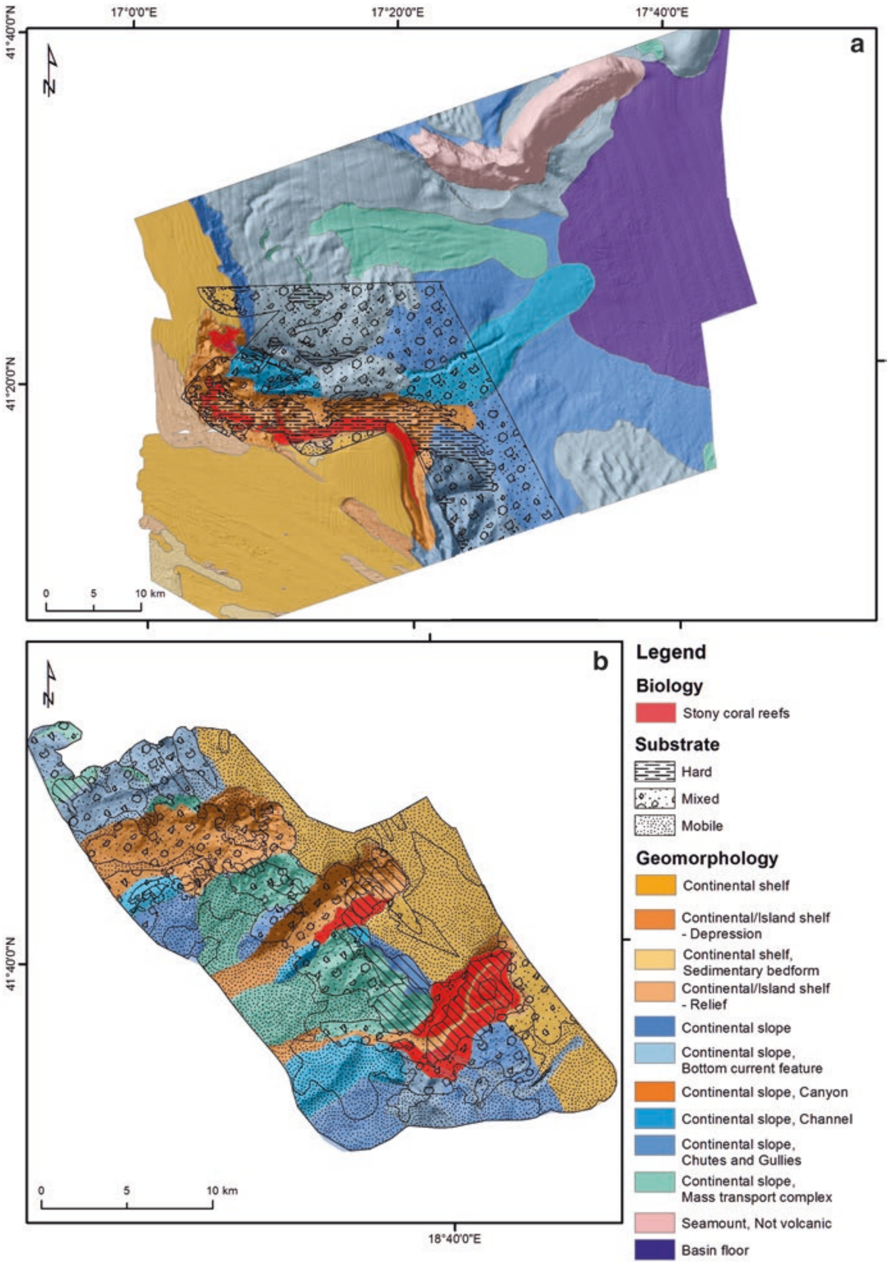


Fig. 16.9 Map of the benthic habitat for Bari Canyon (**a**) and Montenegro continental margin (**b**) built following CoCoNet classification scheme. (© ISMAR-CNR Bologna)

applications of CWCs in the Mediterranean Sea (Cassidaigne Canyon: Fabri et al. 2017; Santa Maria di Leuca and Bari Canyon: Foglini et al. 2016b, 2017; Bargain et al. 2017, 2018) identified MaxEnt as the best method to predict CWC habitat distribution in terms of probability of occurrence. Such an approach makes use of geomorphometric derivatives and oceanographic variables (i.e. temperature, salinity, currents velocity) as input dataset and trains the model with presence-only data (occurrences of CWC coming from bottom samples and ROV images). The model assigns a weight to each variable according to its contribution to CWC preference of a specific area. The validation is carried out using CWC presence-only data and the result is a probability map highlighting the potential sites for CWC growth.

While CWC habitat mapping produces a snapshot of the distribution of the habitat at the moment of the survey, HSM represents a step forward by mapping the potential for future distribution. They are performed on well-known CWC sites in order to choose and train the best model able to automatically find other areas suitable for CWC settling.

16.5 Cold-Water Coral Habitat Mapping Techniques Caveats and Perspectives

We have presented the different types of data (Table 16.1) and techniques used for CWC habitat mapping in the Mediterranean Sea. Top-down *vs* bottom-up approaches to CWC habitat mapping depends upon type, amount and quality of data. The first one is generally used when the available data cover large areas with a coarse spatial resolution and include scarce or no ground-truthing data. The second approach is applied when an extensive ground-truthing dataset is available, allowing one to train models or interpret and validate the results. Both approaches rely upon automatic classification algorithms that have been rarely implemented for CWC habitat in the Mediterranean Sea to date. This is probably because geophysical data are currently only available at a spatial resolution that is too coarse to distinguish features and patterns related to CWC colonies.

The best acoustic resolution can be achieved either by towing instruments near the bottom (like for SSS) or, more commonly, by instrumenting ROVs or AUVs (e.g. Grasmueck et al. 2006, 2007; Huvenne et al. 2011, 2016b; Wynn et al. 2014). This kind of vehicles can follow the topography and mounting the MBES vertically on a ROV would allow for high-resolution surveys of subvertical walls, cliffs or headwall scarps generating also a 3D reconstruction. Some examples are presented in Huvenne et al. (2011, 2016b) and Robert et al. (2014) on the CWC-dominated walls of the Whittard Canyon. However, this technique has not yet been applied to Mediterranean CWC sites.

Bottom samples are fundamental to determine the nature of substrate (hard, soft or firm) and sediment texture and to validate backscatter interpretation (manual or automatic) for top-down approaches or train bottom-up classification algorithms.

Visual inspection is used for first hand qualitative substrate assessment and for biological identification. High defi-

Table 16.1 Table showing the data required for benthic habitat mapping, the information and advantages that we get using them and their limits

Data	Devices for acquisition	Info and advantages	Limits
Bathymetry	MBES (and single beam echosounders)	Water depth (m)	Indirect method (remote sensing)
		Seafloor morphology	Spatial resolution not always adequate to measure ecological processes
		Manual geomorphological interpretation	
		Geomorphometric analysis to support interpretation and extract geomorphological features	
		Large scale to fine scale data	
		High spatial resolution	
Acoustic backscatter	MBES and SSS	Information on seabed substrate (hard/mobile, grain size)	Indirect method
		Enhance some geomorphological features	Noisy
		Qualitative and quantitative (only MBES backscatter) analyses	Influenced by incident angle and morphology/rugosity
		Manual and automatic classification	Shadows (SSS backscatter)
		Large scale to fine scale data	Spatial resolution not always adequate to measure ecological processes
		High spatial resolution	Signal penetrates the sediments
			Possible discrepancy between acoustic response and seafloor substrate
CHIRP profiles	Sub-bottom profiler (SBP)	High resolution stratigraphy (penetration of few metres)	Low penetration
		Support morphological and backscatter interpretation	2D information
		Detection of morphologies related to specific habitats (e.g. coral mounds)	
Seafloor samples	Grab, box corer, corer, dredge, hauls	Ground-truth data for acoustic data analysis	Punctual database
		Information on seafloor geology (lithology, grain size)	Discrepancy in scale between geophysical data and seafloor samples
		Information on mega- and macro-epifauna and infauna	
		Information on palaeobiology	
ROV video and images	Camera	Ground-truth data for acoustic data analysis	Very fine scale → discrepancy in scale between geophysical data and seafloor images
		HD images of seascape, seafloor and habitats	ROV exploration → linear data
		Detailed information on habitats: identification of species, extension, density, health of the organisms, etc.	
		Photo-mosaic → mapping at fine scale → bridge between large and fine scale analyses	

nition images, currently up to ultra-high definition (4k), extracted from cameras mounted on ROVs, permit one to identify not only mega-benthic, but even macro-benthic organisms (>20 mm), to the lowest possible taxonomic rank (species). Further data extracted from ROV images are fundamental to contribute to satisfy the requisites of programs such as MSFD (EU Marine Strategy Framework Directive) aimed at monitoring Good Environmental Status (GES) of benthic habitats, with the lowest possible impact on the seafloor. Despite its diffused application for CWC habitat mapping in Europe and elsewhere, just one study exploited photo-mosaic of ROV images within the Mediterranean region (Vertino et al. 2010), while the application of georeferenced photo-mosaics to Mediterranean CWCs is highly desirable. Nevertheless, biological samples are needed in most cases to properly assess taxonomy. In fact, a large number of taxa cannot be identified from images at species-level, such as some cnidarians or sponges, which were described as morpho-species or morphological categories in some works (e.g. Bell and Barnes 2001).

Seafloor backscatter images are seldom analysed for CWC habitat mapping and HSM. Any interpretation of the seafloor substrate based solely on acoustic reflectivity presents some caveats which can be relevant for CWCs and habitat mapping. High reflectivity (high backscatter intensity) is usually interpreted as an indication of hard bottom (rock or gravel), when it could be in reality draped by soft sediments. In such a case, the retro-diffused signal responded predominantly to an underlying hard substrate more than to the easily-penetrable thin muddy drape. Backscatter data are also influenced by the morphology showing higher intensity in correspondence to steep slopes, such as scarps and canyon flanks that can be covered by a muddy layer. These examples illustrate the inherent ambiguity of backscatter data, and thus the fundamental obligation to validate any interpretation. In addition, backscatter data from MBES are not calibrated to date, although efforts have recently been made in this direction (Lurton and Lamarche 2015). Calibrated MBES in the future would help in overcoming these possible discrepancies between backscatter signal interpretation and seafloor composition. Progress in multibeam technology, such as multi-frequency systems, is also expected to bring about further accuracy in habitat mapping (Hughes Clarke 2015; Brown et al. 2017).

Another promising technology to improve and accelerate the recognition of salient biological traits in a given deep-water habitat (such as CWCs) would be the use of hyperspectral cameras. For example, The Underwater Hyperspectral Imager (UHI) developed by Ecotone is a ROV equipped with hyperspectral cameras and a suite of data processing algorithms. This system records upwelling radiance or reflectance in the entire visible band (390–700 nm) with up to 1 nm resolution, and radiometrically and geometrically processed the data, and finally performs an automatic fine-scale identification of species or communities, to be compared with a library of spectral fingerprints (Pettersen et al. 2014; Johnsen et al. 2016; Foglini et al. 2018). The construction of the library is a critical prerequisite that will require an important and coordinated effort in order to fit all possible situations to be found in the ocean.

Another recent development in habitat mapping is the use of oceanographic data. Indeed, oceanographic variables are important in species and habitat distribution, so that habitat inventories and classification schemes (e.g. CMECS: Madden et al. 2009; EUNIS: Garlparsoro et al. 2012) have considered oceanographic variables for habitat characterisation. Nevertheless, oceanography is only seldom considered in CWC habitat maps and is by now contemplated to be included in Habitat Suitability Models calculations as models of variables (not as long-term measurements), with a spatial resolution much coarser than those of acoustic or ground-truth data (Vincent et al. 2004; Kostylev and Hannah 2007; Degraer et al. 2008; Verfaillie et al. 2009; Brown et al. 2011). Regarding the Mediterranean basin, oceanographic variables have been included in models of CWC habitat suitability in the Bari Canyon and Cassidaigne Canyon (Bargain et al. 2018).

Besides the new sources of data introduced previously, developments are also expected in the classification algorithms themselves. Recently introduced methods with high potential are multi-model ensembles, which integrate different automatic methods, both unsupervised and supervised, without omitting any fundamental aspect for habitat mapping (Diesing et al. 2014). Thus far, the expert's interpretation is the most adopted approach serving CWC habitat mapping in the Mediterranean basin since fundamental to assign a meaning to the classes in which the datasets can be segmented. It appears, therefore, advisable to find the optimal combination of methods for mapping and modelling Mediterranean CWCs.

16.6 Conclusions

It is urgent to establish measures for the sustainable management of such emblematic ecosystems of the deep which are increasingly threatened by climatic and anthropogenic stressors. The integration of habitat mapping methodologies and habitat suitability models is instrumental to deal with these societal problems. Habitat mapping evolves continuously, following the implementation of existing techniques as well as technological ameliorations and advances in marine sciences. Hence, future innovative approaches will strengthen its potential and efficacy in the coming years. The mapping of Mediterranean CWC ecosystems is still in its infancy, but is steadily gaining momentum due to the increasing scientific outcomes. Habitat mapping is a valuable tool to improve the characterisation and evaluation of the status of Mediterranean CWCs by fostering a better accuracy of CWC occurrences in terms of geo-biological and oceanographic aspects and predicting potentially-suitable CWC settings.

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References

Anderson JT, Van Holliday D, Kloser R, et al (2008) Acoustic seabed classification: current practice and future directions. ICES J Mar Sci 65:1004e1011

Anderson OF, Guinotte JM, Rowden AA, et al (2016) Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: implications for the use of broad-scale models in fisheries management. Ocean Coast Manag 120:110–126

Angeletti L, Taviani M, Canese S, et al (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Mediterr Mar Sci 15:263–273

Angeletti L, Canese S, Franchi F, et al (2015a) The "chimney forest" of the deep Montenegrin margin, south-eastern Adriatic Sea. Mar Pet Geol 66:542–554

Angeletti L, Berov D, Foglini F, et al (2015b) Scuba to ROV visual groundtruthing and habitat mapping: Mediterranean and Black Seas examples. Paper presented at the International Meeting of GeoSub2015 – Underwater Geology, Trieste, 13–16 October 2015

Angeletti L, Foglini F, Grande V, et al (2016) Habitat mapping discloses oceanographic patterns underneath. In: GEOHAB – Marine Environment Mapping and Interpretation, Abstract Booklet, Winchester, 2–6 May 2016, p 89

Arantes RCM, Castro CB, Pires DO, et al (2009) Depth and water mass zonation and species associations of cold-water octocoral and stony coral communities in the southwestern Atlantic. Mar Ecol Prog Ser 397:71–79

Bargain A, Marchese F, Savini A, et al (2017) Santa Maria di Leuca Province (Mediterranean Sea): identification of suitable mounds for cold-water coral settlement using geomorphometry proxies and Maxent methods. Front Mar Sci Deep-Sea Environ Ecol. https://doi.org/10.3389/fmars.2017.00338

Bargain A, Foglini F, Pairaud I, et al (2018) Predictive habitat modeling in two Mediterranean canyons including hydrodynamics variables. Prog Oceanogr 168:151–168

Bell JJ, Barnes DKA (2001) Sponge morphological diversity: a qualitative predictor of species diversity? Aquatic Conserv: Mar Freshw Ecosyst 11:109–121

Blaschke T (2010) Object based image analysis for remote sensing. ISPRS J Photogramm 65:2–16

Blondel PH (1996) Segmentation of the Mid-Atlantic Ridge south of the Azores, based on acoustic classification of TOBI data. In: MacLeod CJ, Tyler PA, Walker CL (eds) Tectonic, magmatic, hydrothermal biological segmentation of mid-ocean ridges. Geological Society special publication, vol 118. Geological Society, London, pp 17–28

Boero F, Foglini F, Fraschetti S, et al (2016) CoCoNet: towards coast to coast networks of marine protected areas (from the shore to the high and deep sea), coupled with sea-based wind energy potential. SCI RES Inform Technol Ric Sci Tecnol dell'Inform 6:1–95. https://doi.org/10.2423/i22394303v6Sp1

Bonaldo D, Benetazzo A, Bergamasco A, et al (2016) Interactions among Adriatic continental margin morphology, deep circulation and bedform patterns. Mar Geol 375:82–98

Brown CJ, Smith SJ, Lawton P, et al (2011) Benthic habitat mapping: a review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. Estuar Coast Shelf S 92:502–520

Brown CJ, Sameoto JA, Smith SJ (2012) Multiple methods, maps, and management applications: purpose made seafloor maps in support of ocean management. J Sea Res 72:1–13

Brown CJ, Beaudoin J, Brissette M, et al (2017) Setting the stage for multi-spectral acoustic backscatter research. In: Todd BJ, Brown CJ, Lacharité M, et al (eds) Program and abstracts GeoHab conference. Nova Scotia Geological Survey of Canada, Dartmouth, Open File 8295:41

Bryan TL, Metaxas A (2007) Predicting suitable habitat for deep-water gorgonian corals on the Atlantic and Pacific Continental Margins of North America. Mar Ecol Prog Ser 330:113–126

Buhl-Mortensen L, Buhl-Mortensen P, Dolan MFJ, et al (2012) Habitat complexity and bottom fauna composition at different scales on the continental shelf and slope of northern Norway. Hydrobiologia 685:191–219

Canals M, Puig P, Durrieu de Madron X, et al (2006) Flushing submarine canyons. Nature 444:354–357

Cau A, Moccia D, Follesa MC, et al (2017) Coral forests diversity in the outer shelf of the south Sardinian continental margin. Deep-Sea Res Part 1 Oceanogr Res Pap 122:60–70

Correa T, Grasmueck M, Eberli GP, et al (2012) Variability of cold-water coral mounds in a high sediment input and tidal current regime, Straits of Florida. Sedimentology 59(4):1278–1304

Correa TB, Grasmueck M, Eberli GP, et al (2013) Deep acoustic applications. In: Goodman JA, Purkis SJ, Phinn SR (eds) Coral reef remote sensing. Springer, Dordrecht, pp 253–282

Costello MJ (2009) Distinguishing marine habitat classification concepts for ecological data management. Mar Ecol Prog Ser 397:253–268

Davies AJ, Guinotte JM (2011) Global habitat suitability for framework-forming cold-water corals. PLoS One 6:e18483. https://doi.org/10.1371/journal.pone.0018483

Davies AJ, Wisshak M, Orr JC, et al (2008) Predicting suitable habitats for the cold-water coral *Lophelia pertusa* (Scleractinia). Deep-Sea Res Part 1 Oceanogr Res Pap 55:1048–1062

De Clippele LH, Gateira J, Robert K, et al (2016) Using novel acoustic and visual mapping tools to predict the small-scale spatial distribution of live biogenic reef framework in cold-water coral habitats. Coral Reefs 36:255–268

De Falco G, Tonielli R, Di Martino G, et al (2010) Relationships between multibeam backscatter, sediment grain size and *Posidonia oceanica* seagrass distribution. Cont Shelf Res 30:1941–1950

DeGeest AL, Mullenbach BL, Puig P, et al (2008) Sediment accumulation in the western Gulf of Lions, France: the role of Cap the Creus canyon in linking shelf and slope sediment dispersal systems. Cont Shelf Res 28:2031–2047

Degraer S, Verfaillie E, Willems W, et al (2008) Habitat suitability modelling as a mapping tool for macrobenthic communities: an example from the Belgian part of the North Sea. Cont Shelf Res 28:369–379

Diaz RJ, Solan M, Valente RM (2004) A review of approaches for classifying benthic habitats and evaluating habitat quality. J Environ Manag 73:165–181

Diesing M, Green SL, Stephens D, et al (2014) Mapping seabed sediments: comparison of manual, geostatistical, object-based image analysis and machine learning approaches. Cont Shelf Res 84:107–119

Dolan MFJ, Grehan AJ, Guinan JC, et al (2008) Modelling the local distribution of cold-water corals in relation to bathymetric variables: adding spatial context to deep-sea video data. Deep-Sea Res Part 1 Oceanogr Res Pap 55:1564–1579

Dunn DC, Halpin PN (2009) Rugosity-based regional modelling of hard-bottom habitat. Mar Ecol Prog Ser 377:1–11

Dúran Muñoz P, Sayago-Gil M, Cristobo J, et al (2009) Seabed mapping for selecting cold-water coral protection areas on Hatton Bank, Northeast Atlantic. ICES J Mar Sci 66:2013–2025

Edinger EN, Sherwood OA, Piper DJ, et al (2011) Geological features supporting deep-sea coral habitat in Atlantic Canada. Cont Shelf Res 31:S69–S84

Fabri M-C, Pedel L, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207

Fabri M-C, Bargain A, Pairaud I, et al (2017) Cold-water coral ecosystems in Cassidaigne Canyon: an assessment of their environmental living conditions. Deep-Sea Res Part 2 Top Stud Oceanogr 137:436–453

Foglini F, Angeletti L, Campiani E, et al (2014) Habitat mapping for establishing Coast to Coast Network of marine protected areas in the framework of COCONET Project: from coastal area to deep sea in the South Adriatic (Italy). In: GEOHAB – Marine Environment Mapping and Interpretation, Abstract Volume, Lorne, Australia, 4–8 May 2014, p 32

Foglini F, Campiani E, Trincardi F (2016a) The reshaping of the SouthWest Adriatic Margin by cascading of dense shelf waters. Mar Geol 375:64–81

Foglini F, Bargain A, Angeletti L, et al (2016b) Predictive habitat modelling of cold water coral distribution in the Bari Canyon (Adriatic Sea) with hydrodynamic variables. In: GEOHAB – Marine Environment Mapping and Interpretation, Abstract Booklet, Winchester, UK, 2–6 May 2016, p 116

Foglini F, Bargain A, Angeletti L, et al (2017) The addition of hydrodynamic variables to predictive cold water coral habitat modelling: the Bari Canyon case-study, southwestern Adriatic Sea. In: EGU General Assembly Conference Abstracts, Geophysical Research Abstracts 19:18766

Foglini F, Angeletti L, Bracchi VA, et al (2018) Underwater hyperspectral imaging in the Adriatic Sea: a new technology for benthic habitat mapping and monitoring. In: GEOHAB - Marine Environment Mapping and Interpretation, Abstract Volume, Santa Barbara, USA, 7–11 May 2018, p 45

Fonseca L, Brown C, Calder B, et al (2009) Angular range analysis of acoustic themes from Stanton Banks Ireland: a link between visual interpretation and multibeam echosounder angular signatures. Appl Acoust 70:1298–1304

Fosså JH, Lindberg B, Christesen O, et al (2005) Mapping of *Lophelia* reefs in Norway: experiences and survey methods. In: Freiwald A, Murray Roberts J (eds) Cold-water corals and ecosystems. Springer, Berlin, pp 359–391

Frederiksen R, Jensen A, Westerberg H (1992) The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing. Sarsia 77:157–171

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the central Mediterranean revealed by ROV surveys. Oceanography 22:58–74

Galparsoro I, Connor DW, Borja A, et al (2012) Using EUNIS habitat classification for benthic mapping in European seas: present concerns and future needs. Mar Pollut Bull 64:2630–2638

García-Alegre A, Sánchez F, Gómez-Ballesteros M, et al (2014) Modelling and mapping the local distribution of representative species on the Le Danois bank, El Cachucho marine protected area (Cantabrian Sea). Deep-Sea Res Part 2 Top Stud Oceanogr 106:151–164

Genin A, Dayton PK, Lonsdale PF, et al (1986) Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature 322:59–61

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Grande V, Angeletti L, Campiani E, et al (2015) “Habitat mapping” geodatabase, an integrated interdisciplinary and multi-scale approach for data management. Paper presented at the international meeting GeoSub2015 – underwater geology, Trieste, 13–16 October 2015

Grasmueck M, Eberli GP, Viggiano DA, et al (2006) Autonomous underwater vehicle (AUV) mapping reveals coral mound distribution, morphology, and oceanography in deep water of the Straits of Florida. Geophys Res Lett 33:L23616

Grasmueck M, Eberli GP, Correa TBS, et al (2007) AUV-based environmental characterization of deep-water coral mounds in the straits of Florida. Paper presented at the Offshore technology conference, Houston

Greene HG, Yoklavich MM, Starr RM, et al (1999) A classification scheme for deep seafloor habitats. Oceanol Acta 22:663–678

Greene HG, Bizzarro JJ, O’Connell VM, et al (2007) Construction of digital potential marine benthic habitat maps using a coded classification scheme and its applications. In: Todd BJ, Greene HG (eds) Mapping the seafloor for habitat characterization: Geological Association of Canada, Special Paper 47:141–155

Guinan JC, Grehan AJ, Dolan MFJ, et al (2009a) Quantifying relationships between video observations of cold-water coral and seafloor terrain in Rockall Trough, west of Ireland. Mar Ecol Prog Ser 375:125–138

Guinan J, Brown C, Dolan MFJ, et al (2009b) Ecological niche modelling of the distribution of cold-water coral habitat using underwater remote sensing data. Ecol Inform 4:83–92

Harris PT, Baker EK (2011) Seafloor geomorphology as benthic habitat: GeoHab atlas of seafloor geomorphic features and benthic habitats. Elsevier, Amsterdam

Hirzel AH, Hausser J, Chessel D, et al (2002) Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83(7):2027–2036

Horn BKP (1981) Hill shading and the reflectance map. Proc IEEE 69(1):14–47

Huetten E, Greinert J (2008) Software controlled guidance, recording and postprocessing of seafloor observations by ROV and other towed devices: the software package OFOP. Geophys Res Abstract 10:EGU2008-A-03088

Hughes Clarke JE (2015) Multispectral acoustic backscatter from multibeam, improved classification potential. In: Proceedings of the U.S. hydrographic conference 2015, National Harbor, Maryland, USA, 16th–19th March 2015, p 19

Hughes Clarke JE, Mayer LA, Wells DE (1996) Shallow-water imaging multibeam sonars: a new tool for investigating seafloor processes in the coastal zone and on the continental shelf. Mar Geophys Res 18:607–629

Hughes Clarke JE, Danforth BW, Valentine P (1997) Areal seabed classification using backscatter angular response at 95kHz. In: SACLANTCEN conference on high frequency acoustics in shallow water. NATO SACLANT Undersea Research Centre, Lerici, Italy, 30th June–4th July 1997, pp 243–250

Huvenne VAI, Beyer A, de Haas H, et al (2005) The seabed appearance of different coral bank provinces in the Porcupine Seabight, NE Atlantic: results from sidescan sonar and ROV seabed mapping. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg pp 535–569

Huvenne VAI, Tyler PA, Masson DG, et al (2011) A picture on the wall: innovative mapping reveals cold-water coral refuge in submarine canyon. PLoS One 6:e28755

Huvenne VAI, Bett B, Masson D, et al (2016a) Effectiveness of a deep-sea cold-water coral marine protected area, following eight years of fisheries closure. Biol Conserv 200:60–69

Huvenne VAI, Georgiopoulou A, Chaumillon L, et al (2016b) Novel method to map the morphology of submarine landslide headwall scarps using remotely operated vehicles. In: Lamarche G, Mountjoy J, Bull S, et al (eds) Submarine mass movements and their consequences, advances in natural and technological hazards research, vol 41. Springer International Publishing, Cham, pp 135–144

Jackson DR, Briggs KB (1992) High-frequency bottom backscattering: roughness versus sediment volume scattering. J Acoust Soc Am 92:962–977

Johnsen G, Ludvigsen M, Sørensen A, et al (2016) The use of underwater hyperspectral imaging deployed on remotely operated vehicles – methods and applications. IFAC-Pap OnLine 49:476–481

Kostylev VE, Hannah CG (2007) Process-driven characterization and mapping of seabed habitats. Geol Assoc Can Spec Pap 47:171–184

Kostylev VE, Todd BJ, Fader GB, et al (2001) Benthic habitat mapping on the Scotian Shelf based on multibeam bathymetry, surficial geology and sea floor photographs. Mar Ecol Prog Ser 219:121–137

Lacharité M, Brown CJ, Gazzola V (2017) Multisource multibeam backscatter data: developing a strategy for the production of benthic habitat maps using semi-automated seafloor classification methods. Mar Geophys Res 38:307–322 https://doi.org/10.1007/s11001-017-9331-6

Lamarche G, Orpin AR, Mitchell JS, et al (2016) Benthic habitat mapping. In: Clark MR, Consalvey M, Rowden AA (eds) Biological sampling in the deep sea. Wiley, pp 80–102

Lastras G, Canals M, Ballesteros E, et al (2016) Cold-water corals and anthropogenic impacts in La Fonera submarine canyon head, Northwestern Mediterranean sea. PLoS One 11:e0155729

Le Bas TP (2016) RSOBIA – a new OBIA toolbar and toolbox in ArcMap 10.x for segmentation and classification. In: Kerle N, Gerke M, Lefevre S (eds) GEOBIA 2016: solutions and synergies. University of Twente Faculty of Geo-Information and Earth Observation (ITC), Enschede, pp 14–16, September 2016. https://doi.org/10.3990/2.448

Lecours V, Devillers R, Schneider DC, et al (2015) Spatial scale and geographic context in benthic habitat mapping: review and future directions. Mar Ecol Prog Ser 535:259–284

Lecours V, Dolan MFJ, Micallef A, et al (2016) A review of marine geomorphometry, the quantitative study of the seafloor. Hydrol Earth Syst Sci 20:3207–3244

Lecours V, Devillers R, Simms AE, et al (2017) Towards a framework for terrain attribute selections in environmental studies. Environ Model Softw 89:19–30

Leverette T, Metaxas A (2005) Predicting habitat for two species of deep-water coral on the Canadian Atlantic continental shelf and slope. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin pp 467–479

Lim A, Wheeler AJ, Arnaubec A (2017) High-resolution facies zonation within a cold-water coral mound: the case of the Piddington Mound, Porcupine Seabight, NE Atlantic. Mar Geol 390:120–130

Lo Iacono C, Gràcia E, Diez S, et al (2008) Seafloor characterization and backscatter variability of the Almería Margin (Alboran Sea, SW Mediterranean) based on high-resolution acoustic data. Mar Geol 250:1–18

Lo Iacono C, Gràcia E, Bartolomé R, et al (2012a) The habitats of the Chella Bank, Eastern Alboran Sea (Western Mediterranean). In: Harris P, Baker E (eds) Seafloor geomorphology as benthic habitat: GeoHab Atlas of seafloor geomorphic features and benthic habitats. Elsevier, London, pp 681–687

Lo Iacono C, Orejas C, Gori A, et al (2012b) The habitats of the Cap de Creus continental shelf and Cap de Creus Canyon, northwestern Mediterranean. In: Harris P, Baker E (eds) Seafloor geomorphology as benthic habitat: GeoHab Atlas of seafloor geomorphic features and benthic habitats. Elsevier, London, pp 457–464

Lo Iacono CL, Gràcia E, Ranero CR, et al (2014) The West Melilla cold water coral mounds, Eastern Alboran Sea: morphological characterization and environmental context. Deep-Sea Res Part 2 Top Stud Oceanogr 99:316–326

Ludvigsen M (2010) An ROV toolbox for optical and acoustical seabed investigations. Doctoral dissertation, Norwegian University of Science and Technology

Ludvigsen M, Soreide F (2006) Data fusion on the Ormen Lange shipwreck project. In: OCEANS 2006 MTS/IEEE Boston, Massachusetts, 18–21 September 2006

Lurton X, Lamarche G. (2015) Backscatter measurements by seafloor-mapping sonars. Guidelines and Recommendations. GeoHab report, http://geohab.org/wp-content/uploads/2014/05/BSWG-REPORT-MAY2015.pdf

Madden CJ, Goodin K, Allee RJ, et al (2009) Coastal and marine ecological classification standard. National Oceanic and Atmospheric Administration and NatureServe, Washington DC, pp 107

Malinverno E, Taviani M, Rosso A, et al (2010) Stratigraphic framework of the Apulian deep-water coral province, Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:345–359

Marcon Y (2016) LAPMv2 6.0-user manual. PANGAEA, Bremerhaven

Marsh I, Brown C (2009) Neural network classification of multibeam backscatter and bathymetry data from Stanton Bank (Area IV). Appl Acoust 70:1269–1276

Masson DG, Bett BJ, Billet DSM, et al (2004) The origin of deep-water, coral-topped mounds in the northern Rockal Trough, Northeast Atlantic. Mar Geol 291:159–180

McGonigle C, Brown C, Quinn R, et al (2009) Evaluation of image-based multibeam sonar backscatter classification for benthic habitat discrimination and mapping at Stanton Banks, UK. Estuar Coast Shelf Sci 81:423–437

MESH (2008a) Mapping European seabed habitats. www.searchmesh.net

MESH (2008b) MESH (Mapping European Seabed Habitats): review of standards and protocols for seabed habitat mapping. www.searchmesh.net

Mitchell SC (2005) How useful is the concept of habitat? A critique. Oikos 110:634–638

Morris DW (2003) Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13

Mortensen PB, Buhl-Mortensen L (2004) Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). Mar Biol 144:1223–1238

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Prog Ser 397:37–51

Pettersen R, Johnsen G, Bruheim P, et al (2014) Development of hyperspectral imaging as a bio-optical taxonomic tool for pigmented marine organisms. Org Divers Evol 14:237–246

Remia A, Taviani M (2005) Shallow-buried Pleistocene *Madrepora*-dominated coral munds on a muddy continental slope, Tuscan archipelago, NE Tyrrhenian sea. Facies 50:419–425

Rengstorf AM, Mohn C, Brown C, et al (2014) Predicting the distribution of deep-sea vulnerable marine ecosystems using high-resolution data: considerations and novel approaches. Deep-Sea Res Part 1 Oceanogr Res Pap 93:72–82

Rigol-Sanchez JP, Stuart N, Pulido-Bosch A (2015) ArcGeomorphometry: a toolbox for geomorphometric characterisation of DEMs in the ArcGIS environment. Comput Geosci 85:155–163

Robert K, Jones DOB, Tyler PA, et al (2014) Finding the hotspots within a biodiversity hotspot: fine-scale biological predictions within a submarine canyon using high-resolution acoustic mapping techniques. Mar Ecol 36:1256–1276

Robert K, Jones DOB, Roberts JM, et al (2016) Improving predictive mapping of deep-water habitats: considering multiple model outputs and ensemble techniques. Deep-Sea Res Part 1 Oceanogr Res Pap 113:80–89

Roberts JM, Brown CJ, Long D, et al (2005) Acoustic mapping using a multibeam echosounder reveals cold-water coral reefs and surrounding habitats. Coral Reefs 24:654–669

Roberts JM, Wheeler A, Freiwald A, et al (2009) Cold-water corals. The biology and geology of deep-sea coral habitats. Cambridge University Press, Cambridge, p 334

Ross SW, Rhode M, Brooke S (2017) Deep-sea coral and hardbottom habitats on the west Florida slope, eastern Gulf of Mexico. Deep-Sea Res Part 1 Oceanogr Res Pap 120:14–28

Sandwell DT, Smith WH, Gille S, et al (2006) Bathymetry from space: rationale and requirements for a new, high-resolution altimetric mission. Compt Rendus Geosci 338:1049–1062

Savini A, Corselli C (2010) High-resolution bathymetry and acoustic geophysical data from Santa Maria di Leuca Cold Water Coral province (northern Ionian Sea – Apulian continental slope). Deep-Sea Res Part 2 Top Stud Oceanogr 57:326–344

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the northern Ionian Sea (central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9(7):e102405

Somoza L, Ercilla G, Urgorri V, et al (2014) Detection and mapping of cold-water coral mounds and living *Lophelia* reefs in the Galicia Bank, Atlantic NW Iberia margin. Mar Geol 349:73–90

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, Berlin pp 137–156

Taviani M, Angeletti L, Antolini B, et al (2011) Geo-biology of Mediterranean deep-water coral ecosystems. In: Beatrici D, Braico P, Cappelletto M, et al (eds) Geo-biology of Mediterranean deep-water coral ecosystems. Marine Research at CNR, DTA/6, Rome, pp 705–720

Taviani M, Angeletti L, Beuck L, et al (2016) Reprint of 'On and off the beaten track: Megafaunal sessile life and Adriatic cascading processes'. Mar Geol 375:146–160

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystem. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78

Tillin HM, Rogers SI, Frid CLJ (2008) Approaches to classifying benthic habitat quality. Mar Policy 32:455–464

Tittensor DP, Baco AR, Brewin PE, et al (2009) Predicting global habitat suitability for stony corals on seamounts. J Biogeogr 36:1111–1128

Tong R, Purser A, Unnitham V, et al (2012) Multivariate statistical analysis of distribution of deep-water gorgonian corals in relation to seabed topography on the Norwegian margin. PLoS One 7:e43534

Tong R, Purser A, Guinan J, et al (2013) Modeling the habitat suitability for deep-water gorgonian corals based on terrain variables. Ecol Inform 13:123–132

Trincardi F, Foglini F, Verdicchio G, et al (2007) The impact of cascading currents on the Bari Canyon System, SW-Adriatic margin (central Mediterranean). Mar Geol 246:208–230

Trincardi F, Campiani E, Correggiari A, et al (2014) Bathymetry of the Adriatic Sea: the legacy of the last eustatic cycle and the impact of modern sediment dispersal. J Maps 10:151–158

Urgelés R, Locat J, Schmitt T, et al (2002) The July 1996 flood deposit in the Saguenay Fjord, Quebec, Canada: implications for sources of spatial and temporal backscatter variations. Mar Geol 184:41–60

Verfaillie E, Degraer S, Schelfaut K, et al (2009) A protocol for classifying ecologically relevant marine zones, a statistical approach. Estuar Coast Shelf Sci 83:175–185

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396

Vertino A, Spezzaferri S, Rosso A, et al (2014) Comparing Mediterranean and NE Atlantic cold-water coral mounds: spatial and temporal distribution of benthic carbonate associations. Paper presented at the International Sedimentological Congress (COCARDE symposium S12), Geneva, 18–22 Aug 2014

Vincent MA, Atkins SM, Lumb CM, et al (2004) Marine nature conservation and sustainable development -the Irish Sea Pilot. In: Joint Nature Conservation Committee (ed) Report to Defra. Peterborough, p 176

Wheeler A, Beck T, Thiede J, et al (2005) Deep-water coral mounds on the Porcupine Bank, Irish Margin: preliminary results from the Polarstern ARK-XIX/3a ROV cruise. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Heidelberg, pp 393–402

Wilson MFJ, O'Connell B, Brown C, et al (2007) Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Mar Geod 30:3–35

Wood J (2009) Overview of software packages used in geomorphometry. In: Hengl T, Reuter HI (eds) Geomorphometry: concepts, software, applications. Developments in soil science, vol 33. Elsevier, Amsterdam, pp 257–267

Woodby D, Carlile D, Hulbert L (2009) Predictive modeling of coral distribution in the Central Aleutian Islands, USA. Mar Ecol Prog Ser 397:227–240

Wright DJ, Pendleton M, Boulware J (2012) ArcGIS Benthic Terrain Modeler (BTM), v. 3.0. Environmental Systems Research Institute, NOAA Coastal Services Center, Massachusetts Office of Coastal Zone Management. esriurl.com/5754

Wynn RB, Huvenne VAI, Le Bas T, et al (2014) Autonomous Underwater Vehicles (AUVs): their past, present and future contributions to the advancement of marine geoscience. Mar Geol 352:451–458

Yesson C, Taylor ML, Tittensor DP, et al (2012) Global habitat suitability of cold-water octocorals. J Biogeogr 39:1278–1292

Zajac RN, Lewis RS, Poppe LJ, et al (2003) Responses of infaunal populations to benthoscape structure and the potential importance of transition zones. Limnol Oceanogr 48:829–842

Cross References

Lo Iacono C, Savini A, Huvenne VAI, et al (this volume) Habitat mapping of cold-water corals in the Mediterranean Sea

Rebesco M, Taviani M (this volume) A turbulent story: Mediterranean contourites and cold-water corals

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Drop Chapter Working with Visual Methods, Comparison Among the French Deep-Sea Canyons

17

Maïa Fourt, Adrien Goujard, and Pierre Chevaldonné

Abstract

The MedSeaCan and CorSeaCan cruises (November 2008 to August 2010) took place along the French continental shelf, from the Spanish border to Monaco (MedSeaCan) and the western coast of Corsica (CorSeaCan). They provided a reference state of the ecosystem in the general context of deep-sea canyons, through direct observations with a remotely operated vehicle and a human occupied vehicle. Both devices collected photographic, video and biological samples, and all have been integrated in the specifically designed ZOOlogical Data Exploitation system working platform (Goujard and Fourt. 31 October 2014). These cruises were the very first attempt to systematically explore French Mediterranean deep-sea canyons. The same data acquisition techniques were used throughout the cruises and the same scientific team treated the data. Extensive remotely operated vehicle exploration appears to be an appropriate method for comparing canyons and better apprehend cold-water coral distribution. Moreover, this method gives the possibility to initiate a monitoring programme of the deep-sea benthos.

Keywords

Submarine canyons · Cold-water corals · Mediterranean · Visual method survey · ZOODEX Platform

The MedSeaCan and CorSeaCan cruises took place from November 2008 to August 2010 along the French continental shelf, from the Spanish border to Monaco (MedSeaCan) and the western coast of Corsica (CorSeaCan) with the aim of exploring the benthic ecosystems associated to deep-sea canyons. The study area spanned from 3°35′ to 9°35′E and from 41°25′ to 43°70′N (Fig. 17.1). The canyons, and nearby rocky banks (geological features rising a few meters from the surrounding flat continental shelf, here generally near the head of canyons) were explored from 34 to 802 m depth, with a main focus between 100 and 600 m. A total of 34 canyons and 9 rocky banks were investigated through 475 km of prospection by 264 dives with a "Super Achille" type remotely operated vehicle (ROV) and 23 with the "Rémora 2000" human occupied vehicle (HOV); mean distance explored in canyons was 12.5 km (min. 1 km, max. 27.5 km). Surveys were all conducted on board the Research Vessel '*Minibex*' which was geolocalised by a submetrical GPS and able to localise the ROV by means of a transponder, providing tracks at a cm level precision.

As a first step, bathymetrical exploration of the canyons was conducted to identify the steepest flanks. Prospection by ROV took place going up the steepest flanks and canyon heads perpendicularly to the isobaths, from 600 m depth to the shelf-break. The ROV video transects covered a ca. 3 m wide section, the ROV speed was non-constant (around 850 m h^{-1}) as it was decided depending on the occurring fauna. All transects were filmed at least by a low definition Pan and Tilt camera cumulating 550 h of video records. A total of 21,900 pictures were taken, including species, habitats, anthropogenic impacts and substrate. Further, HD images were taken when a poorly known species or assemblage was detected, when a species showed a specific behavior and also when areas with high biodiversity were encountered (Fourt et al. 2014). Two laser beams 6 cm apart, provided a scale enabling some sample measurements. Beside the video and photo material, 320 samples were collected (biological samples, substrate, water) by ROV or HOV.

From the video/photo material and from the samples the following information was extracted and quantified: occurrence of taxa, litter, trawling marks and changes in facies

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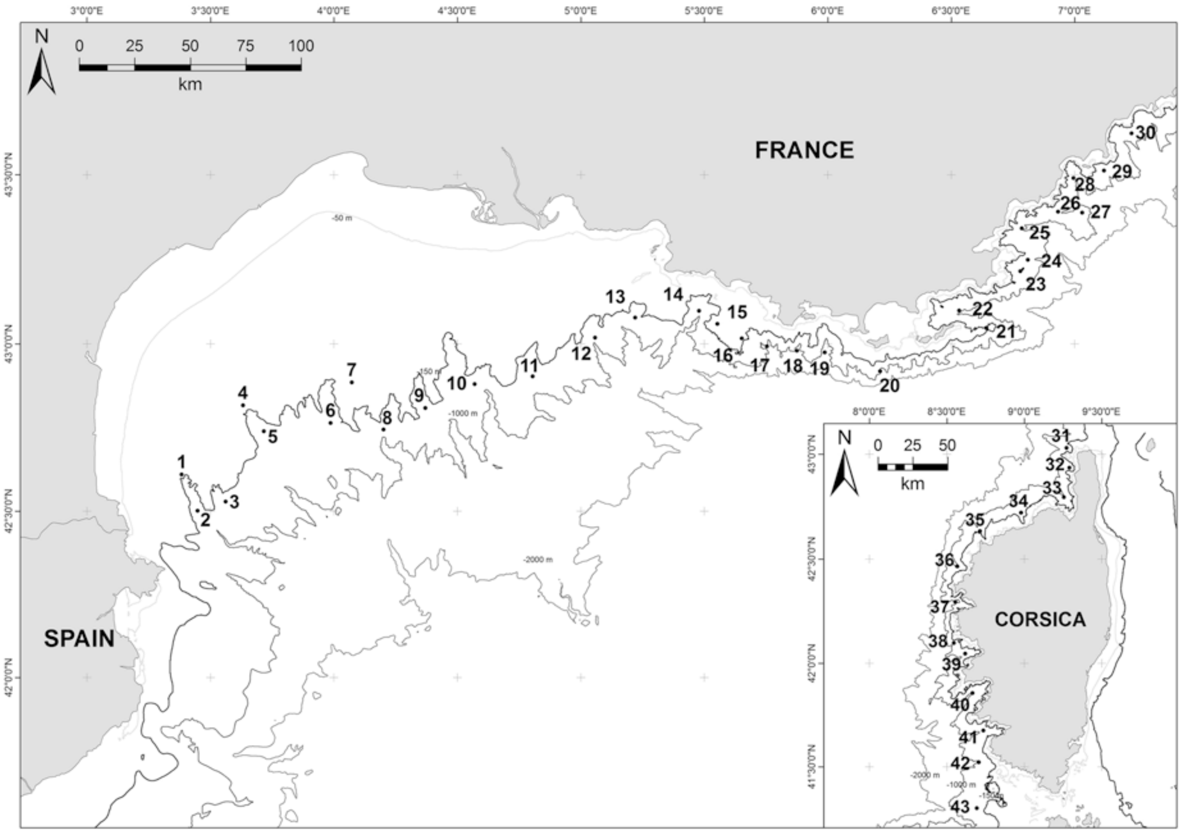

Fig. 17.1 Location of the 43 sites (canyons and rocky banks) explored during the MedSeaCan and CorSeaCan cruises. 1: Lacaze-Duthiers Rocks, 2: Lacaze-Duthiers Canyon, 3: Pruvot Canyon, 4: Sète Rocks, 5: Bourcart Canyon, 6: Marti Canyon, 7: Ichtys Bank, 8: Sète Canyon, 9: Montpellier Canyon, 10: Petit Rhône Canyon, 11: Grand Rhône Canyon, 12: Couronne Canyon, 13: Planier Canyon, 14: Cassidaigne Canyon, 15: Esquine Bank, 16: Blauquières Bank, 17: No-Name Canyon, 18: Sicié Canyon, 19: Toulon Canyon, 20: Porquerolles Canyon, 21: Magaud Bank, 22: Stoechades Canyon, 23: Nioulargue Bank, 24: Pampelonne Canyon, 25: Saint-Tropez Canyon, 26: Dramont Canyon, 27: Méjean Seamount, 28: Cannes Canyon, 29: Juan Canyon, 30: Nice Canyon, 31: North Centuri Canyon, 32: South Centuri Canyon, 33: Saint-Florent Canyon, 34: Ile Rousse Canyon, 35: Calvi Canyon, 36: Galeria Canyon, 37: Porto Canyon, 38: Cargèse Canyon, 39: Sagone Canyon, 40: Ajaccio Canyon, 41: Valinco Canyon, 42: Les Moines Canyon, 43: Asinara Bank

and substrates; each of these observations constituted an "event" along the prospection tracks. The data obtained, was organised and interconnected in the ZOODEX (ZOOlogical Data EXploitation system) working platform (Goujard and Fourt 2014), which provided a friendly environment in which to plot observations and extract information (see Fig. 17.2). ZOODEX was specifically designed for: (1) systematic and homogeneous processing of underwater images along a dive track, (2) storage and linking of data (e.g. photographs, video footage, and samples which offer information on the substrate type, habitat and species identification), (3) easy access and retrieval of the information and, (4) spatial and temporal comparisons (e.g. variability of the bathymetrical distribution of a species within the sites explored). At the core of the system, a Microsoft® Access 2010 database is coupled with a GIS (Geographic Information System). The ZOODEX was used for the post processing of the photographs and video footages. The visual material (photographs and video) was analysed by the same scientific team which highly guarantees a homogeneous treatment of the data. Georeferenced and time-coded events of each dive were described by variables related to: the identification of species, the number of individuals, the nature of the substrate, the presence of given facies of CWCs, qualitative description of the bioturbation (categories used: absent, low, medium, high) and the sessile and mobile biodiversity (categories: low, medium, high), the presence of waste, plankton occurrence, trawl marks, the collection of a biological, substrate or water sample, as well as any other potential comment or observation from the observers. Consequently, each event is contextualised and linked to a dive, a video sequence and to one or several photographs (when available) as shown in Fig. 17.2. Species identification was conducted using the photographic and video material, with the support of a group of 25 specialists in taxonomy; moreover the identification was occasionally performed using biological samples when available. The ZOODEX allows to display the information, images and maps, using different filters such as species names, depth range, sites, habitats, and substrate types as possible entries.

The surveys presented in this chapter covered only a few CWC hotspots. These included live *Lophelia pertusa* occurring only in the Lacaze-Duthiers canyon between 250 and 535 m depth on rocky cliffs, where it formed dense patches with *Madrepora oculata*, but also on silted slopes. In Cassidaigne canyon, large areas were covered by *M. oculata* in a particularly shallow context from 196 to 250 m, along with circalittoral species such as the gorgonian *Paramuricea clavata*. Some isolated colonies of *M. oculata* were also spotted in places where the species was previously unknown such as Bourcart, Sicié and Nice canyons. Although Corsican canyons did not show any of these two CWC species, Les Moines canyon revealed marl walls unexpectedly covered by large populations of the solitary deep-sea coral *Desmophyllum dianthus* between 453 and 617 m (Fig. 17.3). In continental canyons, *D. dianthus* had only been documented as isolated specimens among the other CWCs, however recently a large facies of *D. dianthus* has been discovered in La Fonera can-

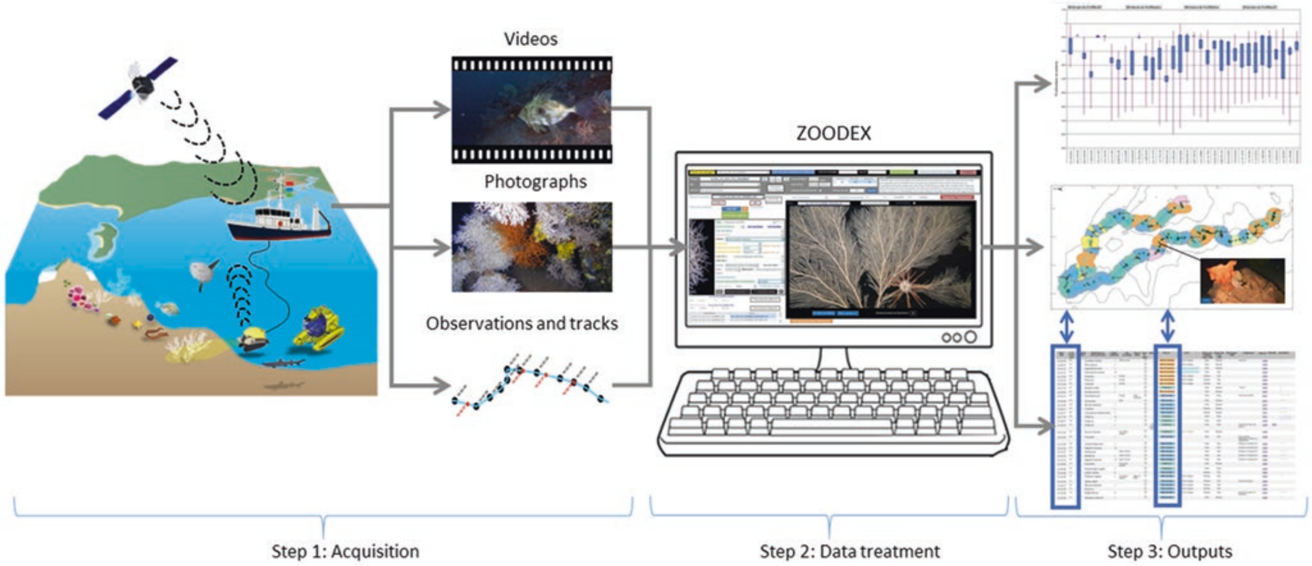

Fig. 17.2 Schematic view of the methodology used for the MedSeaCan and CorSeaCan research cruises. Step 1 consists in the data acquisition including the geolocalised video and photographs; Step 2 includes the data treatment with the ZOODEX platform; Step 3 displays outputs such as (top to bottom): bathymetrical distribution of a species at sites where it occurs, interactive track map with linked events, substrates and photos, table of time-coded observations for a dive with associated information

Fig. 17.3 *Desmophyllum dianthus* covering a marl wall at Les Moines deep-sea canyon, western Corsica, 476 m. The carapace of the squat lobster *Munida* sp. measures about 3 cm. (Photo COMEX/Agence française pour la biodiversité - campagne CorSeaCan)

yon (Catalan margin) (see Aymà et al., this volume; Lastras et al., this volume). In Les Moines canyon, associated fauna consisted of deep-sea oysters *Neopycnodonte zibrowii* (occasionally observed alive), carnivorous sponges *Cladorhiza* cf. *abyssicola* and *Lycopodina hypogea*, as well as teleost fish such as *Benthocometes robustus* (see images in Fourt et al. 2017).

Using an ROV combining a primary low definition continuous video recording together with on-demand HD video/photo acquisition, allows covering and documenting extended geographic areas in a fairly short time, while obtaining high quality images of locations and/or specimens. In the specific case of CWCs, this system offers the possibility to precisely document their occurrence, information that is essential for conservation and management plans.

Furthermore, identifying reference points at specific locations accurately positioned along a track, allows returning to sites and even to specific colonies years later. Some locations were indeed revisited in 2014, 5 years after the MedSeaCan cruises at the Cassidaigne canyon and the Esquine bank (now part of the "Calanques National Park"). Exactly following a past ROV track based only on geographical positioning appeared too complex. However, it was possible to follow a path plotted with remarkable reference points originating from the initial ROV track. Revisiting the same sites demonstrated that the National Park enforcement of a fishery ban in the area appeared effective: fishing lines and ropes, the main anthropogenic impact initially observed on the CWCs of Cassidaigne canyon, had not increase in number after 5 years of protection. In 2014, an experimental 3D reconstruction of the CWC reef area in Cassidaigne canyon, allowed to display the location and orientation of *M. oculata* colonies at a very fine scale, but also to count colonies and sort them in size classes (Fourt et al. 2016).

The data collected during the cruises and processed in the ZOODEX, supply information on spatial and bathymetrical distribution of species, the occurrence and composition of the main megabenthic assemblages as well as on their surrounding geomorphological context. This approach allows a rapid prospection of large areas as well as, for instance, to localise and characterise CWCs, offering an evaluation of the state of conservation of the communities. Further, this method also offers the possibility to return to specific locations and specific individuals (e.g. CWC colonies) to evaluate potential changes over time. The 3D reconstruction of targeted populations may also be appropriate for the survey of population dynamics in selected specific areas.

Acknowledgements We are grateful to the "Agence des Aires Marines Protégées" (now "Agence française pour la biodiversité") for supporting the cruises and their data treatment. We also thank the Comex SA team and the MedSeaCan and CorSeaCan scientific teams.

References

Fourt M, Goujard A, Pérez T, et al (2014) French Mediterranean submarine canyons and deep rocky banks: a regional view for adapted conservation measures. In: Langar H, Bouafif C, Ouerghi A (eds) Proceedings of the 1st Mediterranean symposium on the conservation of dark habitats, Portoroz, Slovenia, 31 October 2014. RAC/SPA Publ. Tunis, pp 33–38

Fourt M, Goujard A, Seguin E, et al (2016) Proposition d'une méthode de suivi temporel 2D en zone profonde & Apport de l'imagerie 3D à la description et au suivi temporel des communautés de grottes sous-marines et des roches profondes. Partenariat «Grottes 3D & MedSeaCan 3D». IMBE-CNRS/GIS Posidonie/Comex SA/Parc National des Calanques/Agence des Aires Marines Protégées No. Rapport Final. Marseille, 114 p

Fourt M, Goujard A, Pérez T, et al (2017) Guide de la faune profonde de la mer Méditerranée. Museum National d'Histoire Naturelle, Paris, 184 p

Goujard A, Fourt M (2014) The information system ZOODEX, a tool for the treatment of image data. In: Langar H, Bouafif C, Ouerghi A (eds) Proceedings of the 1st Mediterranean symposium on the conservation of dark habitats, Portoroz, Slovenia, 31 October 2014. RAC/SPA Publ., Tunis, pp 71–72

Cross References

Aymà A, Aguzzi J, Canals M, et al (this volume) Occurrence of living cold-water corals at large depths within submarine canyons of the northwestern Mediterranean Sea

Lastras G, Sanchez-Vidal A, Canals M (this volume) A cold-water coral habitat in La Fonera submarine canyon, northwestern Mediterranean Sea

18

Review of the Circulation and Characteristics of Intermediate Water Masses of the Mediterranean: Implications for Cold-Water Coral Habitats

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Pierre Testor, Laurent Mortier, Anthony Bosse,
and Xavier du Madron

Abstract

This chapter describes the main features of the circulation and properties of the intermediate water masses of the Mediterranean. Interaction with other water masses is also briefly summarised. Both observational and numerical studies described in the literature are used, as well as some more recent, unpublished data sets. It is shown that the main water mass important to cold-water coral habitats is the Levantine Intermediate Water which forms in the Levantine Sea, Eastern Mediterranean and spreads throughout the entire Mediterranean before leaving via the Gibraltar Strait. This pathway is described as well as the expected temperature and salinity along that pathway. Current speed regimes are estimated from the few studies that exist.

Keywords

Mediterranean sea · Hydrography · Circulation · Intermediate water · Deep water · Cold-water corals

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18.1 Introduction

In this paper, the current understanding of the flow and characteristics of intermediate Mediterranean Sea water masses is described. The motivation to include oceanographic studies in this book is that ocean flows and water properties establish the basic environmental conditions to which sessile organisms are subjected. If conditions are favorable, in terms of temperature, salinity, dissolved oxygen, and organic matter, all of which are maintained adequately by the currents, then cold-water corals (CWC) can thrive. Johnston and Larson (this volume) explain how the functionality and connectivity of CWC are driven both by physical and biological processes, merged through biophysical modeling. Before robust results can be derived from biophysical modeling, the performance of the flow modules must be evaluated against the existing observational and numerical bodies of work presented in this chapter.

In the Mediterranean, as will be described below, evaporation exceeds precipitation when averaged over the basin, and the "reverse estuarine" circulation that results implies a net inflow into the basin (through the Gibraltar Straits). This low input of river runoff, combined with the vertical stability of the thermohaline circulation, make the waters relatively poor in nutrients. Thus, any process that injects nutrients into the ocean, such as deep or intermediate water formation, dense water cascades, or downwelling events around eddies, will control the vitality of the ecosystem along the path of the currents carrying the signal of these processes. Therefore, the conditions described here provide context for the regions where CWC have been discovered. Taviani et al. (2017) and Taviani et al. (2011) (and references therein) identified five discrete provinces: the Southwestern Adriatic, the Northern Ionian, the Sicily Channel, the Alborán Sea, and the Catalan-Provençal-Ligurian canyons, and more recently the Nora

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canyon, offshore Sardinia. Live CWCs have also been found in other places such as scleractinian corals on Eratosthenes Seamount (Galil and Zibrowius 1998; Mitchell et al. 2013), and on the Anaximenes ridge summit south of Turkey, black *Antipathes* coral and occasional *Desmophyllum* corals were observed (Raineault et al. 2013). Epibenthic communities on the Anaxagoras seamount hosted cold-water octocorals (CWCs) and scleractinian corals (Shank et al. 2011). There is new evidence of CWC communities in the Cassidaigne Canyon on the Provençal east of the Gulf of Lion between Marseille and Toulon at depths of the intermediate water (around 500 m) (Fabri et al. 2017). Particular emphasis will be given to flow and water properties at the depths at which CWC are known to thrive: 350–600 m (Taviani et al. 2011), which corresponds to intermediate water masses. A map of the regions where these ocean depths are found is shown in Fig. 18.1, along with the confirmed CWC discoveries above.

Deep water masses will also be briefly described since they are directly linked to the intermediate water through mixing. Near-surface layers are also briefly described since they influence the production and volume flux of the intermediate water masses. Also, in certain places, during dense water formation events, the seafloor may have direct contact with the surface layer, or indirectly through the lateral spreading or downward cascading of these newly-formed waters.

After a description of the approach taken, the paper presents processes related to the spotty, intermittent intermediate water mass formation and transformation. The identifying characteristics, pathways and flow speeds of the Levantine Intermediate Water (LIW) are discussed in the final part of the paper, in subsections for the eastern and western Mediterranean, respectively. The reader will recognise the preponderance of information for the eastern Mediterranean characteristics and flows. One of the reasons for this is the present lack of a systematic review of the LIW in the eastern basin. Besides being of interest in its own right, such a review may provide insight to the apparent low rates of recovery of CWC habitats in the eastern basin compared to the western basin after pan-Mediterranean depletion in the late Pleistocene (Taviani et al. 2011, Taviani, this volume; Vertino et al., this volume). It may help answer the question: "how do today's conditions compare to those of the early Holocene?"

18.2 Approach

This study focuses on the current understanding of the present-day characteristics and circulation, water mass pathways and currents of the Mediterranean below the surface layer and above the deep layer. Because of the large spatial and temporal gaps in the observational data sets available, in particular for subsurface layers, this understanding is based on a variety of sources. Firstly, historical observations, going back to the early to mid twentieth century provide a low resolution set of static views. Naturally, changes have occurred over this time period, many of them probably not known to us because of the sparseness of the observations. In order to piece together a coherent structure, however, we must glean the essential information from these data sets and make conclusions about what is a reasonable mean state.

Newer, unpublished, data sets certainly exist, and a few examples related to the authors' work are presented below. In general, these include CTD cruises, eXpendable BathyThermographs (XBTs), profiling floats, gliders and a few fixed point stations. These platforms measure

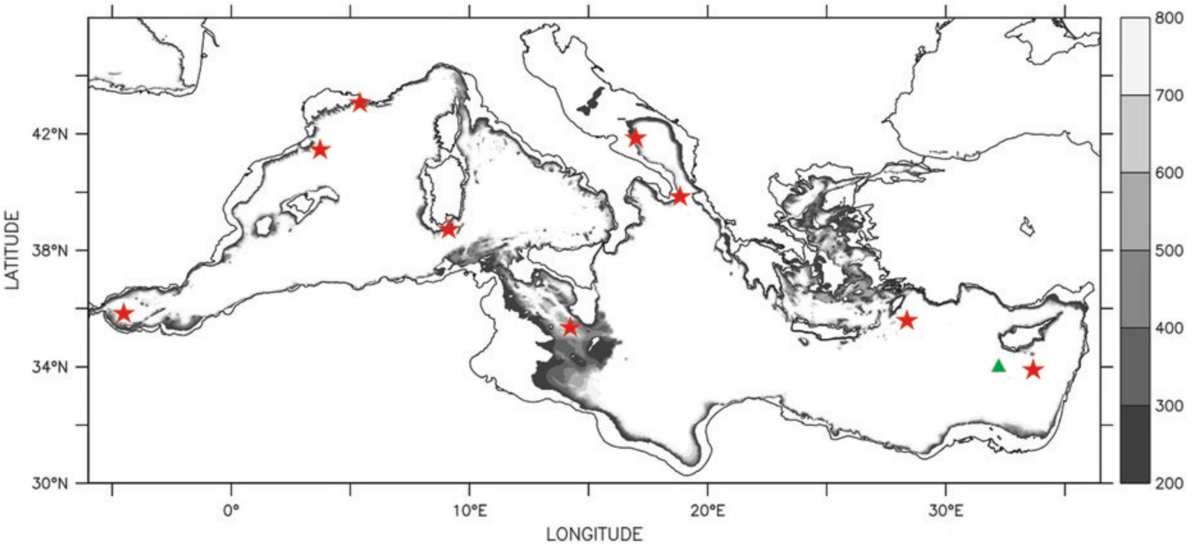


Fig. 18.1 Mediterranean basin and depths at which cold-water corals may be found (dark grey). Stars indicate known locations of living cold-water corals (see references in text). Green triangle is position of CSNet mooring (data in Fig. 18.10). (Source of bathymetry is EMODnet 2017)

temperature, conductivity (except XBT), and pressure. In many cases, dissolved oxygen is also measured, but chlorophyll, nutrient, and inorganic carbon data are sparse. Very few platforms measure properties below 1000 m, and even fewer measure currents directly (at any depth), making characterisation of deep flows extremely difficult. For this reason, currents are usually estimated using the assumption of geostrophic balance, which is wrought with pitfalls in the Mediterranean, in particular because of an unknown reference at the typical maximum observation depth. It should be noted that satellite altimetry (dynamic height and Sea Level Anomaly: SLA) can also aid in calculating ocean currents in a depth-averaged (barotropic) sense, but the intermediate flow may not coincide because of stratification (baroclinic flows). In some regions, these complementary observation platforms have been organised into observatories which operate for extended periods, often providing near real-time information, and associated prediction and assimilation products. For example, the MOOSE in France captured processes related to deep and intermediate water formation, as in Houpert et al. (2016) and Bosse et al. (2016). Where relevant, these have been identified as a potential source of information that could be analysed further to enhance the present, primarily retrospective, study.

One exception to the lack of observable changes is the striking example of the shift in the formation of the Eastern Mediterranean Deep Water (EMDW), in the 1990s, and later the Western Mediterranean Deep Water (WMDW), both of which indirectly affect the overlying intermediate water properties (see below). Another example of observed change is the ongoing change in salinity of the Mediterranean (see Skliris, this volume). Despite these exceptions, most observational data sets are inadequate to describe the spatial or temporal variations, especially in the intermediate layer which is expected (and sometimes observed) to be tremendously complex. Surface layer variability is likely even more complex, but remote sensing and surface drifting platforms have provided a realistic glimpse (Menna et al. 2012; Poulain et al. 2012; Rio et al. 2014).

For these reasons, a second source of information is often used: numerical models and their associated re-analysis data sets. While theoretical considerations and hydrodynamic simulations of varying complexity help in understanding the important processes of intermediate water mass transformation and spreading, and can even provide accurate estimates of water mass production rates and exchanges through straits, they are notoriously bad at prediction or reconstruction of the true ocean state. Nevertheless, through the merging of observational data sets with dynamic formalisms (data assimilation), realistic ocean state estimates can be made and are examined here in addition to published and ongoing observational studies and a thorough review of the Mediterranean structure and dynamics from a 20-year reanalysis from Pinardi et al. (2015).

In this chapter, the current steady-state view emerging from the literature is described, while acknowledging that this is a gross simplification, constantly violated by the rapid transients and long-term changes mentioned above. Despite these violations, the steady-state view is useful as a starting point upon which to base a detailed discussion of cross-basin interactions and to understand the relevant processes and likely ways that said transients spread around the basin.

A summary of what is known about the water masses and formation processes is provided in the next section, after which the spreading and pathways of those water masses are discussed.

18.3 Water Masses

By far, the dominant water mass at depths of 150–400 m and 350–600 m in the eastern and western Mediterranean (respectively) is the Levantine Intermediate Water (LIW). In fact, it is the most voluminous water mass produced in the Mediterranean (Skliris 2014; Lascaratos 1993). The LIW is found throughout the Mediterranean, not just the Levantine region in which it forms (Fig. 18.2). Other intermediate water masses include the Western Intermediate Water (WIW) formed by wintertime cooling of Atlantic Water (AW) in the Western Mediterranean and the Cretan Intermediate Water (CIW) formed in winter time and mostly trapped in the Aegean Sea. The CIW was first identified by Schlitzer et al. (1991) and defined to be Aegean water that spreads out into the Levantine and Ionian at 500–1200 m, i.e., below LIW. These two intermediate waters are produced in much lower quantities and their pathways are not easily identified (Millot and Taupier-Letage 2005a). However, it has been shown by Millot (2013) that the Aegean/Cretan waters contribute significantly to what some call the LIW in the western basin, so the name Eastern Intermediate Water (EIW) was suggested.

18.3.1 The Functioning of the Mediterranean Sea

Future climatic changes will strongly affect the so-called climatic hot-spots regions, and the Mediterranean region is one of them. Its climate is mainly influenced by the presence of the sea, a “miniature ocean” in which typical oceanographic processes of the global ocean occur with a much shorter turnover timescale (one order of magnitude less that the global ocean’s one). The expected rapid response of this water body to the variable atmospheric forcings is documented by a considerable amount of studies about changes in Mediterranean water mass properties and rates of Dense Water Formation (DWF) (e.g., Bethoux and Gentili 1999; Rixen et al. 2005; Schroeder et al. 2006, 2008).

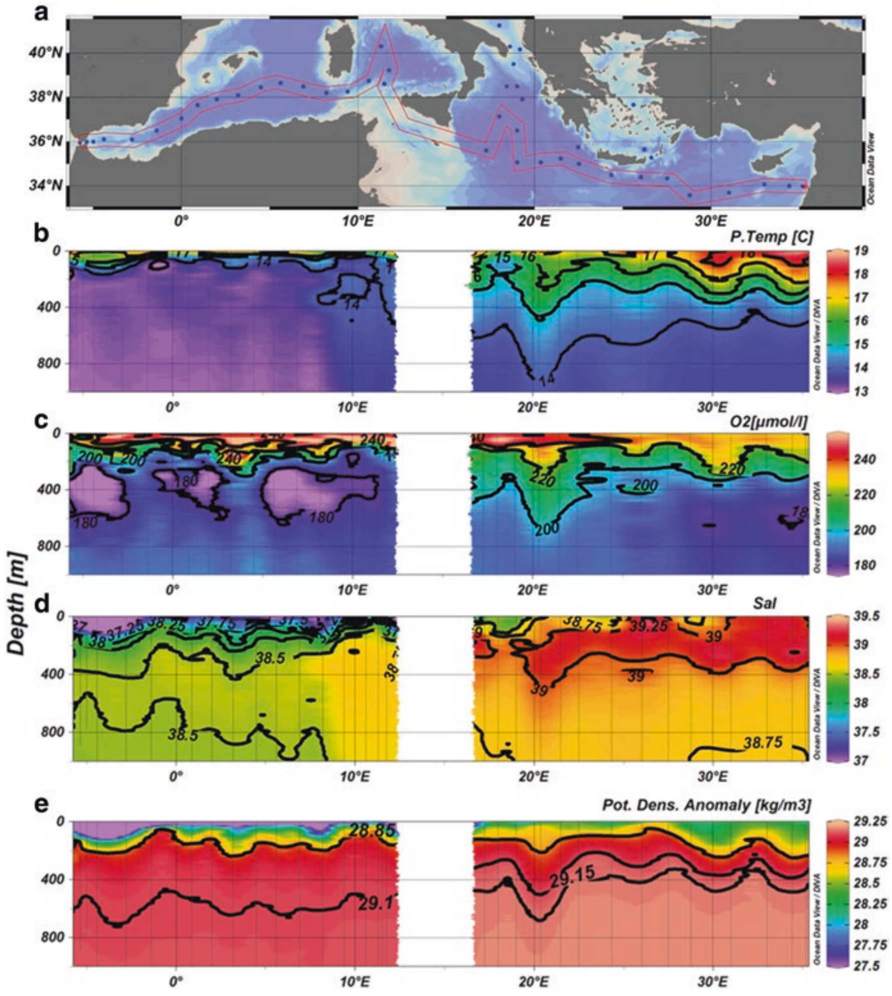


Fig. 18.2 Vertical section along trans-Mediterranean section (**a**) of (**b**) potential temperature, (**c**) dissolved oxygen, (**d**) salinity, and (**e**) potential density anomaly. Levantine Intermediate Water layer growing in thickness and deepening as it spreads from East to West (right to left) indicated by potential density anomaly between 28.85 and 29.1 kg m^{-3}. (Source of data: Tanhua et al. 2013)

There are three main circulation cells: a pan-Mediterranean one, an Eastern Mediterranean one, and a Western Mediterranean one (the latter two separated by the Sicily Channel with a sill depth of about 500 m). The uppermost one is open and brings AW: 15 °C, 36.2) in through the Strait of Gibraltar (sill depth of about 300 m) to make up for the net evaporative losses of the basin. Other masses not formed in the basin include the Black Sea Water and river input. These are restricted to the surface and are not directly relevant to CWC habitats. They do, however, have an effect on the formation of the deeper water masses. Intermediate water with properties of approximately (13.5 °C, 38.4) also exits Gibraltar in a bottom layer (Tsimplis and Bryden 2000). The incoming AW is modified by mixing and air-sea fluxes as it traverses the basin, and some of it leaves the surface layer through densification in both east and west "closed" overturning cells (relatively cold, salty water sinks in sporadic events at particular locations to particular depths). The displaced deeper waters upwell in much broader, slower processes over each basin, then mix with intermediate waters that have formed through less intense densification, which traverse back to the west in complicated ways. Finally, the uppermost part of this intermediate layer, a form of the LIW, exits the Mediterranean in the bottom layer at Gibraltar. An excellent summary of the above with references is provided by Malanotte-Rizzoli et al. (2014) as well as Tsimplis et al. (2006). A schematic is shown in Fig. 18.3. A summary of Mediterranean deep and intermediate water formation is provided next.

18.3.2 Deep Water Formation

The formation of deep water is briefly summarised here in order to understand the intermediate water properties and pathways. There are two main types of deep water in the Mediterranean: Western Mediterranean Deep Water (WMDW) and Eastern Mediterranean Deep Water (EMDW). Each water mass accumulates at depths much greater than the sill depths separating the basins from each other and the Atlantic. The water masses spread along the bottom, mixing with the surroundings which modifies the deep layers.

The WMDW forms in the Gulf of Lions nearly every February–March after intense surface buoyancy loss (evaporation and cooling via latent and sensible means) is applied

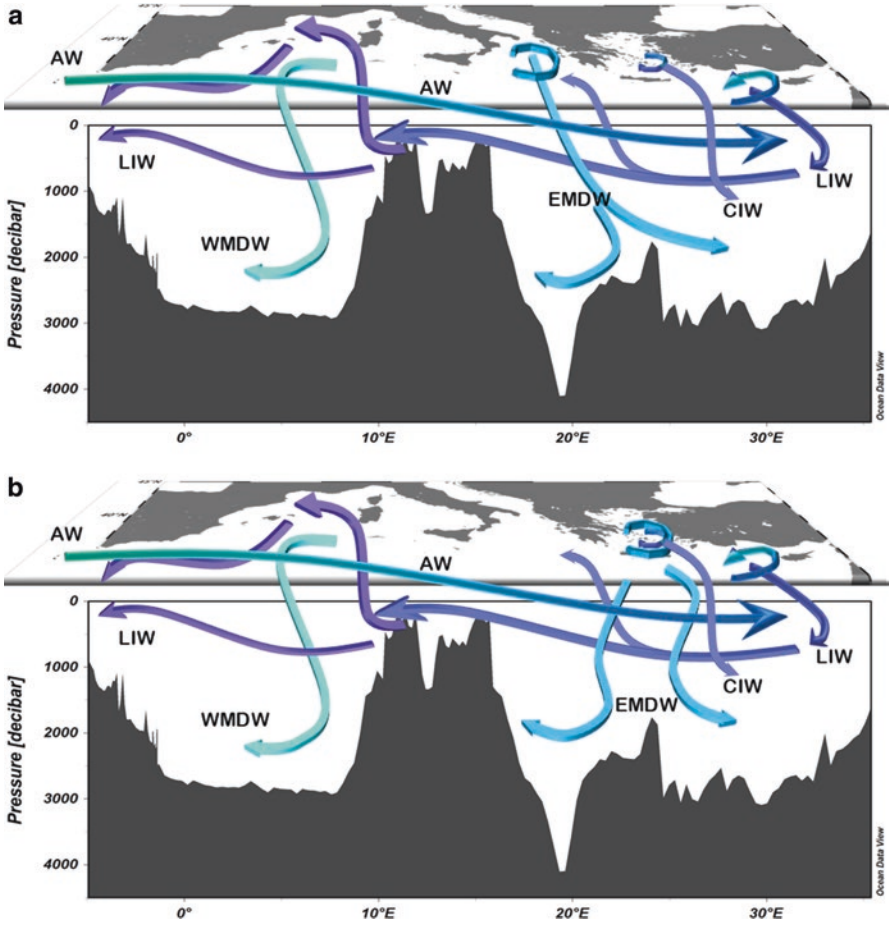


Fig. 18.3 (**a**) The thermohaline of the Mediterranean in the time before and after and (**b**) during the Eastern Mediterranean Transient. (Modified from Tsimplis et al. 2006, figures a and b © Daniel Hayes)

to pre-conditioned waters in the open sea. Strong, destabilising buoyancy loss occurs during occasions with high winds, which also mix the surface layer mechanically. If the surface fluxes are strong, frequent and/or long enough for the given water column properties, WMDW is produced. If not, an intermediate water mass is produced: Western Intermediate Water (WIW). The WIW is cooler and fresher than the LIW that arrives from the eastern Mediterranean. The presence of AW with salinity higher than normal near the surface and the underlying LIW contributes to more efficient production of these two types of water, as less buoyancy loss is required to produce a denser water mass. Therefore, as the AW and LIW properties vary, the volume and density of the water mass formed varies interannually. In recent years WMDW has become progressively warmer and saltier (Schroeder et al. 2010; Houpert et al. 2016). Some years the ocean bottom is reached (about 2400 m) and some years lesser depths are reached (about 1500 m). Dense water production on the shelf can also result in cascading dense water plumes reaching depths from 200 to 2000 m or more (Canals et al. 2006; Durrieu de Madron et al. 2005, 2013).

The EMDW forms either in the southern Adriatic Sea (Fig. 18.3a) or the Aegean Sea (Fig. 18.3b). Evidence points to decadal variability of a "precarious balance" in the source location of EMDW (Roether et al. 2007). In 1989, deep and intermediate water from the Cretan Sea (CDW and CIW) were dense enough to sink to the depths of the Levantine for the first time in instrumental records (Theocharis et al. 1999). Before that, CDW left the Cretan Sea and settled to depths below the LIW, but above EMDW of Adriatic origin. The formation of EMDW in the Adriatic is influenced by the LIW properties and the dense shelf water of the northern Adriatic that cascades along the west coast to mix with the LIW in the South Adriatic cyclonic gyre. This Adriatic Deep Water (ADW) spreads into the depths of the Ionian and Levantine Seas. In the years from 1989 to 1992, the Cretan Sea dominated the formation of EMDW, and this may be explained by an oscillation of the Ionian Circulation which feeds more or less LIW into the southern Adriatic (Borzelli et al. 2009; Gačić et al. 2010, 2011; Theocharis et al. 2014). Harsh weather conditions in the northern Adriatic can trigger the formation and spreading of extremely dense EMDW. See Bensi et al. (2013) for an example in 2012. In all cases of deep water formation, the presence and properties of LIW play a critical part (Wu and Haines 1996; Skliris and Lascaratos 2004).

18.3.3 Levantine Intermediate Water Formation

Levantine Intermediate Water (LIW) is usually defined in the eastern Mediterranean by a potential density anomaly σ_θ of 28.85–29.10 kg m^{-3} (temperature of 15–16 °C and salinity 38.95–39.05) (Lascaratos et al. 1993). Taken together, historical studies (Table 1 of Lascaratos et al. 1993) show wider ranges (28.85–29.15, 14.6–16.4 °C, 38.85–39.15); LIW resides primarily at depths between 150 and 400 m, although naturally it is found at and near the surface in regions in which it is formed and descends as it spreads to other regions. It has been seen as deep as 500 m at the base of the anticyclonic Cyprus Eddy (Hayes et al. 2016). It can be seen as a layer of salinity maximum in those depths throughout the entire Mediterranean, although of different salinity and temperature because of mixing during its spread away from the formation region.

This water mass most likely forms in the Rhodes Gyre (Nielsen 1912; Lacombe and Tchernia 1960; Wüst 1961; Ovchinnikov 1984; Schlitzer et al. 1991; Lascaratos and Nittis 1998), although many authors have suggested other locations (Southern Levantine: Morcos 1972; anticyclonic eddies: Brenner et al. 1991; Northern Levantine: Sur et al. 1992; LIWEX Group 2003). Unfortunately, observations are insufficient to support claims as to the dominance and persistence of the various sources. Rare, direct observations were described in LIWEX Group (2003) when in fact deep water formation was observed in the Rhodes Gyre. In that study, LIW was formed by simple cooling and evaporation of the surface mixed layer, which deepened gradually to 100 m. Since direct observations are scarce, various numerical and reanalysis studies have been carried out. In numerical simulations (Lascaratos and Nittis 1998; Nittis and Lascaratos 1998), mixing to 400 m was simulated in the Rhodes Gyre, favored because the upward-doming isopycnals of the cyclonic gyre reduced the surface density and intermediate stability of the water column underlying the mixed layer. This is believed to be the primary mechanism for LIW formation. A short summary of the above can also be found in Schroeder et al. (2012).

A warmer and drier regional climate in the EMED favours the formation of warmer and saltier intermediate layer, given that LIW is formed by transformation (densification due to evaporation and cooling) and sinking of Levantine Surface Water (LSW). The LSW originates from the modification of AW along its path through the Ionian and the Levantine, where it becomes particularly warm and salty. Hence the climatic conditions along this path are likely to be crucial in eventually determine the heat and salt content of LIW. In this regard, it is worth noting that Cook et al. (2016) reports a recent drought in the Levant (since 1998) which is the driest in the past 500 years. Schroeder et al. (2017) show a change in net evaporation (evaporation minus precipitation, or E-P) in the whole southern part of the EMED, which significantly increased between 1990–1999 and 2000–2015 (the sign of the E-P anomaly time series, from 1980 to 2016, switched in 1998 from negative to positive). So, a prolonged intensification of net evaporation is affecting the region where the eastward pathway of the LSW occurs: this strongly modified LSW will later on transform into a saltier and warmer LIW.

The role of LIW is crucial in determining the amount and characteristics of the deep waters (Wu and Haines 1996) that are formed in and ventilate both the EMED and the WMED. These waters are formed with properties that are mainly determined by the conditions at surface (air-sea exchanges) and the hydrographic preconditioning, i.e. heat and salt contents, of the surface and intermediate waters that contribute to the formation of the deep ones (Schroeder et al. 2010). Thus, changes in air-sea fluxes (of heat and freshwater), interior ocean circulation and mixing can alter the signature of the new deep waters (in terms of T, S, equilibrium depth, volume and layer thickness).

18.4 Water Mass Characteristics and Flows

18.4.1 Eastern Mediterranean

Various mechanisms and locations may generate LIW in the Eastern Mediterranean in winter, which then spreads throughout the basin, eventually leaving through the Sicily Channel, possibly after one or more circuits in the basin. The sill depth at the Sicily Channel is just over 500 m, but the channel is only 35 km wide below 200 m depth. The path this water follows through the basin is not well documented, with most of the available observations sparsely distributed in time and space. These have been supplemented by and compared with numerical simulations, and have been incorporated in re-analyses (models that assimilate historical data). After formation, lateral (isopycnal) spreading and mixing occur, modifying the initial T-S properties. Both mean flow and eddies transport LIW throughout the eastern basin. In some cases, LIW is a distinct, homogeneous layer (thermostad in the core of an eddy), but in other cases it is not, and both mean flow and eddy flux can exist at the same time.

While there are a few early hydrographic studies related to the formation of deep and intermediate water (see above), they do not reveal much information on the dispersion pathways because they do not cover large regions synoptically, nor with statistical significance. The intermediate circulation in the eastern Mediterranean was first estimated by Ovchinnikov (1966). Based on hydrographic cruises, he concluded that the intermediate circulation is a less-intense version of the surface circulation (which cannot be true everywhere and at least not at Sicily and Gibraltar Straits or there would be no balance with the surface Atlantic Water inflow). Gerges (1977) uses a diagnostic model to conclude the intermediate layers of the Levantine Sea move cyclonically around the basin, as was believed to be the case near the surface. In that same study, another cyclonic gyre is illustrated in the Ionian, while there is a weak exchange at the Sicily Channel. Malanotte-Rizzoli and Hecht (1988) summarise the state of knowledge before mesoscale effects were sufficiently observed. Of note is the study of Wüst (1961) showing LIW flowing westwards from the formation region (Rhodes Gyre) and mixing with layers above/below. Other studies show that the salinity maximum is distinct enough to be observed in the Ionian, the Adriatic, and parts of the western Mediterranean with a core value of 38.9 at the Cretan Passage and 38.7 at the Sicily Channel (Malanotte-Rizzoli and Hecht 1988). The dispersion of LIW in the Levantine Sea was described in detail for the first time as part of an Israeli cruise program called Marine Climate in the period 1979–1984 (Hecht et al. 1988), with the new picture emerging that LIW spatial distribution in the Levantine was correlated with mesoscale variability, with LIW often trapped inside anticyclonic eddies. Scales of features resolved were 60–100 km. The fact that mesoscale variability dominated the spreading of LIW within the entire eastern basin was revealed by the POEM cruises as described by Özsoy et al. (1989, 1991). Ozturgut (1976), and Ovchinnikov (1984) also link LIW formation to mesoscale processes, which prove to be a critical aspect of the eastern Mediterranean.

Based on POEM cruises in March of 1989, deep excursions of the 15 °C isotherm (to 500 m) were shown away from the Rhodes Gyre (Özsoy et al. 1993), while near the center of the gyre, very shallow depths of 10 m were observed. These excursions were associated with anticyclonic eddies containing LIW. From 1985 to 1990, dynamic height maps for each POEM cruise at 300 dbar relative to 800 dbar showed long-lived (months to years) anticyclonic eddies intermingled with a weaker cyclonic circulation of the Rhodes Gyre.

Schlitzer et al. (1991) describe the westward spreading and modification of LIW away from what appears to be the source region in the northern Levantine from a ship-based tracer and hydrography experiment. Substantial mixing with water below 500 m is noted, before passing the Sicily Channel. The LIWEX Group (2003), who found that subsequent to Levantine deep and intermediate water mass formation in the Rhodes Gyre and northern Levantine (respectively), LIW subducts under the low density layers of the surface and spreads along isopycnal surfaces. Based on grids of temperature, salinity, and oxygen profiles, it is claimed that one pathway is to the west, into the Aegean and Cretan Seas, with some of the LIW continuing around the cyclonic gyre, heading back east after passing Crete. A second pathway is directly south from the formation region, opposing the cyclonic flow of the gyre, and possibly entering an open sea eddy (Fig. 18.4). Attempts to synthesise available hydrographic observations to estimate LIW pathways were made by Millot and Taupier-Letage (2005a), who show only a few indicative arrows in the eastern Mediterranean. The only suggested direct paths of LIW are the ones from the main formation area in the Rhodes Gyre towards the west along the northern edges of the Cretan Passage and Ionian Seas (Millot and Taupier-Letage 2005a). Other pathways of LIW mentioned in the latter study are the entrainment into wind-induced eddies along the northern coast (Ierapetra and Pelops), the entry of some LIW into the southern Adriatic, and the recirculation at the Sicily Channel.

All of these studies are affected by the same issue: the observational data were of limited spatial and temporal

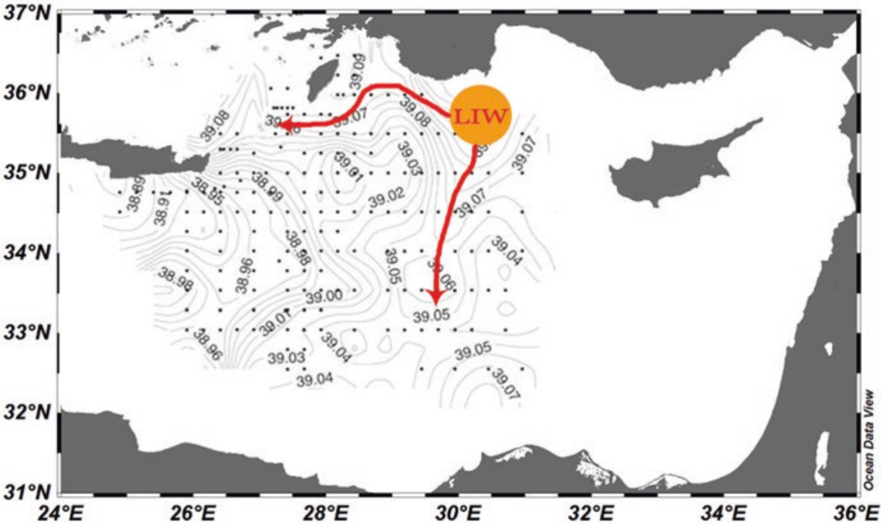


Fig. 18.4 Salinity at potential density anomaly of 29.0 kg m^{-3} from the LIWEX 1995 cruise. Orange oval indicates the region of LIW formation (Northern Levantine). Red arrows indicate likely pathways based on salinity gradient. (Adapted from LIWEX group 2003)

extent and spatial resolution was very low. It is very likely that subbasin (30–150 km), meso- scale (10–30 km) and smaller processes are responsible for the spreading of intermediate water, but were not resolved, or did not occur during the short time of the particular cruise. Further studies have published maps based on model simulations (Wu and Haines 1996; Lascaratos and Nittis 1998) and re-analysis (Pinardi et al. 2015), which solve the problem of resolution and extent, but tend to raise more questions than they answer because of the complex eddy fields and decadal variability revealed. In particular, the model results of Wu and Haines (1996) provide deep insights into the dispersal of LIW throughout the Mediterranean. They find that the LIW formed in their model (prescribed in the Rhodes Gyre by surface relaxation) breaks up in baroclinic eddies (stratified flow instabilities) which can move eastward against the direction of mean flow. The net effect of the eddies could be to transfer LIW north of Cyprus, southward along the coast of Lebanon and Israel (Plate 3 of Wu and Haines 1996). A mean flow to the west out of the gyre is also seen (as in previous modeling studies that did not resolve eddies such as Haines and Wu 1995). This branch enters and leaves the Aegean, joining the Ionian basin. Some of this branch also recirculates eastward in the Mersa-Matruh Gyre, and possibly back to the Rhodes Gyre. The idea of mean and time-varying transports was proven to be valuable in Stratford and Williams (1997), who show that tracers released in the Rhodes Gyre simulated by the GCM of Wu and Haines (1996) not only spread westward into the Aegean under the mean flow, but that eddy fluxes were required to account for the flow southward and eastward. This is also described by Lascaratos and Nittis (1998). Additional evidence for LIW pathways can be seen from the 120-year model run of Wu and Haines (1998). By mapping the mean salinity on the LIW density level (28.95 kg m^{-3}) from the last 20 years, it is possible to discern one branch exiting the Aegean and moving into the Ionian, and eventually the Adriatic, while another branch moves south out of the Rhodes Gyre, then west along the southern Mediterranean coast to the Sicily Channel. There is also an indication of a transport of LIW towards the east out of the Rhodes Gyre (Fig. 18.5).

In a recent numerical reanalysis experiment (Pinardi et al. 2015), the intermediate layer circulation (200–300 m) was computed based on a mean of monthly means over the years 1987–2007 (Fig. 18.6). However, this can be misleading since actual transport of LIW can occur against the mean flow due to time varying flow (Stratford and Williams 1997). In addition, flow in the ocean more closely moves along density layers, not depth layers. For these reasons, the salinity and currents on the 28.95 kg m^{-3} potential density anomaly surface from the Copernicus Marine Environment Monitoring Service (CMEMS 2017) daily model re-analysis output are also computed here. Averages of instantaneous fields from every 10 days of 2016 show the spreading of LIW in many directions away from the south of Crete (Fig. 18.6). This is suggested to be the region where LIW was most recently formed as it has the highest salinities. A branch spreading eastward along the Turkish coast is evident, as well as branches encircling Cyprus and the region south of the Rhodes Gyre. In the latter region the LIW seems to encircle a set of three anticyclones. West of Crete the LIW heads straight west into the Ionian, but also with indications of a branch heading northward into the Adriatic, which is not shown by Pinardi et al. (2015). An instantaneous image from 31 January 2016 (Fig. 18.6) indicates the complex transport processes via geostrophic turbulence. It is nearly impossible to track specific parcels without a separate tracer experiment. Even if this were done, it is not clear that the model can adequately simulate the spreading of LIW. Anti-cyclonic eddies with a core of LIW have been observed numerous times with gliders or profiling floats that were not predicted by operational models. In some cases, similar features were only present in the re-analysis because of assimilated data.

It is also noted from other studies that the Adriatic Sea also accepts LIW as a sub-surface layer overlaying Adriatic water through the Otranto Channel. Over a few years, LIW, circulating cyclonically in the southern Adriatic, preconditions the area for deep convection and deep water

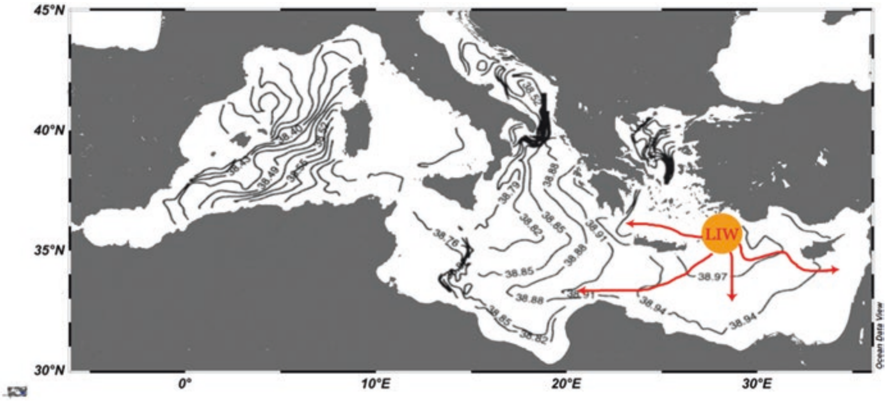


Fig. 18.5 Salinity on the 28.95 kg m^{-3} isopycnal surface from a 20 year average after a 100-year simulation. (Adapted from Wu and Haines 1998). Orange oval indicates the region of LIW formation (Northern Levantine). Red arrows indicate likely pathways based on salinity gradient

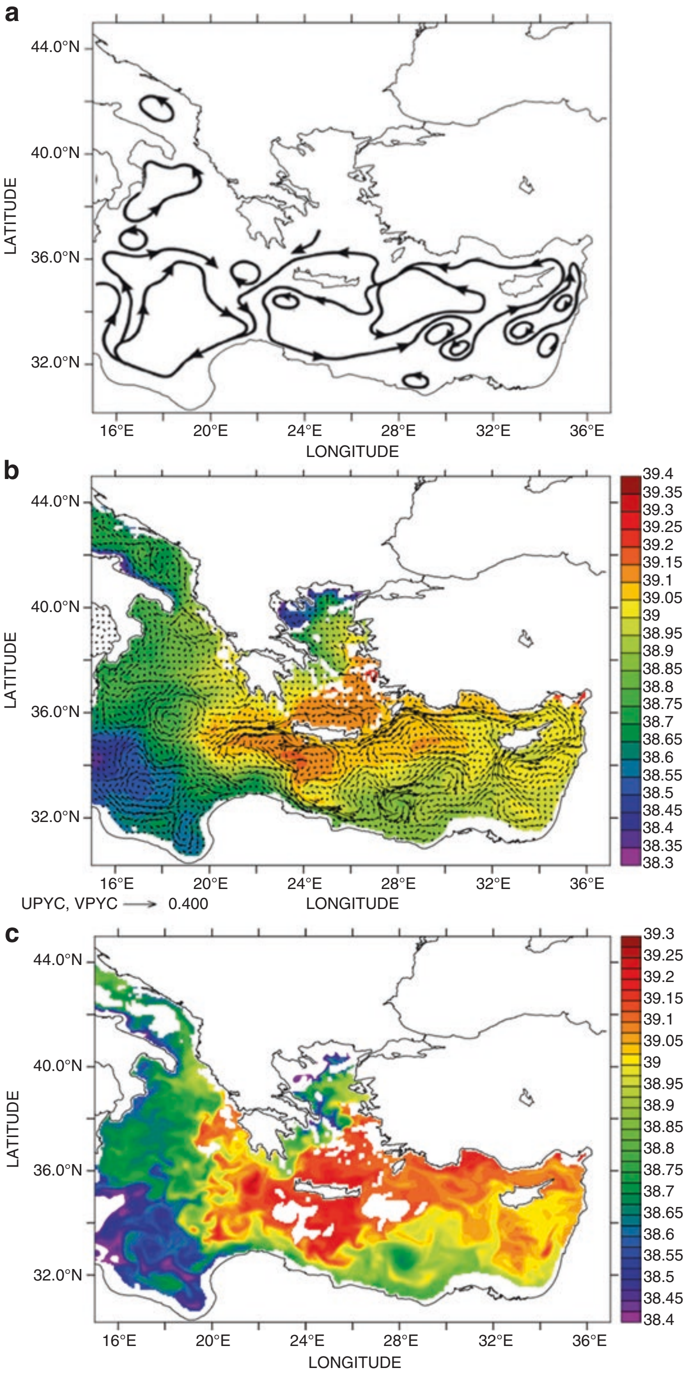


Fig. 18.6 (**a**) Eastern Mediterranean intermediate layer circulation (200–300 m) from Pinardi et al. (2015). (**b**) 2016 average salinity and currents on 28.95 kg m^{-3} σ_θ potential density anomaly from CMEMS (2017). (**c**) Salinity on same density layer for 31 January 2016 instantaneous (white areas are where the isopycnal outcrops). Generated using E.U. Copernicus Marine Service Information

formation that spills back out into the Mediterranean and spreads eastward below existing LIW (Wu and Haines 1996). Pinardi et al. (2015) do not indicate this current in the schematic of the intermediate circulation. Further west, it appears that the Ionian Sea is split from NW to SE by a front in LIW properties. This front generates eddies but is maintained for many years in Wu and Haines (1996). This would indicate a dynamic barrier to spread of LIW in addition to the topographic one further west at the Sicily Channel, although the latter is likely the rate-limiting one.

By far the most extensive study so far regarding the direct measurement of the intermediate water circulation in the Mediterranean is that of Menna and Poulain (2010), who used profiling floats to describe the currents at 350 m. They found that in the Eastern basin, the flow was primarily along bathymetric contours at mean speeds of about 5 cm s^{-1}, except in regions of narrow passages. However, this flow was also dominated by fluctuation, not steady mean flow.

Recent efforts have been made by the authors to map LIW pathways using hydrographic properties measured from pro-

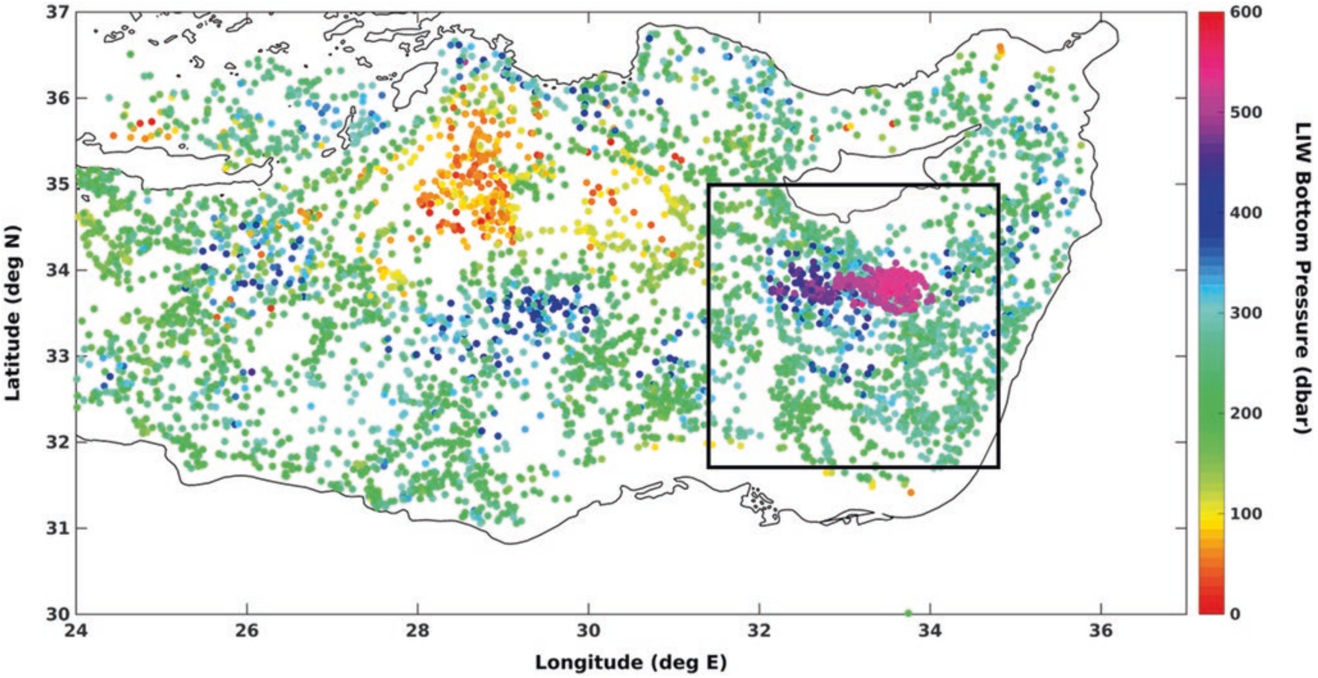


Fig. 18.7 Map of pressure (dbar) of 29.0 kg m^{-3} isopycnal from Argo floats from 2002 to 2014, recent years are plotted on top of previous. The box indicates the region included in the time series (Fig. 18.9). (Modified from Hayes et al. 2014, figures a and b © Daniel Hayes)

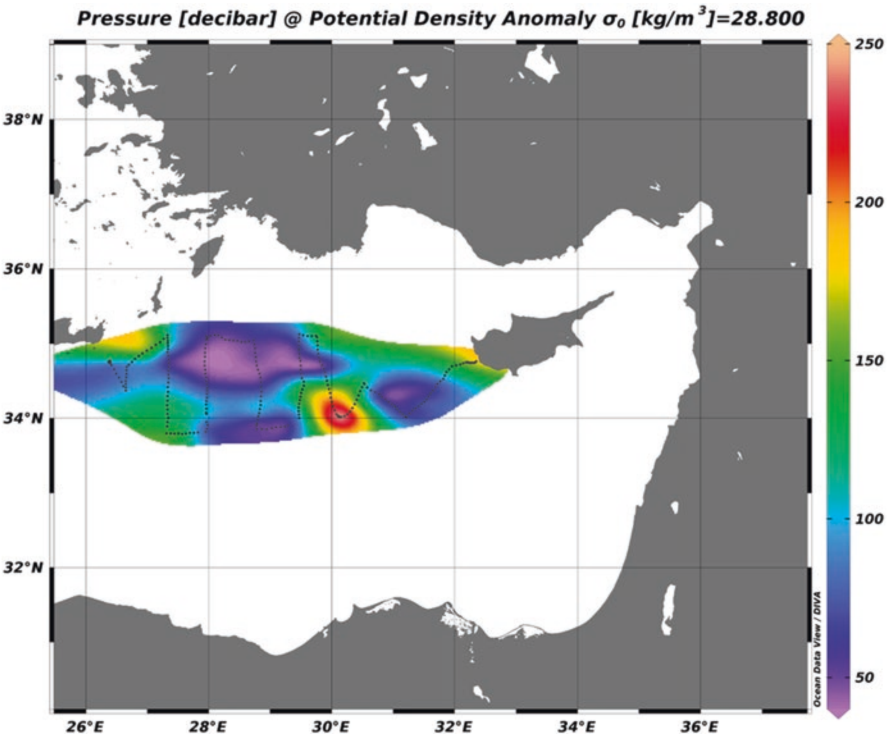
filing floats, gliders and ships (Hayes et al. 2014). The float data were collected and made freely available by the International Argo Program and the national programs that contribute to it (http://www.argo.ucsd.edu, http://argo.jcommops.org). It is part of the Global Ocean Observing System. The glider data are available from PANGEA (Hayes 2017). From a map of the depth of the LIW isopycnal from such data over the 2002–2015 period, a picture of spreading and deepening can be seen (Fig. 18.7). This spreading does not appear to be the same in all directions, but a series of deep/shallow variations are visible around the suspected formation region (Rhodes Gyre). Particularly striking is the depth of LIW in the Cyprus Eddy, south of Cyprus. This multi-lobe dispersion of LIW in depressed isopycnals is consistent with the results of Wu and Haines (1996) and Stratford and Williams (1997).

A glider mission through the Rhodes Gyre was recently carried out from 23 March to 5 June 2016 (Hayes 2017). A pattern of 570 profiles crossing the Rhodes Gyre multiple times was carried out, covering the restratification season (March to June). After interpolation, it is possible to see a similar lobe-like structure to the LIW surface (Fig. 18.8).

Besides pathways, the properties of intermediate water are important for studies of CWC. *In situ* data at intermediate depths from ships, floats, moorings and gliders can be used to track the variability of the LIW temperature and salinity. Hydrographic surveys from 1995 to 2012 and recent data from floats and gliders have been used to determine the properties of LIW in the SE Levantine. For glider and float data, the temperature and salinity were extracted and averaged over time and density windows. Cyprus Basin Oceanography (CYBO) cruise data were extracted from 240 to 260 m depths. This work (Hayes et al. 2014) reveals interannual variability which has yet to be fully explained: a sudden rise in temperature and salinity in 2009, followed by a slow relaxation (Fig. 18.9). Similar variability, using similar data, was found by Krokos et al. (2014).

Ozer et al. (2017) also showed the thermohaline trends and decadal fluctuation of intermediate water masses in south eastern Mediterranean (south of 34°N and east of 30°E). They found significant positive trends in both temperature and salinity, along with decadal variability of LIW over the years 1979–2014. Prior to this period, and on a longer time scale, there is evidence of long-term increasing trends in the LIW core salinity (Rohling and Bryden 1992; see Skliris, this volume) as well as sudden shifts (in the southeastern Mediterranean; Hecht 1992). An excellent summary and review of the cross-basin and temporal distribution of nutrients (Dissolved Inorganic Nitrogen (DIN), Total Nitrogen (TN), Dissolved Inorganic Phosphorous (DIP), Total Phosphorous (TP), Total Organic Carbon (TOC)) and oxygen, as well as the carbonate system, is provided by reports for the Marine Strategy Framework Directive (MSFD) on behalf of the Republic of Cyprus (2012). It is shown that the vertically-integrated concentration of nutrients generally decreases from west to east, and at the same time the nutricline deepens. In particular, the phosphacline shows a much stronger deeping (to over 200 m) towards the east. The oxygen minimum zone ranges from about 500 m to 1000 m and extends deeper with higher concentrations of

Fig. 18.8 Depth of isopycnal 28.8 kg m^{-3} during CRELEV-16 glider mission (23 March to 5 June 2016, 570 profiles). (Source of data is Hayes 2017)



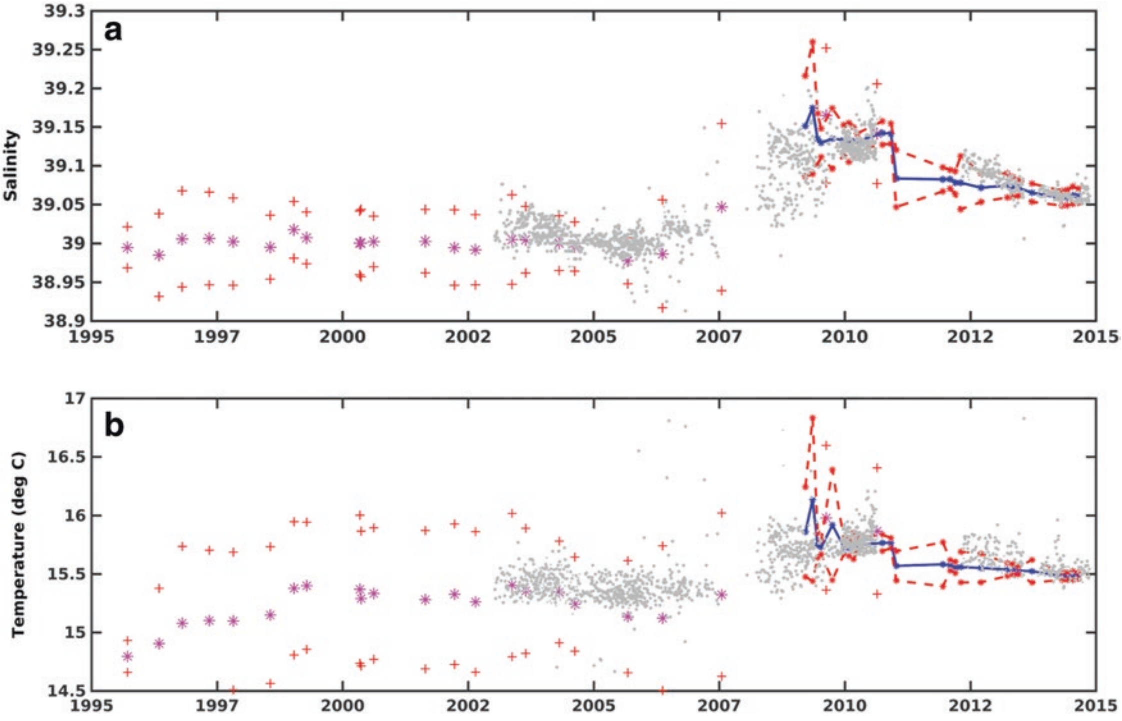


Fig. 18.9 Time series of (**a**) salinity and (**b**) temperature at depth of 29.0 σ_θ within the box of Fig. 18.7. Pink: hydrographic cruise averages, red crosses indicate one standard deviation. Connected blue stars: glider monthly averages with one standard deviation in red dash. Gray dots are float values (not averaged). (Modified from Hayes et al. 2014, figures a and b © Daniel Hayes)

oxygen in the eastern as opposed to the western Mediterranean.

Time series measurements at 265 dbar from a mooring near the Eratosthenes Seamount, close to where CWC sightings occurred (Galil and Zibrowius 1998; Mitchell et al. 2013), show a significant change in temperature (16.3–17.2 and back) and salinity (39.21–39.36 and back) over the five months of the experiment (Fig. 18.10). It is surprising to see

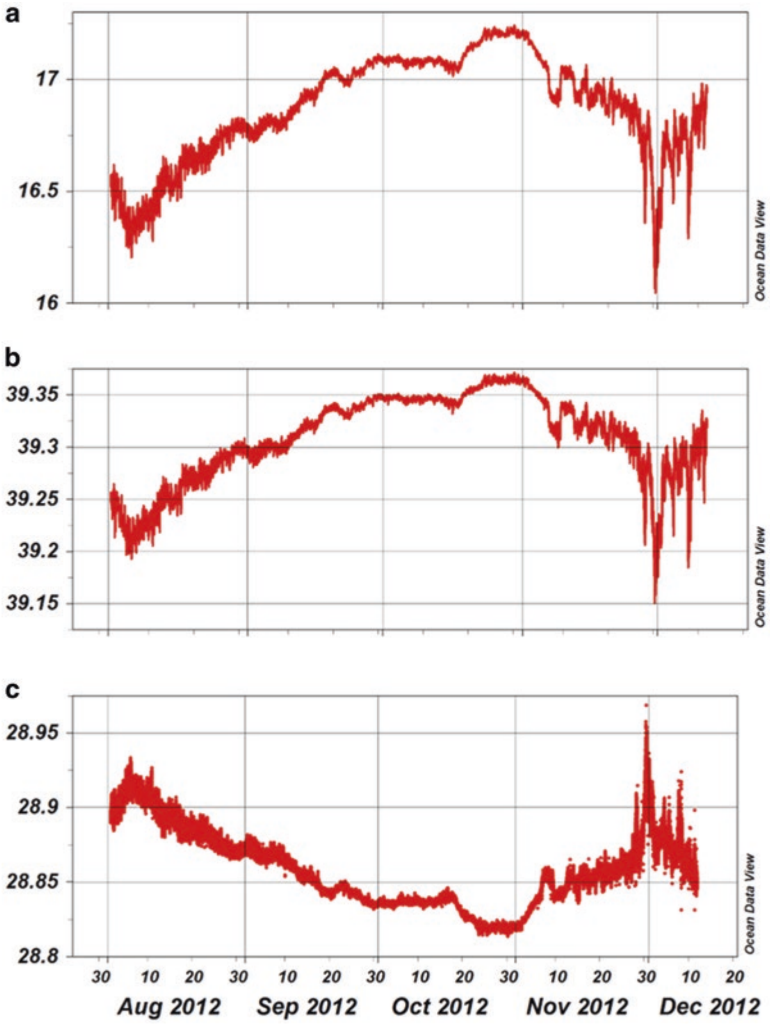


Fig. 18.10 (**a**) Temperature, (**b**) salinity, and (**c**) potential density from a sensor moored at 265 dbar southwest of Cyprus (N33° 53′, E032° 11′), just west of Eratosthenes Seamount. Bottom depth is approximately 2650 m. (Data courtesy CSnet, International, Inc.)

large excursions in temperature and salinity at this depth, but it indicates that the intermediate water is a dynamic water mass in terms of position in the water column and characteristics, even away from the formation and coastal areas (the sea depth is approximately 2650 m in this case.) This is likely due to the various mechanisms and pathways that drive the formation and dispersion of LIW, as well as the decadal variability in the formation of deep waters, which spread into the basin and mix with the LIW the years after its formation.

In summary, intermediate water in the Eastern Mediterranean is exclusively represented by various forms of LIW, possibly from multiple formation origins. LIW spreads throughout the basin at depths of 0–500 m (normally 200–350 m). This lateral spreading via large-scale turbulence seems to be bounded by flow which follows the bathymetric contours cyclonically around the basin. Temperature and salinity vary several tenths of degrees and salinity units (respectively) on scales of hours up to years according to the limited *in situ* observations available. Eventually, LIW exits the Eastern Mediterranean through the Sicily Channel, balancing the inflow of Atlantic Water and the net loss of water through the upper surface (evaporation-precipitation-runoff).

18.4.2 Western Mediterranean

The inflow of fresh surface AW, the evaporation excess over the basin and strong heat losses during winter in specific areas, drive an antiestuarine circulation. As the AW spreads through the basin it is modified: in the eastern Mediterranean it is transformed into salty and warm LIW. While flowing back towards the Western Mediterranean (WMED), it tends to gradually lose its characteristics, due to dilution with adjacent water masses, becoming thus less salty and less warm (and less oxygenated due to respiration processes). In addition to these spatial variations, there are also temporal variations, in particular on the longer time scale. Schroeder et al. (2017) show that since the mid 1990s the temperature (T) and the Salinity (S) of the LIW crossing the Sicily Channel, which divides the EMED and the WMED, have increased by

0.53 °C and 0.13, respectively (i.e. 0.024 °C year^{-1} and 0.006 year^{-1}). Such trends are at least one order of magnitude greater than those reported for the global ocean intermediate layer (Schroeder et al. 2017 and references therein).

Two types of water of eastern Mediterranean origin are found in the Sicily Channel: LIW and Aegean and/or Adriatic Deep Water (summarised in Millot 1999). The latter cascades from about 400 m in the Channel to depths of about 2000 m in the Tyrrhenian Sea resulting in Tyrrhenian Dense Water (TDW) (Millot 1999). The former, LIW, leaves the Eastern Mediterranean via the Sicily Channel, rounding Sardinia to enter the WMEDalong the periphery of the Tyrrhenian Sea in a cyclonic sense. Properties of the LIW core in the WMEDare as follows: temperature from 13 to 14.2 °C, salinity from 38.4 to 38.8, potential density from 29 to 29.10 kg m^{-3}, and depths from 200 to 600 m (Millot 2013). The circulation pattern is summarised in Millot (1999) but with caution that turbulence makes such estimates difficult. Based on hydrographic studies, Millot (1999) concludes that there is a mean current along the west coast of Italy, which diverges at Corsica, with some flow north through the Corsica Channel and some making the loop south then back north around Sardinia first, then as the Western Corsica Current, rejoining downstream of the channel. Once joined, these water masses flow in the Northern Current along the coast of France and Spain. Then, a part flows through the Ibiza Channel (possibly intermittently), while another part flows around Menorca. Some LIW exits at Gibraltar, while some seems to recirculate eastward, but in an unsteady, turbulent way. Meandering and instability of the eastward current along the Algerian coast, and the resulting entrainment of newer LIW coming from the Sicily Channel into Algerian Eddies were noted by Millot and Taupier-Letage (2005b). Testor et al. (2005) has indicated that eddies generated at the southwest corner of Sardinia (Sardinian Eddies) trap LIW, and may transport a significant part of these water masses toward the center of the basin.

An entirely new phenomenon was described by Bosse et al. (2015) in which submesoscale vortices of LIW are generated west of Corsica and Sardinia and populate the basin, significantly influencing the flux of heat and salt from LIW vein to the interior. Normally, LIW is considered to play a critical role for direct influence of the stability of the Gulf of Lions and the strength and timing of the formation of WMDW in wintertime there. Larger scale eddies have been observed previously, Algerian Eddies and Sardinian Eddies, but these were limited to the southern sub-basins (Millot and Taupier-Letage 2005b; Testor and Gascard 2005). According to Testor et al. (2005) the Algerian basin appears to be characterised by two cyclonic large-scale circulations, which are mainly barotropic and have been called the Western and Eastern Algerian Gyres.

As for the Eastern Mediterranean (Fig. 18.6), the intermediate layer circulation of the western Mediterranean is shown according to (Pinardi et al. 2015) (Fig. 18.11). Broad similarities to the LIW circulation shown in Millot (1999) and many other studies exist: the anticyclonic circulation described above west of Corsica. However, the flow along the North African coast seems at odds with the circulation of Millot (1999) and Testor et al. (2005). The salinity and currents on the 28.95 kg m^{-3} potential density anomaly surface from the Copernicus Marine Environment Monitoring Service (CMEMS 2017) daily analysis output for 2016 are plotted for the west in the same way as for the east (Fig. 18.11) and also seem to indicate the same anticyclonic circulation west of Corsica and south of France, but seem to also be at odds with the circulation near the coast of Africa of Pinardi et al. (2015). Averages of the instantaneous 10-day output show good agreement with the schematic Pinardi et al. (2015), with the notable exception of a lack of the westward current along the coast of northern Africa in the simulations. The simulations show an elongated mean cyclonic circulation in the western Algerian gyre with strong eastward flow very near the coast in agreement with Testor et al. (2005). As in the eastern basin, instantaneous fields only vaguely resemble the mean field, indicating that time variable transport could play a significant role and calculating transport based on mean currents should be done with caution. The instantaneous image of the salinity at the 28.95 kg m^{-3} isopycnal again shows complex features, especially in the western Algerian basin and near the Algerian coast. However there are also indications of northward flow along western Sardinia and the continued cyclonic circulation around the basin.

Fabri et al. (2017) show in their study on the Cassidaigne canyon and using a habitat suitability model that the living conditions of CWC communities can be found in areas of the canyon where the substratum shows irregularities, slopes and topographic highs. Concerning environmental variables temperature and high current velocities (with strong interactions between the canyon and the along-slope Northern Current, and wind-induced upwelling) were identified as explanatory factors of the distribution of CWC. Similar explanations can be probably drawn for the Catalan canyons (see Aymà et al., this volume), which are the only ones that are regularly impacted by cascading of dense shelf water cascading and storm-induced downwelling, and were rocky but also partially sedimented substrates take place. These canyons are also sites with higher fluxes of organic matter deriving from the shelf or frontal zones. Along the Catalan margins, CWCs are found solely in the head of the Lacaze-Duthiers, Cap de Creus, and La Fonera canyons. In general, the spotty presence of CWCs is likely a result of local conditions, since LIW borders all of the northern margins of the Mediterranean.

Recently, remarkable changes occurred in the WMED. Once advected to the dense water formation region in the Gulf of Lion (one of the CWC Provinces in Taviani et al. 2011), more salt and heat in the LIW will further

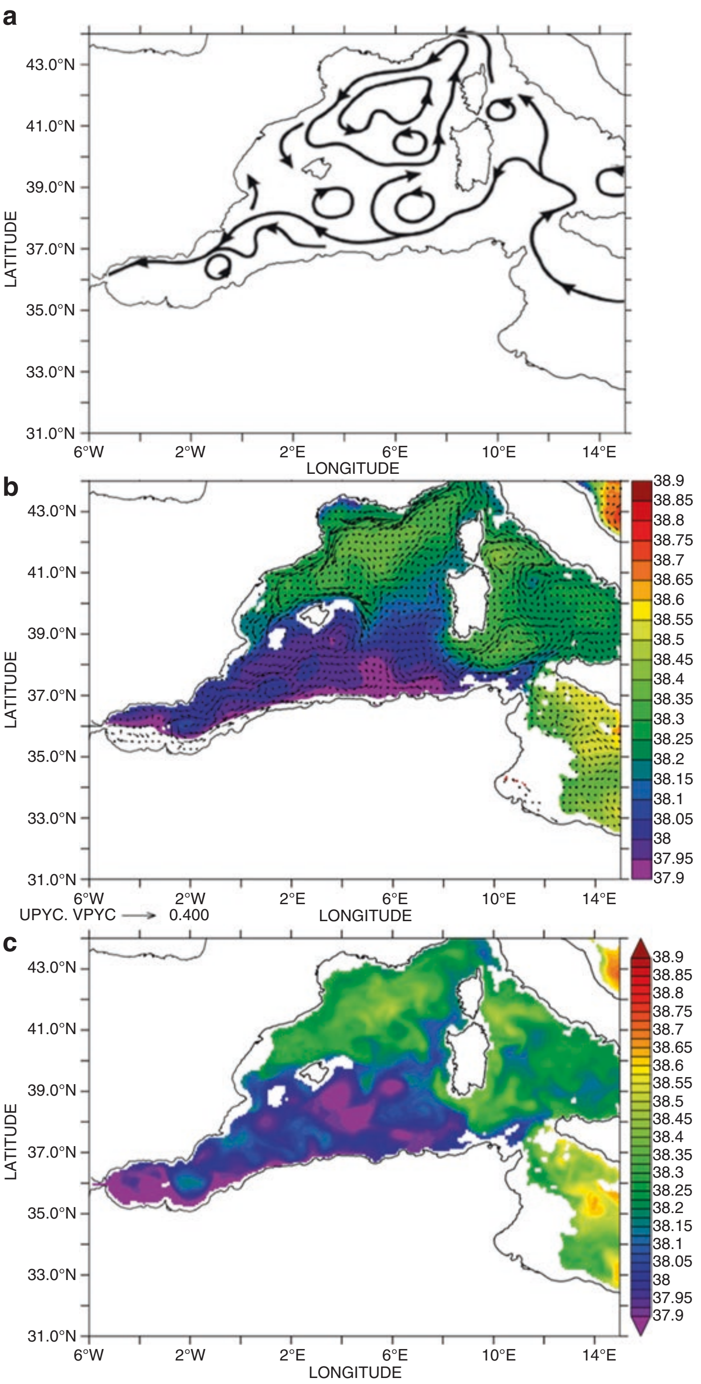


Fig. 18.11 (**a**) Western Mediterranean intermediate layer circulation (200–300) from Pinardi et al. (2015). (**b**) 2016 average salinity and currents on 28.95 kg m^{-3} σ_θ potential density anomaly from CMEMS (2017). (**c**) Salinity on the same isopycnal for 21 July 2016 instantaneous (white areas are where the isopycnal outcrops). Generated using E.U. Copernicus Marine Service Information

enhance the tendency of this site to produce warmer and saltier deep waters (Schroeder et al. 2010). The homogeneous WMDW has long been considered a stable layer to be used to quantify gradual trends in T and S possibly induced by climate change (Schroeder et al. 2016). While deep T and S seem to have increased almost steadily for about half a century (Rohling and Bryden 1992; Krahmann and Schott 1998; Bethoux and Gentili 1999; Rixen et al. 2005; Josey et al. 2011), since 2005 the gradual trend was interrupted by an abrupt jump towards higher T and S (increasing rates were 2.5 times faster than during 1961–2004, see Schroeder et al. 2016), as a consequence of a major DWF event in winter 2004/2005 that set the beginning of the Western Mediterranean Transition (WMT). The WMT is a climate shift that radically changed the basic structure and properties of the intermediate/deep water column in the western basin: T, S and density abruptly increased and the weak stratification has been replaced by a number of vertical gradient inversions. The process of formation of large volumes of anomalous WMDW continued in the following winters (especially in 2005/2006, 2008/2009, 2009/2010, 2010/2011, 2011/2012 and 2012/2013): each winter a new warmer, saltier and denser deep water formed, leading to a stepwise increase of the heat and the salt contents of the WMDW (Houpert et al. 2016; Schroeder et al. 2016). These waters will eventually feed the Mediterranean Outflow Water (MOW) exiting through the Strait of Gibraltar (crossing a CWC province), with potential impacts at the global scale.

Given that all processes of DWF involve the AW and LIW to some extent, all Mediterranean water masses are closely related, such that significant modification to one water mass will also affect the others sooner or later (Rohling et al. 2015).

18.5 Summary

Despite drawbacks associated with the steady-state assumption and the lack of observations, the literature can provide information relevant to the study of CWC, even if crude. For example, progress can be made on understanding pathways of larval spread, and the connection to potential changes in the deep water formation and spreading processes using ocean re-analyses and operational forecasts (CMEMS 2017). As mentioned in Evans et al. (this volume), thriving CWC assemblages occur in the Mediterranean, distributed along the circulation path of the LIW, which appears to be a main driver for CWC distribution in the Mediterranean (Taviani et al. 2011). As the observing system improves, and as the scientific community is able to leverage focused programs on new and existing areas, this cross-basin picture will have to be revised.

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References

Bensi M, Cardin V, Rubino A, et al (2013) Effects of winter convection on the deep layer of the Southern Adriatic Sea in 2012. J Geophys Res Oceans 118:6064–6075. https://doi.org/10.1002/2013JC009432

Bethoux JP, Gentili B (1999) Functioning of the Mediterranean Sea: past and present changes related to freshwater input and climate changes. J Mar Syst 20:33–47. https://doi.org/10.1016/S0924-7963(98)00069-4

Borzelli GLE, Gačić M, Cardin V, et al (2009) Eastern Mediterranean Transient and reversal of the Ionian Sea circulation. Geophys Res Lett 36:L15108. https://doi.org/10.1029/2009GL039261

Bosse A, Testor P, Mortier L, et al (2015) Spreading of Levantine Intermediate Waters by submesoscale coherent vortices in the northwestern Mediterranean Sea as observed with gliders. J Geophys Res Oceans 120:1599–1622. https://doi.org/10.1002/2014JC010263

Bosse A, Testor P, Houpert L, et al (2016) Scales and dynamics of Submesoscale Coherent Vortices formed by deep convection in the northwestern Mediterranean Sea. J Geophys Res Oceans 121:7716–7742. https://doi.org/10.1002/2016JC012144

Brenner S, Rozentraub Z, Bishop J, et al (1991) The mixed-layer/thermocline cycle of a persistent warm core eddy in the eastern Mediterranean. Dyn Atmos Oceans 15:457–476

Canals M, Puig P, de Madron XD, et al (2006) Flushing submarine canyons. Nature 444:354

CMEMS—Copernicus Marine Environment Monitoring Service (2017) Internet web site for product MEDSEA_ANALYSIS_FORECAST_PHYS_006_001. http://marine.copernicus.eu

Cook BI, Anchukaitis KJ, Touchan R, et al (2016) Spatiotemporal drought variability in the Mediterranean over the last 900 years. J Geophys Res Atmos 121:2060–2074. https://doi.org/10.1002/2015JD023929

Durrieu de Madron X, Zervakis V, Theocharis A, et al (2005) Comments on "Cascades of dense water around the world ocean". Progr Oceanogr 64:83–90. https://doi.org/10.1016/j.pocean.2004.08.004

Durrieu de Madron X, Houpert L, Puig P, et al (2013) Interaction of dense shelf water cascading and open-sea convection in the northwestern Mediterranean during winter 2012. Geophys Res Lett 40:1379–1385

EMODnet – European Marine Observation and Data Network (2017) Internet website. http://www.emodnet-bathymetry.eu/

Fabri M-C, Bargain A, Pairaud I, et al (2017) Cold-water coral ecosystems in Cassidaigne Canyon: an assessment of their environmental living conditions. Deep-Sea Res Part 2 Top Stud Oceanogr 137:436–453. https://doi.org/10.1016/j.dsr2.2016.06.006

Gačić M, Borzelli GLE, Civitarese G, et al (2010) Can internal processes sustain reversals of the ocean upper circulation? The Ionian Sea example. Geophys Res Lett 37:L09608. https://doi.org/10.1029/2010GL043216

Gačić M, Civitarese G, Eusebi Borzelli GL, et al (2011) On the relationship between the decadal oscillations of the northern Ionian Sea and the salinity distributions in the eastern Mediterranean. J Geophys Res Oceans 116:C12002. https://doi.org/10.1029/2011JC007280

Galil B, Zibrowius H (1998) First benthos samples from Eratosthenes Seamount, Eastern Mediterranean. Senckenberg Marit 28:111. https://doi.org/10.1007/BF03043142

Gerges MA (1977) A numerical investigation of the circulation in the Mediterranean Sea. Rapp Comm Int Mer Méditerr 24:25–30

Haines K, Wu PL (1995) A modelling study of the thermohaline circulation of the Mediterranean Sea: water formation and dispersal. Oceanol Acta 18:401–417

Hayes DR (2017) Physical oceanography from nine Seaglider missions in the Mediterranean Sea, Eastern Basin, PANGAEA, https://doi.org/10.1594/PANGAEA.860867, Supplement to: Hayes DR; et al (in prep.): physical oceanography of the Eastern Basin of the Mediterranean Sea from 2009 to 2016 as observed from autonomous underwater gliders: data set description. Earth Syst Sci Data Disc

Hayes DR, Georgiou G, Zodiatis G, et al (2014) Levantine intermediate water properties observed in the eastern Levantine from 1995–2014. In: Ocean salinity science and salinity remote sensing workshop, 26–28 November, 2014. Exeter, UK

Hayes DR, Gildor H, Bosse A, et al (2016) On the evolution of the long-lived subsurface mesoscale eddy south of Cyprus. Rapp Comm Int Mer Mediterr 41:84

Hecht A (1992) Abrupt changes in the characteristics of Atlantic and Levantine intermediate waters in the Southeastern Levantine Basin. Oceanol Acta 15:25–42

Hecht A, Pinardi N, Robinson AR (1988) Currents, water masses, eddies and jets in the Mediterranean Levantine Basin. J Phys Oceanogr 18:1320–1353. https://doi.org/10.1175/1520-0485(1988)018<1320:CWMEAJ>2.0.CO;2

Houpert L, Durrieu de Madron X, Testor P, et al (2016) Observations of open-ocean deep convection in the northwestern Mediterranean Sea: seasonal and interannual variability of mixing and deep water masses for the 2007–2013 Period. J Geophys Res Oceans 121:8139–8171

Josey SA, Somot S, Tsimplis M (2011) Impacts of atmospheric modes of variability on Mediterranean Sea surface heat exchange. J Geophys Res 116:C02032. https://doi.org/10.1029/2010JC006685

Krahmann G, Schott F (1998) Longterm increases in Western Mediterranean salinities and temperatures: anthropogenic and climatic sources. Geophys Res Lett 25:4209–4212

Krokos G, Velaoras D, Korres G, et al (2014) On the continuous functioning of an internal mechanism that drives the Eastern Mediterranean thermohaline circulation: the recent activation of the Aegean Sea as a dense water source area. J Mar Syst 129:484–489. https://doi.org/10.1016/j.jmarsys.2013.10.002

Lacombe H, Tchernia P (1960) Quelques traits generaux de l'Hydrologie Mediterrane. Cah Oceanogr 12:527–547

Lascaratos A (1993) Estimation of deep and intermediate water mass formation rates in the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 40:1327–1332. https://doi.org/10.1016/0967-0645(93)90072-U

Lascaratos A, Nittis K (1998) A high-resolution three-dimensional numerical study of intermediate water formation in the Levantine Sea. J Geophys Res 103:18497–18511. https://doi.org/10.1029/98JC01196

Lascaratos A, Williams RG, Tragou E (1993) A mixed-layer study of the formation of Levantine Intermediate Water. J Geophys Res 98:14739–14749

Malanotte-Rizzoli P, Hecht A (1988) Large-scale properties of the eastern Mediterranean: a review. Oceanol Acta 11:323–335

Malanotte-Rizzoli P, Artale V, Borzelli-Eusebi G, et al (2014) Physical forcing and physical/biochemical variability of the Mediterranean Sea: a review of unresolved issues and directions for future research. Ocean Sci 10:281

Menna M, Poulain PM (2010) Mediterranean intermediate circulation estimated from Argo data in 2003–2010. Ocean Sci 6:331–343

Menna M, Poulain P-M, Zodiatis G, et al (2012) On the surface circulation of the Levantine sub-basin derived from Lagrangian drifters and satellite altimetry data. Deep-Sea Res Part 1 Oceanogr Res Pap 65:46–58. https://doi.org/10.1016/j.dsr.2012.02.008

Millot C (1999) Circulation in the western Mediterranean Sea. J Mar Syst 20:423–442

Millot C (2013) Levantine Intermediate Water characteristics: an astounding general misunderstanding! Sci Mar 77:217–232. https://doi.org/10.3989/scimar.03518.13A

Millot C, Taupier-Letage I (2005a) Additional evidence of LIW entrainment across the Algerian subbasin by mesoscale eddies and not by a permanent westward flow. Progr Oceanogr 66:231–250. https://doi.org/10.1016/j.pocean.2004.03.002

Millot C, Taupier-Letage I (2005b) Circulation in the Mediterranean Sea. In: Saliot A (ed) The Mediterranean Sea. Springer, Berlin, Heidelberg, pp 29–66

Mitchell G, Mayer LA, Bell KLC, et al (2013) Exploration of Eratosthenes seamount – a continental fragment being forced down an oceanic trench. In: Bell KLC, ML Brennan (eds) New frontiers in ocean exploration: the E/V Nautilus 2012 field season and summary of Mediterranean exploration. Oceanography 26: 36–41. https://doi.org/10.5670/oceanog.2013.supplement.01

Morcos SA (1972) Sources of Mediterranean intermediate water in the Levantine Sea. In: Gordon AL (ed) Studies in physical oceanography: a tribute to G. Wüst on his 80th birthday. Gordon and Breach, New York, pp 185–206

Nielsen JN (1912) Hydrography of the Mediterranean and adjacent waters. In: Report of the Danish oceanographic expedition 1908–1910 to the Mediterranean and Adjacent Waters, vol 1. Copenhagen, pp 72–191

Nittis K, Lascaratos A (1998) Diagnostic and prognostic numerical studies of LIW formation. J Mar Syst 18:179–195

Ovchinnikov IM (1966) Circulation in the surface and intermediate layers of the Mediterranean. Oceanology 6:49–59

Ovchinnikov IM (1984) The formation of intermediate water in the Mediterranean. Oceanology 24:168–173

Ozer T, Gertman I, Kress N, et al (2017) Interannual thermohaline (1979–2014) and nutrient (2002–2014) dynamics in the Levantine surface and intermediate water masses, SE Mediterranean Sea. Glob Planet Chang 151:60–67. https://doi.org/10.1016/j.gloplacha.2016.04.001

Özsoy E, Hecht A, Ünlüata Ü (1989) Circulation and hydrography of the Levantine Basin. Results of POEM coordinated experiments 1985–1986. Progr Oceanogr 22:125–170. https://doi.org/10.1016/0079-6611(89)90004-9

Özsoy E, Hecht A, Ünlüata Ü, et al (1991) A review of the Levantine Basin circulation and its variability during 1985–1988. Dyn Atmos Ocean 15:421–456. https://doi.org/10.1016/0377-0265(91)90027-D

Özsoy E, Hecht A, Ünlüata Ü, et al (1993) A synthesis of the Levantine Basin circulation and hydrography, 1985–1990. Deep-Sea Res Part 2 Top Stud Oceanogr 40:1075–1119. https://doi.org/10.1016/0967-0645(93)90063-S

Ozturgut E (1976) The Source and spreading of the Levantine Intermediate Water in the Eastern Mediterranean. Saclant ASW Research Centre Memorandum SM-92, La Spezia, p 45

Pinardi N, Zavatarelli M, Adani M, et al (2015) Mediterranean Sea large-scale low-frequency ocean variability and water mass formation rates from 1987 to 2007: a retrospective analysis. Progr Oceanogr 132:318–332. https://doi.org/10.1016/j.pocean.2013.11.003

Poulain P-M, Menna M, Mauri E (2012) Surface geostrophic circulation of the Mediterranean Sea derived from drifter and satellite altimeter data. J Phys Oceanogr 42:973–990. https://doi.org/10.1175/JPO-D-11-0159.1

Raineault NA, Ramey-Balci PA, Shank TM, et al (2013) Exploration of the Anaximander Mountains: Mud volcanoes, cold-seep communities, and cold water corals. Oceanography 26:30–35

Republic of Cyprus, Ministry of Agriculture, Natural Resources, and the Environment Department of Fisheries and Marine Research (2012) Initial assessment of the marine environment of Cyprus Part I – Characteristics. Web link accessed 20170925: http://cdr.eionet.europa.eu/cy/eu/msfd8910/msfd4text/envufw40q/1-Initial_Assesment_Report.pdf/manage_document

Rio M-H, Pascual A, Poulain P-M, et al (2014) Computation of a new mean dynamic topography for the Mediterranean Sea from model outputs, altimeter measurements and oceanographic in situ data. Ocean Sci 10:731–744. https://doi.org/10.5194/os-10-731-2014

Rixen M, Beckers J-M, Levitus S, et al (2005) The Western Mediterranean Deep Water: a proxy for climate change. Geophys Res Lett 32:L12608. https://doi.org/10.1029/2005GL022702

Roether W, Klein B, Manca BB, et al (2007) Transient Eastern Mediterranean deep waters in response to the massive dense-water output of the Aegean Sea in the 1990s. Progr Oceanogr 74:540–571

Rohling EJ, Bryden HL (1992) Man-induced salinity and temperature increases in western Mediterranean deep water. J Geophys Res Oceans 97:11191–11198. https://doi.org/10.1029/92JC00767

Rohling EJ, Marino G, Grant KM (2015) Mediterranean climate and oceanography, and the periodic development of anoxic events (sapropels). Earth-Sci Rev 143:62–97. https://doi.org/10.1016/j.earscirev.2015.01.008

Schlitzer R, Roether W, Oster H, et al (1991) Chlorofluoromethane and oxygen in the Eastern Mediterranean. Deep-Sea Res 38:1531–1551. https://doi.org/10.1016/0198-0149(91)90088-W

Schröder K, Gasparini GP, Tangherlini M, et al (2006) Deep and intermediate water in the western Mediterranean under the influence of the Eastern Mediterranean Transient. Geophys Res Lett 33:L21607. https://doi.org/10.1029/2006GL027121

Schroeder K, Ribotti A, Borghini M, et al (2008) An extensive western Mediterranean deep water renewal between 2004 and 2006. Geophys Res Lett 35:L18605. https://doi.org/10.1029/2008GL035146

Schroeder K, Josey SA, Herrmann M, et al (2010) Abrupt warming and salting of the Western Mediterranean Deep Water after 2005: atmospheric forcings and lateral advection. J Geophys Res Oceans 115:C08029. https://doi.org/10.1029/2009JC005749

Schroeder K, Garcìa-Lafuente J, Josey SA, et al (2012) 3 – Circulation of the Mediterranean Sea and its variability. In: Lionello P (ed) The climate of the Mediterranean region. Elsevier, Oxford, pp 187–256

Schroeder K, Chiggiato J, Bryden HL, et al (2016) Abrupt climate shift in the western Mediterranean Sea. Sci Rep UK 6:23009

Schroeder K, Chiggiato J, Josey SA, et al (2017) Rapid response to climate change in a marginal sea. Sci Rep 7: 4065. https://doi.org/10.1038/s41598-017-04455-5

Shank TM, Herrera S, Cho W, et al (2011) Exploration of the Anaximander mud volcanoes. In: Bell KLC, Fuller S (eds) New frontiers in ocean exploration: the e/v nautilus 2010 field season. Oceanography 24:22–23. https://doi.org/10.5670/oceanog.24.1.supplement

Skliris N (2014) Past, present and future patterns of the thermohaline circulation and characteristic water masses of the Mediterranean Sea. In: The Mediterranean Sea. Springer, pp 29–48

Skliris N, Lascaratos A (2004) Impacts of the Nile River damming on the thermohaline circulation and water mass characteristics of the Mediterranean Sea. J Mar Syst 52:121–143. https://doi.org/10.1016/j.jmarsys.2004.02.005

Stratford K, Williams RG (1997) A tracer study of the formation, dispersal, and renewal of Levantine Intermediate Water. J Geophys Res Oceans 102:12539–12549. https://doi.org/10.1029/97JC00019

Sur HI, Özsoy E, Unluata U (1992) Simultaneous deep and intermediate convection in the northern Levantine Sea, winter 1992. Oceanol Acta 16:33–43

Tanhua T, Hainbucher D, Cardin V, et al (2013) Physical oceanography during METEOR cruise M84/3. In: PANGAEA. Available at: https://doi.org/10.1594/PANGAEA.856632

Taviani M, Vertino A, López Correa M, et al (2011) Pleistocene to recent scleractinian deep-water corals and coral facies in the eastern mediterranean. Facies 57:579–603. https://doi.org/10.1007/s10347-010-0247-8

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78. https://doi.org/10.1016/j.dsr2.2015.12.008

Testor P, Gascard J-C (2005) Large scale flow separation and mesoscale eddy formation in the Algerian Basin. Progr Oceanogr 66:211–230

Testor P, Send U, Gascard J-C, et al (2005) The mean circulation of the southwestern Mediterranean Sea: Algerian Gyres. J Geophys Res 110:C11017. https://doi.org/10.1029/2004JC002861

The LIWEX Group (2003) The Levantine Intermediate Water Experiment (LIWEX) Group: Levantine basin—a laboratory for multiple water mass formation processes. J Geophys Res Oceans 108:8101. https://doi.org/10.1029/2002JC001643

Theocharis A, Nittis K, Kontoyiannis H, et al (1999) Climatic changes in the Aegean Sea influence the Eastern Mediterranean thermohaline circulation (1986–1997). Geophys Res Lett 26:1617–1620

Theocharis A, Krokos G, Velaoras D, et al (2014) An internal mechanism driving the alternation of the eastern Mediterranean dense/deep water sources. In: Eusebi Borzelli GL, Gačić M, Lionello P, et al (eds) The Mediterranean Sea. Wiley, pp 113–137

Tsimplis MN, Bryden HL (2000) Estimation of the transports through the Strait of Gibraltar. Deep-Sea Res Part 1 Oceanogr Res Pap 47:2219–2242. https://doi.org/10.1016/S0967-0637(00)00024-8

Tsimplis MN, Zervakis V, Josey SA, et al (2006) Changes in the oceanography of the Mediterranean Sea and their link to climate variability. Dev Earth Environ Sci 4:227–282

Wu P, Haines K (1996) Modeling the dispersal of Levantine Intermediate Water and its role in Mediterranean deep water formation. J Geophys Res Oceans 101:6591–6607. https://doi.org/10.1029/95JC03555

Wu P, Haines K (1998) The general circulation of the Mediterranean Sea from a 100-year simulation. J Geophys Res Oceans 103:1121–1135. https://doi.org/10.1029/97JC02720

Wüst G (1961) On the vertical circulation of the Mediterranean Sea. J Geophys Res 66:3261–3271. https://doi.org/10.1029/JZ066i010p03261

Cross References

Aymà A, Aguzzi J, Canals M, et al (this volume) Occurrence of living cold-water corals at large depths within submarine canyons of the northwestern Mediterranean Sea

Evans J, Knittweis L, Borg JA, et al (this volume) Cold water corals in the Mediterranean: a history of discovery

Johnston M, Larsson AI (this volume) Perspectives of biophysical modelling with implications on biological connectivity of Mediterranean cold-water corals

Skliris N (this volume) The Mediterranean is getting saltier: from the past to the future

Taviani M (this volume) Changing views about Mediterranean cold-water corals

Vertino A, Taviani M, Coselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Occurrence and Biogeography of Mediterranean Cold-Water Corals

19

Giovanni Chimienti, Marzia Bo, Marco Taviani,
and Francesco Mastrototaro

Abstract

The term cold-water coral *sensu lato* groups taxa with a more or less pronounced frame-building ability (e.g. *Lophelia pertusa* and *Madrepora oculata*) with forest-forming organisms both on hard (e.g. *Leiopathes glaberrima*, *Parantipathes larix*, *Callogorgia verticillata* and *Viminella flagellum*) and soft bottoms (e.g. *Isidella elongata*, *Funiculina quadrangularis* and *Kophobelemnon stelliferum*). Cold-water coral species and their occurrence in the Mediterranean Sea are here reviewed and discussed from a biogeographic point of view, considering geographical areas of occurrence and bathymetric distribution. The present-day occurrence of living cold-water corals is then compared to the main deep currents of the Mediterranean Sea. Due to the proper interaction between topography and a combination of cold, oxygenated and trophic-carrying water masses (i.e. Levantine Intermediate Water, deep waters and cascading effects), cold-water coral communities develop in a mosaic-like situation along the main paths that such water masses follow within the basin. Finally, knowledge gaps and future perspectives in the study of cold-water coral occurrence, distribution and biogeography are highlighted. The currently still scarce knowledge on the Mediterranean deep-sea and on the basin-scale distribution of the most important cold-water corals species represents crucial biogeographical information. This gives fundamental indications on the location of the Mediterranean vulnerable deep marine ecosystems for future management strategies.

Keywords

Cold-water corals · Hard bottoms · Soft bottoms · Biogeography · Mediterranean Sea

19.1 Introduction

The deep Mediterranean Sea is inhabited by a variety of cnidarians distributed on both hard and soft substrata, constituting in favorable places emblematic ecosystems such as 'white coral' bioconstructions, antipatharian and soft coral 'animal forests' (*sensu* Rossi et al. 2017) or sea pen fields. The present-day situation is a transient one achieved through the troubled history of a basin exposed to major geological, climatic and oceanographic vicissitudes in the last million years (Taviani 2002). A commonly shared view is that the whole Mediterranean stenoecious fauna was completely renewed, or at least profoundly reshaped, at the beginning of the Pliocene (i.e. 5.33 Ma; Manzi et al. 2013) following the deleterious oceanographic conditions imposed by the Late Miocene 'Messinian Salinity Crisis' (Por and Dimentman 1985; Taviani 2003; Bianchi et al. 2012; Sabelli and Taviani 2014; Freiwald, this volume). Since then, the colonisation of the deep Mediterranean bottoms was served by the Gibraltar connection with the Atlantic Ocean, which exclusively controls up to present the biogeographic affinity of the basin's bathyal benthos, as documented by the fossil legacy and present composition (Zibrowius 1980; Raffi and Taviani 1984; Fredj and Laubier 1985; Taviani et al. 2011a, b, this volume; Sabelli and Taviani 2014; Vertino et al. 2014, this

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volume). Besides the function of the relatively shallow Gibraltar Strait as corridor and filter for potential Atlantic invaders (Bouchet and Taviani 1992a, b) and/or for Mediterranean migrants (De Mol et al. 2005; Henry et al. 2014), a pivotal role in modeling the present Mediterranean deep water benthos is played by the conspicuous climatic variations which markedly affected this semi-enclosed mid-latitude basin in the Plio-Pleistocene (Taviani 2002; Sabelli and Taviani 2014; Vertino et al. 2014; Dubois-Dauphin et al. 2017).

The aims of this chapter are twofold. Firstly, we present the distribution of coral life at depths >200 m in the Mediterranean Sea, by considering not only the scleractinian settling on hard substrates, but also allied cnidarian assemblages participating in forming antipatharian and octocoral forests, including some colonising soft substrata. Secondly, we discuss the main biogeographic traits of such taxa.

19.1.1 Cold-Water Corals *Sensu lato*

Cold-water corals (CWCs) have been usually defined as deep-water azooxanthellate colonial scleractinian (stony) corals distributed between ca. 200 and 1200 m (Freiwald et al. 2004). Other corals, not necessarily colonial scleractinians, are also included under the label of CWC (Roberts et al. 2006). From a holistic point of view, CWCs can be regarded as those cold-affinity azooxanthellate cnidarians, usually found below 200 m depth in the Mediterranean Sea, many of them acting as habitat formers. This wide definition includes both colonial stony corals building up bioconstructions able to persist for long periods of time after the death of the animals as well as other sessile cnidarians, mostly anthozoans, which can live in large aggregations (*facies*) significantly changing the structural heterogeneity of the environment where they are settled (Buhl-Mortensen et al. 2010). The different species fitting with this definition have been here distinguished for phenotypic sharp features which reflect taxonomic and ecological differences, both for hard and soft bottom species (Fig. 19.1). On hard bottoms, CWCs are broadly represented by the white corals *Desmophyllum dianthus* (Esper, 1794), *Lophelia pertusa* (Linnaeus, 1758) and *Madrepora oculata* Linnaeus, 1758, the black corals *Antipathes dichotoma* Pallas, 1766, *Leiopathes glaberrima* (Esper, 1788) and *Parantipathes larix* (Esper, 1788), the yellow coral *Dendrophyllia cornigera* (Lamarck, 1816), the alcyonaceans *Callogorgia verticillata* (Pallas, 1766) and *Viminella flagellum* (Johnson, 1863), and the stylasterid *Errina aspera* (Linnaeus, 1767) (Fig. 19.1). The alcyonacean *Isidella elongata* (Esper, 1788) and the pennatulaceans *Funiculina quadrangularis* (Pallas, 1766) and *Kophobelemnon stelliferum* (Müller, 1776) represents soft bottom CWCs (Fig. 19.1). Thus, the term CWC as used here groups taxa with a pronounced frame-building ability (e.g. *L. pertusa* and *M. oculata*) with forest-forming organisms both on hard (e.g. *C. verticillata*, *V. flagellum* and Antipatharia) and soft substrata (e.g. *I. elongata* and Pennatulacea). Many of these species belong to the threatened categories reported in the IUCN Red List of Mediterranean Anthozoa (Otero et al. 2017; Otero and Marin, this volume), i.e. 'critically endangered' (*I. elongata*), 'endangered' (*D. dianthus*, *L. pertusa*, *M. oculata*, *L. glaberrima*, *D. cornigera*) and 'vulnerable' (*F. quadrangularis*). Four species are considered 'near threatened' (*A. dichotoma*, *P. larix*, *C. verticillata*, *V. flagellum*) and only one (*K. stelliferum*) has been categorised as 'least concern' (i.e. not considered to be under any known threat of extinction now or in the foreseeable future).

This heterogeneous ensemble has received attention of different quality and quantity, mainly depending on the substratum on which the organisms settle. Deep-sea soft bottom habitats have been historically surveyed much longer than those of hard bottoms due to being easier to sample (e.g. using trawls, dredges, grabs and corers). Notwithstanding, the advances in deep-sea exploration technologies, applied to previously unexplored hard bottoms, have provided in the last decade a wide set of in vivo high quality data about the presence and distribution of CWCs. As a result, even if their exploration only started a few decades ago, deep-sea hard bottom habitats can be considered much more precisely surveyed and explored with respect to soft bottom ones in terms of visual information and data resolution.

In the case of soft bottom CWCs, the traditional and destructive methods used to study incoherent substrata provided an extensive and useful amount of presence data at medium/large scale. On the other hand, these methods provided only weak information about species density, large and small-scale distribution and key habitat features. Moreover, since soft bottoms are affected by trawl fishing, this information may be subject to rapid change due to fishing pressures and biological data for soft bottoms need to be updated often. On the contrary, deep hard bottom CWC habitats are only marginally influenced by bottom trawling, but still suffer the effects of artisanal and recreational fishing activities (e.g. longline) targeting commercial species taking place within or around these ecosystems (D'Onghia et al. 2003; Orejas et al. 2009; Bo et al. 2014a, 2015; Mytilineou et al. 2014). These fishing impacts can be either direct (e.g. mechanic damage and catches) or indirect (e.g. lost fishing gears). Despite pristine (i.e. not impacted whatsoever) examples are nowadays considered to be very limited in the Mediterranean basin (Bo et al. 2015), it is plausible to hypothesise that hard bottoms are, overall, less affected with respect to soft bottoms due to their heterogeneous distribution and relative inaccessibility to the most damaging fishing activities. Because of their high ecosystem value, deep CWC habitats (including both those with frame-building corals and coral

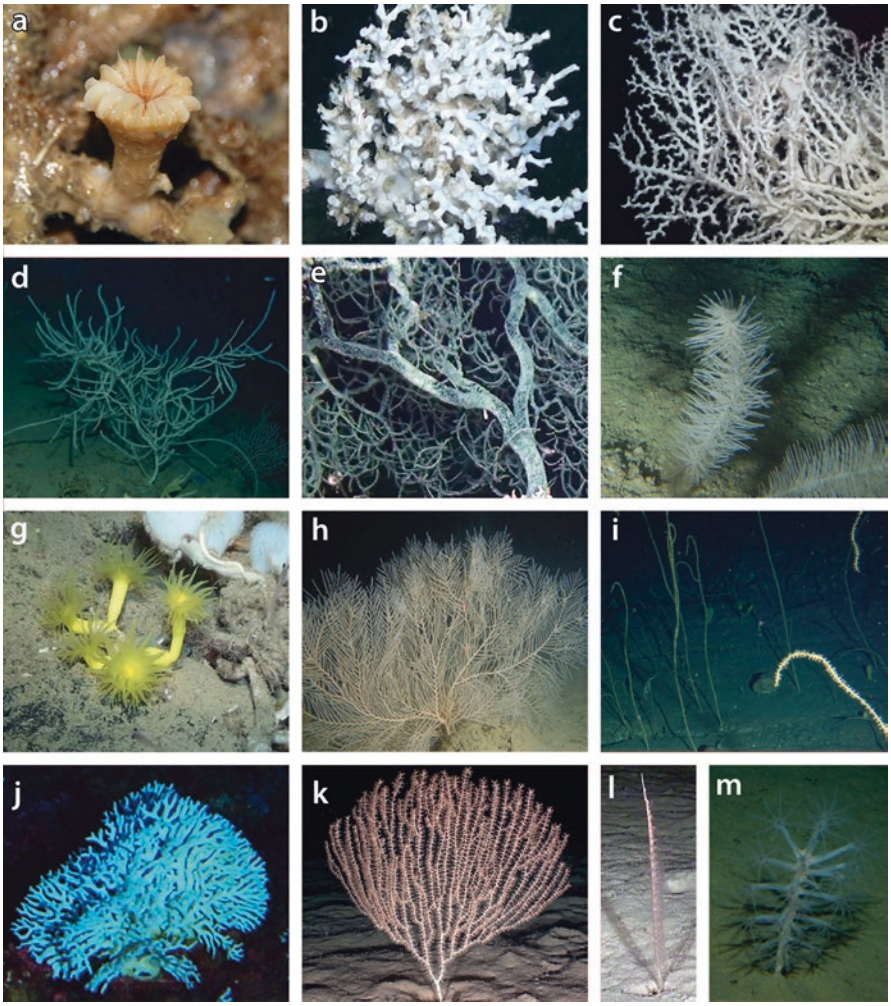


Fig. 19.1 Hard bottom CWCs: (**a**) *Desmophyllum dianthus*, (**b**) *Lophelia pertusa*, (**c**) *Madrepora oculata*, (**d**) *Antipathes dichotoma*, (**e**) *Leiopathes glaberrima*, (**f**) *Parantipathes larix*, (**g**) *Dendrophyllia cornigera*, (**h**) *Callogorgia verticillata*, (**i**) *Viminella flagellum*, (**j**) *Errina aspera*. Soft bottom CWCs: (**k**) *Isidella elongata*, (**l**) *Funiculina quadrangularis*, (**m**) *Kophobelemnon stelliferum*. ((**a**–**c**, **e**, **g**) Courtesy of L. Angeletti; (**d**, **m**) modified from Bo et al. (2011); (**f**) courtesy of Cau A., MIPAAF (Montecristo shoals, Tuscany; 160 m); (**h**) modified from Bo et al. (2014c); (**i**) courtesy of MIPAAF, Regione Sardegna (Porto Corallo, Sardinia; 160 m); (**j**) modified from Salvati et al. (2010); (**k**, **l**) modified from Mastrototaro et al. (2017))

forests) have sparked an exponential interest in the international scientific community and a relevant intensification of the deep Mediterranean seabed exploration (e.g. Hebbeln et al. 2009; Orejas et al. 2009; Vertino et al. 2010; Taviani et al. 2011a; Gori et al. 2013; Savini et al. 2014; Bo et al. 2015).

By-catch and accidental trawling and artisanal fishing (e.g. Tursi et al. 2004; Schembri et al. 2007; Deidun et al. 2010; Mastrototaro et al. 2010; Mytilineou et al. 2014) wryly revealed numerous Mediterranean coral sites, representing a starting point for the study of hard bottom CWC habitats distribution. These findings aroused great interest in the scientific community in the context of the on-going research on deep coral habitats worldwide, contributing to stimulate the carrying of targeted oceanographic missions in these areas and afterwards in other areas with similar hydrological and morphological features. Occasional and sporadic findings of single specimens or sparse populations of living CWC species were soon followed by the extraordinary occurrence of lush coral sites, with highly structured CWC communities, clustered in specific areas where suitable topographic and oceanographic conditions were simultaneously present (e.g. Freiwald 2002; Canals et al. 2006; Orejas et al. 2009; Deidun et al. 2010; Vertino et al. 2010; Taviani et al. 2011a; Gori et al. 2013; Bo et al. 2015; Grinyó et al. 2016). In the case of frame-building corals, such localities are currently known as CWC provinces.

19.2 Mediterranean CWC Occurrences

Areas characterised by a large coral growth and colony density are recognised as CWC provinces (Taviani et al. 2011a). The term "province" has been previously used in the northeast Atlantic to define large coral mound aggregations developing in areas of some square kilometers (e.g. Kozachenko et al. 2002; Wheeler et al. 2005; Huvenne et al. 2005; Henriet et al. 2014). The real biogeographical meaning of the term comes from the Botany, where it defines "*a major division of the biosphere, a phitogeographical subdivision of a region characterized by dominand plant species of similar past history, or a biogeographical zone characterized by a 25–50% endemic flora or fauna*" (Lincoln and Clark 1998). Considering the increasing discoveries of CWC areas and

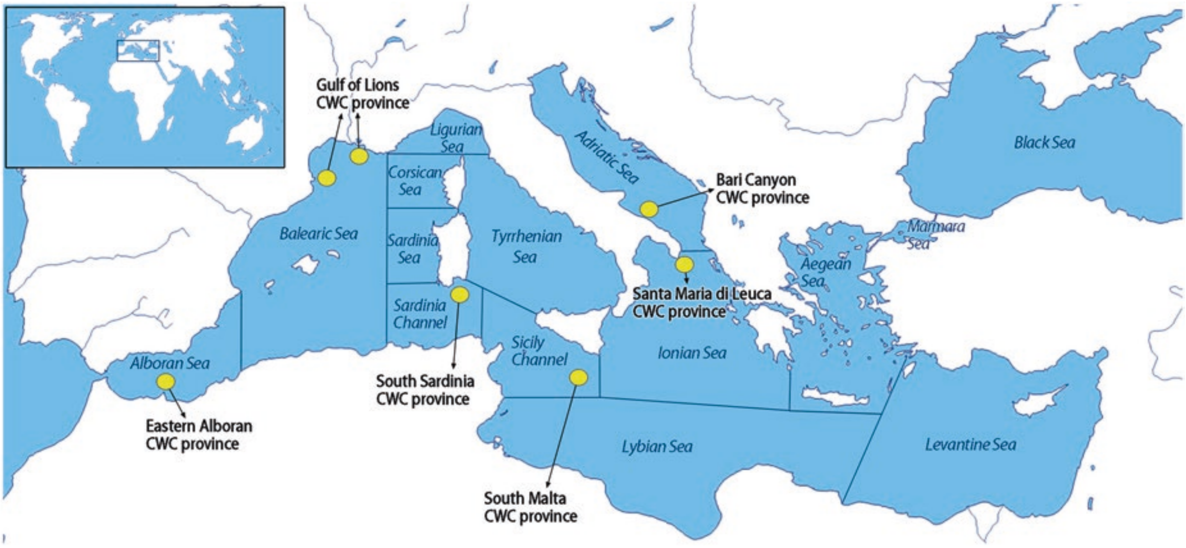


Fig. 19.2 Main sectors of the Mediterranean Sea and location of the six CWC provinces described up to date

their importance, the definition of coral province should be revisited in the future (Chimienti et al. 2018b).

A total of six provinces characterised by the two main framework-forming CWC species, *Madrepora oculata* and *Lophelia pertusa*, has been identified up to date in the Mediterranean Sea (Taviani et al. 2017). These CWC provinces are located, from East to West, in the northern Ionian Sea (Santa Maria di Leuca), in the southwestern Adriatic Sea (Bari Canyon), in the Sicily Channel (South Malta), in the Sardinia Channel (South Sardinia), in the canyons system of the Gulf of Lions and in the eastern Alborán Sea (Fig. 19.2). A description of each CWC province and its environs is provided in the following paragraphs.

19.2.1 Northern Ionian Sea

A large CWC province develops patchy over an area of about 1000 km^2 from 300 to 1100 m depth off Cape Santa Maria di Leuca (Ionian Sea, Italy; Fig. 19.2). This province is by far the best studied deep-sea area of the Mediterranean Sea and the CWC habitat for which most information is available, having been the subject of many research projects and oceanographic missions (e.g. Taviani et al. 2005b, 2011a; Freiwald et al. 2009; Mastrototaro et al. 2010; D'Onghia et al. 2012; Savini et al. 2014). As revealed by acoustic surveys, remotely operated vehicle (ROV) observations and bottom sampling, this CWC province is typified by an array of deep-water coral-rich and coral-poor contexts, or mega-habitats, that provide detritus to bottom sediments, as is usual in CWC banks (Vertino et al. 2010).

Santa Maria di Leuca CWC province (Fig. 19.3) is populated by the emblematic stony corals *M. oculata*, *L. pertusa* and *Desmophyllum dianthus* as well as by the alcyonacean *Callogorgia verticillata*, throughout a wide bathymetric range, from about 450 to 1000 m depth, with a luxuriant coral growth between 500 and 700 m depth (Mastrototaro et al. 2010). On the upper part of the mound field, these corals have been found in mixed aggregations with *Dendrophyllia cornigera* (447–613 m), *Antipathes dichotoma* (630–640 m) and *Leiopathes glaberrima* (200–790 m) (Carlier et al. 2009; Freiwald et al. 2009; Mastrototaro et al. 2010), while a dense population of the sea pen *Kophobelemnon stelliferum* has been found from 404 to 467 m depth on the muddy seabed around the mounds, currently representing the largest population of this species ever found in the Mediterranean Sea (Mastrototaro et al. 2013).

Freiwald et al. (2009) reported the occurrence of living *M. oculata* (670–744 m), *L. pertusa* (603–744 m) and *D. dianthus* about 14 nautical miles (nm) WNW from Santa Maria di Leuca CWC province, at the Gallipoli escarpment. This near-vertical escarpment forming the eastern wall of a major canyon system was characterised by metre-size *L. pertusa* bioconstructions with living corals settled on fossilised coral frameworks. Northern Gallipoli, off the Porto Cesareo Marine Protected Area, some living colonies of *D. cornigera* have been also observed up to 217 m depth (D'Onghia et al. 2016).

19.2.2 Southern Adriatic Sea

The Bari Canyon is an asymmetric East-West oriented two-branch incision located ca. 16 nm offshore from the city of Bari (southern Adriatic Sea, Italy; Fig. 19.2), and characterised by sub-vertical flanks in its southern part and less steep flanks northward. Flanks form a levee complex and evolve basinwards into gentler morphologies at a bathymetric range

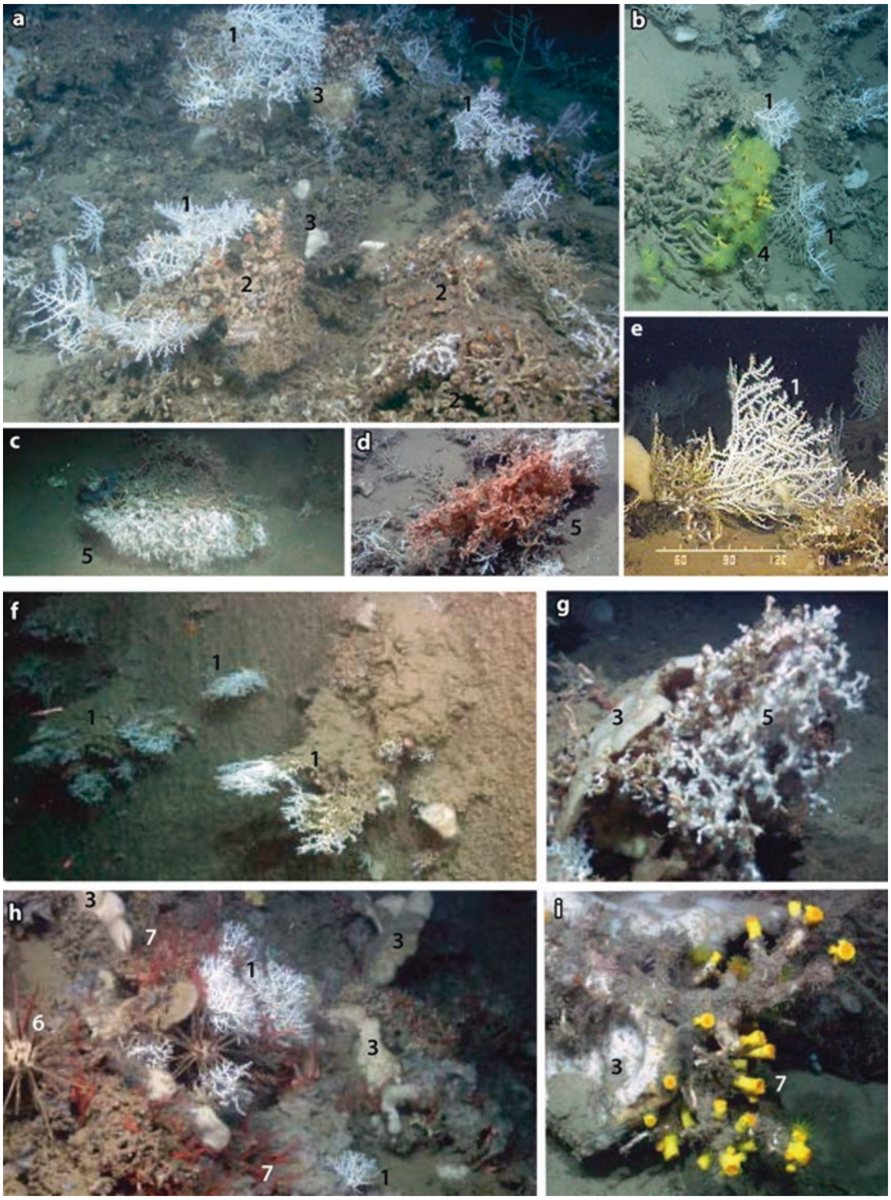


Fig. 19.3 Northern Ionian Sea and southern Adriatic Sea CWC provinces: (**a**–**e**) Santa Maria di Leuca, (**f**–**i**) Bari Canyon. (**a**) Fossil frameworks with living *Madrepora oculata* (*1*), *Desmophyllum dianthus* (*2*) and sponges (*3*); (**b**) *Dendrophyllia cornigera* clusters (*4*) and *M. oculata* (*1*); (**c**) white and (**d**) orange *Lophelia pertusa* colonies (*5*); (**e**) *M. oculata* colonies (*1*) on flat bottom. (**f**) *M. oculata* colonies (*1*) on steep slope; (**g**) *L. pertusa* (*5*) with sponge (*3*); (**h**) fossil frameworks colonised by living *M. oculata* (*1*) and sponges (*3*) with several sea urchins *Cidaris cidaris* (Linnaeus, 1758) (*6*) and ophiuroids (*7*); (**i**) *D. cornigera* (*4*) associated with sponges (*3*). ((**a**–**d**, **f**–**i**) Modified from Freiwald et al. (2011); (**e**) modified from D'Onghia et al. (2008))

of 200–1700 m (Trincardi et al. 2007; Freiwald et al. 2009; Angeletti et al. 2014; D'Onghia et al. 2015). *Madrepora*-dominated build-ups (Fig. 19.3) develop from 280 to 600 m depth, with dense aggregations of *D. dianthus* reported from 490 to 664 m depth (Freiwald et al. 2009, 2011; D'Onghia et al. 2015). *Lophelia pertusa* (306–640 m) and *D. cornigera* (445–494 m) also occur but are less abundant (Freiwald et al. 2009; Angeletti et al. 2014).

About 26 nm northeast of the Bari Canyon CWC province, some CWC growth is present on slumped blocks of the Gondola slide, with *M. oculata* between 184 and 372 m depth and *L. pertusa* colonising deeper hardgrounds, between 674 and 714 m depth (Freiwald et al. 2009; D'Onghia et al. 2016).

On the other side of the Adriatic Sea, diametrically opposite to the Bari Canyon, another CWC area has been recently discovered in a canyon system with depths of down to 400 m off the Montenegro coast (Angeletti et al. 2014). Here rocky blocks, boulders and hardgrounds emerging from the soft sediment are colonised at depths of 420–490 m by a conspicuous CWC assemblage composed of *M. oculata*, small colonies of *L. pertusa*, well-developed *L. glaberrima* colonies, clusters of *D. cornigera* and patchy dense aggregations of *C. verticillata*. In this area, *M. oculata* and *D. cornigera* have been observed down to 540 m depth (Angeletti et al. 2014), while fishermen reported some accidental catches by longline of *M. oculata* and *L. glaberrima* until 1000 m depth (D'Onghia et al. 2016). The occurrence of such a rich CWC community on the southeastern Adriatic margin is significant for the understanding of the connectivity between discontinuous deep-water coral grounds in this sector of the southern Adriatic Sea and especially with the Bari Canyon CWC province (see also Boavida et al., this volume).

South of Bari Canyon, additional CWC sites have been identified on the Apulian margin, off Monopoli and off the Salento peninsula, close to Tricase village. In this last area, the escarpment is incised by several canyons and with a wide apron at the base, likely due to slumping from the margin (Angeletti et al. 2014). The canyon base (720–786 m) is characterised by the presence of blocks colonised by living *D. dianthus* as well as by *L. pertusa* and *M. oculata* colonies. Living CWCs also occur southwards, along the Salento peninsula, in the Otranto Strait (778 m), next to the midline between Italy and Albania, where few colonies of the stony corals *M. oculata* and *L. pertusa* were observed at 775–778 m depth. These recent findings highlight that CWC communities are much commoner in the southern Adriatic than previously supposed, suggesting the presence of an almost continuous belt of patchy CWC sites spread along the southwestern Italian margin, broadly connecting the Adriatic populations (i.e. Bari Canyon) with those present in the northern Ionian Sea (i.e. Santa Maria di Leuca) (Taviani et al. 2011a; Angeletti et al. 2014).

19.2.3 Sicily Channel

Live CWCs occur at various sites in the Sicily Channel between 200 and 1000 m, mainly settling on escarpments, seamounts, and the flanks of volcanic islands (Freiwald et al. 2009). Based upon the accidental collection of live *M. oculata* and *L. pertusa* (Schembri et al. 2007), a CWC province has been defined about 11 nm southwest of Malta (Taviani et al. 2011a, 2015) (Figs. 19.2 and 19.4). This province is characterised by a highly structured CWC community (Deidun et al. 2015). Following a belt dominated by *L. glaberrima* between 200 and 400 m, the white corals *M. ocu-*

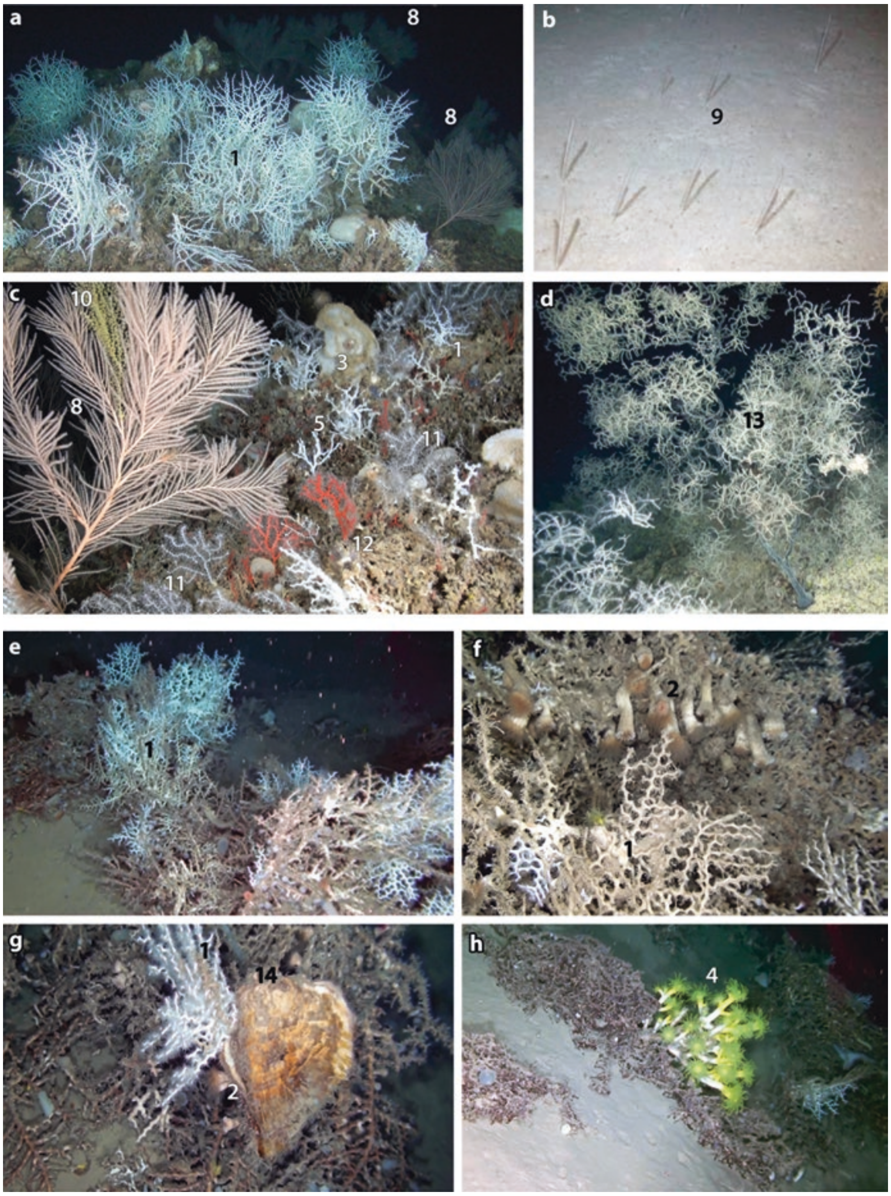


Fig. 19.4 Sicily Channel and South Sardinia CWC provinces: (**a**–**d**) South Malta, (**e**–**h**) South Sardinia. (**a**) *Madrepora oculata* framework (*1*) and *Callogorgia verticillata* (*8*); (**b**) *facies* of *Funiculina quadrangularis* (*9*); (**c**) Mixed aggregation of *C. verticillata* (*8*) parasitised by *Savalia savaglia* (*10*), *M. oculata* (*1*), *Lophelia pertusa* (*5*), *Muriceides lepida* (*11*), *Corallium rubrum* (*12*) and massive sponges (*3*); (**d**) *Leiopathes glaberrima* forest (*13*) with *M. oculata* (*1*). (**e**) *M. oculata* frameworks (*1*); (**f**) Mixed *M. oculata* framework (*1*) and *Desmophyllum dianthus* pseudo-reef (*2*); (**g**) framework of *M. oculata* (*1*) with a living specimen of the deep-sea giant oyster *Neopycnodonte zibrowii* (*14*) settled on *M. oculata* (*1*) and *D. dianthus* (*2*); (**h**) *Dendrophyllia cornigera* (*4*) on dead *M. oculata* rubble. ((**a**–**c**) Photo copyright OCEANA ©LIFE BaĦAR for N2K; (**d**) modified from Freiwald et al. (2011); (**e**–**h**) modified from Taviani et al. (2017))

lata, *L. pertusa* and *D. dianthus* appear at ca. 300 m and then predominate between 390 and 650 m, extending down to 1000 m (Schembri et al. 2007; Freiwald et al. 2009; Knittweis et al., this volume). In addition, living colonies of *D. cornigera* occur, as well as the calcitic gorgonian *Corallium rubrum* (Linnaeus, 1758) here reaching its deepest known record of 1016 m (Freiwald et al. 2009; Costantini et al. 2010; Taviani et al. 2010; Knittweis et al. 2016). *Callogorgia verticillata* is present all along the CWC province with the development of lush gardens from 800 to 1000 m depth (Knittweis et al., this volume). Active CWC recruitment in the area has been suggested since 2007 by the occurrence of small *L. pertusa* colonies living on a lost fishing line at 622–667 m depth (Schembri et al. 2007). On the muddy bottom around the coral banks, from 457 to 611 m depth, the community is dominated by the soft bottom CWC *Isidella elongata* and *Funiculina quadrangularis* (Freiwald et al. 2009). Moreover, a dense *L. glaberrima* forest, comprising more than 2000 colonies with a maximum density of 4–5 adult colonies m^{-2}, was reported 6 nm off the southwestern coasts of Malta along deep (250–400 m) rocky terraces in a marine area exploited by fisheries (Deidun et al. 2015). A rich associated fauna was reported within and in the immediate proximity of the antipatharian forest. Some uncommon species such as large clusters of the giant barnacle *Pachylasma giganteum* (Philippi, 1836) have been found solely in the South Malta CWC province (Schembri et al. 2007). A comprehensive review on the associated fauna of the Mediterranean CWC communities is provided by Rueda et al. (this volume), while Altuna and Poliseno (this volume) offer a comprehensive overview on the CWC taxonomy.

Living CWCs are also present at ca. 500–680 m on the eastern flank of the Nameless Bank (also called Urania Bank) and on the southern flank of Linosa island (Freiwald et al. 2009) as large colonies of *M. oculata* and smaller and less abundant ones of *L. pertusa*. Additionally, *D. cornigera* thrived under overhangs (733 m) and in large caves formed by the volcanic bedrock on the southern slope of the Linosa Trough (Freiwald et al. 2009).

19.2.4 South Sardinia and South Tyrrhenian Sea

A rich CWC site has been recently identified off the southern coast of Sardinia (Fig. 19.2), in the Nora canyon, part of the Capo Spartivento canyon system (Taviani et al. 2017). This area has been named as South Sardinia CWC province, characterised by a flourishing population of *M. oculata* between 380 and 460 m and by the co-occurrence of *D. dianthus*, with only occasional colonies of *L. pertusa* and *D. cornigera* observed at 452 and 440 m, respectively (Taviani et al. 2017) (Fig. 19.4). No direct coral growth on hard substrata has been reported in this CWC province, where corals grow only on dead coral frameworks, probably because of high mud sedimentation. Relatively close to this site, *M. oculata* was recorded northwest of Sicily, on the Aceste Seamount, and *D. dianthus* off northern Sicily, from Enarete Seamount and Filicudi banks (Freiwald et al. 2011).

19.2.5 Gulf of Lions

Lush CWC communities are patchy located in the northwest Mediterranean canyons between Cap de Creus and the Ligurian Sea, in the wide Catalan-Provençal-Ligurian canyon system straddling the Balearic and the Ligurian Sea (Bourcier and Zibrowius 1973; Tunesi et al. 2001; Orejas et al. 2009; Gori et al. 2013; Fabri et al. 2014; Fourt et al. 2015, this volume; Puig and Gili, this volume) (Fig. 19.5). In particular, the Gulf of Lions (Fig. 19.2) is currently considered the core of this large province, where CWCs are settled on the vertical walls of this crescent-shaped continental margin. In this area, the continental shelf width reaches a maximum of ca. 70 km and the shelf break is located at ca. 120 m depth, with the slope incised by numerous submarine canyons that extend down to the continental rise at more than 2000 m depth. The continental margin of the Gulf of Lions displays one of the highest canyon densities of the world (Würtz 2012). Cap de Creus and Lacaze-Duthiers canyons represent the westernmost submarine canyon system of the Gulf of Lions. Well-developed CWC communities have been documented on the rocky flanks of both canyons (Pérès and Picard 1964; Reyss 1964; Orejas et al. 2009; Watremez 2012; Gori et al. 2013; Fourt et al. 2014, this volume; Puig and Gili, this volume). These communities are dominated by *M. oculata*, while *L. pertusa* and *D. cornigera* are less common, being present as isolated colonies or small patches (Orejas et al. 2009; Watremez 2012; Gori et al. 2013). In particular, the population of *M. oculata* found on the southern flank of the Cap de Creus canyon seems to comprise one of the denser populations of this species in the Mediterranean Sea (Orejas et al. 2009), displaying maximum values of around ten colonies m^{-2}, although colony density data are still scarce within the Mediterranean Sea. On the eastern side of the Gulf of Lions, Cassidagne canyon hosts another rich CWC community similar to those of the western canyons (Fabri et al. 2014). The French canyons also host one of the shallower populations of *M. oculata* known for the basin so far (180–210 m depth) co-occurring, in an extraordinary assemblage, with *C. rubrum* and *Paramuricea clavata* (Risso, 1826) (Fig. 19.5). Living *M. oculata* was also found at 280 m depth during a recent exploration of the easternmost French canyons, in the Ligurian Sea (Fourt et al. 2015). The muddy bottoms lying between the canyons of the wide Catalan-Provençal-Ligurian canyon system host patchy populations of *I. elongata* and of the sea pens *K. stelliferum* and *F. quadrangularis*, these two last species sometimes forming mixed aggregations between 208 and 270 m (Fabri et al. 2014).

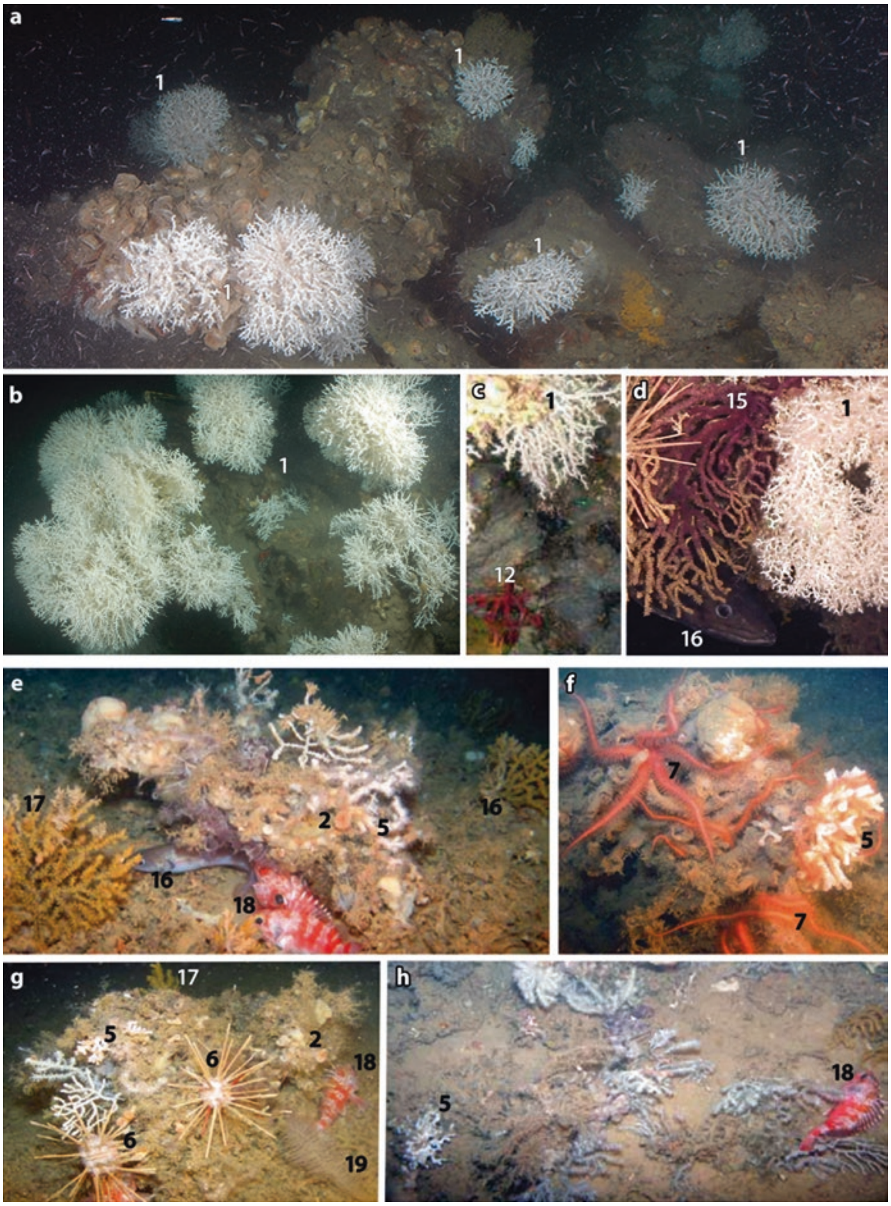


Fig. 19.5 Gulf of Lions and Alborán Sea CWC provinces: (**a**–**d**) Gulf of Lions, (**e**–**h**) Eastern Alborán Sea. (**a**) *Madrepora oculata* colonies (*1*) settled on an oyster reef; (**b**) *facies* of *M. oculata* (*1*); (**c**) mixed aggregation of *M. oculata* (*1*) and *Corallium rubrum* (*12*); (**d**) mixed aggregation of *M. oculata* (*1*) and *Paramuricea clavata* (*15*) with the fish *Conger conger* (Linnaeus, 1758) (*16*). (**e**) Aggregation of *Lophelia pertusa* (*5*), *Desmophyllum dianthus* (*2*), *Acanthogorgia hirsuta* (*17*) and other alcyonaceans on a coral framework, with the urcin *Cidaris cidaris* (*6*) and the fishes *C. conger* (*16*) and *Helicolenus dactylopterus* (Delaroche, 1809) (*18*); (**f**) *L. pertusa* (*5*) on coral framework with ophiuroids; (**g**) coral framework colonised by *L. pertusa* (*5*), *D. dianthus* (*2*), *Parantipathes larix* (*19*), *A. hirsuta* (*17*) and other aclyonacenas, with *C. cidaris* (*6*) and *H. dactylopterus* (*18*). (**h**) Mixed aggregation of white corals (e.g. *L. pertusa*, (*5*) and alcyonaceans on dead coral framework, with *H. dactylopterus* (*18*). ((**a**, **b**) Courtesy of ICM-CSIC/IFM-GEOMAR; (**c**, **d**) modified from Fabri et al. (2014); (**e**–**h**) modified from Hebbeln et al. (2009))

19.2.6 Eastern Alborán Sea

Hebbeln et al. (2009) reported the first large-scale occurrence of CWC assemblages from the Alborán Sea (Fig. 19.2), mainly from El Idrissi Bank, the Alborán Ridge and the East Melilla mounds. This latter area is located East of the Spanish city of Melilla, on the Moroccan coast, while the first two areas lie in the middle between Moroccan and Spanish coasts. El Idrissi bank is characterised by the patchy occurrence of *L. pertusa* between 387 and 676 m depth and *D. cornigera* between 288 and 465 m, together with forest-like aggregations of *L. glaberrima* (452–647 m), a thin *Parantipathes larix* belt (327–382 m) and the occasional occurrence of *C. verticillata* (657 m) and *V. flagellum* (360–432 m). On the soft sediments interspersed with the hard bottom CWC community, local rich aggregations of *I. elongata* (303–434 m) and *K. stelliferum* (reported as *K.* cf. *leuckarti*; 303–618 m) are present (Hebbeln et al. 2009). Proceeding southward, the Alborán Ridge hosts the hard bottom CWC *L. pertusa* (392–539 m), *M. oculata* (423–539 m), *D. cornigera* (423–426 m) and *P. larix* (404–407 m), while the surrounding soft bottom is colonised by *K. stelliferum* (517–602 m) and by occasional colonies of *Pennatula phosphorea* Linnaeus, 1758 (570 m). On the East Melilla seamounts, together with *L. pertusa* (308–365 m), *M. oculata* (200–360 m), *D. cornigera* (310 m) and *P. larix* (296–326 m), the solitary coral *D. dianthus* was found from 308 to 326 m depth (Hebbeln et al. 2009) (Fig. 19.5). Considered collectively, these three areas and some surrounding seamounts (Würtz and Rovere 2015) form a unique CWC province with a rich CWC community of both hard and soft bottom, from ca. 200 to 680 m depth.

A potential interesting area close to this CWC province is the mound field west of the city of Melilla, a few kilometres west of the Cape Tres Forcas, along the upper slope of the Mediterranean Moroccan continental margin, which hosts up to 103 mounds organised in two main clusters from 299 to 590 m depth, with a density of 5 mounds km^{-2}. Although this area may represent a promising new CWC site, only fossil CWC have been found to date (Lo Iacono et al. 2014).

Adjoining to the Alborán Sea, an extraordinary shallow CWC bank was reported by Álvarez-Pérez et al. (2005) in the Gibraltar Strait, with CWC settled mainly on coarse-grained sediments. This bank is characterised by *Lophelia*-dominated frameworks with a preferential depth range of 150–330 m with *M. oculata* and *E. aspera*, as well as the occasional presence of *D. dianthus* and *D. cornigera*. Despite not being very far from the eastern Alborán CWC province (ca. 110 nm), the Gibraltar Strait CWC community can be considered a distinct extra-Mediterranean province because the particular oceanographic conditions, mainly due to the water flowing from the Atlantic Ocean to the MediterraneanSea, give rise to this surprisingly shallow occurrence of CWC.

19.3 Hard Bottom CWCs

Deep hard bottoms have recently received an increasing attention from the scientific community due to the possibility to find CWC communities. Precipitous (e.g. canyon heads and seamount walls) or rugged (e.g. hardgrounds and slumped blocks) topographies can be suitable for the settlement of CWCs (Genin et al. 1986; Würtz 2012; Würtz and Rovere 2015) if coupled with certain oceanographic conditions such as low temperature and enhanced currents, strong enough to prevent burial by deposition of fine sediment and to transport food to the coral polyps (Frederiksen et al. 1992; Thiem et al. 2006; Kiriakoulakis et al. 2007).

19.3.1 The White Triad

Among CWCs, many data on presence and distribution regard the so-called ‘white coral triad’ (Pérès and Picard 1964; Taviani et al. 2005b), namely the solitary coral *D. dianthus* as well as the colonial corals *Madrepora oculata* and *Lophelia pertusa*, this latter recently proposed to be revised in *Desmophyllum pertusum* (Addamo et al. 2015; Addamo, this volume). Although these three species do not represent the only living CWCs in the Mediterranean basin, they have one of the largest bioconstruction capability, promoting the growth of conspicuous structures (Chimienti et al. 2018b). *Desmophyllum dianthus* can provide small, scattered hard substrata on pre-existent coherent substratum and can locally reach high densities (pseudo-colonial bank-building species), being usually the faster white coral colonising a substratum as a sort of pioneer CWC (Aymà et al., this volume; Fourt et al., this volume). The branched stony corals *M. oculata* and *L. pertusa* are able to build-up huge frameworks that in certain cases exceed a metre of height and width per colony (e.g. Pardo et al. 2011; Angeletti et al. 2014; Taviani et al. 2016; Fanelli et al. 2017). The finding of *Madrepora-Lophelia* ‘false chimaeras’ (i.e. coral bushes made from different CWC species) also revealed the ability of CWC larvae to settle on already established living colonies of both the same species or a different one (Tursi et al. 2004; Arnaud-Haond et al. 2015). CWCs frameworks can remain after the death of the polyps (or the death of a portion of the colony), representing a valuable hard substratum for many associated species (Mastrototaro et al. 2010; Vertino et al. 2010). In fact, the highest α-diversity in CWC grounds is shown primarily in the dead part of the coral framework and within the proximal sediments (Freiwald and Wilson 1998; Roberts et al. 2009b). Thus the ecosystem engineer role of these corals is expressed especially with the calcareous framework remaining after the partial death of the colony, which allows the settlement of other corals or other sessile organisms on this calcareous substratum. On a geological time scale, such high-structured build-ups can produce true carbonate mounds, sometimes encompassing many hundred thousands to millions of years of discontinuous coral succession (Wheeler et al. 2007; Taviani et al. 2011a).

Until the advent of deep-sea exploration technologies, CWC frameworks dominated by the so-called white corals were considered present in the Mediterranean Sea only as dead loose corals and skeletal remains of a Pleistocenic prosperity, afterwards shattered by the emerging oceanographic post-glacial conditions (Zibrowius 1980; Delibrias and Taviani 1985). Limited initial findings of living white corals (e.g. Pérès and Picard 1964; Fredj and Laubier 1985; Tunesi and Diviacco 1997; Taviani et al. 2005a, b) and concomitant discoveries of true living deep-sea reefs (e.g. Mastrototaro et al. 2002; Schembri et al. 2007) overturned the concept of extinct (or almost extinct) white corals in the Mediterranean Sea (Taviani, this volume) and, currently, at least 37 different local occurrences of living CWC belonging to the ‘white triad’ have been reported in the literature (Table 19.1; Fig. 19.6). In particular, the presence of *M. oculata* and *L. pertusa* in the Ionian Sea has been well known since more than a century. The first documented finding of these two species in the Mediterranean dates back to the collections

Table 19.1 Occurrence and depth range of CWCs in the Mediterranean Sea

Basin	Area	ID	Depth (m)	Species	References
Atlantic Ocean	Gibraltar Strait	1	150–330	*D. dianthus*	Álvarez–Pérez et al. (2005)
			150–330	*L. pertusa*	
			150–330	*M. oculata*	
			–	*D. cornigera*	
			150–330	*E. aspera*	
Alboran Sea	**Eastern Alboran CWC province**	**2**	308–410	*D. dianthus*	Hebbeln et al. (2009), Pardo et al. (2011), Aguilar et al. (2013), Maldonado et al. (2013), and Würtz and Rovere (2015)
			308–676	*L. pertusa*	
			200–539	*M. oculata*	
			320–410	*A. dichotoma*	
			320–400	*A. subpinnata*	
			462–647	*L. glaberrima*	
			296–458	*P. larix*	
			288–465	*D. cornigera*	
			320–657	*C. verticillata*	
			90–500	*V. flagellum*	
			303–434	*I. elongata*	
			303–618	*K. stelliferum*	
	Avempace Bank, Los Olivos Shoal and Off Motril	3	350–400	*L. pertusa*	Ocaña et al. (2000), Pardo et al. (2011), and Aguilar et al. (2013)
			350–400	*M. oculata*	
			350–400	*A. dichotoma*	
			350–400	*C. verticillata*	
			350–400	*I. elongata*	
			150–300	*F. quadrangularis*	
			150–400	*K. stelliferum*	
	Chella Bank	4	243–486	*L. pertusa*	Hebbeln et al. (2009), Pardo et al. (2011), Lo Iacono et al. (2012), and Aguilar et al. (2013)
			118–486	*M. oculata*	
			300	*A. dichotoma*	
			300	*P. larix*	
			125–300	*D. cornigera*	
			118–400	*C. verticillata*	
			118–130	*V. flagellum*	
			320–497	*K. stelliferum*	
Balearic Sea	Mallorca Channel and Emile Baudot Escarpment	5	300–950	*D. dianthus*	Aguilar et al. (2013, 2014), de la Torriente et al. (2014), and Mastrototaro et al. (2017)
			–	*A. dichotoma*	
			–	*L. glaberrima*	
			–	*P. larix*	
			–	*C. verticillata*	
			90–500	*V. flagellum*	
			480–615	*I. elongata*	
			473–616	*F. quadrangularis*	
	Menorca Channel	6	180–330	*D. cornigera*	Gori et al. (2014b), López–González et al. (2015), and Grinyó et al. (2016)
			92–187	*A. dichotoma*	
			115–200	*L. glaberrima*	
			100–360	*C. verticillata*	
			100–360	*V. flagellum*	
			112–267	*F. quadrangularis*	
	Northeast Menorca	7	301–1163	*D. dianthus*	Montagna et al. (2006)
	South Catalonia	8	418–1656	*I. elongata*	Maynou and Cartes (2012) and Cartes et al. (2013)
	La Fonera Canyon	9	130–370	*M. oculata*	Lastras et al. (2016)
			130–325	*D. cornigera*	

(continued)

Table 19.1 (continued)

Basin	Area	ID	Depth (m)	Species	References
	Gulf of Lions CWC province	**10**	246–541	*D. dianthus*	Bourcier and Zibrowius (1973), Zibrowius (2003), Orejas et al. (2009), Fourt and Goujard (2012), Gori et al. (2013), Fabri et al. (2014), and Fourt et al. (2014, 2015)
			180–541	*L. pertusa*	
			180–541	*M. oculata*	
			200–210	*A. dichotoma*	
			200–350	*L. glaberrima*	
			200–250	*P. larix*	
			185–537	*D. cornigera*	
			200–420	*C. verticillata*	
			100–400	*V. flagellum*	
			375–543	*I. elongata*	
			80–270	*F. quadrangularis*	
			200–500	*K. stelliferum*	
Ligurian Sea	South-West Nice	11	280	*M. oculata*	Fabri et al. (2014) and Fourt et al. (2014, 2015)
			300	*A. dichotoma*	
			100–400	*V. flagellum*	
			208–445	*F. quadrangularis*	
	Off Bergeggi (Transylvania wreck)	12	630	*M. oculata*	Gay pers. comm.
	Vado Ligure Canyon	13	344	*L. glaberrima*	Bo pers. comm.
	Mantice Shoal	14	80–120	*D. cornigera*	Bo et al. (2014c)
	Gulf of Tigullio	15	212–561	*M. oculata*	Rossi (1958), Tunesi and Diviacco (1997), and Tunesi et al. (2001)
			173–257	*F. quadrangularis*	
	Santa Lucia Bank	16	140–210	*A. subpinnata*	Bo et al. (2014c)
			140–210	*A. dichotoma*	
			140–210	*L. glaberrima*	
			140–210	*P. larix*	
			140–210	*D. cornigera*	
			200	*V. flagellum*	
	Off Punta Mesco/ Levante Canyon	17	200–560	*M. oculata*	Fanelli et al. (2017)
Corsican Sea	West Corse	18	100–550	*C. verticillata*	Fourt et al. (2014)
			100–400	*V. flagellum*	
	South Corse	19	480	*D. dianthus*	Fourt et al. (2014)
Tyrrhenian Sea	Tuscan Archipelago	20	100–200	*A. dichotoma*	Morri et al. (1991) and Bo et al. (2014b)
			100–200	*A. subpinnata*	
			100–200	*L. glaberrima*	
			150–200	*P. larix*	
			150–200	*D. cornigera*	
			100–200	*C. verticillata*	
			100–200	*V. flagellum*	
			97–200	*K. stelliferum*	
			275–280	*F. quadrangularis*	
	Off Civitavecchia	21	–	*D. dianthus*	Taviani et al. (2016)
	Tavolara Canyon	22	150–280	*P. larix*	Cau pers. comm.
			150–260	*D. cornigera*	
			170–250	*F. quadrangularis*	
	Off Ponza and Palmarola	23	130–300	*A. dichotoma*	Ingrassia et al. (2016) and Bo pers. comm.
			130–300	*L. glaberrima*	
			100–220	*P. larix*	
			194–220	*C. verticillata*	
	Off Ventotene	24	420	*D. dianthus*	Bortoluzzi pers. comm.
			420	*L. glaberrima*	
	Palinuro seamount	25	210	*L. glaberrima*	Bo pers. comm.
			120–250	*D. cornigera*	

(continued)

Table 19.1 (continued)

Basin	Area	ID	Depth (m)	Species	References
	St Eufemia Gulf	26	90–120	*A. dichotoma*	Porporato et al. (2009) and Bo et al. (2012)
			90–120	*P. larix*	
			90–120	*C. verticillata*	
			70–400	*F. quadrangularis*	
			70–130	*K. stelliferum*	
	Gioia Canyon	27	450	*I. elongata*	Pierdomenico et al. (2016)
			130–410	*F. quadrangularis*	
			450	*K. stelliferum*	
	Enarete Seamount and Filicudi Bank	28	–	*D. dianthus*	Freiwald et al. (2011)
			–	*D. cornigera*	
	Marco Bank and Aceste Seamount	29	–	*M. oculata*	Freiwald et al. (2011) and Bo et al. (2014c)
			200–250	*A. dichotoma*	
			240–280	*L. glaberrima*	
			240–280	*C. verticillata*	
			260	*V. flagellum*	
Sardinia Sea and Sardinia Channel	Asinara Gulf (Corazzata Roma wreck)	30	1200	*D. dianthus*	Gay pers. comm.
	Southwest Sardinia	31	120–200	*A. dichotoma*	Bo et al. (2015)
			120–200	*L. glaberrima*	
			115–210	*P. larix*	
			115–210	*C. verticillata*	
			115–210	*I. elongata*	
	South Sardinia CWC province	**32**	380–460	*D. dianthus*	Cau et al. (2015) and Taviani et al. (2015)
			452	*L. pertusa*	
			380–460	*M. oculata*	
			330–450	*D. cornigera*	
			340	*V. flagellum*	
Sicily Channel	Off Pantelleria	33	120–240	*V. flagellum*	Giusti et al. (2012)
	Nameless Bank (Urania Bank)	34	509–604	*L. pertusa*	Freiwald et al. (2009, 2011)
			509–613	*M. oculata*	
	Linosa Through	35	669–679	*L. pertusa*	Freiwald et al. (2009, 2011)
			669–679	*M. oculata*	
			733	*D. cornigera*	
			487	*A. dichotoma*	Angeletti pers. comm.
			477–495	*V. flagellum*	
	Lampedusa shoals	36	270	*D. cornigera*	Bo pers. comm.
	Gela Basin	37	–	*D. dianthus*	Angeletti pers. comm.
			–	*L. pertusa*	
	Malta and **South Malta CWC province**	**38**	390–617	*D. dianthus*	Schembri et al. (2007), Freiwald et al. (2009), Deidun et al. (2015), Evans et al. (2016), and Knittweis et al. (this volume)
			390–667	*L. pertusa*	
			200–1000	*M. oculata*	
			100–400	*A. subpinnata*	
			200–800	*L. glaberrima*	
			–	*D. cornigera*	
			200–1000	*C. verticillata*	
			300–400	*V. flagellum*	
			457–611	*I. elongata*	
			–	*K. stelliferum*	
			457–611	*F. quadrangularis*	
	Malta Escarpment	39	310–315	*A. dichotoma*	Angeletti et al. (2015)
			310–315	*L. glaberrima*	
			300–310	*F. quadrangularis*	

(continued)

Table 19.1 (continued)

Basin	Area	ID	Depth (m)	Species	References
Ionian Sea	Messina Strait	40	90–220	*E. aspera*	Giacobbe (2001), Giacobbe et al. (2007), and Salvati et al. (2010)
	Amendolara Bank	41	120–180	*D. cornigera*	Bo et al. (2014c)
	Off Porto Cesareo	42	100–217	*D. cornigera*	D'Onghia et al. (2016)
	Gallipoli Escarpment	43	740	*D. dianthus*	Freiwald et al. (2009, 2011)
			603–744	*L. pertusa*	
			670–744	*M. oculata*	
	Santa Maria di Leuca CWC province	**44**	525–1100	*D. dianthus*	Mastrototaro et al. (2002, 2010, 2013), Tursi et al. (2004), Taviani et al. (2005a, b), Carlier et al. (2009), Freiwald et al. (2009, 2011), Gori et al. (2014b), Savini et al. (2014), and D'Onghia et al. (2016)
			469–1100	*L. pertusa*	
			425–1100	*M. oculata*	
			630–640	*A. dichotoma*	
			200–790	*L. glaberrima*	
			447–613	*D. cornigera*	
			425–910	*C. verticillata*	
			404–467	*K. stelliferum*	
	Northwest Kerkyra	45	496–508	*D. dianthus*	Taviani et al. (2015)
			413–535	*L. glaberrima*	
	Southwest Cephalonia	46	483–634	*D. dianthus*	Mytilineou et al. (2014)
			516–600	*A. dichotoma*	
			367–634	*L. glaberrima*	
			478–719	*I. elongata*	
Adriatic Sea	Tricase and Otranto escarpements	47	720–786	*D. dianthus*	Angeletti et al. (2014)
			720–786	*L. pertusa*	
			720–786	*M. oculata*	
	Off Monopoli	48	558	*M. oculata*	D'Onghia et al. (2016)
	Bari Canyon CWC province	**49**	490–664	*D. dianthus*	Freiwald et al. (2009, 2011), Angeletti et al. (2014), Gori et al. (2014b), and D'Onghia et al. (2015)
			306–640	*L. pertusa*	
			280–600	*M. oculata*	
			400–500	*A. dichotoma*	
			400–500	*L. glaberrima*	
			445–494	*D. cornigera*	
	Gondola slide	50	674–714	*L. pertusa*	Freiwald et al. (2009, 2011) and D'Onghia et al. (2016)
			184–372	*M. oculata*	
	Pomo/Jabuka pits	51	200	*F. quadrangularis*	Martinelli et al. (2013) and Bastari et al. (2017)
	Montenegrian margin	52	420–490	*D. dianthus*	Angeletti et al. (2014), D'Onghia et al. (2016), and Angeletti pers. comm.
			420–490	*L. pertusa*	
			420–1000	*M. oculata*	
			420–440	*A. dichotoma*	
			420–1000	*L. glaberrima*	
			420–540	*D. cornigera*	
			420–490	*C. verticillata*	
Aegean Sea	South Crete	53	520–620	*D. cornigera*	Smith et al. (2009)
	Karpathos	54	600	*D. cornigera*	Gori et al. (2014b)
	Chios	55	60–200	*C. verticillata*	Vafidis et al. (1994)
	Antipsara	56	420	*D. cornigera*	Gori et al. (2014b)
	Kyra Panayia/Mount Athos	57	200–270	*D. cornigera*	Vafidis et al. (1994) and Gori et al. (2014b)
			60–200	*C. verticillata*	
	Northwest Lesbos	58	–	*D. cornigera*	Vafidis et al. (1994, 1997)
			60–200	*C. verticillata*	
	Thassos trough	59	300–350	*L. pertusa*	Vafidis et al. (1997)
			300–350	*M. oculata*	
Marmara Sea	Marmara trough	60	900–1200	*D. dianthus*	Taviani et al. (2011b)
Levantine Sea	South Cyprus	61	–	*D. dianthus*	Taviani et al. (2016)

ID numbers correspond to those in the maps within the text. CWC provinces are reported in bold

Fig. 19.6 Distribution of the white corals (i.e. *Desmophyllum dianthus*, *Lophelia pertusa* and *Madrepora oculata*) in the Mediterranean Sea. Numbers refer to the area ID given in Table 19.1

made by the Austrian research ship Pola in 1891 off Santa Maria di Leuca, where *M. oculata* and *L. pertusa* were dredged from a depth of 760 m (Steindachner 1891; Marenzeller 1893). Other Mediterranean reports of living white corals came a century later, from the Ligurian Sea, by Tunesi and Diviacco (1997), while the collection and identification of coral by-catch from the eastern Ligurian Sea occurred frequently in-between (Orsi-Relini pers. comm.). Meanwhile, similar single particular observations were made by Reyss (1964) and Bourcier and Zibrowius (1973) in the Gulf of Lions, as well as by Vafidis et al. (1997) in the Aegean Sea. A remarkable development in CWC exploration history came in 2000 with the accidental finding of a huge number of living colonies of *M. oculata* and *L. pertusa* between 630 and 1100 m depth during trawl fishing operations again off Cape Santa Maria di Leuca, in the northern Ionian Sea (Mastrototaro et al. 2002). This occurrence, expanded by further intentional coral sampling efforts, provided a large collection of living CWCs and the precise location of this first discovered CWC province in the Mediterranean Sea (Tursi et al. 2004). The finding of another two CWC provinces occurred in 2005 and 2007 in the Alborán Sea and in the Sicily Channel, respectively, by Álvarez-Pérez et al. (2005) and Schembri et al. (2007). In the same period, 2006, several CWC sites were reported in the Sicily Channel and southern Tyrrhenian Sea (Freiwald et al. 2011). The possible presence of a rich CWC assemblage in the Gulf of Lions canyons system was highlighted by Zibrowius (2003) after the observation and the dredging of white coral colonies, respectively during the cruises CYATOX1 in 1995 and DEPRO96 in 1996. A lush CWC assemblage in the area, discovered in 2006, was then described by Orejas et al. (2009). In the same year, the Bari Canyon CWC province was firstly explored by Freiwald et al. (2009) after the finding of relatively fresh-looking dead white corals dredged few years before by Trincardi et al. (2007). Finally, a sixth CWC province was recently documented by Taviani et al. (2017) in the Nora Canyon (southern Sardinia). The six CWC provinces currently recognised have been identified based on the occurrence of the 'white triad', with mainly *M. oculata*-dominated frameworks in four of the six provinces (i.e. Bari Canyon, South Malta, South Sardinia and Gulf of Lions) and both *M. oculata* and *L. pertusa* frameworks in the other two (i.e. Santa Maria di Leuca and eastern Alborán), while *D. dianthus* is widespread with discrete abundances in all the CWC provinces.

Within the whole Mediterranean Sea, the three white coral species are currently known from a bathymetric range of 180–1100 m depth, with different ranges for each subbasin (Fig. 19.7). From the westernmost Alborán Sea and the Gibraltar sill to the easternmost Marmara and Cyprus basins, the Mediterranean is speckled with white corals occurrences except for the African coasts, historically less explored, from where only the eastern Alborán CWC province is currently known (Fig. 19.6). *Madrepora oculata* and *D. dianthus* are usually dominant in shallower areas with respect to *L. pertusa* (e.g. Mastrototaro et al. 2010; Gori et al. 2013), despite showing almost the same bathymetric range within the basin (Fig. 19.7). This different bathymetric range of dominance of *M. oculata* and *L. pertusa* can be due to the physiological differences (e.g. growth rates, feeding ecology, metabolism, sensitivity to temperature changes, sensitivity to ocean acidification) recently assessed from Mediterranean specimens of the two species (Orejas et al. 2011; Gori et al. 2014a; Movilla et al. 2014; Naumann et al. 2014; Reynaud and Ferrier-Pagès, this volume). *Lophelia pertusa* seems to be better adapted to lower temperatures, while *M. oculata* seems to exhibit a greater ability to grow in warmer waters (Naumann et al. 2014). In

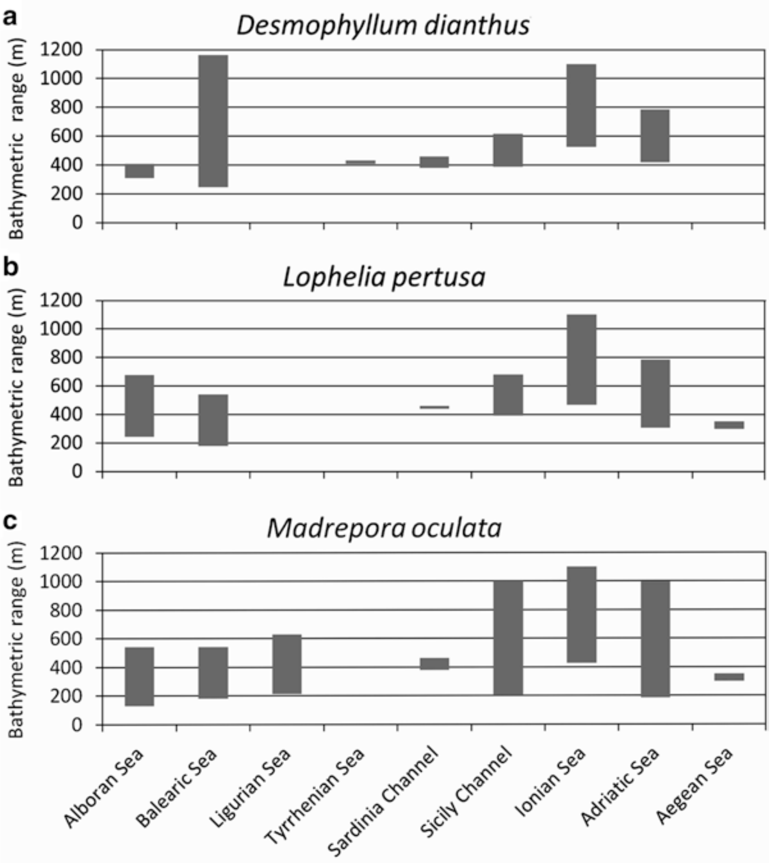


Fig. 19.7 Bathymetric range of the white corals (**a**) *Desmophyllum dianthus*, (**b**) *Lophelia pertusa* and (**c**) *Madrepora oculata* in the Mediterranean Sea

fact, an inverse South-North gradient in the relative abundance of *M. oculata* and *L. pertusa* seems to be present from the North Atlantic (e.g. the Norwegian shelves) to the Mediterranean Sea, with a density increase of *M. oculata* and a decrease of *L. pertusa* from North to South (Arnaud-Haond et al. 2015). It would be worthwhile to explore the deeper areas of the known Mediterranean CWC provinces to assess if dominance by *L. pertusa* occurs in deeper waters, as it is the case in the Gulf of Lions canyon system (Gori et al. 2013).

19.3.2 Black CWCs: Antipatharia

Besides white corals, which are the main actors of the currently defined CWC provinces (Taviani et al. 2011a), there are other conspicuous anthozoans that, in the past decades, also proved to be exceptional habitat structuring species. The Mediterranean black coral fauna comprises at least three species that conform to the criteria defining CWCs in this context – *Antipathes dichotoma*, *Leiopathes glaberrima* and *Parantipathes larix* (Fig. 19.1) – even if their depth range usually embraces also a large part of the continental shelf above 200 m depth. *Antipathes dichotoma* is a large black coral (colonies up to 1.5 m tall and wide) with loose, long, flexible branches. It is currently considered a typical Atlanto-Mediterranean species (Opresko 2009; Bo et al. 2011; Altuna and Poliseno, this volume; Bo and Bavestrello, this volume). Even though this species has never been reported to form extremely dense aggregations (0.1 colonies m^{-2}) (Bo et al. 2011, 2012, 2015), it usually co-occurs with other CWCs in multi-specific assemblages (Bo et al. 2011, 2012, 2015; Pardo et al. 2011; Mytilineou et al. 2014; Cau et al. 2015, 2017). *Leiopathes glaberrima* is a tall, arborescent species characterised by a branched canopy that may exceed 2 m in height and width in the largest specimens (Bo et al. 2015; Bo and Bavestrello, this volume). The species belonging to this genus are characterised by an extraordinary longevity, being considered among the oldest-living creatures on Earth (Roark et al. 2006). The radiocarbon dating of a *Leiopathes* colony from Hawaiian waters revealed an extraordinary age of 4265 years (Roark et al. 2006; Wagner and Opresko 2015) and Atlanto-Mediterranean *L. glaberrima* colonies were found to be as old as 2000 years (Carreiro-Silva et al. 2013; Bo et al. 2015). Although growth rates vary among individuals and depends on locality and depth, the occurrence of millennial specimens was hypothesised to reflect a long-term stability of undisturbed deep biocoenoses, particularly surprising for a semi-enclosed, heavily exploited basin such as the Mediterranean Sea (Bo et al. 2015). Finally, *P. larix* represents the third black coral species frequently occurring from the shelf edge to the bathyal depths in the Mediterranean basin. This species shows monopodial or sparsely branched colonies up to

Fig. 19.8 Distribution of the black corals (i.e. *Antipathes dichotoma*, *Leiopathes glaberrima* and *Parantipathes larix*) in the Mediterranean Sea. Numbers refer to the area ID given in Table 19.1

2 m tall with a characteristic bottlebrush habitus (Bo et al. 2014b). Both *L. glaberrima* and *P. larix* can aggregate in extensive patches reaching very high densities (4 colonies m^{-2} and 2.5 colonies m^{-2}, respectively for *P. larix* and *L. glaberrima*) (Bo et al. 2014b, 2015). They may form mono-specific forests or co-occur with other CWCs (Bo et al. 2014b, 2015; Ingrassia et al. 2016).

All Mediterranean black corals thrive on hard bottoms, especially on ridges, terraces and the flanks of canyons and seamounts, where they can exploit the currents (Freiwald et al. 2009; Bo et al. 2014c, 2015; Angeletti et al. 2015). Nevertheless some records provide evidence of populations thriving in heavily silted environments, suggesting a certain tolerance to sedimentation (Bo et al. 2012, 2014c). Habitat preferences, slow growth rates, late maturity and short larval dispersal (Miller 1998) are among the principal factors that may drive the distribution and aggregation patterns of these large arborescent anthozoans.

Black corals have been mainly found in the western basin, mostly in the Sicily Channel, Sardinia Channel, South Adriatic Sea and Aegean Sea (Fig. 19.8), albeit it is worthy to mention that the eastern basin has been much less explored than the western one. In particular, luxuriant antipatharian forests have been documented for the eastern Alborán Sea and the South Malta CWC provinces, southwest Sardinia, along the Ligurian and Tyrrhenian coasts and off Montenegro (Table 19.1; Fig. 19.8) (Bo et al. 2009, 2011, 2014b, c, 2015; Pardo et al. 2011; Angeletti et al. 2014; Deidun et al. 2015; Bo and Bavestrello, this volume; Knittweiss et al., this volume). Within the basin, *L. glaberrima* is widespread from 120 to 1000 m depth, while *A. dichotoma* and *P. larix* show an unevenly distribution at 90–645 and 90–460 m depth, respectively (Table 19.1; Fig. 19.9). In the deeper areas, *P. larix* is a more occasional species, while *A. dichotoma* and *L. glaberrima* are commonly reported within CWCs provinces together with frame-building corals (Mastrototaro et al. 2010; Freiwald et al. 2011; Pardo et al. 2011; Angeletti et al. 2014; Fabri et al. 2014; Deidun et al. 2015).

A fourth common black coral species in the Mediterranean Sea, *Antipathella subpinnata* (Ellis and Solander, 1786), can be occasionally found on deep rocky bottoms down to 600 m depth (Deidun et al. 2015). However this species is not considered here since its peak of abundance is located within the deep circalittoral zone, between 60 and 150 m depth (Bo et al. 2009). Apart from *A. subpinnata*, which is considered to be a Tethyan relict (Bo et al. 2008), the other species have numerous congenerics in the nearby Atlantic supporting their origin from this ocean.

19.3.3 Yellow CWCs: *Dendrophyllia cornigera*

The so-called yellow and pink corals, i.e. *D. cornigera* and *Dendrophyllia ramea* (Linnaeus, 1758), are the most important Mediterranean colonial Dendrophylliidae corals (see also Altuna and Poliseno, this volume). Originally, they were considered by Pérès and Picard (1964) as typical hard bottom coral species in shallower waters with respect to *M. oculata* and *L. pertusa*, and these authors' "offshore deep rock community" was included in the circalittoral zone, unlike the bathyal white corals. Pérès and Picard's view about *Dendrophyllia* was biased by the still imprecise information available, including a certain difficulty on how to distinguish these species (Zibrowius 2003). As shown by Zibrowius (1980), the two *Dendrophyllia* species differ in geographical and depth distribution, and are not ecologically equivalent. In particular, *D. ramea* is a shallower species, effectively developing in the circalittoral zone (e.g. Orejas et al. 2017, this volume), while *D. cornigera*

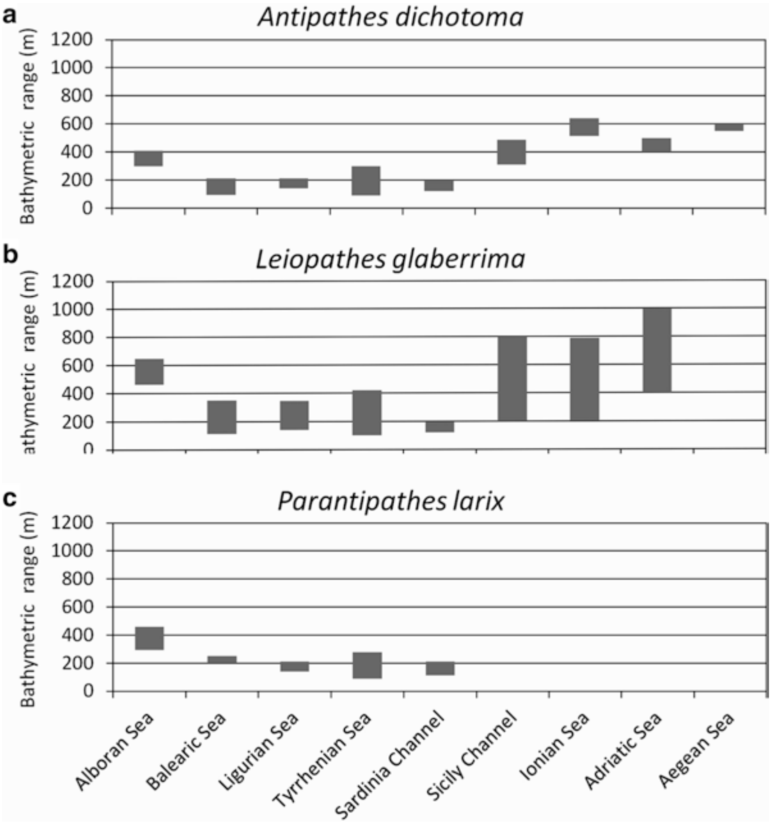


Fig. 19.9 Bathymetric distribution of the black corals (**a**) *Antipathes dichotoma*, (**b**) *Leiopathes glaberrima* and (**c**) *Parantipathes larix* in the Mediterranean Sea

reaches greater depths, also colonising the bathyal zone. For this reason, only *D. cornigera* is here considered as a CWC coral (Fig. 19.1). This scleractinian coral shows an irregularly branched, rigid morphology and can exceed 30 cm in height. Colonies show typical sulfur-yellow polyps on the top of a coral framework anchored on flat or gently sloping hard bottoms, where they usually keep their individuality without forming complex carbonate frames. Nevertheless, they can occur with relatively high densities, as at Mantice Shoal (Ligurian Sea, 80–120 m; Bo et al. 2014a) and Amendolara Bank (Ionian Sea, 120–180 m; Bo pers. comm.), where *D. cornigera* colonies form dense aggregations on flat muddy bottoms without any consistent anchorage.

The currently known distribution of *D. cornigera* in the Mediterranean Sea shows this species to be widespread from the eastern to the western side of the basin (Freiwald et al. 2009; Orejas et al. 2009; Bo et al. 2011, 2014a, 2015; Salomidi et al. 2010; Gori et al. 2013; Cau et al. 2015). However no large monospecific aggregations over 200 m depth have been found to date in the Mediterranean Sea (Fig. 19.10). As for the ‘white triad’, this yellow coral occurs in all the six CWC provinces identified, with a bathymetric range of 80–733 m (Table 19.1, Fig. 19.11). *Dendrophyllia cornigera* usually colonises the shallower horizons of CWC banks, often bathymetrically preceding white and black corals. This different bathymetric/distributional range could be due to the capacity of this species to maintain physiological functions until 16 °C, resulting in its dominance where temperatures are too warm for the other CWC species (Gori et al. 2014b).

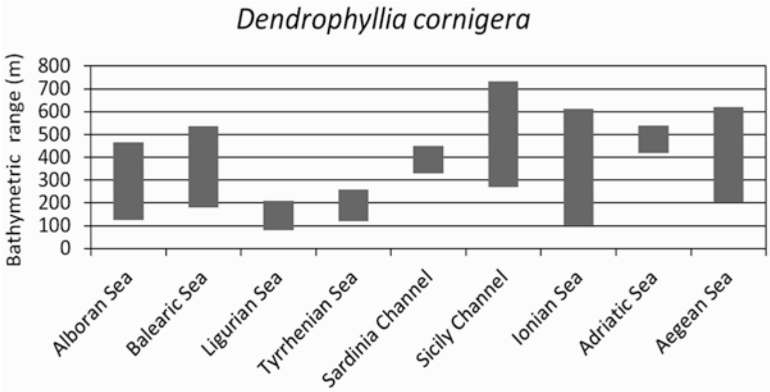
Large beds of dead *D. cornigera* colonies in a natural upright and spaced position were reported on the Vercelli Seamount (Central Tyrrhenian Sea; 200 m depth) and the Marco Bank (northwest Sicily; 200–250 m) (Bo et al. 2014c) suggesting that this species may suffer heavy mass mortality events due to still unkwnon reasons. Similar situations have been related to the high hydrothermal activities present in the Tyrrhenian basin (Bavestrello et al. 2014).

19.3.4 Alcyonacea: Soft CWCs on Hard Bottoms

Among deep-sea alcyonaceans, the Primnoidae *Callogorgia verticillata* and the Ellisellidae *Viminella flagellum* (Fig. 19.1; see also Altuna and Poliseno, this volume) currently represent the most common Mediterranean hard bottom CWC species. *Callogorgia verticillata* is characterised by branched feathery fan-like colonies often exceeding 1 m in height and forming dense aggregations. It is an Atlanto-Mediterranean species with a wide distribution over the entire Atlantic Ocean (Braga-Henriques et al. 2013; Bullimore et al. 2013; Locke et al. 2013), as well as within the Mediterranean Sea. It has been found in the Alborán Sea (Pardo et al. 2011), in the Gulf of Lions (Fabri et al. 2014), in the Tyrrhenian Sea (Bo et al. 2011, 2012, 2014b,

Fig. 19.10 Distribution of the yellow coral *Dendrophyllia cornigera* in the Mediterranean Sea. Numbers refer to the area ID given in Table 19.1

Fig. 19.11 Bathymetric distribution of the yellow coral *Dendrophyllia cornigera* in the Mediterranean Sea



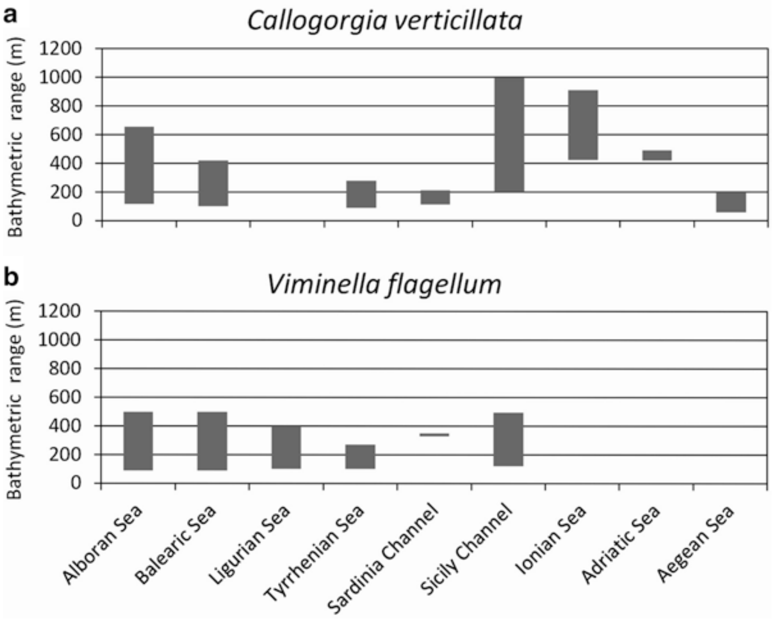
2015; Cau et al. 2015, 2017), in the Sicily Channel (Knittweis et al., this volume), in the Ionian Sea (Tursi et al. 2004), in the South Adriatic Sea (Angeletti et al. 2014) and in the Aegean Sea (Vafidis et al. 1994) (Table 19.1; Fig. 19.12). *Callogorgia verticillata* shows a wide bathymetric range, from 90 to 1000 m depth, with the deepest records in the Sicily Channel and in the Ionian Sea (Mastrototaro et al. 2010; Knittweis et al., this volume) (Fig. 19.13). In particular, *C. verticillata* has been observed in four of the six identified provinces (i.e. Santa Maria di Leuca, South Malta, Gulf of Lions and eastern Alborán) usually forming patchily-distributed but locally-dense aggregations from 400 to 1000 m depth. Important forests have been reported also from shallower sites, such as northwest Sicily (240–280 m) (Bo et al. 2014c) and St Eufemia Gulf (southern Tyrrhenian Sea; 90–120 m) on flat, heavily silted hardgrounds (Bo et al. 2012).

Gardens of *C. verticillata* are often mixed with other CWC species, creating an extremely heterogeneous and three-dimensional habitat (Angeletti et al. 2014). This is also the case of the less known *V. flagellum* (Aguilar et al. 2011; Giusti et al. 2012). This tall, whip alcyonacean is also an Atlanto-Mediterranean species, so far reported in the Mediterranean Sea only from the western basin with relatively few records. It seems to have preferences for deep circalittoral hard substrata (from 90 to 200 m depth) where it forms dense *facies* (Giusti et al. 2012), although it has been sighted down to 500 m depth (Table 19.1; Fig. 19.13) (Aguilar et al. 2013). Large *facies* of *V. flagellum* are known from numerous banks and seamounts in the Alborán Sea and around the Balearic Islands (Lo Iacono et al. 2012; Aguilar et al. 2013; Maldonado et al. 2013), along the French canyons and Corsican coasts (Carpine and Grasshoff 1975; Fourt and Goujard 2012; Fabri et al. 2014), in the Sicily Channel (Giusti et al. 2012), northwest Sicily (Bo et al. 2014c) and southern Sardinia (Cau et al. 2015, 2017) (Table 19.1).

Within the Mediterranean basin, large alcyonacean forests are known from the Gulf of Lions canyon system, Ligurian and Tyrrhenian Sea, northwest Sardinia, around the Maltese islands and off Montenegro (Fig. 19.12). From an ecological point of view, the large and tall colonies of *C. verticillata* and *V. flagellum*, as well as those of other arbo-

Fig. 19.12 Distribution of the hard bottom alcyonaceans *Callogorgia verticillata* and V*iminella flagellum* in the Mediterranean Sea. Numbers refer to the area ID given in Table 19.1

Fig. 19.13 Bathymetric range of the alcyonaceans (**a**) *Callogorgia verticillata* and (**b**) *Viminella flagellum* in the Mediterranean Sea



rescent anthozoans, provide a three-dimensional animal forest to a wide array of small to medium sized species, especially other alcyonaceans that thrive in these environments occasionally forming aggregations, including *Acanthogorgia hirsuta* Gray, 1857, *Swiftia pallida* Madsen, 1970, *Bebryce mollis* Philippi, 1842, *Paramuricea macrospina* (Koch, 1882), *Muriceides lepida* Carpine and Grasshoff, 1975, *Villogorgia bebrycoides* (Koch, 1887) and *Placogorgia* spp. (Mastrototaro et al. 2010; Freiwald et al. 2011; Pardo et al. 2011; Bo et al. 2012, 2014c, 2015; Giusti et al. 2012; Angeletti et al. 2014; Cau et al. 2015, 2017; Grinyó et al. 2016).

19.3.5 Stylasteridae: The Case of *Errina aspera*

Due to their branched calcareous skeleton, hydroids belonging to the Family Stylasteridae are considered habitat-forming species (Etnoyer and Morgan 2005). *Errina aspera* (Fig. 19.1) is the only Stylasteridae species actually found alive in the Mediterranean Sea (Cairns 1983; Zibrowius and Cairns 1992; Schuchert 2008; Altuna and Poliseno, this volume). This hydroid can form dense aggregations of branched calcareous colonies both in the Atlantic Ocean and in the Mediterranean Sea (Salvati et al. 2010). Despite *E. aspera* has been reported in relatively few Atlantic sites (Zibrowius and Cairns 1992), it is considered an important component of deep coral communities (Heifetz 2002). In the Mediterranean Sea this species is currently found only in the Messina Strait, at depths between 80 and 230 m (Giacobbe 2001; Giacobbe et al. 2007), where it forms monospecific stands showing exceptionally high densities of about 100 colonies m^{-2} (Salvati et al. 2010). Despite the Messina Strait's population is the only one found so far in the Mediterranean Sea, other large aggregations of *E. aspera* might occur even deeper in the basin, as it happens in the Gibraltar Strait (Álvarez-Pérez et al. 2005). Peculiar hydrodynamic regimes, as those occurring in strait regions, could be important environmental constraints for this species.

19.4 Soft Bottom CWCs

Soft bottom CWCs inhabit extensive regions of the seabed thanks to their ability to exploit sedimentary bottoms. Thus, in theory, such species could take advantage of the extensive bathyal muddy bottoms occurring in the Mediterranean Sea.

The massive exploitation of deep-sea benthic habitats started in the first few decades of the last century with the relentless development of trawl fishing activities on soft bottoms populated by commercial shrimps, such as the red shrimps *Aristeus antennatus* (Risso, 1816) and *Aristaeomorpha foliacea* (Risso, 1827) as well as the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). With progress in fishing gear technology, trawling now has a heavy devastating mechanical impact on deep-sea soft bottom habitats (see also Otero and Marin, this volume), including bathyal seabeds characterised by viscous mud with a very fluid superficial layer (normally occurring at depths between 250 and 500 m) as well as the firm and compact mud (found at 500–1000 m depth) *sensu* Pérès and Picard (1964). Aggregations of the sea pen *Funiculina quadrangularis* and of the alcyonacean *Isidella elongata*, which develop respectively on the two soft bottoms with the above cited edaphic features, almost completely disappeared from most of the trawlable bottoms of the Mediterranean Sea as documented for the Catalan coasts, French canyons, Ligurian Sea, Sicily Channel and Ionian Sea (D'Onghia et al. 2003; Maynou and Cartes 2012; Cartes et al. 2013; Mastrototaro et al. 2013, 2015; Fabri et al. 2014; Petović et al. 2016). Cartes et al. (2013) report the complete extirpation of *I. elongata* from a trawled fishing ground off the Ebro Delta due to a low fishing activity over a period of 15 years. The impact of trawling can be locally accelerated by other fishing practices characterised by high removal rate such as longlines (Mytilineou et al. 2014). Considering that this decline was already reported back in 1970s–1980s of the past century (Arena and Li Greci 1973; Relini et al. 1986) and that nowadays *I. elongata* occurs only occasionally in fishing discard, it is plausible to hypothesise that, given the slow growth rate of the species, the potential for recovery of the populations is practically nil under continuous fishing pressure.

In spite of the widespread decline of Mediterranean muddy-bottom CWC aggregations, some of these sensitive communities still persist in certain restricted areas. This mainly happens in areas not accessible to trawling, such as near hard bottom coral banks, canyon flanks or accidentally preserved areas (Mastrototaro et al. 2013, 2015, 2017; Fabri et al. 2014; Bo et al. 2015; Pierdomenico et al. 2016). In fact, together with suitable oceanographic and edaphic features, human pressure now also contributes in determining CWCs distribution.

19.4.1 *Isidella elongata*

The candelabrum-shaped alcyonacean *I. elongata* (Fig. 19.1), also known as bamboo coral, usually forms dense aggregations on Mediterranean bathyal muddy bottoms between 500 and 1650 m depth (and occasionally shallower, up to 115 m depth) on relatively flat bottoms with a slope of less than 5% (Maurin 1962; Pérès and Picard 1964; Bellan-Santini 1985; Maynou and Cartes 2012; Bo et al. 2015; Mastrototaro et al. 2017; Altuna and Poliseno, this volume; Rueda et al., this volume). Carpine (1970) reported *I. elongata* as one of the most common coral species on bathyal soft bottoms in the western Mediterranean Sea and, 16 years later, Relini et al. (1986) reported this species as part of the trawling coral bycatch. Laubier and Emig (1993) emphasised the ecological role of *I. elongata* as a habitat former, as a secondary biological hard substratum for epibiotic species, and as a spawning substratum for the egg masses and eggcases of cephalopods and sharks. Nevertheless, the actual conservation status of this soft bottom CWC is somewhat precarious (GFCM 2009) and it is actually a rare species (Bo et al. 2015; Mastrototaro et al. 2015, 2017), categorised as critically endangered by the IUCN (Otero et al. 2017). Conspicuous aggregations of *I. elongata* are currently known from El Idrissi Bank in the eastern Alborán CWC province (Hebbeln et al. 2009), in the Mallorca Channel (Mastrototaro et al. 2017), off the southern Catalonian coasts (Maynou and Cartes 2012; Cartes et al. 2013), on the soft bottoms interspersed in the Gulf of Lions canyon system (Fabri et al. 2014), in the muddy enclave at the base of the Carloforte shoal (southwest Sardinia; Bo et al. 2015) and on the muddy bottoms around the Maltese CWC province (Freiwald et al. 2009), while occasional occurrences have also been reported from Greek waters (Mytilineou et al. 2014) (Table 19.1; Figs. 19.14 and 19.15). Almost all these known *I. elongata* gardens occur in the immediate proximity of hard coral banks, canyon systems or rough topographies which protect

Fig. 19.14 Distribution of the soft bottom alcyonacean *Isidella elongata* in the Mediterranean Sea. Numbers refer to the area ID given in Table 19.1

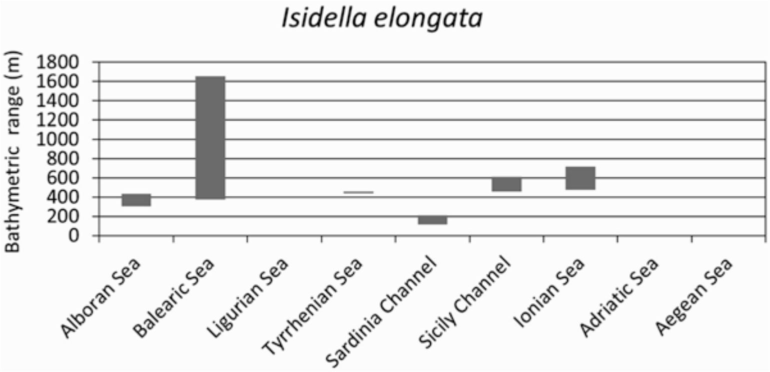


Fig. 19.15 Bathymetric distribution of the bamboo coral *Isidella elongata* in the Mediterranean Sea

them from trawling. The only exception is the muddy seabed of the Mallorca Channel seamounts field where, however, trawling is forbidden because of the occurrence of submarine electricity cables (Acosta et al. 2004; Mastrototaro et al. 2017). The scarce *I. elongata* sites currently remained in the Mediterranean Sea (Fig. 19.14), someway protected from trawling, show high densities due to the marked tendency of this species to form aggregations.

19.4.2 Pennatulacea

Pennatulaceans, most commonly known as sea pens, are peculiar colonial octocorals characterised by a more or less distinct feather-like appearance and strongly adapted to live on muddy, sandy or detritic bottoms where they may occasionally form dense aggregations. Sea pens fields have been listed as vulnerable marine ecosystems (VMES) and, similarly to other aggregating anthozoans, they are able to structure the environment and attract vagile fauna (Pardo et al. 2011; Baillon et al. 2012; Mastrototaro et al. 2013; Rueda et al., this volume). However, a general picture of these soft bottom populations in pristine conditions is still biased by a reduced number of direct observations, poor knowledge of the ecology and biology of these species, as well as the influence of the anthropic trawling pressure. Compared to hard bottom aggregations of CWCs, however, those occurring on mud or on sand seem to respond differently to the constraining parameters of settling, such as larval dispersal and habitat suitability and the result is a patchy distribution on a large scale. Quantitative data on sea pens in the discard from trawling is variable in this sense, but still always present (Colloca et al. 2003; Massutí and Reñones 2005; Abad et al. 2007; Maynou and Cartes 2012; Mastrototaro et al. 2013; Fabri et al. 2014; Chimienti et al. 2015, 2018a). The sea pen discard, together with that of other benthic species, motivates the creation of Large Marine Protected Areas on soft-bottoms (Bastari et al. 2016; Otero and Marin, this volume).

Pennatulaceans often live in moderately high energy environments, as is usual for deep-sea soft bottom species (Gage

Fig. 19.16 Distribution of the deep-sea pennatulaceans *Funiculina quadrangularis* and *Kophobelemnon stelliferum* in the Mediterranean Sea. Numbers refer to the area ID given in Table 19.1

and Tyler 1991). In the Mediterranean Sea there are at least two major groups of sea pens, separated on the basis of their main bathymetric distribution. *Pennatula rubra* (Ellis, 1761), *Veretillum cynomorium* (Pallas, 1766) and *Pteroeides spinosum* (Ellis, 1764) have a preference for the continental shelf and therefore are not strictly considered CWCs (Gori et al. 2017). On the contrary, other species such as *F. quadrangularis* and *Kophobelemnon stelliferum* (Fig. 19.1) thrive in the deepest part of the basin, occasionally forming dense fields (*facies*). These species show a wide distribution in the Mediterranean Sea (Fig. 19.16) from the western to the eastern basins, where an appreciable bottom current is necessary mainly for trophic reasons. Thus pennatulaceans are often most common in the more hydrodynamically active areas such as the bases of seamounts, canyon or ridges, slightly sloping escarpments and continental slopes (Williams 2011).

As for *I. elongata*, deep-sea pennatulacean aggregations are also affected by intense destructive fishing practices and the formerly common *facies* of *F. quadrangularis* have almost completely disappeared from many Mediterranean areas due to trawl fishing (D'Onghia et al. 2003; Sardà et al. 2004; Otero and Marin, this volume). Because of its large size and dense aggregations, *F. quadrangularis* is often present as bycatch although with shrinking abundance (Arena and Li Greci 1973; Relini et al. 1986; Colloca et al. 2003; Voultsiadou et al. 2011; Bastari et al. 2018) and it is therefore considered a vulnerable species (Otero et al. 2017; Otero and Marin, this volume). This whip-like pennatulacean is still locally dominant on the bathyal soft bottom community around the Maltese CWC bank (Freiwald et al. 2009), on the muddy bottoms off the Gulf of Tigullio (Ligurian Sea; Tunesi et al. 2001), in the Gulf of Lions Canyon system until the Cannes and Var canyons, southwest the city of Nice (Fabri et al. 2014) and in the Mallorca Channel (Table 19.1; Fig. 19.17). Further occasional occurrences are in Alborán Sea, along the Catalan coasts, French canyons, Gulf of Naples, South Tyrrhenian and Adriatic Sea (Ocaña et al. 2000; Porporato et al. 2009; Pardo et al. 2011; Bo et al. 2012; Aguilar et al. 2013; Cartes et al. 2013; Fabri et al. 2014; Pierdomenico et al. 2016; Bastari et al. 2018).

Kophobelemnon stelliferum is considered a cosmopolitan species distributed from the Atlantic to the Pacific Ocean both along the continental shelf and on the slope always on muddy bottoms (Carpine 1970; Ocaña et al. 2000; Mastrototaro et al. 2013). This species represents another deep-sea pennatulacean able to form large aggregations as for example in the Santa Maria di Leuca CWC province at depths of 404–467 m (Mastrototaro et al. 2013). This represents the only Mediterranean *facies* of *K. stelliferum* studied so far, while other relevant occurrences are reported in the western basin from the eastern Alborán CWC province (300–618 m) to the Gulf of Lions (200–500 m) and the southern Tyrrhenian Sea (Gili and Pagès 1987; Ocaña et al. 2000; Hebbeln et al. 2009; Pardo et al. 2011; Bo et al. 2012; Fabri et al. 2014; Pierdomenico et al. 2016) (Table 19.1; Fig. 19.17).

Within the Santa Maria di Leuca *K. stelliferum* aggregation, another deep-sea North Atlantic pennatulacean, *Protoptilum carpenteri* Kölliker, 1872, was found from 240 to 451 m depth. The presence of this rare species is most probably due to the protection from the trawl fishing offered by hard substrata and coral mounds (Mastrototaro et al. 2015). Perhaps not by chance, the second occurrence of this species in the Mediterranean Sea is in another deep-sea CWC oasis, i.e. the *I. elongata facies* in the Balearic Sea (Mastrototaro et al. 2017).

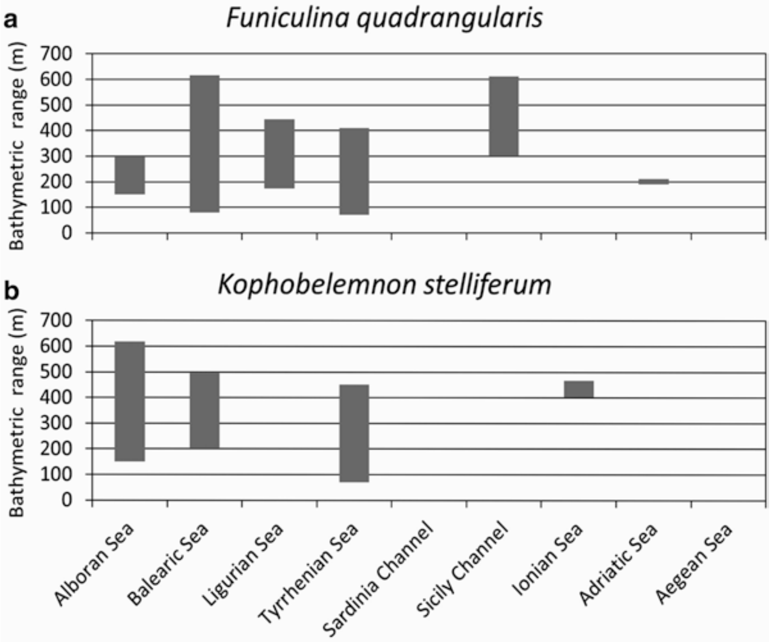


Fig. 19.17 Bathymetric range of the pennatulaceans (**a**) *Funiculina quadrangularis* and (**b**) *Kophobelemnon stelliferum* in the Mediterranean Sea

Pennatula phosphorea Linnaeus, 1758 and *Virgularia mirabilis* (Müller, 1776) represents another two pennatulacean species which can occur also in the deep-sea. However, they are not considered in the present review because no data about consistent habitat-forming aggregations of these species in the deep-sea are available, to our best knowledge, in the literature.

19.5 Corals and Currents: A Juxtaposition

The occurrence of living CWCs in the Mediterranean Sea does not completely overlap with the findings of subfossil CWCs, particularly in the eastern Mediterranean basin (e.g. Taviani et al. 2011a). Despite the possibility of still undiscovered CWC sites, this partial mismatch between living and subfossil CWCs distributions may represents a proxy of a dynamic response of these corals to environmental factors that drive their settlement and that, eventually, determine their demise through time and space (Taviani et al. 2017). Occurrence, distribution and abundance of CWC species are strongly influenced by several abiotic factors such as the availability of appropriate substrata, seawater temperature, oxygen concentration, aragonite saturation state, water flow regimes and food supply (Frederiksen et al. 1992; Davies et al. 2008; Dullo et al. 2008; Orejas et al. 2009; Roberts et al. 2009b; Gori et al. 2013). In particular, appropriate currents are considered as one of the main governing factors in CWC distribution, since they supply corals with food and prevent burial of the corals by sediments (Thiem et al. 2006; Roberts et al. 2009a). Mediterranean CWCs growth and distribution is currently considered mainly influenced by the Levantine Intermediate Water (LIW), the largest water mass moving in the basin, formed in the northern portion of the eastern Mediterranean and flowing westward (Robinson et al. 2001; Millot and Taupier-Letage 2005; Hayes et al. this volume). These water masses fill all the CWC sites and provinces of both hard and soft bottoms, and supply food to the corals, facilitating also the larva transport and contributing as well to counteract sedimentation (Fig. 19.18).

From the eastern Mediterranean Sea, the LIW mass flows along the southern continental slope of the Cretan arc to the Peloponnesus peninsula, between about 250 and 600 m depth (Robinson et al. 2001; Manca et al. 2004; Millot and Taupier-Letage 2005). Part of the LIW reaches the Adriatic Sea and forms a gyre from the Balkan to the Italian coasts while the remaining LIW vein continues westward through the Sicily Channel and the Tyrrhenian Sea.

Along their entire course, LIW masses are involved in the offshore formation of Mediterranean deep waters, such as the Aegean Deep Water in the eastern Mediterranean, the Adriatic Deep Water in the central Mediterranean and the Tyrrhenian Deep Water in the western Mediterranean basin (Millot and Taupier-Letage 2005). These dense deep-water masses generally follow the circulation of the LIW and contribute with oxygen and food supply to the deeper CWC communities. In particular, cold North Adriatic Deep Water (ADW), formed in the shallow northern Adriatic through cold wind forcing, represents one of the densest water masses in the Mediterranean Sea (Cushman-Roisin et al. 2001). This water mass flows southward and cascades along the southwestern margin of the Adriatic sub-basin, proceding south-

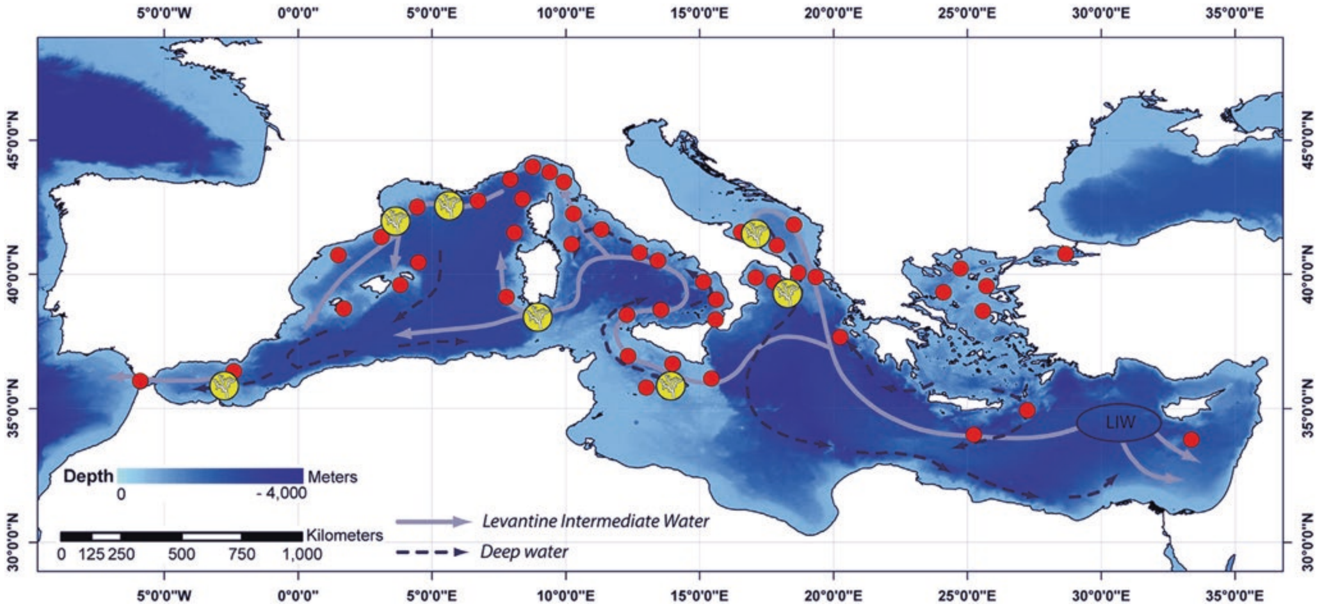


Fig. 19.18 Distribution of CWC sites (*red dots*) and provinces (*yellow dots*) in the Mediterranean Sea and the main paths of flow of the LIW (Levantine Intermediate Water) and deep water masses within the basin. (Modified from Taviani et al. 2017)

ward through the Otranto Strait and passing along the Apulian Plateau into the Ionian Sea and the Levantine Basin (Vilibic and Orlic 2002). The Bari Canyon and the Apulian Adriatic CWC sites are bathed by such dense water masses which flow between 400 and 700 m depth (Vilibic and Orlic 2002; Angeletti et al. 2014). LIW and ADW masses seem to be responsible for the extraordinary CWC growth of the southern Adriatic Sea, feeding the CWC sites off Montenegro and the ones along the coasts of Apulia, where the two CWC provinces of Bari Canyon and Santa Maria di Leuca are present (Fig. 19.18). Not surprisingly, vigorous coral growth in the Bari Canyon is the best between 300 and 600 m depth (Freiwald et al. 2009; D'Onghia et al. 2015). The CWC community off Montenegro, developing between 420 and 490 m depth with occasional deeper coral occurrences at 540 m (Angeletti et al. 2014), also benefits from LIW and partly from the ADW. Considering its recent discovery and that this CWC site has only been partially explored, it is possible that a deeper community supported by the ADW could be present. The cold, oxygenated and less saline ADW flows through the Otranto Channel and moves in geostrophic balance along the 600–1000 m isobaths through the Santa Maria di Leuca CWC province (Budillon et al. 2010), carrying particulate matter and nutrients that provide a crucial source for biological activity in deep waters (De Lazzari et al. 1999; Angeletti et al. 2014). In this CWC province, the maximum coral growth has been observed between 500 and 700 m depth (Freiwald et al. 2009; Budillon et al. 2010).

The second LIW branch bypasses the southern Adriatic and proceeds westwards along the Calabria-Sicilian margin, passing through the Sicily Channel and reaching the Tyrrhenian Sea. Along this path, the Malta CWC province and the other CWC sites benefit from this oxygenated and food-rich water mass flow (Millot and Taupier-Letage 2005) together with the deep water masses mainly following the LIW circulation (Fig. 19.18). Once reaching the northern Sicily coasts, the LIW mainly circulates cyclonically around the Tyrrhenian basin, at about 200–600 m depth (Millot and Taupier-Letage 2005). Here, the lush antipatharian gardens can benefit from a turbulent hydrodynamic regime boosting their filtering activity and, ultimately, their growth and reproduction.

In the Tyrrhenian Sea, a LIW vein flows northwards through the Corsica Channel (sill at about 400 m depth) while the remaining LIW flows out through the Sardinia Channel. This LIW mass intercepts the South Sardinia CWC province together with the deeper Tyrrhenian Deep Water that outflows into the Algero-Provençal basin, as well as the Western Mediterranean Deep Water flowing eastward (Astraldi et al. 2002). Taviani et al. (2017) report the presence of LIW (ca. 200–600 m depth) and cooler and less saline water masses (Tyrrhenian Deep Water and western Mediterranean Deep Water, below ca. 600 m depth) bathing the South Sardinia CWC community.

South of Sardinia, part of the LIW mass can fill the Algerian margin and flow towards the central sub-basin, while a second vein flows northwards along the western Sardinia and Corsica slopes, between 250 and 450 m depth (Gana et al. 2015). This second vein joins with the Corsica Channel one, participating in the wintertime formation of deep waters in the Ligurian and the Provençal margin. The LIW mass continues along the French and the Spanish slope and most of it outflows through the Gibraltar Strait, while the remainder that bypasses the Strait can continue along the North Africa slope. In this way, the CWC provinces of the Gulf of Lions and the eastern Alborán Sea can benefit from food and oxygen carried by the LIW masses, together with the other CWC sites unevenly distributed along the path of the LIW (Fig. 19.18).

Some of the canyons featuring the Gulf of Lions seabed are also affected by periodic arrivals of dense shelf water cascades during wintertime (Durrieu de Madron et al. 2005; Canals et al. 2006; Palanques et al. 2006; Puig et al. 2008; Puig and Gili, this volume). These cascading events act as a significant natural carbon sequestration and deep-sea ecosystem fueling mechanism by carrying dissolved and particulate organic matter to the deep-sea through cold shelf waters and supporting the large CWC province living in the area (Canals et al. 2006; Orejas et al. 2009). Moreover, this cascading cold water mass is responsible for reduced sediment accumulation rates that fully fits with CWC settlement and development (White et al. 2005).

Thanks to the interaction between topography and a combination of cold, oxygenated and food-carrying water masses (i.e. LIW, deep waters and cascading effects), CWC communities broadly develop in a mosaic-like situation on both hard and soft bottoms along the main path followed by the LIW within the basin (Fig. 19.18), as already highlighted for the white corals sites (e.g. Taviani et al. 2017). Few exceptions include localised hydrodynamic features, as for example the case of *Errina aspera* in the Messina Strait. In this area, the upwelling of the LIW masses through the *E. aspera* aggregation explains this peculiar occurrence (Giacobbe et al. 2007). Despite the presence of suitable substrata for the setting of *E. aspera* in closeby areas, this stylasterid has not been observed where the Messina Strait LIW upwelling does not operate (Giacobbe 2001).

19.6 Knowledge Gaps

The last two decades represented an extraordinary turning point for the investigation of the deep Mediterranean habitats, completely changing our perspective on deep-sea biodiversity. ROV footage contributed to giving a visual identity to the assemblages that were listed and partially characterised in the first bionomic efforts (e.g. Pérès and Picard 1964). Despite the large sampling effort carried out, a lot still needs to be done and information is still discontinuous and unevenly available within the Mediterranean Sea. Future perspectives in researching CWC biogeography may concern the individuation and the exploration of other potential CWC sites along the LIW main pathway (Fig. 19.18). Scleractinians occur in areas where the interaction between currents and topography can generate high-speed flow (e.g. White et al. 2005, 2007; Dorschel et al. 2007; Mienis et al. 2007; Orejas et al. 2009). A similar relation has been evidenced for non-scleractinian CWCs, highlighting the close connection between deep corals and turbulent hydrodynamic regimes (Genin et al. 1986; Bo et al. 2014b). New investigations along canyons, ridges and seamounts, possibly at deeper depths, would enhance our knowledge on CWC communities and of their biogeography as modulated by local environmental constraints. This will help to optimise habitat models predicting the location of new provinces mainly based on the seabed topography and hydrodynamic conditions. Even more crucial would be the exploration of the environs of the currently known CWC sites, possibly exploring them deeper than at present and using high-performing equipment such as workclass ROVs (i.e. multitasking ROVs able to reach depth of some thousand of metres). This could help to the potential discovery of other continuous CWC belts, as it has been the case along the Apulian margin (Angeletti et al. 2014).

Deep soft bottoms have been studied for a longer time with respect to hard ones but, paradoxically, they are those for which the least is known, especially in terms of coral occurrence and distribution. Knowledge gaps are probably linked to the scarce employment of direct visual techniques on muddy areas (e.g. ROVs), the low taxonomic resolution in the identification of macro and megabenthic species, the high degree of impact on soft bottoms as well as the overall limited scientific exploitment of invertebrate bycatch data on different temporal and geographic scales (Chimienti et al. 2015, 2018a; Petović et al. 2016; Terribile et al. 2015; Altuna and Poliseno, this volume; Rueda et al., this volume). On bathyal soft bottoms, untrawled areas can hosts pristine or low-impacted CWC communities (e.g. Bo et al. 2015; Mastrototaro et al. 2017) whose study could increase our knowledge of their ecological features. This will also provide the opportunity to understand if and how these communities respond differently to environmental constraints with respect to stressed communities, and which factors drive aggregation patterns.

A greater attention to the benthic bycatch from fisheries would result in more information on the occurrence of new species, rare species, as well as species (such as antipatharians, pennatulaceans or alcyonaceans) becaming rare over a certain temporal scale. The removal rates, together with detailed studies on benthos taxonomy, ecology and biology, would be exceptionally relevant to quantify the populations and their distribution. This will also help to define specific Mediterranean guidelines to preserve deep-water animal forests, for example through the implementation of Deep-Sea Fishery Restricted Areas (see Otero and Marin, this volume). The establishment of such areas would present a unique opportunity to evaluate the recovery potential, rate and patterns of deep-water communities (Tudela et al. 2004).

The filling of knowledge gaps on the affinity of the deep species, based on distribution, oceanographic patterns as well as on population genetics and larval dispersal abilities, would contribute towards understanding the biogeography of the Mediterranean CWCs.

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References

Abad E, Preciado I, Serrano A, et al (2007) Demersal and epibenthic assemblages of trawlable grounds in the northern Alboran Sea (western Mediterranean). Sci Mar 71:513–524

Acosta J, Canals M, Carbó A, et al (2004) Sea floor morphology and plio-quaternary sedimentary cover of the Mallorca channel, Balearic Islands, western Mediterranean. Mar Geol 206:165–179

Addamo AM, Vertino A, Stolarski J, et al (2015) Merging scleractinian genera: the overwhelming genetic similarity between solitary *Desmophyllum* and colonial *Lophelia*. BMC Evol Biol 16:108. https://doi.org/10.1186/s12862-016-0654-8

Aguilar R, Correa ML, Calcinai B, et al (2011) First records of *Asbestopluma hypogea* Vacelet and Boury-Esnault, 1996 (Porifera, Demospongiae Cladorhizidae) on seamounts and in bathyal settings of the Mediterranean Sea. Zootaxa 2925:33–40

Aguilar R, Pastor X, García S, et al (2013) Importance of seamount-like feature for conserving Mediterranean marine habitats and threatened species. OCEANA, Madrid

Aguilar R, Serrano A, García S, et al (2014) Vulnerable habitats and species in the deep-sea Emile Baudot Escarpment (South Balearic Islands) surveyed by ROV. In: Langar H, Bouafif C, Ouerghi A (eds) Proceedings of the 1st Mediterranean symposium on the conservation of dark habitats, Slovenia, 31 October 2014, pp 15–20

Álvarez-Pérez G, Busquets P, De Mol B, et al (2005) Deep-water coral occurrences in the Strait of Gibraltar. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 207–221

Angeletti L, Taviani M, Canese S, et al (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Mediterr Mar Sci 15:225–238

Angeletti L, Mecho A, Doya C, et al (2015) First report of live deep-water cnidarian assemblages from the Malta Escarpment. Ital J Zool 82:1–7. https://doi.org/10.1080/11250003.2015.1026416

Arena P, Li Greci F (1973) Indagine sulle condizioni faunistiche e sui rendimenti di pesca dei fondali batiali della Sicilia occidentale e della bordura settentrionale dei banchi della soglia Siculo-Tunisina. Quad Lab Tecnol Pesca 1:157–201

Arnaud-Haond S, Van den Beld IMJ, Becheler R, et al (2015) Two “pillars” of cold-water coral reefs along Atlantic European margins: prevalent association of *Madrepora oculata* with *Lophelia pertusa*, from reef to colony scale. Deep-Sea Res Part 2 Top Stud Oceanogr 145:110–119. https://doi.org/10.1016/j.dsr2.2015.07.013

Astraldi M, Gasparini GP, Vetrano A, et al (2002) Hydrographic characteristics and interannual variability of water masses in the central Mediterranean: a sensitivity test for longterm changes in the Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 49:661–680

Baillon S, Hamel JF, Wareham VE, et al (2012) Deep cold-water corals as nurseries for fish larvae. Front Ecol Environ 10:351–356. https://doi.org/10.1890/120022

Bastari A, Micheli F, Ferretti F, et al (2016) Large marine protected areas (LMPAs) in the Mediterranean Sea: the opportunity of the Adriatic Sea. Mar Policy 68:165–177

Bastari A, Pica D, Ferretti F, et al (2018) Sea pens in the Mediterranean Sea: habitat suitability and opportunities for ecosystem recovery. ICES J Mar Sci. https://doi.org/10.1093/icesjms/fsy010

Bavestrello G, Bo M, Canese S, et al (2014) The red coral populations of the gulfs of Naples and Salerno: human impact and deep mass mortalities. Ital J Zool 81:552–563

Bellan-Santini D (1985) The Mediterranean benthos: reflections and problems raised by a classification of the benthic assemblages. In: Moraitou-Apostolopoulou M, Kiortsis V (eds) Mediterranean marine ecosystems. Plenum Press, New York, pp 19–48

Bianchi CN, Morri C, Chiantore M, et al (2012) Mediterranean Sea biodiversity between the legacy from the past and a future of change. In: Stambler N (ed) Life in the Mediterranean Sea: a look at habitat changes. Nova Science Publishers, New York, pp 1–55

Bo M, Tazioli S, Spanò N, et al (2008) *Antipathella subpinnata* (Antipatharia, Myriopathidae) in Italian seas. Ital J Zool 75:185–195

Bo M, Bavestrello G, Canese S, et al (2009) Characteristics of a black coral meadow in the twilight zone of the central Mediterranean Sea. Mar Ecol Progr Ser 397:53–61

Bo M, Bavestrello G, Canese S (2011) Coral assemblage off the Calabrian Coast (South Italy) with new observations on living colonies of *Antipathes dichotoma*. Ital J Zool 78:231–242

Bo M, Canese S, Spaggiari C, et al (2012) Deep coral oases in the South Tyrrhenian Sea. PLoS One 7:e49870. https://doi.org/10.1371/journal.pone.0049870

Bo M, Bava S, Canese S, et al (2014a) Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. Biol Conserv 171:167–176

Bo M, Canese S, Bavestrello G (2014b) Discovering Mediterranean black coral forests: *Parantipathes larix* (Anthozoa: Hexacorallia) in the Tuscan Archipelago, Italy. Ital J Zool 81:112–125

Bo M, Cerrano C, Canese S, et al (2014c) The coral assemblages of an off-shore deep Mediterranean rocky bank (NW Sicily, Italy). Mar Ecol 35:332–342. https://doi.org/10.1111/maec.12089

Bo M, Bavestrello G, Angiolillo M, et al (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS One 10:e0119393. https://doi.org/10.1371/journal.pone.0119393

Bouchet P, Taviani M (1992a) La colonizzazione dei bacini a soglia. Il caso del Mar Mediterraneo. Lavori della Società Italiana di. Malacologia 24:120–130

Bouchet P, Taviani M (1992b) The Mediterranean deep-sea fauna: pseudopopulations of Atlantic species? Deep-Sea Res Part 1 Oceanogr Res Pap 39:169–184

Bourcier M, Zibrowius H (1973) Les “boues rouges” déversées dans le canyon de la Cassidaigne (region de Marseille). Observations en soucoupe plongeante SP350 (juin 1971) et résultats de dragages. Téthys 4:811–841

Braga-Henriques A, Porteiro FM, Ribeiro PA, et al (2013) Diversity, distribution and spatial structure of the cold-water coral fauna of the Azores (NE Atlantic). Biogeosciences 10:4009–4036. https://doi.org/10.5194/bg-10-4009-2013

Budillon G, Lo Bue N, Siena G, et al (2010) Hydrographic characteristics of water masses and circulation in the northern Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:441–457. https://doi.org/10.1016/j.dsr2.2009.08.017

Buhl-Mortensen L, Vanreusel A, Gooday A, et al (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Mar Ecol Evol Perspect 31:21–50

Bullimore R, Foster N, Howell K (2013) Coral-characterized benthic assemblages of the deep northeast Atlantic: defining "Coral Gardens" to support future habitat mapping efforts. ICES J Mar Sci 70:511–522

Cairns SD (1983) A generic revision of the Stylasterina (Coelenterata: Hydrozoa). Part I. Description of the genera. Bull Mar Sci 33:427–508

Canals M, Puig P, Durrieu de Madron X, et al (2006) Flushing submarine canyons. Nature 444:354–357

Carlier A, Le Guilloux E, Olu K, et al (2009) Trophic relationships in a deep Mediterranean cold-water coral bank (Santa Maria di Leuca, Ionian Sea). Mar Ecol Progr Ser 397:125–137

Carpine C (1970) Ecologie de l'étage bathyal dans la Méditerranée occidentale. Mém Inst Océanogr Monaco 2:1–146

Carpine C, Grasshoff M (1975) Les gorgonaires de la Méditerranée. Bull Inst Océanogr Monaco 71:1–140

Carreiro-Silva M, Andrews AH, Braga-Henriques A, et al (2013) Variability in growth rates of long-lived black coral *Leiopathes* sp. from the Azores. Mar Ecol Progr Ser 473:189–199

Cartes JE, Lo Iacono C, Mamouridis V, et al (2013) Geomorphological, trophic and human influences on the bamboo coral *Isidella elongata* assemblages in the deep Mediterranean: to what extent does *Isidella* form habitat for fish and invertebrates? Deep-Sea Res Part 1 Oceanogr Res Pap 76:52–65

Cau A, Follesa MC, Moccia D, et al (2015) Deepwater corals biodiversity along roche du large ecosystems with different habitat complexity along the south Sardinia continental margin (CW Mediterranean Sea). Mar Biol 162:1865–1878

Cau A, Moccia D, Follesa MC, et al (2017) Coral forests diversity in the outer shelf of the South Sardinian continental margin. Deep-Sea Res Part 1 Oceanogr Res Pap. https://doi.org/10.1016/j.dsr.2017.01.016

Chimienti G, Maiorano P, Mastrototaro F (2015) *Pennatula rubra facies* in the Ionian Sea (Central Mediterranean). Biol Mar Mediterr 22:76–80

Chimienti G, Angeletti L, Mastrototaro F (2018a) Withdrawal behaviour of the red sea pen *Pennatula rubra* (Cnidaria: Pennatulacea). Eur Zool J 85:64–70. https://doi.org/10.1080/24750263.2018.1438530

Chimienti G, Bo M, Mastrototaro F (2018b) Know the distribution to assess the changes: Mediterranean cold-water coral bioconstructions. Rend Lincei Sci Fis Nat. https://doi.org/10.1007/s12210-018-0718-3

Colloca F, Cardinale M, Belluscio A, et al (2003) Structure and diversity of demersal assemblages in the central Mediterranean Sea. Estuar Coast Shelf Sci 56:469–480. https://doi.org/10.1016/S0272-7714(02)00196-8

Costantini F, Taviani M, Remia A, et al (2010) Deep-water *Corallium rubrum* (L., 1758) from the Mediterranean Sea preliminary genetic characterisation. Mar Ecol Evol Perspect 31:261–269

Cushman-Roisin B, Gacic M, Poulain PM, et al (2001) Physical oceanography of the Adriatic Sea: past, present and future. Kluwer Academic Publishers, Dordrecht, p 304

D'Onghia G, Mastrototaro F, Matarrese A, et al (2003) Biodiversity of the upper slope demersal community in the eastern Mediterranean: preliminary comparison between two areas with and without trawl fishing. J Northwest Atl Fish Sci 31:263

D'Onghia G, Mastrototaro F, Maiorano P, et al (2008) Cold water corals: a biodiversity "hot-spot" in the Mediterranean Sea. JMBA Global Marine Environment (published on line), pp 32–33

D'Onghia G, Maiorano P, Carlucci, et al (2012) Comparing deep-sea fish fauna between coral and non-coral "megahabitats" in the Santa Maria di Leuca cold-water coral Province (Mediterranean Sea). PLoS One 7:e44509. https://doi.org/10.1371/journal.pone.0044509

D'Onghia G, Capezzuto F, Cardone F, et al (2015) Macro- and megafauna recorded in the submarine Bari canyon (southern Adriatic, Mediterranean Sea) using different tools. Mediterr Mar Sci 16:180–196. https://doi.org/10.12681/mms.1082

D'Onghia G, Calculli C, Capezzuto F, et al (2016) New records of cold-water coral sites and fish fauna characterization of a potential network existing in the Mediterranean Sea. Mar Ecol 1–25. https://doi.org/10.1111/maec.12356

Davies AJ, Wisshak M, Orr JC, et al (2008) Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). Deep-Sea Res Part 1 Oceanogr Res Pap 55:1048–1062

De Lazzari A, Boldrin A, Rabitti S, et al (1999) Variability and downward fluxes of particulate matter in the Otranto Strait area. J Mar Syst 20:399–413

De Mol B, Henriet JP, Canals M (2005) Development of coral banks in Porcupine Seabight: do they have Mediterranean ancestors? In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 515–533

Deidun A, Tsounis G, Balzan F, et al (2010) Records of black coral (Antipatharia) and red coral (*Corallium rubrum*) fishing activities in the Maltese Islands. Mar Biodivers Rec 3:e90

Deidun A, Andaloro F, Bavestrello G, et al (2015) First characterisation of a *Leiopathes glaberrima* (Cnidaria: Anthozoa: Antipatharia) forest in Maltese exploited fishing grounds. Ital J Zool 82:271–280

Delibrias G, Taviani M (1985) Dating the death of Mediterranean deep-sea scleractinian corals. Mar Geol 62:175–180

Dorschel B, Hebbeln D, Foubert A (2007) Hydrodynamics and cold-water coral *facies* distribution related to recent sedimentary processes at Galway Mound west of Ireland. Mar Geol 244:184–195

Dubois-Dauphin Q, Montagna P, Sian G, et al (2017) Hydrological variations of the intermediate water masses of the western Mediterranean Sea during the past 20 ka inferred from neodymium isotopic composition in foraminifera and cold-water corals. Clim Past 13:1737. https://doi.org/10.5194/cp-13-17-2017

Dullo WC, Flögel S, Rüggeberg A (2008) Cold-water coral growth in relation to the hydrography of the Celtic and Nordic European continental margin. Mar Ecol Progr Ser 371:165–176

Durrieu de Madron X, Zervakis V, Theocharis A, et al (2005) Comments on "Cascades of dense water around the world ocean". Progr Oceanogr 64:83–90. https://doi.org/10.1016/j.pocean.2004.08.004

Etnoyer P, Morgan LE (2005) Habitat-forming deep-sea corals in the northeast Pacific Ocean. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 331–343

Evans J, Aguilar R, Alvarez H, et al (2016) Recent evidence that the deep sea around Malta is a biodiversity hotspot. In: Rapport du Congrès de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée, vol 41, p 463

Fabri MC, Pedel L, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207

Fanelli E, Delbono I, Ivaldi R, et al (2017) Cold-water coral *Madrepora oculata* in the eastern Ligurian Sea (NW Mediterranean): historical and recent findings. Aquat Conserv 27:965–975. https://doi.org/10.1002/aqc.2751

Fourt M, Goujard A (2012) Rapport final de la campagne MEDSEACAN (Têtes des canyons méditerranéens continentaux) novembre 2008–avril 2010. Partenariat Agence des aires marines protégées–GIS Posidonie, GIS Posidonie Publ, p 218

Fourt M, Michez N, Chevaldonné, et al (2014) Exploration visuelle des canyons et bancs rocheux profonds en Méditerranée française: apports à la typologie nationale des habitats profonds. In: Langar H, Bouafif C, Ouerghi A (eds) Proceedings of the 1st Mediterranean symposium on the conservation of dark habitats, Portoroz, Slovenia, 31 October 2014. RAC/SPA Publications, Tunis, pp 33–38

Fourt M, Goujard A, Canese S, et al (2015) Rapport de la campagne océanographique "Ramoge Exploration canyon et roches profondes 2015". Accord Ramoge-Agence des aires marines protégées, p 81

Frederiksen R, Jensen A, Westerberg H (1992) The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing. Sarsia 77:157–171

Fredj G, Laubier L (1985) The deep Mediterranean benthos. In: Moraitou-Apostopoulou M, Kiortsis V (eds) Mediterranean marine ecosystems (NATO conference series). Plenum Press, New York, pp 169–188

Freiwald A (2002) Reef-forming cold-water corals. In: Ocean margin systems. Springer, New York, pp 365–385

Freiwald A, Wilson JB (1998) Taphonomy of modern deep, cold-temperate water coral reefs. Hist Biol 13:37–52

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs. UNEP-WCMC, Cambridge, p 84

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74. https://doi.org/10.5670/oceanog.2009.06

Freiwald A, Boetius A, Bohrmann G (2011) Deep water ecosystems of the Eastern Mediterranean, Cruise No. 70, Leg 1–3. METEOR-Berichte, p 312

Gage JS, Tyler PA (1991) Deep-sea biology – a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge, p 504

Gana S, Iudicone D, Ghenim L, et al (2015) Monitoring water masses properties by Glider in Sardinia Channel during summer 2014. In: Geophys Res Abstr 17, EGU General Assembly 2015, Vienne, April 2016, p 14252

Genin A, Dayton PK, Lonsdale PF, et al (1986) Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature 322:59–61

GFCM (General Fisheries Commission for the Mediterranean) (2009) Criteria for the identification of sensitive habitats of relevance for the management of priority species. In: Meeting of the Sub-Committee on Marine Environment and Ecosystems (SCMEE), Malaga, Spain

Giacobbe S (2001) Distribuzione areale e batimetrica della *facies* a *Errina aspera* L. (Hydrozoa, Stylasteridae) nello Stretto di Messina. Biol Mar Mediterr 8:246–251

Giacobbe S, Laria G, Spanò N (2007) Hard bottom assemblages in the Strait of Messina: distribution of *Errina aspera* L. (Hydrozoa: Stylasteridae). In: Rapport du Congrès de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée, vol 38, p 485

Gili JM, Pagès F (1987) Pennatuláceos (Cnidaria, Anthozoa) recolectados en la plataforma continental catalana (Mediterráneo occidental). Miscellania Zoológica 11:25–39

Giusti M, Bo M, Bavestrello G, et al (2012) Record of *Viminella flagellum* (Alcyonacea: Ellisellidae) in Italian waters (Mediterranean Sea). Mar Biodivers Rec 5:e34. https://doi.org/10.1017/S1755267211000510

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060. https://doi.org/10.5194/bg-10-2049-2013

Gori A, Grover R, Orejas C, et al (2014a) Uptake of dissolved free aminoacids by four cold-water coral species from the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 99:42–50

Gori A, Reynaud S, Orejas C, et al (2014b) Physiological performance of the cold-water coral *Dendrophyllia cornigera* reveals its preference for temperate environments. Coral Reefs. https://doi.org/10.1007/s00338-014-1167-9

Gori A, Bavestrello G, Grinyó J, et al (2017) Animal forests in deep coastal bottoms and continental shelf of the Mediterranean Sea. In: Rossi S (ed) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1–28. https://doi.org/10.1007/978-3-319-17001-5_5-2

Grinyó J, Gori A, Ambroso S, et al (2016) Diversity, distribution and population size structure of deep Mediterranean gorgonian assemblages (Menorca Channel, Western Mediterranean Sea). Progr Oceanogr 145:42–56. https://doi.org/10.1016/j.pocean.2016.05.001

Hebbeln D, Wienberg C, Beuck L, et al (2009) Report and preliminary results of RV POSEIDON Cruise POS 385 "Cold-Water Corals of the Alboran Sea (western Mediterranean Sea)", vol 273. Universität Bremen, Berichte, Fachbereich Geowissenschaften, p 79

Heifetz J (2002) Coral in Alaska: distribution, abundance, and species associations. Hydrobiologia 471:19–28

Henriet JP, Hamoumi N, Da Silva AC, et al (2014) Carbonate mounds: from paradox to World Heritage. Mar Geol 352:89–110. https://doi.org/10.1016/j.margeo.2014.01.008

Henry LA, Frank N, Hebbeln D, et al (2014) Global ocean conveyor lowers extinction risk in the deep sea. Deep-Sea Res Part 1 Oceanogr Res Pap 88:8–16

Huvenne VAI, Beyer A, de Haas H, et al (2005) The seabed appearance of different coral bank provinces in the Porcupine Seabight, NE Atlantic: results from sidescan sonar and ROV seabed mapping. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 535–569

Ingrassia M, Macelloni L, Bosman A, et al (2016) Black coral (Anthozoa, Antipatharia) forest near the western Pontine Islands (Tyrrhenian Sea). Mar Biodivers 46:285–290. https://doi.org/10.1007/s12526-015-0315-y

López-González PJ, Grinyó J, Gili JM (2015) *Chironephthya mediterranea* n. sp. (Octocorallia, Alcyonacea, Nidaliidae), the first species of the genus discovered in the Mediterranean Sea. Mar Biodivers 45:667–688. https://link.springer.com/article/10.1007/s12526-014-0269-5

Kiriakoulakis K, Freiwald A, Fisher E, et al (2007) Organic matter quality and supply to deep-water coral/mound systems of the NW European Continental Margin. Int J Earth Sci 96:159–170

Knittweis L, Aguilar R, Alvarez H, et al (2016) New depth record of the precious red coral *Corallium rubrum* for the Mediterranean. In: Rapport du Congrès de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 41, p 467

Kozachenko M, Wheeler A, Beyer A, et al (2002) A four dimensional prospective of the sedimentary processes and their interactions with Ireland's deep-water coral carbonate mound ecosystems: Belgica carbonate mound province, Eastern Porcupine Seabight, NE Atlantic. Geophysical Research Abstracts 4, Abstr EGS02-A-02529, 27th General Assembly of the European Geophysical Society, Nice, 21–26 April 2002

de la Torriente A, Aguilar R, Serrano A, et al (2014) Sur de Almería – Seco de los Olivos. Fundación Biodiversidad del Ministerio de Agricultura, Alimentación y Medio Ambiente (ed) Proyecto LIFE+ INDEMARES, p 102

Lastras G, Canals M, Ballesteros E, et al (2016) Cold-water corals and anthropogenic impacts in La Fonera submarine canyon head, northwestern Mediterranean Sea. PLoS One 11:e0155729. https://doi.org/10.1371/journal.pone.0155729

Laubier L, Emig CC (1993) La faune benthique profonde de Méditerranée. In: Della Croce FR (ed) Symposium Mediterranen Seas 2000. Istituto di Scienze Ambientali Marine, S. Margherita Ligure, pp 397–428

Lincoln RJB, Clark GA (1998) A dictionary of ecology, evolution and systematics. Cambridge University Press, Cambridge, p 361

Lo Iacono C, Gràcia E, Bartolomé R, et al (2012) Habitats of the Chella Bank. Eastern Alborán Sea (Western Mediterranean). In: Harris P, Baker E (eds) Seafloor Geomorphology as Benthic Habitat: GeoHab Atlas of seafloor geomorphic features and benthic habitats. Elsevier, pp 681–687

Lo Iacono C, Gràcia E, Ranero CR, et al (2014) The West Melilla cold-water coral mounds, eastern Alboran Sea: morphological characterization and environmental context. Deep-Sea Res Part 2 Top Stud Oceanogr 99:316–326. https://doi.org/10.1016/j.dsr2.2013.07.006

Locke JM, Bilewitch JP, Coates KA (2013) Scleractinia, Octocorallia and Antipatharia of Bermuda's reefs and deep-water coral communities: a taxonomic perspective including new records. In: Sheppard C (ed) Coral reefs of the world, vol 4. Coral reefs of the UK Overseas territories. Springer, Dordrecht, pp 189–200

Maldonado M, López-Acosta M, Sánchez-Tocino L, et al (2013) The rare, giant gorgonian *Ellisella paraplexauroides*: demographics and conservation concerns. Mar Ecol Progr Ser 479:127–141

Manca B, Burca M, Giorgetti A, et al (2004) Physical and biochemical averaged vertical profiles in the Mediterranean regions: an important tool to trace the climatology of water masses and to validate incoming data from operational oceanography. J Mar Syst 48:83–116

Manzi V, Gennari R, Hilgen F, et al (2013) Age refinement of the Messinian salinity crisis onset in the Mediterranean. Terra Nova 25:315–322

von Marenzeller E (1893) Zoologische Ergebnisse. II. Polych ten des Grundes, gesammelt 1890, 1891 und 1892. Sitzungb Kaiserl Ak Wiss Math Naturwiss Cl 60:25–48

Martinelli M, Morello EB, Isajlović I, et al (2013) Towed underwater television towards the quantification of Norway lobster, squat lobsters and sea pens in the Adriatic Sea. Acta Adriat 54:3–12

Massutí E, Reñones O (2005) Demersal resources assemblages in the trawl fishing grounds off the Balearic Islands (western Mediterranean). Sci Mar 69:167–181

Mastrototaro F, Matarrese A, Tursi A (2002) Un mare di coralli nel Mar Ionio. Biol Mar Mediterr 9:616–619

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral ecosystem off cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

Mastrototaro F, Maiorano P, Vertino A, et al (2013) A *facies* of *Kophobelemnon* (Cnidaria, Octocorallia) from Santa Maria di Leuca coral province (Mediterranean Sea). Mar Ecol 34:313–320

Mastrototaro F, Chimienti G, Capezzuto F, et al (2015) First record of *Protoptilum carpenteri* (Cnidaria: Octocorallia: Pennatulacea) in the Mediterranean Sea. Ital J Zool 82:61–68

Mastrototaro F, Chimienti G, Acosta J, et al (2017) *Isidella elongata* (Cnidaria: Alcyonacea) *facies* in the western Mediterranean Sea: visual surveys and descriptions of its ecological role. Eur Zool J 84:209–225. https://doi.org/10.1080/24750263.2017.1315745

Maurin C (1962) Etude des fonds chalutables de la Méditerranée occidentale (écologie et pêche) «Président-Théodore-Tissier» 1957 à 1960 et «Thalassa» 1960 et 1961. Rev Trav Inst Pêches Maritimes 26:163–218

Maynou F, Cartes JE (2012) Effects of trawling on fish and invertebrates from deep-sea coral facies of *Isidella elongata* in the western Mediterranean. J Mar Biol Assoc UK 92:1501–1507. https://doi.org/10.1017/S0025315411001603

Mienis F, de Stigter HC, White M, et al (2007) Hydrodynamic controls on coldwater coral growth and carbonate mound development at the SW and SE Rockall Trough Margin, NE Atlantic Ocean. Deep-Sea Res Part 1 Oceanogr Res Pap 54:1655–1674

Miller KJ (1998) Short-distance dispersal of black coral larvae: inference from spatial analysis of colony genotypes. Mar Ecol Progr Ser 163:225–233

Millot C, Taupier-Letage I (2005) Circulation in the Mediterranean Sea. In: The handbook of environmental chemistry 5K. Springer, Berlin, pp 29–66

Montagna P, McCulloch M, Taviani M, et al (2006) Phosphorus in cold-water corals as a proxy for seawater nutrient chemistry. Science 312:1788–1791. https://doi.org/10.1126/science.1128139

Morri C, Bavestrello G, Nike Bianchi C (1991) Faunal and ecological notes on some benthic cnidarian species from the Tuscan Archipelago and eastern Ligurian Sea (Western Mediterranean). Boll Mus Ist Biol Univ Genova 54–55:27–47

Movilla J, Gori A, Calvo E, et al (2014) Resistance of two Mediterranean cold-water coral species to low-pH conditions. Water 6:59–67

Mytilineou C, Smith CJ, Anastasopoulou A, et al (2014) New cold-water coral occurrences in the eastern Ionian Sea: results from experimental long line fishing. Deep-Sea Res Part 2 Top Stud Oceanogr 99:146–157

Naumann MS, Orejas C, Ferrier-Pages C (2014) Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. Deep-Sea Res Part 2 Top Stud Oceanogr 99:36–41

Ocaña A, Sánchez Tocino L, López-González PJ (2000) Consideraciones faunísticas y biogeográficas de los antozoos (Cnidaria: Anthozoa) de la costa de Granada (Mar de Alborán). Zool Baetica 11:51–65

Opresko DM (2009) A new name for the Hawaiian Antipatharian coral formerly known as *Antipathes dichotoma* (Cnidaria: Anthozoa: Antipatharia). Pac Sci 63:277–291

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51

Orejas C, Ferrier-Pages C, Reynaud S, et al (2011) Long-term growth rates of four Mediterranean cold-water coral species maintained in aquaria. Mar Ecol Progr Ser 429:57–65

Orejas C, Gori A, Jiménez C, et al (2017) First in situ documentation of a population of the coral *Dendrophyllia ramea* off Cyprus (Levantine Sea) and evidence of human impacts. Galaxea J Coral Reef Stud 19:15–16

Otero MM, Numa C, Bo M, et al (2017) Overview of the conservation status of Mediterranean anthozoans. IUCN, Málaga, p 73

Palanques A, Durrieu de Madron X, Puig P, et al (2006) Suspended sediment fluxes and transport processes in the Gulf of Lions submarine canyons. The role of storms and dense water cascading. Mar Geol 234:43–61. https://doi.org/10.1016/j.margeo.2006.09.002

Pardo E, Aguilar R, García S, et al (2011) Documentación de arrecifes de corales de agua fría en el Mediterráneo occidental (Mar de Alborán). Chronica Naturae 1:20–34

Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la Mer Méditerranée. Recueil Trav Station Mar Endoume 31:1–137

Petović S, Marković O, Ikica Z, et al (2016) Effects of bottom trawling on the benthic assemblages in the south Adriatic Sea (Montenegro). Acta Adriat 57:81–91

Pierdomenico M, Martorelli E, Dominguez-Carrió C, et al (2016) Seafloor characterization and benthic megafaunal distribution of an active submarine canyon and surrounding sectors: the case of Gioia Canyon (southern Tyrrhenian Sea). J Mar Syst 157:101–117

Por FD, Dimentman C (1985) Continuity of Messinian biota in the Mediterranean basin. In: Stanley DJ, Wezel FC (eds) Geologic evolution of the Mediterranean Basin. Springer, Heidelberg, pp 545–556

Porporato E, De Domenico F, Mangano MC, et al (2009) The pennatulacean fauna from southern Tyrrhenian Sea. Biol Mar Mediterr 16:292–293

Puig P, Palanques A, Orange DL, et al (2008) Dense shelf water cascades and sedimentary furrow formation in the Cap de Creus Canyon, northwestern Mediterranean Sea. Cont Shelf Res 28:2017–2030. https://doi.org/10.1016/j.csr.2008.05.002

Raffi S, Taviani M (1984) An outline of the late Tertiary to Recent History of the Mediterranean deep-sea mollusks faunas. Int Coll on

Mediterranean Neogene Marine Megafaunal Palaeoenvironments and Biogeography. Ann Géol Pays Héllén 32:257–261

Relini G, Peirano A, Tunesi L, et al (1986) Osservazioni sulle comunità dei fondi strascicatoli del Mar Ligure Centro-Orientale. Boll Mus Ist Biol Univ Genova 52:139–161

Reyss D (1964) Contribution à l'étude du rech Lacaze-Duthiers, vallée sous-marine des coôtes du Roussillon. Vie Milieu 15:1–146

Roark E, Guilderson TP, Dunbar RB, et al (2006) Radiocarbon-based ages and growth rates of Hawaiian deep-sea corals. Mar Ecol Progr Ser 327:1–14

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Roberts JM, Davies AJ, Henry LA (2009a) Mingulay reef complex: an interdisciplinary study of cold-water coral habitat, hydrography and biodiversity. Mar Ecol Progr Ser 397:139–151

Roberts JM, Wheeler A, Freiwald A, et al (2009b) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334. https://doi.org/10.1017/CBO9780511581588

Robinson AR, Leslie W, Theocharis A, et al (2001) Mediterranean sea circulation. Encyclopedia of ocean science 3. Academic, San Diego, pp 1689–1705

Rossi L (1958) Contributo allo studio della fauna di profondità vivente presso la Riviera ligure di levante. Annali del Museo Civico di Storia Naturale "Giacomo Doria". Genova 2:1–13

Rossi S, Bramanti L, Gori A, et al (2017) An overview of the animal forests of the world. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1–26. https://doi.org/10.1007/978-3-319-17001-5_1-1

Sabelli B, Taviani M (2014) The making of the Mediterranean molluscan biodiversity. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 285–306. https://doi.org/10.1007/978-94-007-6704-1_16

Salomidi M, Zibrowius H, Issaris Y, et al (2010) *Dendrophyllia* in Greek waters, Mediterranean Sea, with first record of *D. ramea* (Cnidaria, Scleractinia) from the area. Mediterr Mar Sci 11:189–194

Salvati E, Angiolillo M, Bo M, et al (2010) The population of *Errina aspera* (Hydrozoa: Stylasteridae) of the Messina Strait (Mediterranean Sea). J Mar Biol Assoc UK 90:1331–1336. https://doi.org/10.1017/S0025315410000950

Sardà F, Calafat A, Flexas MM, et al (2004) An introduction to Mediterranean deep-sea biology. Sci Mar 68:7–38

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108. https://doi.org/10.1371/journal.pone.0087108

Schembri PJ, Dimech M, Camilleri M, et al (2007) Living deep water *Lophelia* and *Madrepora* corals in Maltese waters (Strait of Sicily, Mediterranean Sea). Cah Biol Mar 48:77–84

Schuchert P (2008) The European athecate hydroids and their medusa (Hydrozoa, Cnidaria): Filifera part 3. Rev Suisse Zool 115:221–302

Smith C, Sakellariou D, Mccoy F, et al (2009) Deep coral environments south of Crete. In: Proceedings of the 9th symposium on oceanography & fisheries, Patra, 1, pp 665–668

Steindachner F (1891) Veröffentlichungen der Commission für Erforschung des östlichen Mittelmeeres. Vorläufiger Bericht über die zoologischen Arbeiten im Sommer 1891. Sitzungb Kaiserl Ak Wiss Math Naturwiss Cl 1:435–447

Taviani M (2002) The Mediterranean benthos from Late Miocene up to Present: ten million years of dramatic climatic and geological vicissitudes. Biol Mar Mediterr 9:445–463

Taviani M (2003) Shaping the biogeography of the Mediterranean basin: one geologist's perspective. In: Marine biogeography of the Mediterranean Sea: patterns and dynamics of biodiversity. Biogeographia 24:15–22

Taviani M, Freiwald A, Zibrowius H (2005a) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Taviani M, Remia A, Corselli C, et al (2005b) First geo-marine survey of living cold-water *Lophelia* reefs in the Ionian Sea (Mediterranean basin). Facies 50:409–417

Taviani M, Freiwald A, Beuck L (2010) The deepest known occurrence of the precious red coral *Corallium rubrum* (L. 1758) in the Mediterranean Sea. In: Bussoletti E, Cottingham D, Bruckner A, et al (eds) Proceedings of the international workshop on red coral science, management, trade: lessons from the Mediterranean. NOOA Technical Memorandum CRCP-13. NOOA, Silver Spring, pp 87–93

Taviani M, Angeletti L, Antolini B, et al (2011a) Geo-biology of Mediterranean deep-water coral ecosystems. In: Brugnoli E, Cavaretta G, et al (eds) Marine research at CNR. Dipartamento Terra e Ambiente, Consiglio Nazionale delle Ricerche, Roma, pp 705–720

Taviani M, Vertino A, López Correa M, et al (2011b) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603. https://doi.org/10.1007/s10347-010-0247-8

Taviani M, Angeletti L, Beuck L, et al (2015) Reprint of 'On and off the beaten track: Megafaunal sessile life and Adriatic cascading processes'. Mar Geol 375:146–160. https://doi.org/10.1016/j.margeo.2015.10.003

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78. https://doi.org/10.1016/j.dsr2.2015.12.008

Terribile K, Evans J, Knittweis L, Schembri PJ (2015) Maximising MEDITS: using data collected from trawl surveys to characterise the benthic and demersal assemblages of the circalittoral and deeper waters around the Maltese Islands (Central Mediterranean). Reg Stud Mar Sci. https://doi.org/10.1016/j.rsma.2015.07.006

Thiem Ø, Ravagnan E, Fosså JH, et al (2006) Food supply mechanisms for cold-water corals along a continental shelf edge. J Mar Syst 60:207–219

Trincardi F, Foglini F, Verdicchio G, et al (2007) The impact of cascading currents on the Bari Canyon System, SW-Adriatic Margin (Central Mediterranean). Mar Geol 246:208–230

Tudela S, Simard F, Skinner J, et al (2004) The Mediterranean deep-sea ecosystems: a proposal for their conservation. In: The Mediterranean deep-sea ecosystems: an overview of their diversity, structure, functioning and anthropogenic impacts, with a proposal for conservation. IUCN, Málaga and WWF, Rome, pp 39–47

Tunesi L, Diviacco G (1997) Observation by submersible on the bottoms off shore Portofino Promontory (Ligurian Sea). In: Atti del 12°Congresso dell'Associazione Italiana di Oceanologia e Limnologia, pp 61–74

Tunesi L, Diviacco G, Mo G (2001) Observation by submersible on the biocoenosis of the deep-sea corals off Portofino Promontory (northwestern Mediterranean Sea). In: Martin Willison JH, et al (eds) Proceedings of the first international symposium on deep-sea corals, Ecology Action Centre and Nova Scotia Museum, Halifax, pp 76–87

Tursi A, Mastrototaro F, Matarrese A, et al (2004) Biodiversity of the white coral reefs in the Ionian Sea (Central Mediterranean). Chem Ecol 20:107–116

Vafidis D, Koukouras A, Voultsiadou-Koukoura E (1994) Octocoral fauna of the Aegean Sea with a check list of the Mediterranean species: new information, faunal comparisons. Ann Inst Océanogr (Monaco) 70:217–230

Vafidis D, Koukouras A, Voultsiadou-Koukoura E (1997) Actiniaria, Corallimorpharia and Scleractinia (Hexacorallia, Anthozoa) of the Aegean Sea, with a checklist of the Eastern Mediterranean and Black Sea species. Isr J Zool 43:55–70

Vertino A, Savini A, Rosso AI, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML coral province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396. https://doi.org/10.1016/j.dsr2.2009.08.023

Vertino A, Stolarski J, Bosellini FR, et al (2014) Mediterranean corals through time: from Miocene to present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 257–274. https://doi.org/10.1007/978-94-007-6704-1_14

Vilibic I, Orlic M (2002) Adriatic water masses, their rates of formation and transport through the Otranto Strait. Deep-Sea Res Part 1 Oceanogr Res Pap 49:1321–1340

Voultsiadou E, Fryganiotis C, Porra M, et al (2011) Diversity of invertebrate discards in small and medium scale Aegean Sea fisheries. Open Mar Biol J 5:73–81

Wagner D, Opresko DM (2015) Description of a new species of *Leiopathes* (Antipatharia: Leiopathidae) from the Hawaiian Islands. Zootaxa 3974:277–289

Watremez P (2012) Canyon heads in the French Mediterranean. Overview of results from the MEDSEACAN and CORSEACAN campaigns (2008–2010). In: Würtz M (ed) Mediterranean submarine canyons: ecology and governance. IUCN, Gland/Málaga, pp 105–112

Wheeler AJ, Beck T, Thiede J, et al (2005) Deep-water cold-water coral carbonate mounds on the Porcupine Bank, Irish margin: preliminary results from Polarstern ARK-XIX/3a ROV cruise. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 323–333

Wheeler AJ, Beyer A, Freiwald A, et al (2007) Morphology and environment of cold-water coral carbonate mounds on the NW European margin. Int J Earth Sci 96:37–56

White M, Mohn C, de Stigter H, et al (2005) Deepwater coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall Trough, NE Atlantic. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 503–514

White M, Roberts JM, van Weering T (2007) Do bottom intensified diurnal tidal currents shape the alignment of carbonate mounds in the NE Atlantic? Geo-Mar Lett 27:391–397

Williams GC (2011) The global diversity of Sea Pens (Cnidaria: Octocorallia: Pennatulacea). PLoS One 6:e22747. https://doi.org/10.1371/journal.pone.0022747

Würtz M (ed) (2012) Mediterranean submarine canyons: ecology and governance. IUCN, Gland/Málaga, p 216

Würtz M, Rovere M (eds) (2015) Atlas of the Mediterranean seamounts and seamount-like structures. IUCN, Gland, p 276

Zibrowius H (1980) Les scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mém Inst Océanogr Monaco 11:1–284

Zibrowius H (2003) The "white coral community", canyon and seamount faunas of the deep Mediterranean Sea. RAC/SPA – Regional Activity Centre for Specially Protected Areas, Tunis

Zibrowius H, Cairns SD (1992) Revision of the northeast Atlantic and Mediterranean Stylasteridæ (Cnidaria: Hydrozoa). Mém Mus Hist Nat Westerberg 153:1–136

Cross References

Addamo A (this volume) *Desmophyllum dianthus* genetics and more

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Aymà A, Aguzzi J, Canals M, et al (this volume) Occurrence of living cold-water corals at large depths within submarine canyons of the northwestern Mediterranean Sea

Bo M, Bavestrello G (this volume) Mediterranean black coral communities

Boavida J, Becheler R, Addamo A, et al (this volume) Past, present and future connectivity of Mediterranean cold-water corals: patterns, drivers and fate in a technically and environmentally changing world

Fourt M, Goujard A, Chevaldonné P (this volume) Working with visual methods, comparison among the French deep-sea canyons

Freiwald A (this volume) Messinian salinity crisis: what happened to cold-water corals?

Hayes D, Schroeder K, Poulain, PM, et al (this volume) Review of the circulation and characteristics of intermediate water masses of the Mediterranean – implications for cold-water coral habitats

Knittweis L, Evans J, Aguilar R, et al (this volume) Recent discoveries of extensive cold-water coral assemblages in Maltese waters

Orejas C, Jiménez C, Gori A, et al (this volume) Corals of Aphrodite: *Dendrophyllia ramea* communities of Cyprus

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Puig P, Gili JM (this volume) Submarine canyons in the Mediterranean: a shelter for cold-water corals

Reynaud S, Ferrier-Pagès C (this volume) Biology and ecophysiology of Mediterranean cold-water corals

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Taviani M (this volume) Changing views about Mediterranean cold-water corals

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Drop Chapter Gorgonian and Black Coral Assemblages in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea

20

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Abstract

Coral gardens are increasingly being reported at 40–200 m depth in the Mediterranean Sea. These coral assemblages are composed of gorgonians from shallow coastal rocky bottoms extending their distribution to deeper areas, as well as by gorgonians and black corals with distribution restricted to the continental shelf and upper slope. Gorgonians and black corals are among the main structural species in deep benthic ecosystems, providing shelter and reproductive grounds for a highly diverse associated fauna. Due to their branching morphology and erect position, these deep coral gardens are extremely vulnerable to several fishing activities (bottom trawling, long-lines and trammel net fishing) and should consequently be protected through an ecosystem-based fishery management.

Keywords

Gorgonians · Black corals · Deep-coastal bottoms · Continental shelf · Mediterranean Sea

Technological development has recently increased the accessibility of technical diving, remotely operated vehicles (ROV) and manned submersibles to ecological research, resulting in a significant rise in the scientific exploration of deep-sea Mediterranean environments by means of visual methods. Such studies have revealed the presence of dense and highly diverse coral gardens composed by gorgonians and black corals in several locations of the Mediterranean Sea, from 40 to 200 m depth (Fig. 20.1; Grinyó et al. 2016; Gori et al. 2017; Altuna and Poliseno, this volume). These branching organisms are among the main ecosystem engineers (*sensu* Jones et al. 1994) in deep Mediterranean benthic communities, generating complex three-dimensional frameworks that enhance the spatial heterogeneity of the seabed, favouring a highly diverse associated fauna (Bo et al. 2012, 2015; Rueda et al., this volume). Furthermore, by capturing plankton and particulate organic matter suspended in the water, gorgonians and black corals play an important ecological role in the benthic-pelagic coupling, determining a significant flow of matter and energy from the pelagic to the benthic system (Gili and Coma 1998; Rossi et al. 2017; Reynaud and Ferrier-Pagès, this volume).

Gorgonian species typically inhabiting Mediterranean shallow coastal rocky bottoms above 40 m depth (*Eunicella singularis*, *E. cavolinii*, *Leptogorgia sarmentosa*, *Paramuricea clavata* and *Corallium rubrum*) can extend their bathymetric distribution to deeper coastal areas and the continental shelf (approx. 40–130 m depth) (Bo et al. 2008; Rossi et al. 2008; Cerrano et al. 2010; Gori et al. 2011; Angiolillo et al. 2016; Grinyó et al. 2016) (Fig. 20.2). Similarly, *E. cavolinii* and *P. clavata* have been reported forming dense populations at similar depths on top of Mediterranean seamounts (70–100 m depth) (Bo et al. 2011).

On the continental shelf, the gorgonian *Paramuricea macrospina* forms extensive populations on maërl beds (Grinyó et al. 2016) and rocky outcrops (Bo et al. 2012) from 65 to 130 m depth (Fig. 20.2) (see also chapter by Chimienti et al., this volume and by Altuna and Poliseno, this volume). This species has also been observed on shallow-water rocky

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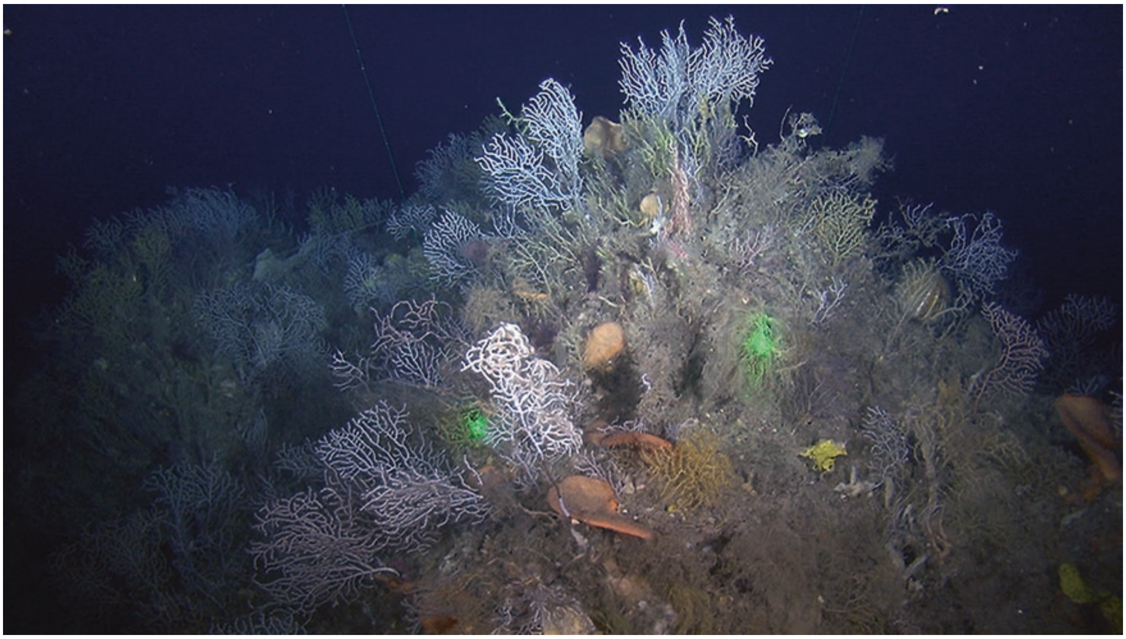

Fig. 20.1 Deep coral garden composed of *Eunicella cavolinii*, *Acanthogorgia hirsuta* and *Paramuricea macrospina* at 160 m depth near Cap Formentor (Menorca Channel, Western Mediterranean Sea), green dots are the laser beams, which are 50 cm apart. (Photo credits: ICM-CSIC and IFM-GEOMAR)

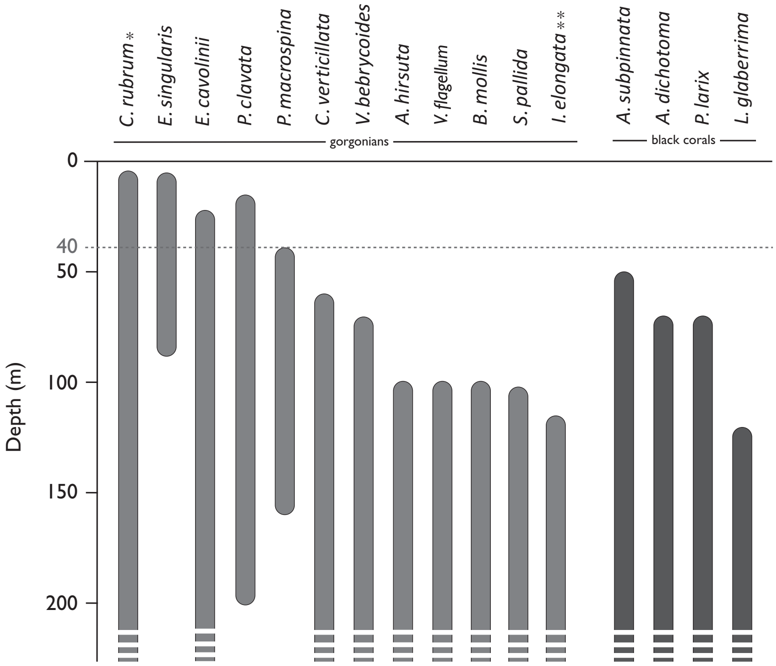

Fig. 20.2 Bathymetric distribution of Mediterranean gorgonian and black coral species in coastal bottoms and continental shelf of the Mediterranean Sea (based on the literature reviewed in Gori et al. 2017); * precious coral, ** bamboo coral

bottoms under the particular hydrodynamic conditions of the Sea of Marmara (Vafidis et al. 1994; Topçu and Öztürk 2015). Additionally, it was reported associated to cold-water corals (CWC) at 540–830 m depth (Mastrototaro et al. 2010; Vertino et al. 2010; Chimienti et al., this volume), whether these records should be confirmed by examination of specimens. Recent studies have shown that shelf edge environments sustain maximum diversity and abundance of Mediterranean gorgonians (Bo et al. 2015; Grinyó et al. 2016; Cau et al. 2017; Altuna and Poliseno, this volume). Indeed, up to ten species of gorgonians (*P. clavata, P. macrospina, E. cavolinii, C. rubrum, Villogorgia bebrycoides, Acanthogorgia hirsuta, Callogorgia verticillata, Swiftia pallida, Viminella flagellum* and *Bebryce mollis*) generate high complex coral gardens on rocky bottoms located at 100–200 m depth in the Menorca Channel (Grinyó et al. 2016), the Montecristo Shoals (Bo et al. 2014a) as well as along the South Sardinia continental margin (Bo et al. 2015; Cau et al. 2015, 2017) (Fig. 20.2) (see also Chimienti et al., this volume). High gorgonian diversity on the shelf edge could result from the merging of species with shallower and deeper distributions, causing a mid-domain effect (Colwell and Lees 2000; Grinyó et al. 2016). Black corals (*Antipathella subpinnata*, *Antipathes dichotoma, Parantipathes larix* and *Leiopathes glaberrima*) can also be found within these assemblages (Cau et al. 2015; Grinyó et al. 2016), becoming dominant in the deeper rocky shoals of the continental slope (130–200 m depth) (Bo et al. 2015; Ingrassia et al. 2016; Bo and Bavestrello, this volume). The bamboo coral *Isidella elongata*, which can be considered the main tree-like species dwelling in deep bathyal muds (Cartes et al. 2013; Mastrototaro et al. 2017; Altuna and Poliseno, this volume; Chimienti et al., this volume), also occurs in muddy bottoms around these rocky shoals at 115–210 m depth (Bo et al. 2015). This species is highly treated by bottom-trawling fishing (Maynou and Cartes 2012; Otero and Marin, this volume); its populations have suffered such a strong reduction in its geographical extent that this species is the only anthozoan so far categorised as Critically Endangered within the IUCN Red List (Otero et al. 2017; Otero and Marin, this volume).

Finally, in the Strait of Gibraltar and Alborán Sea, at the westernmost limit of the Mediterranean Sea, several Atlantic species from the Lusitanian and Mauritanian biogeographical provinces can be also found together with typical Mediterranean species in both coastal and continental shelf gorgonian assemblages (Ocaña et al. 2000; Altuna and Poliseno, this volume; Chimienti et al., this volume; López-González unpublished data).

Due to their branching morphology and erect position, gorgonians and black corals are among the most frequent anthozoan species in the fishing discard, as they easily get entangled in nets and long-lines (Cartes et al. 2013; Mytilineou et al. 2014; Deidun et al. 2015; Otero and Marin, this volume). The gorgonians *L. sarmentosa* and *Eunicella verrucosa*, previously common on the deep continental shelf (Carpine and Grasshoff 1975), have been severely affected by bottom trawling (Gili et al. 1987), resulting in a drastic reduction of their abundances (Gori et al. 2011). Fishing impacts can cause the direct removal of organisms (especially bottom trawling and long-line fishing) or partial damage to the colonies (especially trammel net and long-line fishing), which can lead to overgrowth by other fast-growing organisms (Mortensen et al. 2005; Bo et al. 2014b). These impacts can have far-reaching and long-lasting effects due to the slow growth rates and slow population dynamics of Mediterranean gorgonians and black corals (Linares et al. 2007; Bo et al. 2015; Bramanti et al., this volume; Lartaud et al., this volume). For this reason, the conservation of deep benthic communities in coastal and off-shore areas should be accomplished through an ecosystem-based management approach (Fabri et al. 2014; Otero and Marin, this volume).

References

Angiolillo M, Gori A, Canese S, et al (2016) Distribution and population structure of deep-dwelling red coral in NW Mediterranean. Mar Ecol 37:237–473

Bo M, Tazioli S, Spanò N, et al (2008) Antipathella subpinnata (Antipatharia, Myriopathidae) in Italian seas. Ital J Zool 75:185–195

Bo M, Bertolino M, Borghini M, et al (2011) Characteristics of the mesophotic megabenthic assemblage of the Vercelli Seamount (North Tyrrhenian Sea). PLoS One 6:e16357

Bo M, Canese S, Spaggiari C, et al (2012) Deep coral oases in the South Tyrrhenian Sea. PLoS One 7:e49870

Bo M, Canese S, Bavestrello G (2014a) Discovering Mediterranean black coral forests: Parantipathes larix (Anthozoa: Hexacorallia) in the Tuscan Archipelago. Ital J Zool 81:112–125

Bo M, Bava S, Canese S, et al (2014b) Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. Biol Conserv 171:167–176

Bo M, Bavestrello G, Angiolillo A, et al (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS One 10:e0119393

Carpine C, Grasshoff M (1975) Les gorgonaires de la Mediterranée. Bull l'Institut Océanogr Monaco 71:1–140

Cartes JE, Lo Iacono C, Mamouridis V, et al (2013) Geomorphological, trophic and human influences on the bamboo coral *Isidella elongata* assemblages in the deep Mediterranean: to what extent does Isidella form habitat for fish and invertebrates? Deep-Sea Res Part 1 Oceanogr Res Pap 76:52–65

Cau A, Follesa MC, Moccia D, et al (2015) Deepwater corals biodiversity along roche du large ecosystems with different habitat complexity along the south Sardinia continental margin (CW Mediterranean Sea). Mar Biol 162:1865–1878

Cau A, Moccia D, Follesa MC, et al (2017) Coral forests diversity in the outer shelf of the south Sardinian continental margin. Deep-Sea Res Part 1 Oceanogr Res Pap 122:60–70

Cerrano C, Danovaro R, Gambi C, et al (2010) Gold coral (*Savalia savaglia*) and gorgonian forests enhance benthic biodiversity and ecosystem functioning in the mesophotic zone. Biodivers Conserv 19:153–167

Colwell RK, Lees DC (2000) The mid-domain effect: geometric constraints on the geography of species richness. Trends Ecol Evol 15:70–76

Deidun A, Andaloro F, Bavestrello G, et al (2015) First characterization of a *Leiopathes glaberrima* (Cnidaria: Anthozoa: Antipatharia) forest in Maltese exploited fishing grounds. Ital J Zool 82:271–280

Fabri MC, Pedel L, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207

Gili JM, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol Evol 13:316–321

Gili JM, Ros JD, Pagès F (1987) Types of bottoms and benthic Cnidaria from the trawling grounds (littoral and bathyal) off Catalonia (NE Spain). Vie et Milieu 37:85–98

Gori A, Rossi S, Berganzo E, et al (2011) Spatial distribution patterns of the gorgonians *Eunicella singularis, Paramuricea clavata*, and *Leptogorgia sarmentosa* (Cape of Creus, Northwestern Mediterranean Sea). Mar Biol 158:143–158

Gori A, Bavestrello G, Grinyó J, et al (2017) Animal forests in deep coastal bottoms and continental shelf of the Mediterranean Sea. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 207–234

Grinyó J, Gori A, Ambroso S, et al (2016) Distribution and population size structure of unexpectedly well-preserved deep Mediterranean gorgonian assemblages (Menorca Channel, western Mediterranean Sea). Prog Oceanogr 145:42–56

Ingrassia M, Macelloni L, Bosman A, et al (2016) Black coral (Anthozoa, Antipatharia) forest near the western Pontine Islands (Tyrrhenian Sea). Mar Biodivers 46:285–290

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 29:373–386

Linares C, Doak DF, Coma R, et al (2007) Life history and viability of a long lived marine invertebrate: the octocoral *Paramuricea clavata*. Ecology 88:918–928

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

Mastrototaro F, Chimienti G, Acosta J, et al (2017) *Isidella elongata* (Cnidaria: Alcyonacea) facies in the western Mediterranean Sea: visual surveys and descriptions of its ecological role. Eur Zool J 84:209–225

Maynou F, Cartes JE (2012) Effects of trawling on fishes and invertebrates from deep-sea coral facies of *Isidella elongata* in the western Mediterranean. J Mar Biol Assoc UK 92:1501–1507

Mortensen PB, Buhl-Mortensen L, Gordon Jr DC, et al (2005) Evidence of fisheries damage to deep-water gorgonians in the Northeast Channel, Nova Scotia. In: Thomas J, Barnes P (eds) Proceeding from the symposium on the effects of fishing activities on Benthic habitats: linking geology, biology, socioeconomics and management. American Fisheries Society Symposium, November 12–14, 2002, Florida, USA

Mytilineou C, Smith CJ, Anastasopoulou A, et al (2014) New cold-water coral occurrences in the Eastern Ionian Sea: results from experimental long line fishing. Deep-Sea Res Part 2 Top Stud Oceanogr 99:146–157

Ocaña A, Sánchez-Tocino L, López-González PJ (2000) Consideraciones faunísticas de los antozoos (Cnidaria: Anthozoa) de la costa de Granada (Mar de Alborán). Zool Baetica 11:56–65

Otero MM, Numa C, Bo M, et al (2017) Overview of the conservation status of Mediterranean anthozoans. IUCN, Malaga

Rossi S, Tsounis G, Orejas C, et al (2008) Survey of deep-dwelling red coral (*Corallium rubrum*) populations at Cap de Creus (NW Mediterranean). Mar Biol 154:533–545

Rossi S, Coppari M, Viladrich N (2017) Benthic-pelagic coupling: new perspectives in the animal forests. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 855–886

Topçu EN, Öztürk B (2015) Composition and abundance of octocorals in the Sea of Marmara, where the Mediterranean meets the Black Sea. Sci Mar 79:125–135

Vafidis D, Koukouras A, Voultsiadou-Koukoura E (1994) Octocoral fauna of the Aegean Sea with a check list of the Mediterranean species: new information, faunal comparisons. Ann Inst Oceanogr 70:217–229

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Mound Province (Mediterranean). Deep-Sea Res Part 1 Oceanogr Res Pap 57:380–396

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals.

Bo M, Bavestrello G (this volume) Mediterranean black coral communities.

Bramanti L, Santangelo G, Benedetti MC, et al (this volume) Demography and conservation of deep corals: the study of population structure and dynamics.

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals.

Lartaud F, Mouchi V, Chapron L, et al (this volume) Growth patterns of Mediterranean calcifying cold-water corals.

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement.

Reynaud S, Ferrier-Pagès C (this volume) Biology and ecophysiology of Mediterranean cold-water corals.

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas.

21

Drop Chapter Mediterranean Black Coral Communities

Marzia Bo and Giorgio Bavestrello

Abstract

Remotely operated vehicle (ROV) investigations of the Mediterranean deep continental shelf and bathyal zone have provided, in the last decade, a large amount of data concerning an enigmatic group of anthozoans: the black corals. Taxonomic investigations as well as ecological and biological studies contributed to unveil the diversity, population structure, environmental preferences, bathymetric and geographical distribution of these corals. Remotely operated vehicle footage and accidental bycatch data have provided evidences of large impact by fishing activities on the Mediterranean black coral forests such that today, due also to their important ecological role as structuring species, they are considered part of vulnerable marine ecosystems and conservation strategies need to be developed targeting their protection.

Keywords

Antipatharia · CWCs · Animal forests · Habitat-forming species · Mediterranean Sea

Antipatharians, commonly known as black corals due to their dark, chitinous skeleton, constitute a small order of colonial anthozoans (approximately 240 species) showing a wide geographical and bathymetrical distribution (Wagner et al. 2012; Altuna and Poliseno, this volume). Known to form very rich communities in shallow-water tropical reefs (Tazioli et al. 2007), they also occur in deep waters, from the circalittoral zone to the abyssal plains, in polar and temperate regions (Pax et al. 1987; Opresko 2002; Opresko and Sanchez 2005; Tazioli et al. 2007; Bo et al. 2018; Chimienti et al., this volume). Characterised by six-tentacles polyps and a spiny skeleton, they display a very wide range of corallum morphologies, but typically they have an arborescent or flabellate appearance (Altuna and Poliseno, this volume).

Antipatharians are among the most enigmatic anthozoans of the Mediterranean basin. Despite they have been known for centuries due to occasional fishermen bycatch and most of them have been described over 200 years ago, the species belonging to this group have always been poorly studied in this region (Bo et al., in press). During the last decade, the ecological aspects of these anthozoans have been progressively revealed and recent explorations have highlighted their capability of forming large forests (Bo et al. 2008, 2012a, 2014a, 2018).

Four species of black corals have been described as stable components of the Mediterranean fauna (Opresko and Försterra 2004): *Antipathes dichotoma* Pallas, 1766, (Family Antipathidae), *Parantipathes larix* (Esper, 1790) (Family Schizopathidae), *Leiopathes glaberrima* (Esper, 1792) (Family Leiopathidae), and *Antipathella subpinnata* (Ellis and Solander, 1786) (Family Myriopathidae) (Fig. 21.1). Additionally, there is *Antipathes fragilis* Gravier, 1918 whose type species was lost and its taxonomic position is highly dubious. A sixth species has recently been found once in the Gibraltar area, *Antipathella wollastoni* (Gray, 1857), however, this black coral is far more common in the Atlantic basin (Ocaña et al. 2007). Finally, recent deep explorations are revealing new Atlantic entrances in the westernmost areas of the Mediterranean basin that are currently under taxonomic investigation (Bo et al., in press).

Thanks to deep explorations, black corals, once considered rare species, have been extensively recorded in the Alborán Sea, in the whole western basin, in the Sicily Channel and in the Aegean Sea, with *L. glaberrima* being the only one, so far, reported for the most extreme Levantine basin (Bo et al. 2008, 2018; Altuna and Poliseno, this volume; Chimienti et al., this volume). Particularly abundant along the continental shelf break, where they form mono or multispecific forests together with sponges and gorgonians, they are found also along the upper bathyal slope and mixed

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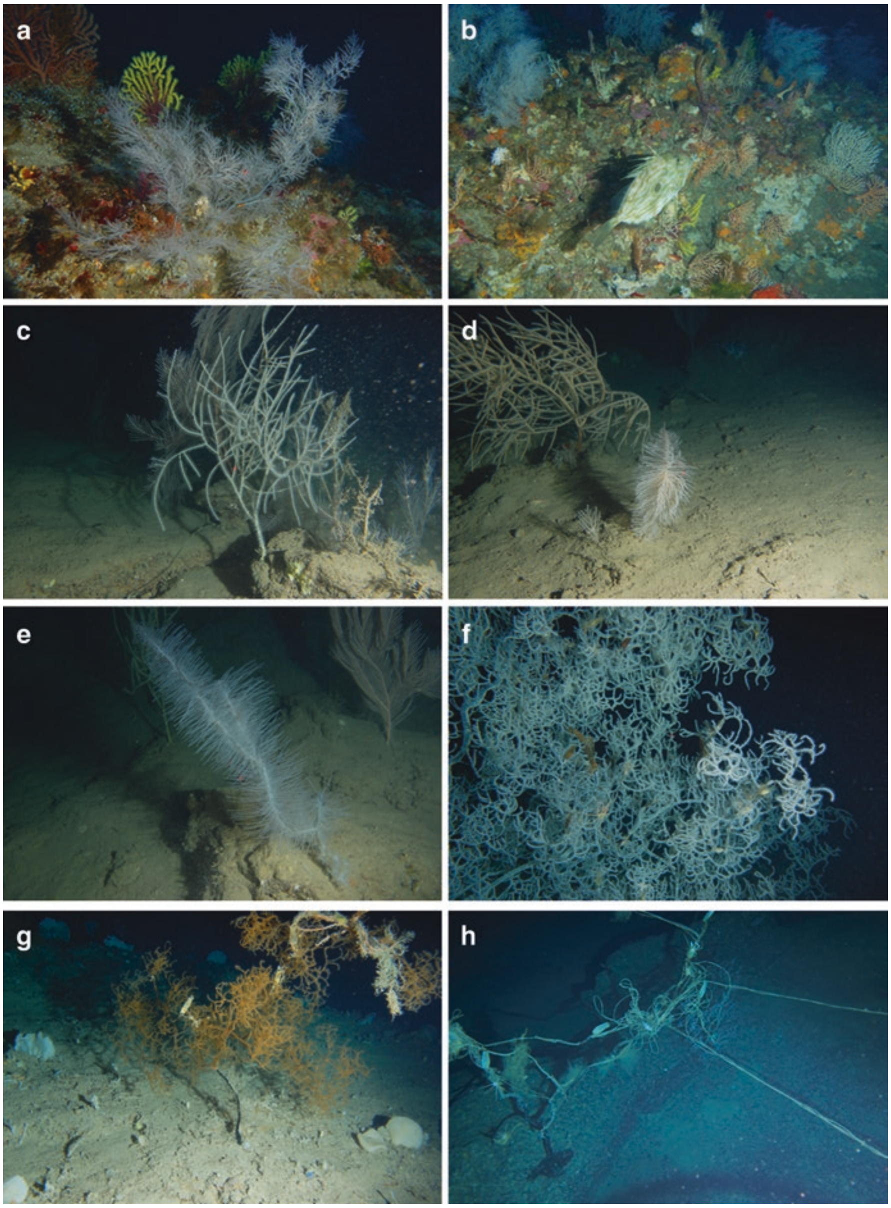

Fig. 21.1 Most common Mediterranean black corals. (**a**) Circa-littoral mixed assemblage of *Antipathella subpinnata* and *Paramuricea clavata* (Favazzina shoals, Calabria, 70 m); (**b**) The commercial species *Zeus faber* moving in a black coral and gorgonian mixed assemblage (Favazzina shoals, Calabria, 70 m); (**c**–**e**) Branched colonies of *Antipathes dichotoma* and bottle-brush colonies of *Parantipathes larix* in a *roche du large* ecosystem (St. Eufemia Gulf, 120 m); (**f**) Branched ramifications of *Leiopathes glaberrima* as refuge for crabs and nursery for catsharks' eggs (Carloforte Shoal, 200 m); (**g**–**h**) Evidences of fishing impact on colonies of *L. glaberrima* (Montecristo shoals, 200 m and Ponza Island, 300 m)

with reef building cold-water corals (CWCs) (Bo et al. 2009, 2012b; Mastrototaro et al. 2010; Fabri and Pedel 2012; Fabri et al. 2014; Angeletti et al. 2014). Occasional records have been made below 1000 m depth (Fabri and Pedel 2012).

From an ecological point of view, they can be considered one of the dominant structuring components of the Mediterranean animal forests between shallow-water gorgonian assemblages and deep-water reefs (Bo et al. 2018). This situation is particularly well represented along the Italian continental shelf. The coral canopy formed by these species, commonly exceeding two meters high, is an optimal refuge for a rich associated sessile and vagile fauna, occasionally spending here also the reproductive phases of their life cycles (Gaino et al. 2013). Excluding some sporadic cases of commercial employment for the jewelry trade reported in the 1980s in Malta (Deidun et al. 2010), the major anthropic impact they suffer is the fishing impact, particularly artisanal and recreational activities carried out by means of nets and longlines on deep rocky shoals; in addition, bottom trawling has been hypothesised to have indirect impacts on hard bottom communities due to the resuspension of silt (Bo et al. 2014b, 2018). Various evidences suggest that black corals, due to their arborescent morphology and their occurrence in dense aggregations, are highly catchable by means of bottom fishing gears operating on hardgrounds and therefore are among the most common components of fishermen bycatch (Mytilineou et al. 2014; Otero and Marin, this volume). A large number of populations can be considered greatly impacted such that the picture we have today of their distribution might have suffered a great change.

Due to their role of ecosystem engineers, their slow growth rates, their great longevity and slow recovery ability after a mechanical impact, these species, and the ecosystem they sustain, are considered extremely sensitive and are therefore listed as vulnerable marine ecosystems (VMEs). The entire Order Antipatharia is listed in CITES Appendix II, as well as in Annex III of Berna Convention, while Mediterranean species have been recently included in Annex II of the Barcelona Convention. They have also been listed as Near Threatened in the IUCN Red List under the Mediterranean regional assessment, with *L. glaberrima*, due to its millenial life span, being the only one listed as Endangered. Currently, the occurrence of black coral forests in a Marine Protected Area is reported only for France (Fabri et al. 2014), nevertheless, there are some specific management initiatives to preserve black coral resources, such as that carried out by the Maltese government (Deidun et al. 2010). In addition, self-regulations of the fishing grounds by artisanal fishing fleets have been promoted in Spain (Gili et al. 2011) as well as local management initiatives, including the creation or expansion of Sites of Community Importance over offshore areas of particular relevance (Bo et al. 2014a, b).

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References

Angeletti L, Taviani M, Canese S, et al (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Mediterr Mar Sci 15:263–273

Bo M, Tazioli S, Spanò N, et al (2008) *Antipathella subpinnata* (Antipatharia, Myriopathidae) in Italian seas. Ital J Zool 75:185–195

Bo M, Bavestrello G, Canese S, et al (2009) Characteristics of a black coral meadow in the twilight zone of the Central Mediterranean Sea. Mar Ecol Progr Ser 397:53–61

Bo M, Bavestrello G, Canese S, et al (2012a) Coral assemblages off the Calabrian Coast (South Italy) with new observations on living colonies of *Antipathes dichotoma*. Ital J Zool 78:231–242

Bo M, Canese S, Spaggiari C, et al (2012b) Deep coral oases in the South Tyrrhenian Sea. PLoS One 7:e49870

Bo M, Canese S, Bavestrello G (2014a) Discovering Mediterranean black coral forests: *Parantipathes larix* (Anthozoa: Hexacorallia) in the Tuscan Archipelago, Italy. Ital J Zool 81:112–125

Bo M, Bava S, Canese S, et al (2014b) Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. Biol Conserv 171:167–176

Bo M, Bavestrello G, Angiolillo M, et al (2018) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS One 10:e0119393

Bo M, Barucca M, Biscotti MA, et al (in press) Phylogenetic relationships of Mediterranean black corals (Cnidaria: Anthozoa: Hexacorallia) and implications for classification within the order Antipatharia. Invertebr Syst 32:1102–1110

Deidun A, Tsounis G, Balzan F, et al (2010) Records of black coral (Antipatharia) and red coral (*Corallium rubrum*) fishing activities in the Maltese Islands. Mar Biodivers Rec 3:e90

Fabri MC, Pedel L (2012) Habitats particuliers du bathyal et de l'abyssal/SRM MO. Ifremer. https://doi.org/10.13155/34118

Fabri MC, Pedel L, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207

Gaino E, Bavestrello G, Boyer M, et al (2013) Biological and ecological relevance of black corals (Antipatharia) in the benthic environment. In: Liñán-Cabello MA (ed) Corals: classification, habitat and ecological significance. NOVA Science Publishers, New York, pp 37–74

Gili JM, Madurell T, Requena S, et al (2011) Caracterización física y ecológica del área marina del Cap de Creus. Informe final área LIFE+INDEMARES (LIFE07/NAT/E/000732). Fundación Biodiversidad, Instituto de Ciencias del Mar/CSIC Barcelona, Madrid, 272 p

Mastrototaro F, d'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

Mytilineou C, Smith CJ, Anastasopoulou A, et al (2014) New cold-water coral occurrences in the Eastern Ionian Sea: results from experimental long line fishing. Deep-Sea Res Part 2 Top Stud Oceanogr 99:146–157

Ocaña O, Opresko DM, et al (2007) First record of the black coral *Antipathella wollastoni* (Anthozoa: Antipatharia) outside of Macaronesian waters. Rev Acad Can Cien 18:125–138

Opresko DM (2002) Revision of the Antipatharia (Cnidaria: Anthozoa). Part II. Schizopathidae. Zool Med 76:411–442

Opresko DM, Försterra G (2004) Orden Antipatharia (corales negros o espinosos). In: Hofrichter R (ed) El Mar Mediterraneo: fauna, flora, ecologia. Omega, Barcelona, pp 506–509

Opresko DM, Sanchez J (2005) Caribbean shallow-water black corals (Cnidaria: Anthozoa: Antipatharia). Caribb J Sci 41:492–507

Pax F, van-Praët M, Doumenc D (1987) Ordre des Antipathaires. In: Doumenc D (ed) Traité de Zoologie: Anatomie, Systématique, Biologie, vol 3. Cnidaires Anthozoaires, Masson, pp 189–210

Tazioli S, Bo M, Boyer M, et al (2007) Ecology of some common antipatharians from the Marine Park of Bunaken (North Sulawesi, Indonesia). Zool Stud 46:227–241

Wagner D, Luck DG, Toonen RJ (2012) The biology and ecology of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). Adv Mar Biol 63:67–132

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Drop Chapter
Recent Discoveries of Extensive Cold-Water Coral Assemblages in Maltese Waters

22

Leyla Knittweis, Julian Evans, Ricardo Aguilar,
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Abstract

Recent deep-water remotely operated vehicle surveys around the Maltese Islands resulted in the discovery of highly diverse habitats, including extensive hard bottom areas dominated by gorgonians and living cold-water corals with a rich variety of associated fauna. Black coral (*Leiopathes glaberrima*) forests were dominant at 200–400 m, whilst stony reef-forming corals (in particular *Madrepora oculata*) were most abundant in waters deeper than 500 m. The gorgonian *Callogorgia verticillata* was dominant in places over the entire depth range, but was particularly abundant at depths of 800–1000 m. Such cold-water coral assemblages are of high conservation interest, and offshore marine protected areas are urgently required in order to protect these very diverse, but highly vulnerable, deep-sea habitats.

Keywords

Alcyonacea · Anthozoa · Antipatharia · Biodiversity · Central Mediterranean · Scleractinia · Sicily channel

Malta hosts one of the six cold-water coral (CWC) provinces known from the Mediterranean, the ‘South Malta CWC province’ (Taviani et al. 2017; see also Chimienti et al., this volume). Observations of the deep sea surrounding the Maltese Islands are scant and, with few exceptions (Freiwald et al. 2009; Costantini et al. 2010), are mainly based on trawl surveys of sedimentary bottoms. In June–July 2015, remotely operated vehicle (ROV) surveys in Maltese waters were carried out by the research vessel ‘*Oceana Ranger*’ as part of the project ‘LIFE BaĦAR for N2K’ (“Benthic Habitat Research for Marine Natura 2000 Site Designation”; see http://lifebahar.org.mt). The surveys were carried out within the 25-nautical mile Fisheries Management Zone (Fig. 22.1a) around the Maltese Islands, and mostly focused on previously unstudied deep-sea areas such as the Malta Trough.

The ROV surveys revealed new areas with extensive and diverse CWC assemblages at depths of 300–1000 m extending some 20 km along the edge of the Malta Graben. The most abundant habitat-forming species on escarpments included the scleractinian *Madrepora oculata*, the antipatharian *Leiopathes glaberrima* and the alcyonacean *Callogorgia verticillata* (Figs. 22.1b and 22.2a). Several other locally abundant habitat-forming species were also encountered, including *Acanthogorgia hirsuta*, *Corallium rubrum*, *Dendrobrachia bonsai*, *Lophelia pertusa*, *Muriceides lepida*, *Paramuricea macrospina*, *Placogorgia massiliensis*, *Swiftia pallida* and *Villogorgia bebrycoides* (Fig. 22.2b). Colonies of the precious red coral *C. rubrum* were observed at depths of down to 1016 m, which represents the first time that this species has been recorded at depths exceeding 800 m (Knittweis et al. 2016). A high diversity of associated fauna (especially sponges, echinoderms, molluscs, crustaceans and fish) was also present.

The depth distribution of the corals and alcyonaceans revealed a vertical stratification in the presence of the main habitat-forming taxa. *L. glaberrima* was the dominant species at depths of 200–400 m, where it formed black coral forests, while the framework-forming *M. oculata* dominated in deeper waters, with peak abundances at depths of 500–700 m. Alcyonaceans had a more patchy distribution but *C. verticillata* was dominant in places, particularly at depths of 800–1000 m.

These recent findings indicate that the deep sea around Malta represents an important biodiversity hotspot with a variety of different assemblages dominated by sessile suspension feeders (mainly cnidarians) as habitat-forming taxa. The Malta Trough, in particular, seems to serve as a conduit for Levantine Intermediate Water (LIW) (Freiwald et al. 2009; Chimienti et al., this volume; Hayes et al., this volume), trans-

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https://doi.org/10.1007/978-3-319-91608-8_22

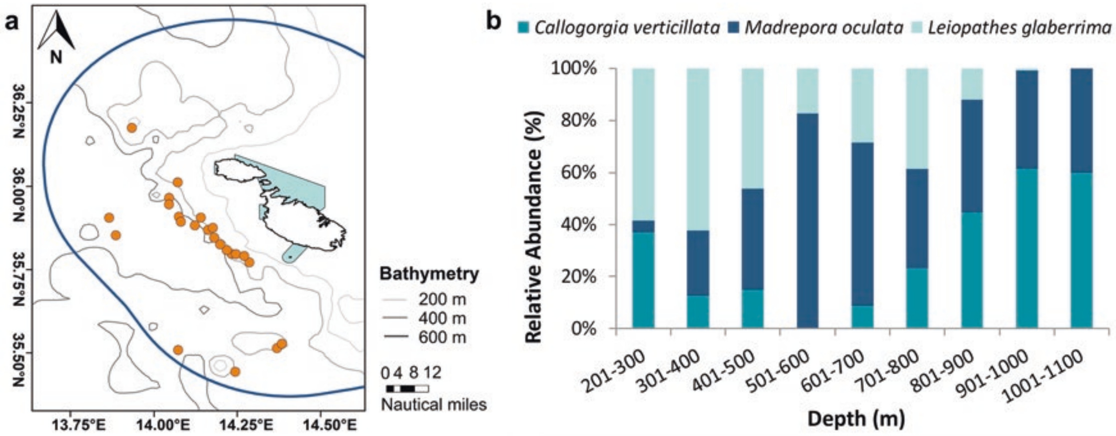

Fig. 22.1 (**a**) Map of the Maltese Islands showing the sites with living cold-water corals (orange circles), identified during the 2015 survey. The partial extent of the 25-nautical mile Fisheries Management Zone (dark blue oval around the Maltese Islands), and the location of current Marine Protected Areas for benthic habitats in Maltese waters (light blue shading) are also shown. (**b**) Relative abundance (as percent of total sightings) of the three main habitat-forming species, *Callogorgia verticillata* (n = 312), *Madrepora oculata* (n = 387) and *Leiopathes glaberrima* (n = 252), recorded from different depth intervals

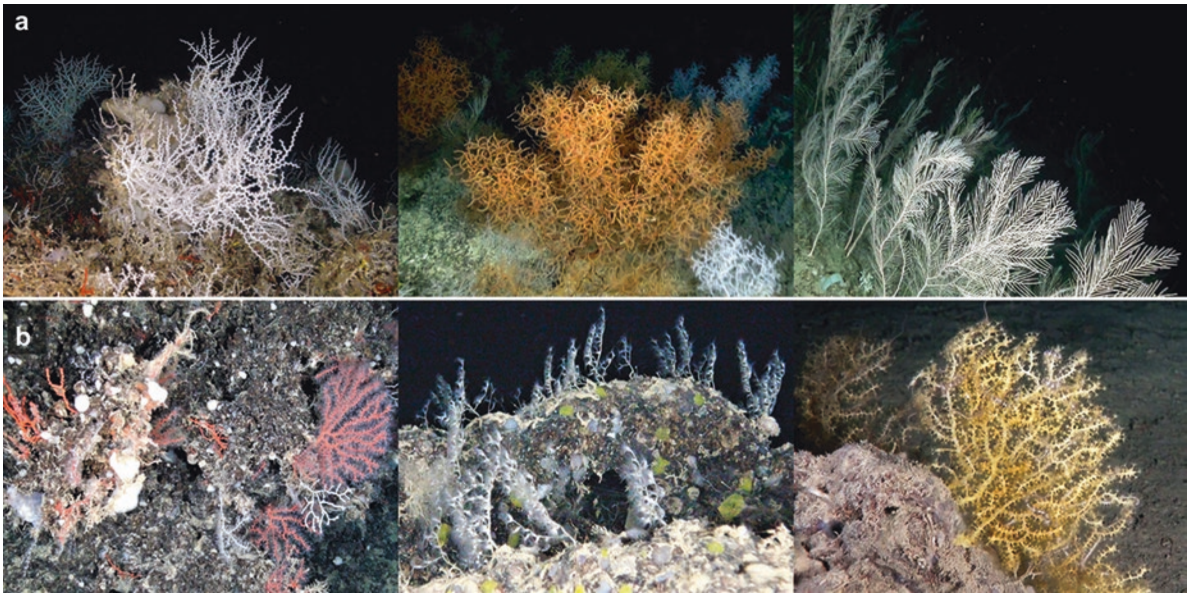

Fig. 22.2 (**a**) Coral and alcyonacean assemblages formed by *Madrepora oculata* (left), *Leiopathes glaberrima* (centre), and *Callogorgia verticillata* (right), found at depths of 300–1000 m in Maltese waters. (**b**) Examples of locally abundant habitat-forming species: *Corallium rubrum* (left), *Dendrobrachia bonsai* (centre), and *Paramuricea macrospina* (right). (Photo copyright: OCEANA © LIFE BaĦAR for N2K)

porting seston and thus providing favourable conditions for suspension feeders, which in turn provide habitats to a large diversity of associated fauna. Similarly, newly discovered CWC grounds off Sardinia were found to occur at depths corresponding to the core of the LIW (Taviani et al. 2017).

Cold-water coral reefs are included in Annex I of the EU ‘Habitats Directive’ (Natural habitat types of Community interest whose conservation requires the designation of special areas of conservation; Council Directive 92/43/EEC), and are listed in the UNEP/MAP/RAC-SPA “Reference list of marine habitat types for the selection of sites to be included in the national inventories of natural sites of conservation interest” (UNEP/MAP/RAC-SPA 2006). Moreover, several of the identified species (*C. rubrum, L. pertusa, L. glaberrima, M. occulata*) are designated as ‘endangered’ in the IUCN Red List of anthozoans in the Mediterranean (IUCN 2016). The present results thus highlight the need for the relevant authorities to consider establishment of offshore marine protected areas in order to protect these very diverse, but highly vulnerable, deep-sea habitats.

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References

Costantini F, Taviani M, Remia A, et al (2010) Deep-water *Corallium rubrum* (L., 1758) from the Mediterranean Sea: preliminary genetic characterisation. Mar Ecol 31:261–269

Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. OJ L 206, 22.7.1992. https://eur-lex.europa.eu/eli/dir/1992/43/oj

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

IUCN (2016) The IUCN Red List of anthozoans in the Mediterranean. Available via IUCN. https://www.iucn.org/sites/dev/files/import/downloads/anzothoa_fact_sheet_final_baja.pdf. Accessed 5 Jan 2017

Knittweis L, Aguilar R, Alvarez H, et al (2016) New depth record of the precious red coral *Corallium rubrum* for the Mediterranean. Rapp Comm Int Mer Médit 41:467

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78. https://doi.org/10.1016/j.dsr2.2015.12.008

UNEP-MAP-RAC/SPA (2006) Reference list of marine habitat types for the selection of sites to be included in the national inventories of natural sites of conservation interest. Available via RAC/SPA. http://www.rac-spa.org/sites/default/files/doc_fsd/lrhm_en.pdf. Accessed 5 Jan 2017

Cross References

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Hayes D, Schroeder K, Poulain, PM, et al (this volume) Review of the circulation and characteristics of intermediate water masses of the Mediterranean – implications for cold-water coral habitats

23

Drop Chapter Corals of Aphrodite: *Dendrophyllia ramea* Populations of Cyprus

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Abstract

The deep-sea of the Levantine Mediterranean basin is still a fairly undiscovered world. The outer insular shelf of Cyprus, a gateway to the deep realm, is not an exception, as very few deep areas in the waters surrounding this island have been explored up to now. Here we present a brief overview of the discovery of an extraordinary population of the scleractinian *Dendrophyllia ramea* at depths, substrate and densities which were previously unknown for this species. Our efforts in better defining the habitat of this unique and fragile coral population, along with solid evidence of alarming destruction (albeit unintentional) from fishing activity, will hopefully urge local authorities into enforcing protection/conservation measures.

Keywords

Cold-water corals · Deep-water scleractinians · Conservation · Levantine Mediterranean

The deep-sea realm of the island of Cyprus is still a world to be discovered. Aside from oil industry geological surveys, the scarce scientific information available until the last years was only focused on the Eratosthenes Seamount (Galil and Zibrowius 1998; Bell et al. 2011; Mayer et al. 2011; Wachsmann et al. 2011; Bell and Brennan 2013; Cornwell et al. 2013; Mitchell et al. 2013; unpublished cruise report from Research Vessel (RV) Merian 2011). The morphological and biological complexity of the regions around the Cyprus insular margin, from the continental shelf down to the bathyal and abyssal sectors has not been explored until now, and consequently it is largely unknown. The scarce information from these areas comes frequently from the local fishermen who are highly experienced in the area.

As part of the research project CYCLAMEN (TOTAL foundation), in 2015 we conducted a research cruise on board the RV Aegaeo (HCRM – Greece) in Cypriot waters off Protaras (South-eastern coast), with the aim of exploring for the first time the outer shelf- upper slope region, between 150 and 400 m depth, focusing on the cold-water coral (CWC) communities. Previous information on the presence of corals in the area was reported by local fishermen who found splendid specimens of *Dendrophyllia* colonies (Fig. 23.1a). Before this cruise, it was thought that the main species inhabiting the area was *Dendrophyllia cornigera* as the skeletons from corals provided by fishermen represented the only evidence available. However, after our exploration and sample collection with the remotely operated vehicle

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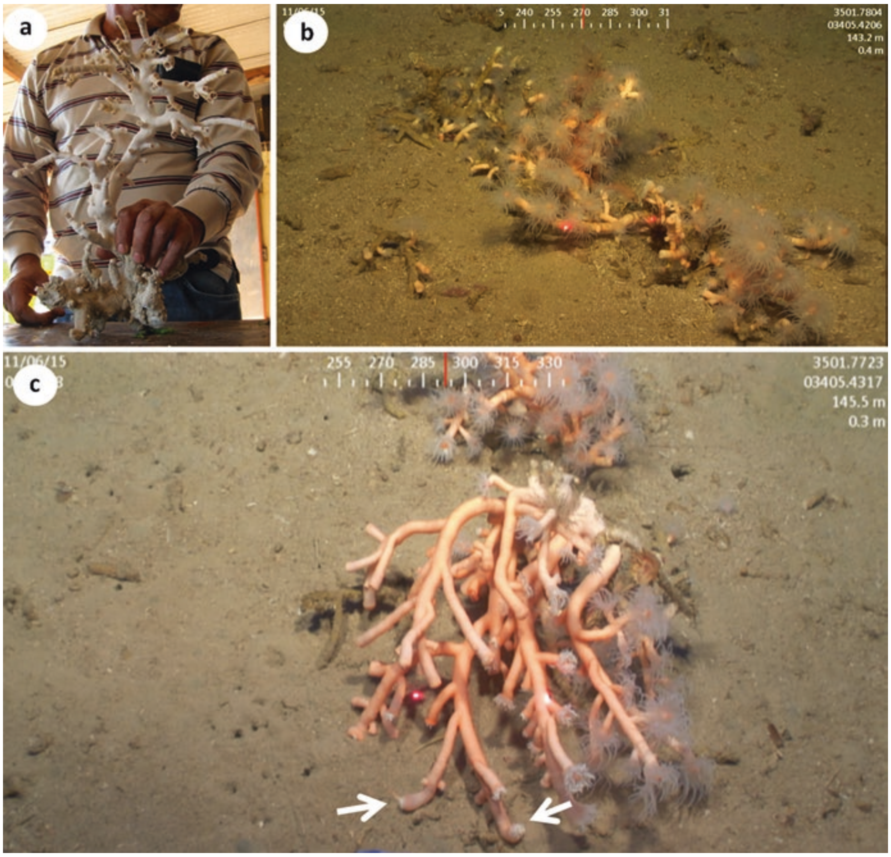

Fig. 23.1 (**a**) Skeleton of a *Dendrophyllia* sp. specimen collected by a local fisherman, (**b**) large colony of *D. ramea* off Protaras at ca. 145 m depth. Distance between the laser pointers is 10 cm, (**c**) colony of *D. ramea* lying on the sandy substrate. White arrows point out to two polyps growing away from the sediment. (Photographs: **a**: © Carlos Jiménez; **b** and **c**: © CYCLAMEN project (With permission from JCRS: Galaxea J. Coral Reef Stud. 19: 15–16, Orejas et al. 2017 Fig. 1b))

(ROV) MAXROV and subsequent preliminary molecular analysis (mitochondrial COI and nuclear histone H3), there was evidence indicating that the Dendrophyllidae inhabiting the soft bottoms off Protaras was a rather slender form of *D. ramea* (Fig. 23.1b, Orejas et al. 2017). These findings were quite unexpected since *D. ramea* is described inhabiting hard-substrates normally shallower than 100 m depth (e.g. Zibrowius 1980; Brito and Ocaña 2004; Salvati et al. 2004; Orejas et al. 2017 and references therein; see Altuna and Poliseno, this volume; Chimienti et al., this volume). An isolated *D. ramea* colony in the Ionian Sea was found established on a shallow sedimentary slope; however, the coral most probably was attached to the underlying hard-substrate (Salomidi et al. 2010).

The *D. ramea* colonies found in the area off Protaras displayed a variety of growth forms with some specimens of very large dimensions (~40 to 50 cm length; Fig. 23.1b). Interestingly, some live colonies were over the seafloor with the basal portions conspicuously turned up or exposed. These colonies displayed a singular polyp growth orientation in which the tips appear to re-direct the growth axis away from the sedimentary bottom (Fig. 23.1c). This orientated growth could be a response to periodic disturbances that cause upturning of entire colonies and possibly fragmentation. Abundant small-sized (~5 to 10 cm length) branches scattered on the bottom suggest physical disturbances are far from negligible in the study site. Strong surges related to seasonal storms able to destroy and fragment the largest colonies, are not expected to affect the *Dendrophyllia* population, being deeper than the maximal depth of wave action known in the Mediterranean Sea. However, strong bottom currents could presumably affect locally the stability of small colonies. The most plausible explanation for the high frequency of upturned colonies observed is the impact of fishing activities (recreational and, on a lesser extent, commercial). Fishing pressure (e.g. bottom nets) is significant in the area of the *Dendrophyllia* population (Orejas et al. 2017); the history of this activity is being currently under revision (Jiménez et al. work in progress).

At a first glance, the *Dendrophyllia* population seemed to be poor in terms of associated species. However, after a closer inspection of the coral specimens collected during the cruise, an abundant associated fauna was found, with 48 species being identified as epibionts on the corals (Fig. 23.2, Jiménez et al. 2016a). Bryozoans and serpulid polychaetes were most represented on the dead portions of the coral colonies.

Beside the coral population, other biocoenoses have been observed in the surveyed areas: (1) bottoms dominated by Cidaridae sea urchins (115–240 m depth), (2) bottoms dominated by *Cerianthus* sp. (105–175 m depth), (3) bottoms dominated by *Alcyonium palmatum* (120–145 m depth)

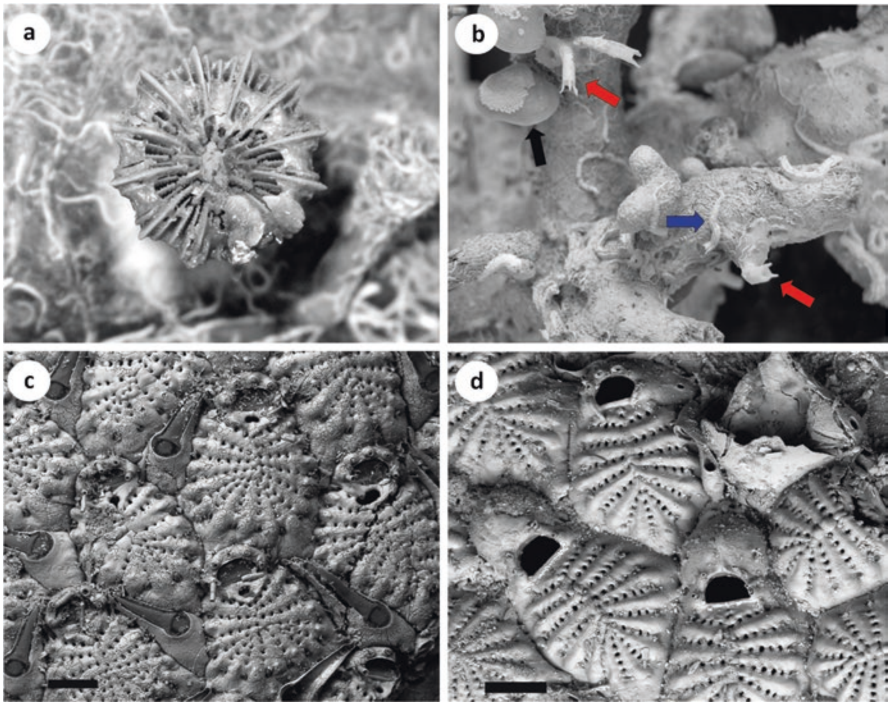

Fig. 23.2 Examples of the biodiversity found associated to the specimens of *Dendrophyllia ramea* collected off Protaras; (**a**) specimen of the solitary coral *Caryophyllia calveri*, (**b**) specimens of the polychaetes *Placostegus tridentatus* (red arrows) and *Janita frimbiata* (blue arrow) and the bryozoans *Escharina vulgaris* (black arrow), (**c**) specimens of the bryozoans *Puellina hincksi*; scale bar = 100 μm and (**d**) specimens of the bryozoan *Puellina pedunculata*; scale bar = 100 μm. (Photographs: © C. Jiménez and K. Achilleos)

and (4) bottoms dominated by pennatulaceans (~130 m depth). These first explorations point out a relatively rich and diverse megabenthic fauna in this area of the Levantine Mediterranean basin, which remains unexplored in most parts, and where more research efforts are needed especially in the deep benthic realm. Studies on deep-sea benthic habitats will contribute to enlarge the knowledge on the biodiversity of the Levantine deep-sea realm contributing also to detect the potential occurrence of non –indigenous invasive species, a threat that has been documented since years in shallow waters for the eastern Mediterranean and completely unstudied in deep-sea areas (see Galil, this volume). As recently as 2017, on two independent events, fishermen from Protaras utilising bottom nets inside the area with corals caught in their nets (aside from *Dendrophyllia* colonies) a juvenile and a young adult of the invasive lionfish (*Pterois miles*), which is spreading around Cyprus and the Levantine Sea in general (Jimenez et al. 2016b and work in progress).

The discovery of *D. ramea* populations off Protaras also plays an important role regarding the need of conservation of such a remarkable assemblage. There is only one more record of this species in the Levantine basin (Lebanon, http://eu.oceana.org/en/our-work/expeditions/deep-sea-lebanon-2016/overview) but in that case, located on hard-substrate. The IUCN (International Union for Nature Conservation) has recently published a report on the current status of the Mediterranean Anthozoans (Otero et al. 2017). The coral *D. ramea* is included in this report, as well as in the IUCN Mediterranean Red list, being categorised as "Vulnerable". Recently the species has also been included in the Annex II of Barcelona Convention. Currently, the results of our study, together with other initiatives (e.g. PROTOMEDEA project to suggest management areas in Greece and Cyprus) are forming the basis for proposing to the local authorities the protection of the area around the *Dendrophyllia* populations.

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References

Bell KLC, Brennan ML (2013) New frontiers in ocean exploration: the E/V Nautilus 2012 field season and summary of Mediterranean exploration. Oceanography 26, 64 pp. https://doi.org/10.5670/oceanog.2013.supplement.01

Bell RJ, Mayer L, Konnaris K, et al (2011) Potential marine mammal-induced seafloor scours on Eratosthenes Seamount. In: Bell KLC, Fuller S (eds) New frontiers in ocean exploration: the E/V Nautilus 2010 field season. Oceanography 24:31. https://doi.org/10.5670/oceanog.24.1.supplement

Brito A, Ocaña O (2004) Corales de las Islas Canarias. Francisco Lemus, Tenerife, 477 pp

Cornwell K, Opaiţ A, Benjamin W, et al (2013) Archaeological discoveries on Eratosthenes Seamount. Oceanography 26:40–43

Galil B, Zibrowius H (1998) First benthos samples from Eratosthenes Seamount. East Mediterr Senckenberg Marit 28:111–121

Jiménez C, Achilleos K, Abu Alhaija R, et al (2016a) Living in close quarters: epibionts on *Dendrophyllia ramea* deep-water coral (Cyprus and Menorca channel). Rapp Comm Int Mer Médit 41:466

Jimenez C, Petrou A, Andreou V, et al (2016b) Veni, vidi, vici: the successful establishment of the lionfish *Pterois miles* in Cyprus (Levantine Sea). Rapp Comm Int Mer Médit 41:417

Mayer L, Bell KLC, Ballard, et al (2011) Discovery of sinkholes and seeps on Eratosthenes Seamount. In: New frontiers in ocean exploration: the E/V Nautilus 2010 field season. Oceanography 24:28–29

Mitchell G, Mayer L, Bell KLC, et al (2013) Exploration of Eratosthenes Seamount—a continental fragment being forced down an Oceanic trench. Oceanography 26:36–41

Orejas C, Gori A, Jiménez C, et al (2017) First in situ documentation of a population of the coral *Dendrophyllia ramea* off Cyprus (Levantine Sea) and evidence of human impacts. Galaxea J Coral Reef Stud 19:15–16

Otero MM, Numa C, Bo M, et al (2017) Overview of the conservation status of Mediterranean anthozoans. In: UICN (ed). Málaga, Spain

Salomidi M, Zibrowius H, Issaris Y, et al (2010) *Dendrophyllia* in Greek waters, Mediterranean Sea, with the first record of *D. ramea* (Cnidaria, Scleractinia) from the area. Mediterr Mar Sci 11:189–194

Salvati E, Tunesi L, Molinari A (2004) Presence of the Scleractinian *Dendrophyllia ramea* in the shallow waters of Mediterranean Morocco (Al Hoceima, Alboran Sea). Rapp Comm Int Mer Médit 37:547

Wachsmann S, Demesticha S, Chryssoheri I, et al (2011) Archaeological discoveries on Eratosthenes Seamount. In: New frontiers in ocean exploration: the E/V Nautilus 2010 field season. Oceanography 24:30

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Memoires de l'Institut Oceanographique Fondation Albert 1er, Prince de Monaco 11

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Galil BS (this volume) The spread of non-indigenous species in the Mediterranean – a threat to cold-water corals?

Drop Chapter
Cold-Water Corals in Fluid Venting Submarine Structures

24

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Abstract

A relationship between scleractinian cold-water corals and fluid venting submarine structures has been observed in Mediterranean and adjacent areas. Mud volcanoes and mud diapirs promote different substrate types for biological colonisation: from muddy bottoms with chemosynthesis-based communities and typical bathyal soft bottom fauna to hard bottoms with sessile solitary and colonial scleractinian cold-water corals, sponges, octocorals and antipatharians. Fluid venting submarine structures provide an elevated position for the development of sessile suspension feeders, including scleractinian cold-water corals, where an interaction of the currents with the local topography generally accelerates the water flow. This facilitates the supply of suspended food particles and the development of carbonate mounds mainly built by scleractinian cold-water corals. Methane-derived authigenic carbonates provide hard substrates, which represent a prerequisite for larvae settlement of some scleractinian cold-water corals and further development of polyps and colonies in those elevated areas. These factors make FVSS an appropriate place for the development of habitats conformed by scleractinian cold-water corals as well as genuine and singular biodiversity hotspots.

Keywords

Cold-water coral · Seepage · Authigenic carbonates · Habitat · Mediterranean Sea

Both colonial and solitary scleractinian cold-water corals (CWCs), as well as other sessile cnidarians (e.g. antipatharians, octocorals, etc.), have been widely documented from fluid venting submarine structures (FVSS) of the Mediterranean Sea (e.g. western Alborán Sea, southeastern Adriatic Sea) (Margreth et al. 2011; Somoza et al. 2012; Angeletti et al. 2015; Rüggeberg and Foubert, this volume; Wienberg, this volume) and adjacent areas exposed to Mediterranean water masses (e.g. Gulf of Cádiz) (Wienberg et al. 2009; León et al. 2012; Palomino et al. 2016; Rueda et al. 2016). During the last decades, FVSS mainly driven by tectonic processes have been detected in bathyal areas with compressive (e.g. Gulf of Cádiz, Mediterranean Ridge, Western Alborán Sea) and extensional (e.g. Black Sea, Tyrrhenian Sea) settings. The uplift of massive plastic sedimentary rocks as mud diapirs (MDs) and the vertical migration and extrusion of fluids (hydrocarbon, brines, etc.) and muddy sediments as mud volcanoes (MVs) promote different substrate types for biological colonisation. Particularly, muddy bottoms composed of gas-rich mud breccias may be later replaced by hard bottoms of methane-derived authigenic carbonates (MDACs) (slabs, chimneys, crusts, etc.), according to the development stages of the MVs and MDs proposed by León et al. (2007), which was later adapted by Palomino et al. (2016) to different seepage and bottom current scenarios. This model proposes a biological differentiation from chemosynthesis-based communities with typical bathyal soft-bottom fauna (e.g. sea pens) in anoxic mud breccia bottoms where fluid venting occurs, to communities dominated by hard bottom sessile solitary and colonial suspension feeders such as scleractinian CWCs, sponges, octocorals (gorgonians and soft corals) and antipatharians. The development of MVs through time, according to this model, generally starts with an active fluid flow and mud extrusion that build up the volcanic edifice where benthic communities associated with seepage (mainly chemosynthetic bacteria as well as chemosymbiotic bivalves and polychaetes) are favoured (Fig. 24.1a). This first stage is followed by moderate

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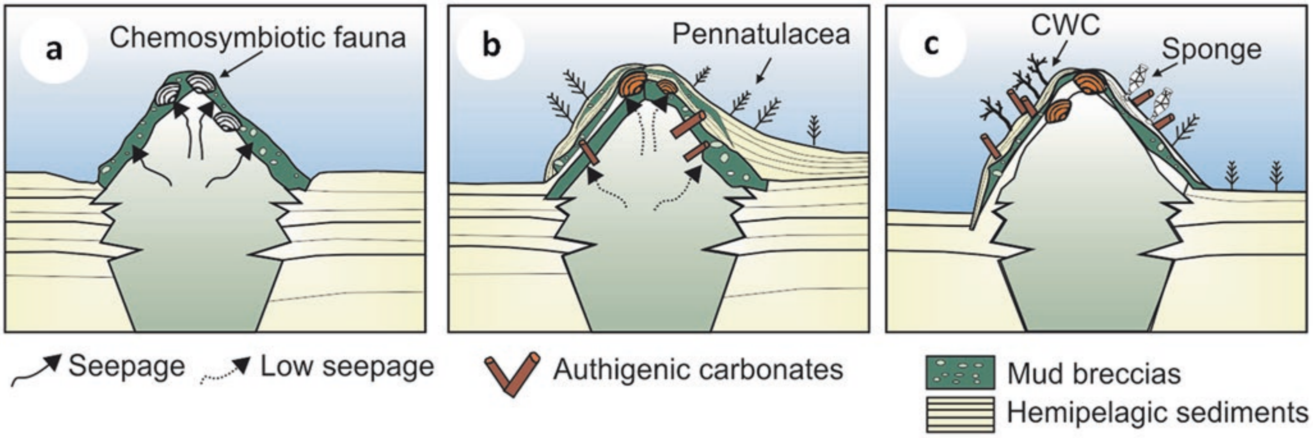

Fig. 24.1 Development of mud volcanoes through time: (**a**) active fluid flow and mud extrusion with the establishment of chemosymbiotic fauna, (**b**) moderate to low seepage and formation of MDACs as well as the colonisation of soft bottoms by typical soft bottom fauna (e.g. sea pens), and (**c**) MDACs exhumed in some areas and colonised by scleractinian CWCs and other sessile suspension feeders (e.g. sponges, antipatharians, octocorals). (Modified from Palomino et al. 2016)

to low seepage that promotes the formation of MDACs by methane anaerobic oxidation by different archeobacteria. Contourite deposits can occur on MVs and MDs flanks as result of a higher bottom current velocity. These deposits are generally colonised by soft bottom epifauna such as sea pens (e.g. *Kophobelemnon, Funiculina*), crinoids (e.g. *Leptometra*), solitary scleractinians (e.g. *Flabellum*) and both desmosponges (e.g. *Thenea*) and hexactinellid sponges (e.g. *Pheronema, Hyalonema*) (Fig. 24.1b). Finally, the development is characterised by latent conditions where the MDACs are exhumed by bottom current action and colonised by hard bottom sessile suspension feeders (e.g. scleractinian CWCs) which further increase the bottom complexity, the biological productivity and the biodiversity. In this stage, bottom currents should be strong enough for promoting a continuous availability of food particles for the scleractinian CWCs and other sessile suspension feeders such as the octocorals and the antipatharians (Fig. 24.1c).

Unlike other types of FVSS (e.g. pockmarks), MVs and MDs provide an elevated position for the development of scleractinian CWCs and other sessile suspension feeders (e.g. antipatharians, sponges, sea pens) with respect to adjacent bottoms. As observed in other elevated seafloor structures (e.g. ridges, seamounts), scleractinian CWCs and other suspension feeders of MVs and MDs could be benefited from the interaction of the currents with the local topography, which accelerates the water flow (Genin et al. 1986). Strong bottom currents also facilitate the supply of suspended food particles and the development of carbonate mounds mainly built by scleractinian CWCs and of other vulnerable marine ecosystems (VMEs) (e.g. sponge fields) in these FVSS (Freiwald and Roberts 2005). Suspended sediments can also be trapped and baffled into the coral framework, contributing to coral mound stabilisation and growth. Nevertheless, when sedimentation rates are higher than scleractinian CWC growth rates or when a new migration and extrusion of muddy sediments occurs in FVSS, deposits can lead to the burial and ultimate demise of the habitats conformed by all these sessile organisms (León et al. 2007; Wienberg et al. 2010; Margreth et al. 2011; Mienis et al. 2012). The MDACs are formed inside sediments of MVs and MDs, and exhumed where bottom currents are strong enough to remobilise unconsolidated surficial sediments (Magalhães et al. 2012). These MDACs increase the seafloor habitat complexity by providing different types of hard substrates (e.g. crusts, chimneys, slabs), which represents a prerequisite for larvae settlement of some scleractinian CWCs and further development of polyps and colonies in those elevated areas that have an adequate food supply (Angeletti et al. 2015; Rueda et al. 2016). Hovland et al. (1998) proposed the “Hydraulic theory” that links scleractinian CWC growth to seepage in FVSS, because fluid flow may provide an extra local input of nutrients throughout the seabed where scleractinian CWCs develop. In addition, bacterial productivity (heterotrophic and chemosynthetic) seems to increase in FVSS when compared to adjacent soft bottoms without seepage, and this has been hypothesised to act as extra nutrient sources for higher trophic organisms such as scleractinian CWCs. Nevertheless, this theory is under debate and no clear evidence has been found yet on the relationship between those habitat-forming organisms and seepage.

In the Montenegrin margin (southeastern Adriatic Sea), a spectacular field of exhumed and vertically-placed chimneys related to hydrocarbon venting serves as substrate for a wide variety of sessile megafauna, including scleractinian CWCs (e.g. *Madrepora oculata, Dendrophyllia cornigera, Caryophyllia* sp.), large octocorals (e.g. *Callogorgia* *verticillata*), antipatharians (e.g. *Leiopathes*) and desmosponges (e.g. *Pachastrella*) (Angeletti et al. 2015). In the Gulf of Cádiz, scleractinian CWCs (e.g. *M. oculata*, *Lophelia pertusa* and *D. cornigera*) as well as antipatharians (*Anthipathella, Leiopathes*) and large sponges (e.g. *Petrosia* sp., *Asconema setubalense*) colonise MDACs of some FVSS (e.g. Gazul MV) (Palomino et al. 2016; Rueda et al. 2016). The presence of scleractinian CWCs in these FVSS also promotes the occurrence of typical associated species such as the polychaete *Eunice norvegica* and the gastropod *Hirtomurex* (=*Coralliophila*) *squamosa* (Rueda et al. 2016, this volume). FVSS with CWCs are very sensitive to some human activities impacting the seabed such as mining and trawling (see Otero and Marin, this volume), and policy measures of conservation must be taken in order to protect the singular occurrence of a combination of two different habitats included in the EU Habitat Directive (92/43/EEC) such as the *Reefs* (Habitat 1170) and the *Submarine structures made by leaking gases* (Habitat 1180). Nevertheless, CWCs are sometimes located in low trawling activity areas because of the presence of hard bottoms and strong bottom currents, which altogether result in higher abundances and biomasses of benthic organisms (Rueda et al. 2016, this volume).

Although there are still some knowledge gaps on the relationship between CWCs and FVSS, the case study in the Mediterranean and adjacent areas suggests that the combination of: (a) the stable hard substrate provided by MDACs for larval settlement and colonial development; (b) the elevated position on a mound-like structure which accelerates the water flow and increases the supply of suspended food particles, makes some FVSS a suitable place for the development of habitats conformed by scleractinian CWCs as well as genuine and singular biodiversity hotspots.

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References

Angeletti L, Canese S, Franchi F, et al (2015) The "chimney forest" of the deep Montenegrin margin, southeastern Adriatic Sea. Mar Pet Geol 66:542–554

Freiwald A, Roberts JM (2005) Cold-water corals and ecosystems. Springer, Heidelberg, p 1243

Genin A, Dayton PK, Lonsdale PF, et al (1986) Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature 322:59–61

Hovland M, Mortensen PB, Brattegard T, et al (1998) Ahermatypic coral banks off mid-Norway: evidence for a link with seepage of light hydrocarbons. PALAIOS 13:189–200

León R, Somoza L, Medialdea T, et al (2007) Sea-floor features related to hydrocarbon seeps in deepwater carbonate mud mounds of the Gulf of Cádiz: from mud flows to carbonate precipitates. Geo-Mar Lett 27:237–247

León R, Somoza L, Medialdea T, et al (2012) New discoveries of mud volcanoes on the Moroccan Atlantic continental margin (Gulf of Cadiz): morpho-structural characterization. Geo-Mar Lett 32:473–488

Magalhães VH, Pinheiro LM, Ivanov MK, et al (2012) Formation processes of methane-derived authigenic carbonates from the Gulf of Cadiz. Sediment Geol 243–244:155–168

Margreth S, Gennari G, Rüggeberg A, et al (2011) Growth and demise of cold-water coral ecosystems on mud volcanoes in the West Alboran Sea: the messages from planktonic and benthic foraminifera. Mar Geol 282:26–39

Mienis F, De Stigter HC, De Haas H, et al (2012) Hydrodynamic conditions in a cold-water coral mound area on the Renard Ridge, southern Gulf of Cadiz. J Mar Syst 96–97:61–71

Palomino D, López-González N, Vázquez JT, et al (2016) Multidisciplinary study of mud volcanoes and diapirs and their relationship to seepages and bottom currents in the Gulf of Cádiz continental slope (northeastern sector). Mar Geol 378:196–212

Rueda JL, González-García E, Krutzky C, et al (2016) From chemosynthesis-based communities to cold-water corals: new records of vulnerable deep-sea habitats for the Gulf of Cádiz. Mar Biodivers 46:473–482

Somoza L, Medialdea T, León R, et al (2012) Structure of mud volcano systems and pockmarks in the region of the Ceuta Contourite Depositional System (Western Alborán Sea). Mar Geol 332–334:4–26

Wienberg C, Hebbeln D, Fink HG, et al (2009) Scleractinian cold-water corals in the Gulf of Cádiz-first clues about their spatial and temporal distribution. Deep-Sea Res Part 1 Oceanogr Res Pap 56:1873–1893

Wienberg C, Frank N, Mertens KN, et al (2010) Glacial cold-water coral growth in the Gulf of Cádiz: implications of increased palaeo-productivity. Earth Planet Sci Lett 298:405–416

Cross References

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Rüeggeberg A, Foubert A (this volume) Cold-water corals and mud volcanoes: life on a dynamic substrate

Wienberg C (this volume) A deglacial cold-water coral boom in the Alborán Sea: from coral mounds and species dominance

Drop Chapter Cold-Water Corals and Mud Volcanoes: Life on a Dynamic Substrate

25

Andres Rüggeberg and Anneleen Foubert

Abstract

Mud volcanoes are prominent features in distinct areas of the Mediterranean Sea and the Gulf of Cádiz. Cold-water corals use these elevated structures as substrate and develop coral reefs during periods of suitable environmental conditions. So far, this partnership has only been reported from the Alborán Sea and the Gulf of Cádiz, where they occurred during the Bølling-Allerød to early Holocene and during the mid to late Holocene.

Keywords

Cold-water corals · Mud volcanoes · Substrate availability · Environmental control

Reef-building cold-water corals (CWC) like *Lophelia pertusa* and *Madrepora oculata* are prominent features within the Mediterranean Sea and the Gulf of Cádiz (e.g., Freiwald et al. 2009; Wienberg et al. 2009; Altuna and Poliseno, this volume; Chimienti et al., this volume; Rueda et al., this volume). However, most of the reported occurrences refer to fossil remnants while living occurrences are less abundant and exhibit a rather scattered distribution pattern compared to those known from the North Atlantic (Fig. 25.1a; Fink et al. 2015; see Taviani et al., this volume; Vertino et al., this volume). Flögel et al. (2014) described the CWC appearance in these areas from patchy growth forms with small colonies including larger patches of fine-grained sediments or coral rubble to only small and frequently isolated branches/colonies or even single living polyps. The main habitat of the coral reefs in the Mediterranean Sea is at intermediate depths between 250 and 650 m (Freiwald et al. 2009; see Chimienti et al., this volume) but also deeper for the mainly fossil corals in the Gulf of Cádiz. These corals have been described on escarpments and ridges (Foubert et al. 2008; Knittweiss et al., this volume), on knolls and banks (De Mol et al. 2012; Lo Iacono et al., this volume) and mounds (Taviani et al. 2005; Comas and Pinheiro 2007; Lo Iacono et al., this volume), at cliffs and canyons (e.g., Freiwald et al. 2009; Orejas et al. 2009; Fabri et al. 2014; Angeletti et al., this volume; Aymà et al., this volume; Fourt et al., this volume; Lastras et al., this volume; Puig and Gili, this volume) and on mud volcanoes (e.g., Wienberg et al. 2009; Margreth et al. 2011; Palomino et al., this volume). Gardner (2001) was one of the first to report CWC debris overlying mud breccia on an inactive mud volcano from the Gulf of Cádiz offshore Morocco. The temporal and spatial distribution of reef-building CWCs in the Mediterranean Sea and the Gulf of Cádiz has been related to areas with high surface productivity and vigorous intermediate water mass circulation (Wienberg et al. 2010; Fink et al. 2015), however, these bioherms also need a nucleation point, a substratum.

Mud volcanoes are one possible niche for CWCs to inhabit. In the Mediterranean Sea and the Gulf of Cádiz (see Palomino et al., this volume) they have been frequently reported in areas evidencing a dynamic sub-seafloor with active seepage of fluids and hydrocarbons (Fig. 25.1a). In the Gulf of Cádiz mud volcanoes are clustered in distinct fluid venting provinces like the Spanish-Moroccan and El Arraiche fields along the Moroccan margin (Gardner 2001; Van Rensbergen et al. 2005) or the Guadalquivir diapiric ridge and Tasyo fields along the Spanish margin (Somoza et al. 2003). In the eastern Mediterranean, mud volcanoes were first discovered west of Crete on the Mediterranean Ridge (Cita et al. 1981). Intensive investigation followed with the discovery of numerous new mud volcanoes (Limonov et al. 1996) being active since 1 Ma on the northern margin of the Mediterranean Ridge (Robertson and Ocean Drilling Program Leg 160 Scientific Party 1998) and even longer since 3 Ma along the Calabrian Arc (Praeg et al. 2009). Occurrence of mud volcanism and diapirism in the eastern Mediterranean is also recorded in an extensional setting of

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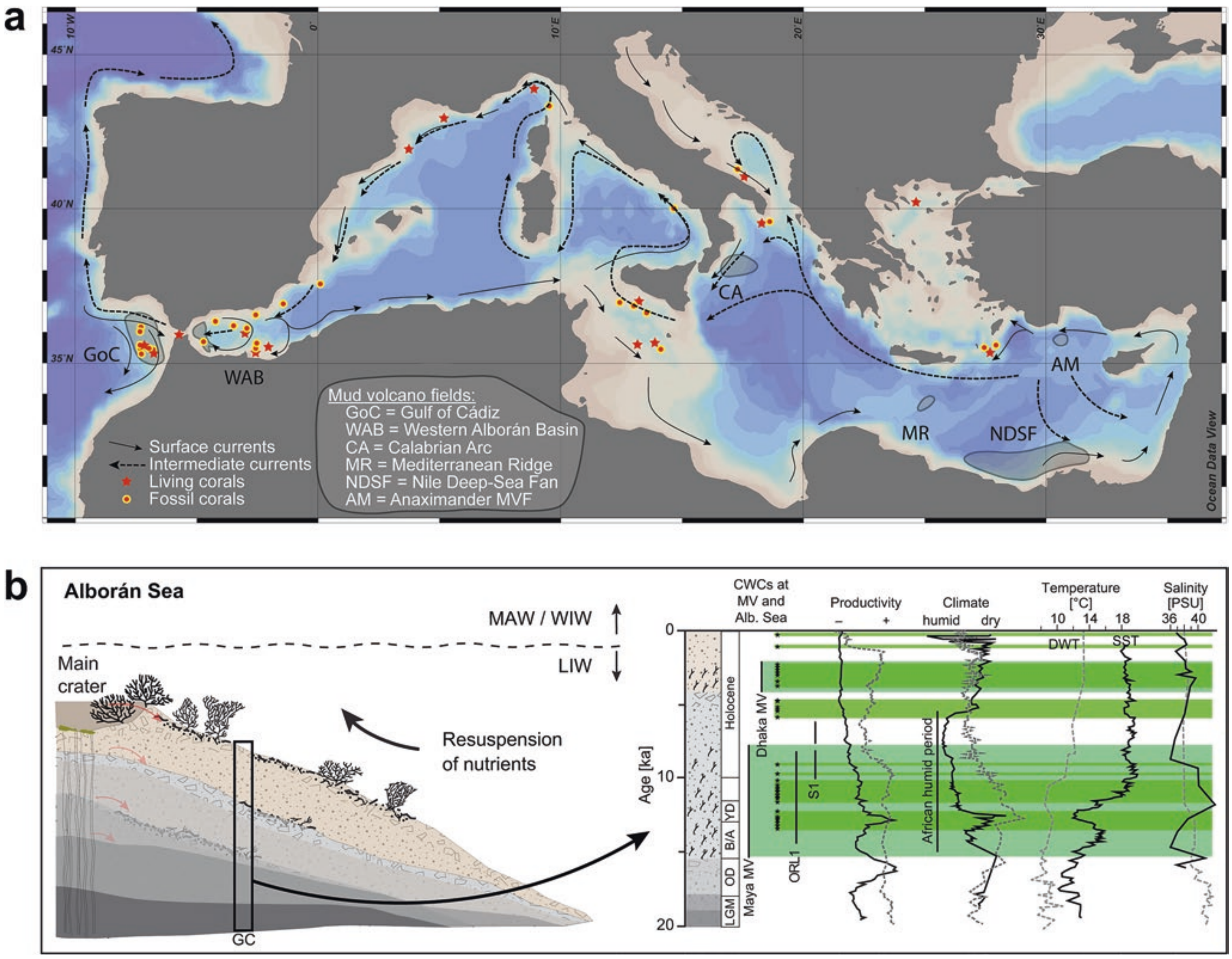

Fig. 25.1 (**a**) Overview map of the Mediterranean Sea showing the mud volcano provinces, the reefal cold-water coral areas and the general ocean circulation pattern in the Mediterranean Sea (Modified from Fink et al. 2015 and references therein). Black arrows correspond to surface water circulation, dotted black arrows to the intermediate water circulation, respectively. Indicated are the sampling sites of fossil corals (circles) and living occurrences (stars) solely considering the two framework-forming species *Lophelia pertusa* and *Madrepora oculata* (From Fink et al. 2015). Co-occurrence of mud volcanoes and cold-water corals has been reported for the GoC and the WAB. Map by Ocean Data View (Schlitzer 2016). (**b**) Idealised schematic of a mud volcano and a core log from a gravity corer (GC) with alternating sediments of episodic mud flows, coral settlement on mud breccia and later burial phases (modified after Spezzaferri et al. 2015 and Margreth et al. 2011). For the settlement of reef-building corals habitable conditions within the right nutrient window and a well-defined hydrodynamic regime are required. In the Alborán Sea, these conditions occurred during Organic Rich Layer 1 (ORL1) (14.5–8.2 ka, Jimenez-Espejo et al. 2008) and during the later Holocene [coral dates from McCulloch et al. (2010), Margreth et al. (2011), Fink et al. (2013), and Stalder et al. (2015)]. Potential drivers controlling coral development are productivity [reconstructions from Rodrigo-Gámiz et al. (2011, solid black) and Fink et al. (2013, dotted grey)], water mass properties [temperature: Deep Water Temperature (DWT, dotted grey) from Cacho et al. (2006), Sea Surface Temperature (SST, solid black) from Cacho et al. (2001); Salinity reconstructions from Emeis et al. (2000, solid black) and Cacho et al. (2006, dotted grey)], which are influenced by regional climatic conditions [reconstructions from Adkins et al. (2006, solid black) and Fink et al. (2013, dotted grey)]. African humid period occurred between 14.8 and 5.5 ka (deMenocal et al. 2000). *MAW* Modified Atlantic Water, *WIW* Winter Intermediate Water, *LIW* Levantine Intermediate Water, *LGM* Last Glacial Maximum, *OD* Older Dryas, *B/A* Bølling-Allerød, *YD* Younger Dryas, *S1* Sapropel layer 1. Light green layers indicate CWC occurrences at Maya and Dhaka mud volcanoes, dark green layers highlight occurrences of dated corals from the Alborán Sea

the Nile Deep Sea Fan (Dupré et al. 2007). In the western Mediterranean, mud volcanoes are relative scarce features only reported from the Alborán Sea, where they are related to mud diapirs and active sediment and fluid flow in a back-arc basin setting (e.g., Comas et al. 2010). Several expeditions revealed the existence of mud volcanoes, pockmarks and seepage-related structures on both the Spanish and the Moroccan margin of the West Alborán Basin (Gennari et al. 2013). Mud volcanoes are dome-shaped formations on the seafloor of up to 10 km in diameter and 700 m in height, which are created by the release of mud charged with hydrocarbon-rich fluids derived from the sub-seafloor.

However, their common appearance in the Mediterranean Sea is generally smaller being 100–200 m high and 1–5 km across (Woodside et al. 2006). During their active phase, the build-up of pressure in wet and gassy sediments below faults leads to periodical eruptions of mud and fluids with rock fragments, the so-called mud breccia (Cita et al. 1981), a semi-liquid, clayey matrix containing various amounts of heterogenic rock fragments and clasts derived from the geological section through which the mud ascends (Cita et al. 1981; Staffini et al. 1993; Dimitrov 2002; Kopf 2002). Successive episodes of mud flows as a result of degassing processes in the deep sub-seafloor and the progressive accumulation of extruded mud breccia build up the cone-shaped edifice, forming the mud volcano (Fig. 25.1b). If not visually ground-truthed by remotely operated vehicles (ROVs) or deep-towed camera, the identification of mud volcanoes through (gravity) coring is necessary to retrieve sequences with greyish mud breccia sediment from targets selected on the basis of multibeam bathymetry/backscatter or side-scan sonar (Fig. 25.1b). As most of the mud volcanoes are presently not active (e.g., Niemann et al. 2006), their surficial sediment consists mainly of hemipelagic foraminifera-rich sandy mud.

It is the habitat complexity with clasts exhumed by the mud breccia and possible authigenic carbonates as remnants of cold-seep communities, which provide the basis for new life – as hard substrate for a new community of CWCs and/or other species to grow and develop (see also Palomino et al., this volume). The occurrence of hard substrata on mud volcanoes allows the preferential settlement of sessile organisms attached to the seafloor (León et al. 2007) – not possible on the soft sediments of the surrounding seafloor. However, if substrate availability would be the only controlling factor, coral patches and reefs would be thriving on the summits and flanks of mud volcanoes – if not temporarily disturbed by mud volcano activity. Besides substrate availability and the absence of destructive extrusive events, other environmental factors control the distribution of CWC growth in those vulnerable environments. Comparable to what has been suggested by Becker et al. (2009) for the Gulf of Mexico or León et al. (2012) and Somoza et al. (2003) for the Gulf of Cádiz, mud breccia and authigenic carbonate substrata together with the higher productivity and stronger hydrodynamic processes at the interface between two water masses (surface or upper intermediate with lower intermediate, Fig. 25.1b) drive the CWC communities at mud volcanoes in the western Mediterranean and the Gulf of Cádiz (Fink et al. 2013; Stalder et al. 2015; Palomino et al., this volume). The nucleation of corals on mud breccia in the fossil record has been described by Margreth et al. (2011) for the Maya (~15 ka) and Dhaka (~4 ka) mud volcanoes in the western Alborán Sea indicating that the coral reefs possibly lasted for some hundreds to thousands of years (based on ^{14}C age dates of sediments) before environmental conditions (dissolved oxygen, salinity and density, nutrient availability) changed and they became buried by a hemipelagic sediment cover.

Dated coral fragments (McCulloch et al. 2010; Fink et al. 2013; Stalder et al. 2015) support the occurrence of reefs in the Alborán Sea during Organic Rich Layer 1 (ORL 1, 14.5–8.2 ka; Jimenez-Espejo et al. 2008) and the African humid period (deMenocal et al. 2000; Castañeda et al. 2009) and after sapropel layer 1 (<6 ky; Rohling 1994). Both episodes are marked by pulses or periods of higher productivity or enhanced nutrient supply to the surface waters and a change in climatic conditions – from dry to humid climates or vice versa (Fig. 25.1b). Rising seawater temperatures and salinities occurred during ORL1 indicating a cooler episode at the onset of coral growth. At a later stage ~10 ka the coral reefs experienced a change in water masses to much higher temperatures in conjunction with the rising sea level. At that time the African humid period intensified leading to a decrease in productivity and possibly decreasing oxygen contents in the bottom waters (Fink et al. 2015). The CWCs of the Late Holocene profit from more stable oceanographic (T, S, O_2) and drier climatic conditions. Their growth stopped around 2 ka at Dhaka mud volcano; only a few records of CWC in the Alborán Sea are reported for the past 1.5 kyr during times with high climatic variability and lower surface productivity (Fig. 25.1b).

The occurrence of CWC on mud volcanoes, which provide a (temporal) niche for a higher diverse benthic community compared to the adjacent soft bottoms (see Palomino et al., this volume; see Rueda et al., this volume), is the result of the complex interplay of environmental processes. The examples of the Alborán Sea are corroborated by the occurrences in the Gulf of Cádiz, evidencing that nutrition and its distribution through currents at the interface of water masses are the most important processes. However, they can vary in strength pending on the prevailing and dominating climatic factors. Therefore, the complexity of the benthic ecosystems needs more continuous and integrated monitoring of the extrinsic controlling factors to better understand their proliferation and limitation of growth on temporal substrates available at the surface of mud volcanoes.

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References

Adkins J, deMenocal P, Eshel G (2006) The "African humid period" and the record of marine upwelling from excess 230th in Ocean Drilling Program Hole 658C. 21, PA4203. https://doi.org/10.1029/2005PA001200

Becker EL, Cordes EE, Macko SA, et al (2009) Importance of seep primary production to *Lophelia pertusa* and associated fauna in the Gulf of Mexico. Deep-Sea Res Part 1 Oceanogr Res Pap 56:786–800

Cacho I, Grimalt JO, Canals M, et al (2001) Variability of the Western Mediterranean sea surface temperatures during the last 25000 years and its connection with the Northern Hemisphere climatic changes. Paleoceanography 16:40–52

Cacho I, Shackleton N, Elderfield H, et al (2006) Glacial rapid variability in deep-water temperature and d18O from the Western Mediterranean Sea. Quart Sci Rev 25:3294–3311

Castañeda IS, Mulitza S, Schefuß E, et al (2009) Wet phases in the Sahara/Sahel region and human migration patterns in North Africa. Proc Natl Acad Sci 106:20159–20163

Cita MB, Ryan WFB, Paggi L (1981) Prometheus mud-breccia: an example of shale diapirism in the Western Mediterranean Ridge. Annales Géologiques des Pays Hélléniques 30:543–570

Comas MC, Pinheiro ML (2007) Discovery of carbonate mounds in the Alboran Sea: the Melilla mound field. 1st International Conference of the Moroccan Association of Petroleum Geologists (MAPG) in association with the American Association of Petroleum Geologists (AAPG), Marrakesh, October 28–31, Abstract Book:73

Comas MC, Pinheiro LM, Ivanov MK, et al (2010) The Alboran Sea Leg-1: look into mud volcanoes, carbonate mounds and climate changes. IOC Tech Ser 94:8–64

De Mol B, Amblas D, Calafat A, et al (2012) Cold-water coral colonization of Alboran Sea Knolls, Western Mediterranean Sea. In: Harris PT, Baker EK (eds) Seafloor geomorphology as benthic habitat. Elsevier, London, pp 819–829

Dimitrov LI (2002) Mud volcanoes—the most important pathway for degassing deeply buried sediments. Earth Sci Rev 59:49–76

Dupré S, Woodside J, Foucher J-P, et al (2007) Seafloor geological studies above active gas chimneys off Egypt (Central Nile Deep Sea Fan). Deep-Sea Res Part 1 Oceanogr Res Pap 54:1146–1172

Emeis KC, Struck U, Schulz HM, et al (2000) Temperature and salinity of Mediterranean Sea surface waters over the last 16,000 years: constraints on the physical environment of S1 sapropel formation based on stable oxygen isotopes and alkenone unsaturation ratios. Palaeogeogr Palaeoclimatol Palaeoecol 158:259–280

Fabri MC, Pedel L, Beuck L, et al (2014) Mega- fauna of vulnerable marine ecosystems in French mediterranean submarine canyons: Spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207

Fink HG, Wienberg C, De Pol-Holz R, et al (2013) Cold-water coral growth in the Alboran Sea related to high productivity during the Late Pleistocene and Holocene. Mar Geol 339:71–82

Fink HG, Wienberg C, De Pol-Holz R, et al (2015) Spatio-temporal distribution patterns of Mediterranean cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) during the past 14,000 years. Deep-Sea Res Part 1 Oceanogr Res Pap 103:37–48

Flögel S, Dullo WC, Pfannkuche O, et al (2014) Geochemical and physical constraints for the occurrence of living cold-water corals. Deep-Sea Res Part 2 Top Stud Oceanogr 99:19–26

Foubert A, Depreiter D, Beck T, et al (2008) Carbonate mounds in a mud volcano province off north-west Morocco: key to processes and controls. Mar Geol 248:74–96

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Gardner JM (2001) Mud volcanoes revealed and sampled on the western Moroccan continental margin. Geophys Res Lett 28:339–342

Gennari G, Spezzaferri S, Comas MC, et al (2013) Sedimentary sources of the mud-breccia and mud volcanic activity in the Western Alboran Basin. Mar Geol 339:83–95

Jimenez-Espejo FJ, Martinez-Ruiz F, Rogerson M, et al (2008) Detrital input, productivity fluctuations, and water mass circulation in the westernmost Mediterranean Sea since the Last Glacial Maximum. Geochem Geophys Geosyst 9:Q11U02

Kopf AJ (2002) Significance of mud volcanism. Rev Geophys 40:1005

León R, Somoza L, Medialdea T, et al (2007) Sea-floor features related to hydrocarbon seeps in deepwater carbonate-mud mounds of the Gulf of Cádiz: from mud flows to carbonate precipitates. Geo-Mar Lett 27:237–247

Léon R, Somoza L, Medialdea T, et al (2012) New discoveries of mud volcanoes on the Moroccan Atlantic continental margin (Gulf od Cádiz): morphostructural characterization. Geo-Mar Let 32:473–488

Limonov AV, Dimitrov L, Ivanov MK, et al (1996) Mud volcanism and fluid venting in the eastern part of the Eastern Mediterranean Ridge. Initial results of the geological, geophysical and geochemical investigations during the Fifth UNESCO-ESF "Training through Research" Cruise of R/V Logachev (July–September 1995): UNESCO Reports in Marine Science 68, p 173

Margreth S, Gennari G, Rüggeberg A, et al (2011) Growth and demise of cold-water coral ecosystems on mud volcanoes in the West Alboran Sea: the messages from the planktonic and benthic foraminifera. Mar Geol 282:26–39

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the Younger Dryas. Earth Planet Sci Lett 298:143–152

deMenocal P, Ortiz J, Guilderson T, et al (2000) Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing. Quat Sci Rev 19:347–361

Niemann H, Duarte J, Hensen C, et al (2006) Microbial methane turnover at mud volcanoes of the Gulf of Cadiz. Geochim Cosmochim Acta 70:5336–5335

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Prog Ser 397:37–51

Praeg D, Ceramicola S, Barbieri R, et al (2009) Tectonically-driven mud volcanism since the late Pliocene on the Calabrian accretionary prism, central Mediterranean Sea. Mar Pet Geol 26:1849–1865

Robertson AHF, Emeis KC, Richter C (1998) Collision-related break-up of a carbonate platform (Eratosthenes Seamount) and mud volcanism on the Mediterranean Ridge: preliminary synthesis and implication of tectonic results of ODP Leg 160 in the Eastern Mediterranean Sea. In: Cramp A, MacLeod CJ, Lee SV, et al (eds) Geological evolution of ocean basins: results from the ocean drilling program, vol 131. Geological Society, London, Special Publications, pp 243–271

Rodrigo-Gámiz M, Martínez-Ruiz F, Jiménez-Espejo FJ, et al (2011) Impact of climate variability in the western Mediterranean during the last 20,000 years: oceanic and atmospheric responses. Quat Sci Rev 30:2018–2034

Rohling EJ (1994) Review and new aspects concerning the formation of eastern Mediterranean sapropels. Mar Geol 122:1–28

Schlitzer R (2016) Ocean data view. http://odv.awi.de

Somoza L, Diaz-del-Rio V, Leon R, et al (2003) Seabed morphology and hydrocarbon seepage in the Gulf of Cádiz mud volcano area: acoustic imagery, multibeam and ultra-high resolution seismic data. Mar Geol 195:153–176

Spezzaferri S, Rüggeberg A, Stalder C, et al (2015) Benthic Foraminiferal assemblages from cold-water coral ecosystems. In: Spezzaferri S, Rüggeberg A, Stalder C (eds) Atlas of benthic foraminifera from cold-water coral reefs, vol 44. Cushman Foundation Special Publication, pp 20–48

Staffini F, Spezzaferri S, Aghib F (1993) Mud diapirs of the Mediterranean Ridge: sedimentological and micropaleontological study of the mud breccia. Riv Ital Paleontol Stratigr 99:225–254

Stalder C, Vertino A, Rosso A, et al (2015) Microfossils, a key to unravel cold-water carbonate mound evolution through time: evidence from the Eastern Alboran Sea. PLoS One 10:e0140223. https://doi.org/10.1371/journal.pone.0140223

Taviani M, Remia A, Corselli C, et al (2005) First geo-marine survey of living cold-water *Lophelia* reefs in the lonian Sea (Mediterranean basin). Facies 50:409–417

Van Rensbergen P, Depreiter D, Pannemans B, et al (2005) The El Arraiche mud volcano field at the Moroccan Atlantic slope, Gulf of Cadiz. Mar Geol 219:1–17

Wienberg C, Hebbeln D, Fink HG, et al (2009) Scleractinian cold-water corals in the Gulf of Cádiz—first clues about their spatial and temporal distribution. Deep-Sea Res Part 1 Oceanogr Res Pap 56:1873–1893

Wienberg C, Frank N, Mertens KN, et al (2010) Glacial cold-water coral growth in the Gulf of Cádiz: implications of increased palaeo-productivity. Earth Planet Sci Lett 298:405–416

Woodside JM, David L, Frantzis A, et al (2006) Gouge marks on deep-sea mud volcanoes in the eastern Mediterranean: caused by Cuvier's beaked whales? Deep-Sea Res Part 1 Oceanogr Res Pap 53:1762–1771

Cross-References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Angeletti L, Bargain A, Campiani E, et al (this volume) Cold-water coral habitat mapping in the Mediterranean Sea: methodologies and perspectives

Aymà A, Aguzzi J, Canals M, et al (this volume) Occurrence of living cold-water corals at large depths within submarine canyons of the northwestern Mediterranean Sea

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Fourt M, Goujard A, Chevaldonné P (this volume) Working with visual methods, comparison among the French deep-sea canyons

Knittweis L, Evans J, Aguilar R, et al (this volume) Recent discoveries of extensive cold-water coral assemblages in Maltese waters

Lastras G, Sanchez-Vidal A, Canals M (this volume) A cold-water coral habitat in La Fonera submarine canyon, northwestern Mediterranean Sea

Lo Iacono C, Savini A, Huvenne VAI, et al (this volume) Habitat mapping of cold-water corals in the Mediterranean Sea

Palomino D, Rueda JL, Vázquez JT, et al (this volume) Cold-water corals in fluid venting submarine structures

Puig P, Gili JM (this volume) Submarine canyons in the Mediterranean: a shelter for cold-water corals

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Occurrence of Living Cold-Water Corals at Large Depths Within Submarine Canyons of the Northwestern Mediterranean Sea

26

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Abstract

In the northwestern Mediterranean Sea, cold-water corals *Madrepora oculata*, *Lophelia pertusa*, *Dendrophyllia cornigera* and *Desmophyllum dianthus* have been mostly described at relatively shallow depths (i.e. <400 m). Here, we report the results of the inspection of the large, deeply incised Cap de Creus, La Fonera and Blanes submarine canyons in order to assess the presence of cold-water corals at depths between 600 and 1500 m. Two complementary methodologies were applied: remotely operated vehicle dives for *in situ* observation, and Agassiz trawls to get biological samples. Remotely operated vehicle videos pictured aggregations of specimens of the solitary *D. dianthus* at 1409 m depth in La Fonera Canyon, which seemed to be alive. This is the first *in situ* observation of this species at such depths in the northwestern Mediterranean Sea. Agassiz trawl samples provided living *M. oculata* and *L. pertusa* in Blanes Canyon at 1200 and 900 m depth, respectively. They also yielded living *D. dianthus* in Cap de Creus Canyon at 900 m and in Blanes Canyon at 900 and 1200 m depth. Jointly with other recently published results, our findings demonstrate that submarine canyons in the northwestern Mediterranean Sea host significant cold-water coral populations, locally extending to water depths below 1000 m.

Keywords

Northwestern Mediterranean Sea · Submarine canyons · Cold-water corals (CWC) · Deep water · Remotely operated vehicle (ROV) · Agassiz trawl (AGT)

26.1 Introduction

Deep-sea ecosystems constitute the largest biome on Earth. They cover more than 65% of the planet surface and encompass more than 95% of the global biosphere (Danovaro et al. 2010). The beginning of the exploration of the deep Mediterranean Sea dates back to the end of the eighteenth century (Ryland 2000), and the sampling effort has constantly increased since then. In the western Mediterranean Sea several studies have been carried out, mostly by trawling, in order to obtain comprehensive faunal lists and define the geographic and bathymetric distribution ranges of species (Cartes and Sarda 1989; Bouchet and Taviani 1992; Cartes et al. 1993, 2009; Abello et al. 2002; D'Onghia et al. 2004, this volume; Galil 2004; Sion et al. 2004; Papiol et al. 2012; Aguzzi et al. 2013; Fanelli et al. 2013; Tecchio et al. 2013; Mecho et al. 2014a, b; Rueda et al., this volume).

The search for cold-water corals (CWCs) progressively gained scientific and socioeconomic interest, especially in the last two decades (Roberts et al. 2006, 2009). Similarly to shallow-water tropical corals, deep-sea CWC reefs host high biodiversity (Henry and Roberts 2007; Mastrototaro et al. 2010; Purser et al. 2013) as they represent a refuge, nursery and feeding ground for many species of crustaceans, fishes and other groups (Husebo et al. 2002; Roberts et al. 2006,

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2009; D'Onghia et al. 2010, this volume; Purser et al. 2013). CWCs settle in seabed areas exposed to currents strong enough to prevent excessive sedimentation and carry food particles to sustain polyps and colonies (Frederiksen et al. 1992; White et al. 2005; Dullo et al. 2008; Davies et al. 2009). Such physical conditions often occur in escarpments, seamounts and submarine canyons (Canals et al. 2006; Thiem et al. 2006; Kiriakoulakis et al. 2007), which subsequently become key-habitats for the recruitment and maintenance of stocks of commercially exploited resources (Sardà and Cartes 1993; Cartes et al. 1994; Company et al. 2008). It should be kept in mind that the occurrence of large submarine canyons deeply incising continental margin segments adds heterogeneity to deep-sea habitats and an ecological complexity not yet fully explored (Canals et al. 2013).

Cold-water coral communities commonly occur in marine waters with temperatures between 4 and 12 °C (Freiwald et al. 2004). These temperatures can be found between 50 and 1000 m depth at high latitudes and at larger depths (up to 4000 m) at low latitudes (Roberts et al. 2006, 2009). In contrast, the Mediterranean Sea presents warmer deep water masses at 12–14 °C below the thermocline (i.e. at approximately 200 m depth; Borghini et al. 2014), which results in limiting conditions for the growth of the majority of CWCs (Freiwald et al. 2004). This notwithstanding, several species such as *Madrepora oculata* (Linnaeus, 1758), *Lophelia pertusa* (Linnaeus, 1758), *Desmophyllum dianthus* (Esper, 1794) and *Dendrophyllia cornigera* (Lamarck, 1816) have been identified in the Mediterranean Sea (Tursi et al. 2004; Hebbeln et al. 2009; Orejas et al. 2009; Mastrototaro et al. 2010; Gori et al. 2013; Rogers 2013; Angeletti et al. 2015; Lastras et al. 2016; Addamo, this volume; Altuna and Poliseno, this volume; Chimienti et al., this volume) (Table 26.1). Of these, *M. oculata* and *L. pertusa* are the most relevant CWC species in terms of abundance and biomass, forming large-sized colonies that provide shelter, food and nursery to deep-sea fauna (D'Onghia et al. 2010, this volume; Rueda et al., this volume). The cosmopolitan *D. dianthus* is a solitary species appearing in the Mediterranean Sea in association with *L. pertusa* and *M. oculata* (Pérès and Picard 1964; Taviani et al. 2005; Reveillaud et al. 2008; Heindel et al. 2010; Addamo, this volume). In some circumstances, it can form pseudo-colonies with the skeletons of older individuals providing the substratum on which younger individuals, including other CWC species, grow as observed in banks off New Zealand and Chile (Squires 1965; Cairns and Stanley 1982; Försterra et al. 2005, 2017; Jantzen et al. 2013).

To date, CWCs below 300 m have been reported in several locations in the Mediterranean Basin (reviewed by Lastras et al. 2016; Altuna and Poliseno, this volume). The occurrence of *M. oculata* and *L. pertusa* has been reported down to 1100 m depth in Santa Maria di Leuca, at the mouth of the Adriatic Sea (Tursi et al. 2004; Mastrototaro et al. 2010), and down to 600 m depth in the Bari Canyon, in the southern Adriatic Sea (Freiwald et al. 2009; D'Onghia et al. 2010). In Sardinian canyons, *M. oculata* has been identified from 380 to 460 m depth, with occasional presence of *L. pertusa* (Taviani et al. 2017). In the northwestern Mediterranean Sea, *M. oculata* has been found in the Cassidaigne Canyon, east of Marseille, from 200 m down to 1000 m, co-occurring with *Corallium rubrum* colonies in the depth range of 200–325 m (Reyss 1970; Zibrowius 1980; Fiala-Medioni et al. 2012; Fabri et al. 2014). Also, Fanelli et al. (2017) recognised *M. oculata* from 525 to 575 m depth at Levante Canyon in the eastern Ligurian Sea, where small *D. dianthus* colonies were also identified. *Dendrophyllia cornigera* was located within a narrow depth interval from 447 to 501 m in the Ionian Sea (Freiwald et al. 2009; Mastrototaro et al. 2010) with *D. dianthus* occurring between 425 and 1100 m in the same locations (Cairns 1995; Tursi et al. 2004; Mastrototaro et al. 2010).

In the North Catalan margin of the northwestern Mediterranean Sea these species have mostly been reported at shallower depths within submarine canyons. The upper flanks of Cap de Creus Canyon host healthy communities of *M. oculata* laying over patches of hard substrate at depths from 129 m down to 400 m and possibly deeper although not inspected due to ROV operational limitations (Rossi et al. 2008; Orejas et al. 2009; Lastras et al. 2011; Lo Iacono et al. 2012; Gori et al. 2013; Puig and Gili, this volume). Also, isolated colonies of *L. pertusa*, *D. dianthus* and *D. cornigera* have been found associated to *M. oculata* communities in the same canyon (Orejas et al. 2009; Lo Iacono et al. 2012; Gori et al. 2013; Puig and Gili, this volume). The recently explored head of La Fonera Canyon revealed the presence of healthy communities of *M. oculata* and *D. cornigera* at relatively shallow water depth ranges, i.e. between 129 and 369 m and 131 and 325 m, respectively (Lastras et al. 2016). Again, ROV operational limitations prevented exploration at larger depths. In the Lacaze-Duthiers Canyon head, *L. pertusa* and *M. oculata* were found at greater depths, ranging between 350 and 541 and 246 and 531 m, respectively (Gori et al. 2013; Lartaud et al. 2013).

In this study, we present the results of a thoughtful exploration of the deep reaches of large submarine canyons in the North Catalan margin thus providing, to our best knowledge, the first *in situ* evidence about the presence of living speci-

Table 26.1 Recorded distribution, depth range (m) and sampling methods applied in different studies of cold-water coral species *Lophelia pertusa, Madrepora oculata, Dendrophyllia cornigera* and *Desmophyllum dianthus* in the Mediterranean Sea

Basin	Location	Depth range (m)	Sampling method	References
Lophelia pertusa				
Ionian Sea	SML	425–1100	Trawl hauls	Tursi et al. (2004)
Ionian Sea	SML	300–1100	ROV, dredges	Taviani et al. (2005)
Ionian Sea	SC	395–617	Trawl hauls	Schembri et al. (2007)
Ionian Sea	SML	520–1100	ROV, trawl hauls	Carlier et al. (2009)
Ionian Sea	SC	509–679	ROV	Freiwald et al. (2009)
Ionian Sea	SML	469–1100	ROV	Mastrototaro et al. (2010)
Alboran Sea	SoG	150–300	Grab sampling	Álvarez-Pérez et al. (2005)
Alboran Sea	MM	539–675	ROV	Hebbeln et al. (2009)
NWMed	NCM	100–400	ROV	Lo Iacono et al. (2012)
NWMed	NCM	<400	ROV	Gori et al. (2013)
NWMed	GoL	531–554	ROV	Fabri et al. (2014)
NWMed	GoL	300–535	ROV	Fiala-Medoni et al. (2012)
Madrepora oculata				
Ionian Sea	SML	425–1100	Trawl hauls	Tursi et al. (2004)
Ionian Sea	SML	300–1100	ROV, dredges	Taviani et al. (2005)
Ionian Sea	SC	395–617	Trawl hauls	Schembri et al. (2007)
Ionian Sea	SML	520–700	ROV, trawl hauls	Carlier et al. (2009)
Ionian Sea	SC	509–679	ROV	Freiwald et al. (2009)
Ionian Sea	SML	425–1100	ROV	Mastrototaro et al. (2010)
Alboran Sea	SoG	150–300	Grab sampling	Álvarez-Pérez et al. (2005)
Alboran Sea	MM	539–675	ROV	Hebbeln et al. (2009)
NWMed	GoL	210–510	Submersible	Bourcier and Zibrowius (1973)
NWMed	NCM	150	ROV	Lastras et al. (2016)
NWMed	GoL	300	Submersible, dredges	Zibrowius (2003)
NWMed	NCM	125	ROV	Rossi et al. (2008)
NWMed	NCM	180–300	ROV	Orejas et al. (2009)
NWMed	NCM	100–400	ROV	Lo Iacono et al. (2012)
NWMed	GoL	246–531	ROV	Gori et al. (2013)
NWMed	GoL	531–554	ROV	Fabri et al. (2014)
NWMed	NCM	129–369	ROV	Lastras et al. (2016)
NWMed	GoL	220–500	ROV	Fiala-Medoni et al. (2012)
Ligurian Sea	LC	540–545	ROV	Fanelli et al. (2017)
Dendrophyllia cornigera				
Ionian Sea	SML	447–501	ROV	Mastrototaro et al. (2010)
Alboran Sea	MM	622	ROV	Hebbeln et al. (2009)
NWMed	NCM	100–400	ROV	Lo Iacono et al. (2012)
NWMed	NCM	131–297	ROV	Lastras et al. (2016)
NWMed	GoL	220–330	ROV	Fiala-Medoni et al. (2012)
Desmophyllum dianthus				
Ionian Sea	SML	425–1100	Trawl hauls	Tursi et al. (2004)
Ionian Sea	SC	395–617	Trawl hauls	Schembri et al. (2007)
Ionian Sea	SML	520–1100	ROV, trawl hauls	Carlier et al. (2009)
Ionian Sea	SML	525–1100	ROV	Mastrototaro et al. (2010)
NWMed	NCM	100–400	ROV	Lo Iacono et al. (2012)
NWMed	GoL	280–535	ROV	Fiala-Medoni et al. (2012)

GoL Gulf of Lion, *LC* Levante Canyon, *MM* Malaga mounds, *NCM* North Catalan margin, *NWMed* Northwestern Mediterranean margin, *SML* Santa Maria di Leuca, *SC* Sicily Channel, *SoG* Strait of Gibraltar

mens of the solitary CWC *D. dianthus* down to 1400 m depth. This finding, together with the dead fragments of *L. pertusa* and *M. oculata* retrieved at remarkable depths in the same area are of broad relevance for Mediterranean deep-sea ecology and highlight the interest of North Catalan submarine canyons in terms of new CWC occurrences, subsequently leading to a southward extension of the Gulf of Lion CWC province, which could be now re-named "Gulf of Lion and North Catalan canyons CWC province".

26.2 Study Area

We inspected three large submarine canyons from the North Catalan margin. Cap de Creus Canyon follows a WNW-ESE direction, is 95 km long and ends at 2150 m depth (Amblas et al. 2006). Its head is located 5 km northeast of the tip of Cap de Creus coastal promontory. The 105 km long La Fonera Canyon (also known as Palamos Canyon), has a N-S oriented head that leads to a NW-SE narrow and V-shaped upper course, followed by broader middle and lower reaches that vanish at the base of the slope at 2540 m depth (Amblas et al. 2006). The nearest shoreline is at only 0.8 km from the tip of the westernmost head branch of La Fonera Canyon (Lastras et al. 2011). Among the canyons investigated here, the southernmost one is Blanes Canyon, which extends along 180 km from its head, at less than 4 km from the nearest shoreline, to its mouth at 2600 m depth (Lastras et al. 2011). Blanes Canyon is roughly oriented N-S along its head, upper, and middle course, and then turns SE in its lower course, where some prominent meanders occur (Amblas et al. 2006).

The closeness of the three canyon heads to the shoreline enhances their trapping ability of coastal and shelf flows (Canals et al. 2013). All of them are able to capture dense waters that form seasonally and escape from the continental shelf to the bathyal domain, carrying sediment, food, pollutants and litter (Canals et al. 2006, 2013; Ulses et al. 2008; Tubau et al. 2015), as well as sediment-laden flows that result from severe coastal storms (Palanques et al. 2005, 2006; Martin et al. 2006; Sanchez-Vidal et al. 2012). Of the three inspected canyons, the most efficient one in trapping and conveying larger volumes of dense shelf water is Cap de Creus (Ulses et al. 2008). All of them share abrupt heads and upper courses with steep walls where rocky outcrops and large boulders are common despite the dominant bottom type is mud (Lastras et al. 2011). Canyon floors, where an axial incision is occasionally observed, are rather flat and usually sediment-covered.

The oceanography of the study area is characterised by the Northern Current, a steady mesoscale current flowing south-westward over the outer shelf and slope where the investigated submarine canyons are incised (Millot 1999). The Northern Current has a baroclinic component from the sea surface to approximately 400 m depth associated with a shelf-slope density front that separates colder, fresher waters over the continental shelf from warmer, saltier waters over the outer continental margin and basin (Font et al. 1988).

26.3 Materials and Methods

26.3.1 Data Collection

In summer 2011 the three canyons (Cap de Creus, La Fonera and Blanes) were systematically inspected and sampled from north to south (Fig. 26.1) by using the research vessel *Sarmiento de Gamboa*. Two complementary methods were applied: a remotely operated vehicle (ROV) and an Agassiz trawl (AGT) to respectively video-inspect and collect biological samples from the bottom.

The ROV "*Liropus 2000*" was equipped with a HD Kongsberg OE 14-502A camera, with a horizontal resolution of 800 TV lines per picture height, a 1920 (H) × 1080 (V) picture elements video, and a 10 × optical zoom. Aligned to the HD camera, the ROV had also a pair of parallel laser beams mounted 15 cm apart one from each other, which allowed measurements on the bottom including the sizing of animals and other items in the imagery. Ten ROV video-dives were conducted along transects at an approximated height of 50–100 cm off bottom, and at low speed (up to 1.2 knots) (Table 26.2). The dives were performed along canyon axes in an upward direction, starting at 900, 1200, and 1500 m reference depths (Fig. 26.1). Other dives were carried out along a transect ascending the northern wall of La Fonera Canyon. The duration of the ROV video records was, on average, 113 min, resulting in a total of 19 h of faunal and geomorphological observations (Table 26.2).

In all dives oceanographic parameters known to directly affect the presence and growth of CWC colonies (Roberts et al. 2006, 2009), such as salinity and temperature were continuously recorded by means of a SBE37 CTD installed in the ROVs payload (Table 26.3). The benthic terrain modelling tool (BTM) of ArcGis 10.2.1 software was used to calculate slope values from bathymetry data.

We used an AGT to sample benthic fauna, as this tool allows greater manoeuvrability in geomorphologically complex environments, such as canyons, than larger otter trawling devices (i.e. the otter trawl Maireta System-OTMS, or commercial trawling nets) (Holme and McIntyre 1971). The dredge was endowed with a 6 mm mesh size net, with 2.5 × 1.2 m of horizontal and vertical opening, respectively. AGT sampling was conducted 24 h after ROV dives, along the axes of the three canyons, resulting in hauls at 900, 1200 and 1500 m reference depths (Table 26.4). In total 8 AGT hauls were performed in a down canyon direction, resulting in a total swept area of 0.154 km^2.

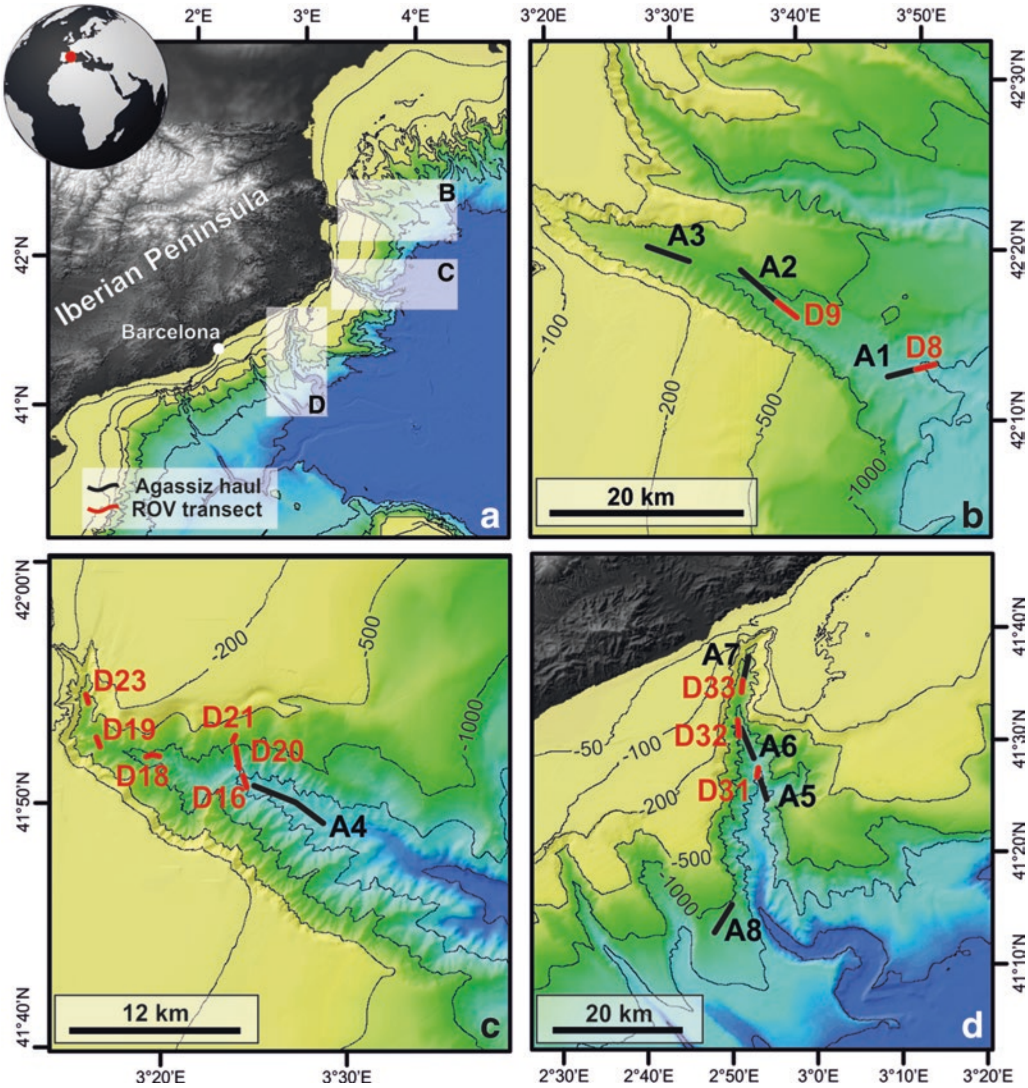


Fig. 26.1 (**a**) General location of ROV dives (D, red lines) and Agassiz trawl hauls (A, black lines) within (**b**) Cap de Creus, (**c**) La Fonera and (**d**) Blanes submarine canyons of the North Catalan continental margin. (© GRC Geociències Marines, Universitat de Barcelona)

Table 26.2 Reference data for the ROV dives in terms of location and reference depth (700, 900, 1200 and 1500 m), date within year 2011, initial and final transect location (latitude and longitude), duration of video record (min), depth range (m, from deeper to shallower as dives were performed upwards) and swept area (m^2)

Dive no.	Location	Date	Initial location	Final location	min	m	m^2	CWC Y/N
8	CCC-1500 axis	05/07	42°13′14″N 03°48′48″E	42°13′14″N 03°48′48″E	159	1570–1490	6456	N
9	CCC-1200 axis	05/07	42°16′53″N 03°38′44″E	42°17′25″N 03°37′45″E	97	1215–1200	5789	N
16	LFC-1500 axis	08/07	41°51′00″N 03°24′25″E	41°51′31″N 03°23′59″E	141	1570–1510	4136	N
18	LFC-1200 axis	09/07	41°51′53″N 03°20′22″E	41°05′03″N 03°19′45″E	119	1215–1155	3485	N
19	LFC-900 axis	09/07	41°52′25″N 03°16′45″E	41°52′49″N 03°16′40″E	83	985–860	2467	N
20	LFC-1500 lower N wall	09/07	41°51′30″N 03°23′56″E	41°52′48″N 03°16′40″E	238	1500–980	5582	Y

(continued)

Table 26.2 (continued)

Dive no.	Location	Date	Initial location	Final location	min	m	m²	CWC Y/N
21	LFC-900 mid N wall	10/07	41°52′26″N 03°23′57″E	41°52′47″N 03°23′55″E	100	985–750	2063	N
23	LFC-700 upper N wall	10/07	41°54′10″N 03°16′09″E	41°53′46″N 03°16′09″E	150	730–600	2509	Y
31	BC-1500 axis	13/07	41°07′02″N 02°52′50″E	41°07′40″N 03°52′44″E	71	1520–1500	1870	N
32	BC-1200 axis	13/07	41°01′14″N 02°50′45″E	41°01′29″N 02°50′42″E	60	1225–1200	1892	N
33	BC-900 axis	13/07	41°04′15″N 02°50′48″E	41°04′31″N 02°50′52″E	68	910–900	1753	N

CCC Cap de Creus Canyon, *LFC* La Fonera Canyon, *BC* Blanes Canyon

Table 26.3 Mean values for temperature (T) and salinity (S) reported for every dive

Dive no.	Dive	T (°C)	SD	S (PSU)	SD
8	CCC-1500 axis	13.15	0.029	38.41	0.007
9	CCC-1200 axis	13.15	0.011	38.42	0.010
16	LFC-1500 axis	13.17	0.004	38.40	0.029
18	LFC-1200 axis	13.15	0.002	38.42	0.028
19	LFC-900 axis	13.21	0.009	38.44	0.019
20	LFC-1500 lower N wall	13.16	0.008	38.47	0.004
21	LFC-900 mid N wall	13.20	0.040	38.48	0.007
23	LFC-700 upper N wall	13.28	0.005	38.47	0.007
31	BC-1500 axis	13.17	0.003	38.45	0.002
32	BC-1200 axis	13.15	0.002	38.45	0.003
33	BC-900 axis	13.24	0.004	38.45	0.003

SD standard deviation. For location codes and reference depths see Table 26.2

Table 26.4 Reference data for the Agassiz trawl (AGT) sampling stations, including location, depth range (m, from shallower to deeper as trawls were performed downwards) and trawled area (m²)

AGT no.	Location	m	km²	CWC Y/N
1	CCC-1500 axis	1408–1554	0.01009	N
2	CCC-1200 axis	1018–1236	0.01368	N
3	CCC-900 axis	771–880	0.00657	Y
4	LFC-1900 axis	1526–2289	0.0152	N
5	BC-1500 axis	1477–1569	0.00584	N
6	BC-1200 axis	1204–1424	0.00627	Y
7	BC-900 axis	752–864	0.09237	Y
8	BC-1100 open slope	1063–1159	0.00602	N

For location codes and reference depths see Table 26.2

26.3.2 Video and Hauling Data Treatment

Video footage from ROV was analysed in slow motion (i.e. at 50% of the recording speed). CWC individuals' identification was resolved to the lowest possible taxonomical level whereas the associated fauna was identified at genus level. The software ArcGis 10.2.1 allowed calculating the length of the different sections in each transect where colonies were found. The software *Image J* was used to determine the area frame by frame, by taking the known distance (15 cm) between the two ROV laser points that appeared on the imagery as a reference, also assuming an averaged ROV constant speed of 1.2 knots over the bottom. The separation between the two laser points allowed, in addition, compensating for ROV seabed height changes during navigation.

Agassiz trawl samples were sorted on board, cleaned, counted, and finally weighted. Determining if well preserved coral specimens collected with AGT were actually alive or not was dubious. Therefore, the total weight of fragments was used as a proxy for present or past biomass in each study area.

26.4 Results

26.4.1 ROV Video-Observations

The dense concentrations of CWCs found in the lower and upper northern flank of La Fonera Canyon contrast with their absence in the ROV dives at Cap de Creus and Blanes canyons (Table 26.2). The living colonies of *Desmophyllum dianthus* in La Fonera Canyon were particularly noticeable in dives no. 20 (1400 m depth) and 23 (600 m depth) (Fig. 26.2a–c), being dive no. 20 the only one conducted across the canyon wall (Fig. 26.2b). In this transect, seabed slope values were ranging from 16° to 30°. CWC individuals were identified on a 10 m high rock step with slope values of 16°, within the 1420–1400 m depth range. Dive no. 23 was conducted at 680 m depth along the canyon axis (Fig. 26.2c), and, in contrast with dive no. 20, slope values were less than 6°.

Hundreds of *D. dianthus* specimens grouped in several clusters of different sizes (i.e. up to several tens of recognisable individuals) were found along dive no. 20 (Fig. 26.3a), settling on a vertical rocky wall. Most corals were hanging from the rocky outcrop with their calyx looking either down or sideward. Many of them were observed as inhabiting rock protrusions and bumps with no or little soft sediment on top (Fig. 26.3b). The spaces in between coral clusters or sparse

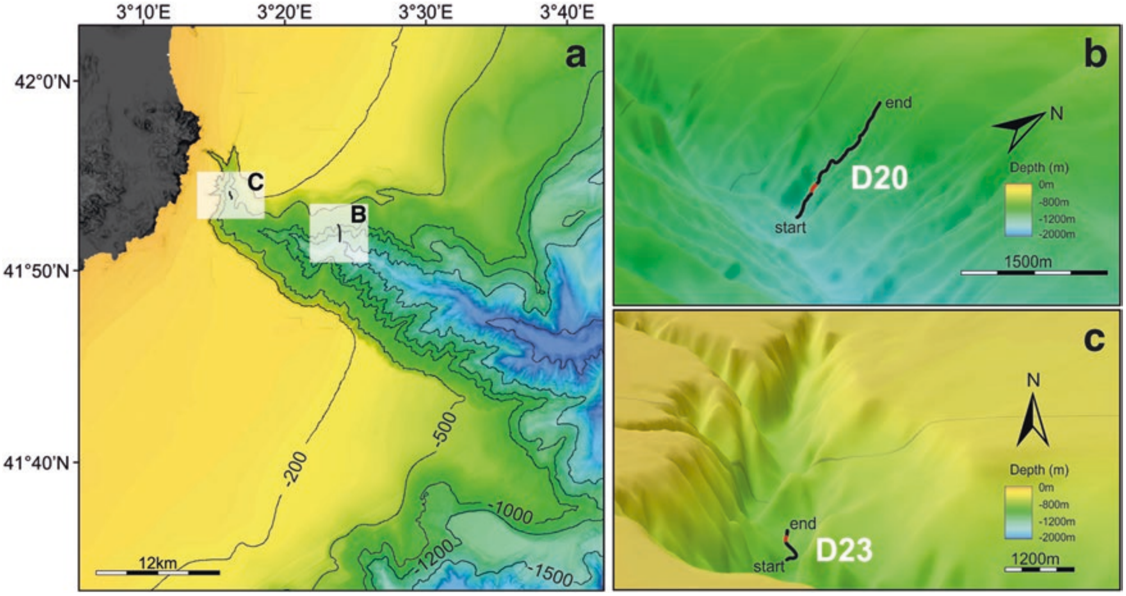


Fig. 26.2 (**a**) Location of the ROV dives (D) in La Fonera Canyon where living cold-water corals (CWCs) were observed. 3-D plots show the precise location of dives 20 (**b**) and 23 (**c**). Red segments indicate the location of CWCs. (© GRC Geociències Marines, Universitat de Barcelona)

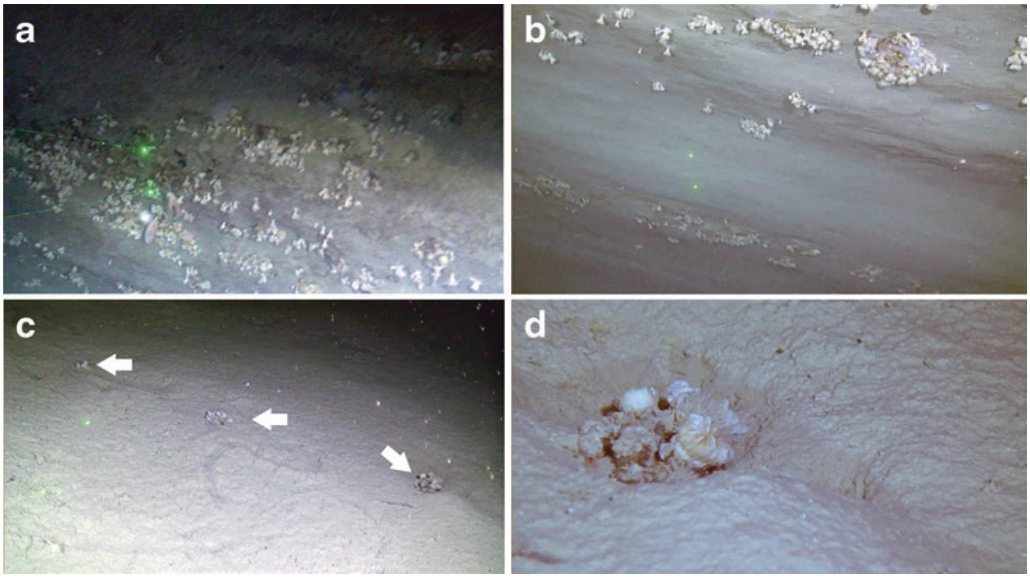


Fig. 26.3 (**a**) ROV video capture showing *Desmophyllum dianthus* in a rock outcrop in La Fonera canyon at 1409 m depth. (**b**) *D. dianthus* specimens attached to a near-vertical rock outcrop. (**c**) and (**d**) *D. dianthus* clusters lying on a soft muddy bottom at the foot of the escarpment after detachment from the outcrop. Distance amongst green laser dots is 15 cm. (© GRC Geociències Marines, Universitat de Barcelona)

individuals were just barren rock. Detached coral clusters were also found settling onto the soft bottom at the base of the escarpment (Fig. 26.3c, d).

Individuals of *D. dianthus* were also located attached to a rocky outcrop during dive no. 23 (Fig. 26.4a). Again, hundreds of individuals were detected hanging with their calix looking downward or sideward. This ROV transect presented higher density values of *D. dianthus* individuals than dive no. 20. Specimens formed aggregations, resting on a vertical hard substrate with vertical slope and also in places where soft sediment accumulated. We detected associated fauna amidst of *D. dianthus* specimens (Fig. 26.4b). In ROV imagery decapod crustaceans, echinoids, anemones and holothurians were observed between coral clusters attached to the outcrop. Holothurians, identified as *Holothuria forskali*, were the most abundant group, followed by echinoids, all belonging to genus *Gracilechinus*. Decapod crustaceans identified as *Munida* sp. were observed sheltering in spaces between coral aggregations. Actiniae were the less abundant group. Also, we noticed the presence of several specimens belonging to classes Polychaeta and Bivalvia, but it was not possible identifying them at the species level on the video imagery.

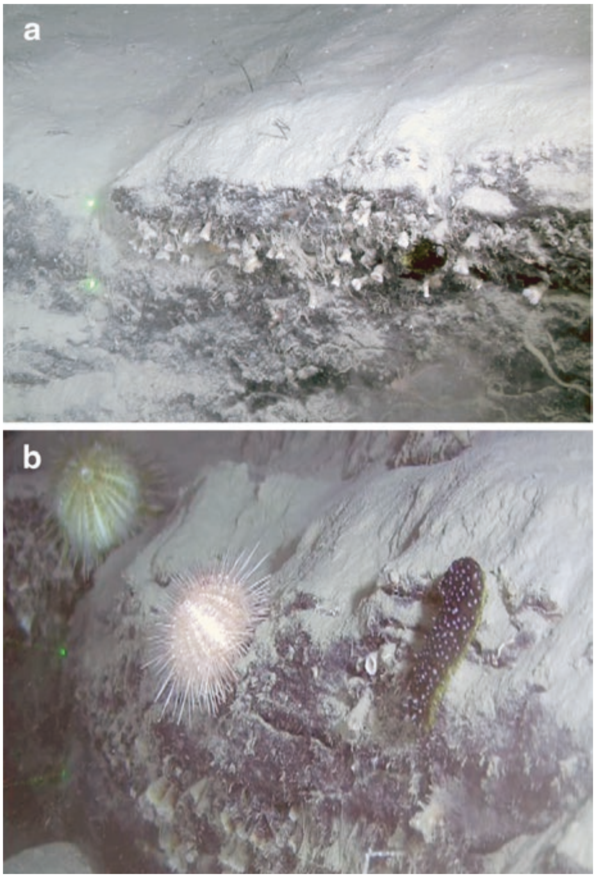


Fig. 26.4 *Desmophyllum dianthus* community at 680 m of water depth in La Fonera canyon. (**a**) ROV video screenshot showing a number of individuals settling on a vertical to overhanging rock outcrop with their calyxes looking downwards. (**b**) Living echinoderms and holothurians associated to the *D. dianthus* community. (© GRC Geociències Marines, Universitat de Barcelona)

Regarding temperature and salinity, similar mean values were observed between canyons, and differences between dives were also very small (see Table 26.3). For dives D20 and D23, where CWCs occurred, mean temperature values were 13.16 ± 0.01 °C and 13.28 ± 0.01 °C, respectively. The same salinity mean value was recorded in both dives (38.47 ± 0.01 PSU).

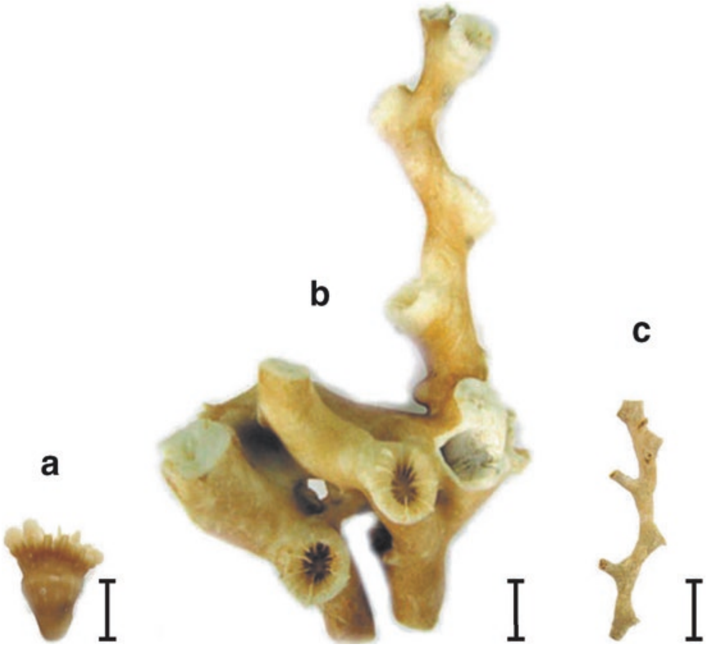
26.4.2 Agassiz Trawling

Agassiz trawl sampling yielded three species of CWCs: *Lophelia pertusa*, *Madrepora oculata* and *D. dianthus* (Fig. 26.5). In Blanes Canyon where all the three species were present, *L. pertusa* was sampled at trawl 7 (752–864 m) yielding 11.477 g, *M. oculata* at trawl 6 (1204–1424 m) with 244 g, and *D. dianthus* at both trawls and depths, with 1084 and 2050 g, respectively (Fig. 26.1 and Tables 26.4 and 26.5).

Weight of *L. pertusa* per unit area for trawl 7 was 124.3 kg/km^2, while *D. dianthus* presented higher values at the deeper trawl 6 than at the shallower trawl 7 (i.e. 326.9 kg/km^2 vs. 11.7 kg/km^2). At trawl 7, the weight of *M. oculata* per unit area was about 39 kg/km^2 (Table 26.5).

The solitary coral *D. dianthus* was also sampled in Cap de Creus Canyon by AGT at trawl 3 from 771 to 880 m of water depth, with 3 g and an estimated weight of 0.46 kg/km^2. Such isolated occurrence of *D. dianthus* was also observed with ROV on rock escarpments in La Fonera Canyon at 1400 and 680 m depth. By contrast, in Blanes Canyon, *D. dianthus* appeared in association to *M. oculata* at 1200 m depth in trawl 6, and with *L. pertusa* at 900 m depth in trawl 7 (Table 26.4). Some specimens of *L. pertusa* recovered from Blanes Canyon in trawl 7 also had associated fauna, mainly polychaetes.

Fig. 26.5 Fragments of cold-water corals retrieved by Agassiz trawling. (**a**) *Desmophyllum dianthus* recovered in Agassiz trawl 7 (752–864 m depth) within Blanes Canyon. (**b**) and (**c**) *Madrepora oculata* and *Lophelia pertusa* recovered in Agassiz trawl 6 (1204–1424 m depth) within Blanes canyon. Scale bars: 1 cm. (© GRC Geociències Marines, Universitat de Barcelona)



Interaction between CWC and marine litter was observed in samples retrieved from AGT 7 (752–864 m depth) in Blanes Canyon. There, a noticeable *L. pertusa* colony had grown around and over nylon ropes from an old net (Fig. 26.6).

26.5. Discussion

Living colonies of *Madrepora oculata* and *Lophelia pertusa* in the northwestern Mediterranean Sea had been previously reported between 180 and 400 m depth in Cap de Creus Canyon by Rossi et al. (2008), Orejas et al. (2009), and Gori et al. (2013) and down to 400 m depth by Lo Iacono et al. (2012) and Gori et al. (2013), mostly on hard substrata (Fig. 26.7) (see also Altuna and Poliseno, this volume; Chimienti et al., this volume; Fourt et al., this volume). *M. oculata* had also been reported at shallower depths (i.e. 155 m) in La Fonera Canyon (Lastras et al. 2011, 2016) (Fig. 26.7).

Our findings in the North Catalan canyons constitute the deepest confirmed record in the entire Mediterranean Sea for *Desmophyllum dianthus*, which was found at depths below 1400 m (Fig. 26.7). Previously, only one single specimen of *D. dianthus* had been reported after retrieval by trawl hauling at 1758 m in the Balearic Basin, although it is unclear if it was dead or alive (Cartes et al. 2009).

Table 26.5 Biomass of cold-water coral species retrieved in Agassiz trawls (AGT) in terms of total weight (kg) and estimated biomass (kg/km^2)

Species	AGT no.	Location	kg	kg/km^2
Madrepora oculata	6	BC-1200 axis	0.244	38.92
Lophelia pertusa	7	BC-900 axis	11.477	124.25
Desmophyllum dianthus	3	CCC-900 axis	0.003	0.46
Desmophyllum dianthus	6	BC-1200 axis	2.050	326.95
Desmophyllum dianthus	7	BC-900 axis	1.084	11.74

For location codes and reference depths see Table 26.2

Our video images show colonies of *D. dianthus* attached to a rock outcrop, evidencing that these are not dead colonies drifted by the currents. Similarly, Jantzen et al. (2013) and Försterra et al. (2017) in Chilean waters, as well as Fourt et al. (this volume), in the canyons of the Gulf of Lion, in the northwestern Mediterranean Sea, also observed colonies of *D. dianthus* in downward and sideward positions in deep water locations, similar to those observed in our study. By contrast, *M. oculata* and *L. pertusa* did not present polyp tissue or any other evidence that allow us to confirm that the specimens sampled with AGT were alive. Whereas more data would be required to corroborate the occurrence of living specimens of both corals, the good state of preservation of individuals, together with the fact that *L. pertusa* was retrieved as growing on a nylon wire (as a proxy of age), suggest that living deep-sea corals likely occur in the canyon axis, or at least inhabited this environment in very recent times. Our findings for *M. oculata* and *L. pertusa* colonies are of relevance, as they could point out to a possible extension of the currently known distribution range of the species in the western Mediterranean Sea, down to 1200 and 900 m depth, respectively (Fig. 26.7). In the investigated depths of the studied canyons, the retrieved fragments of colonies showed that *M. oculata* and *L. pertusa* did not appear associated to each other but with *D. dianthus*, which is another frequent contributor to CWC communities (Pérès and Picard 1964).

Beyond our study area, living CWCs in the Mediterranean Sea have been identified off Thassos Island in the Aegean Sea, the southern Adriatic, the Ionian Sea, the Sicily Channel, the Tyrrhenian Sea, the Ligurian Sea, the Gulf of Lion and the Strait of Gibraltar (Freiwald et al. 2009; Taviani

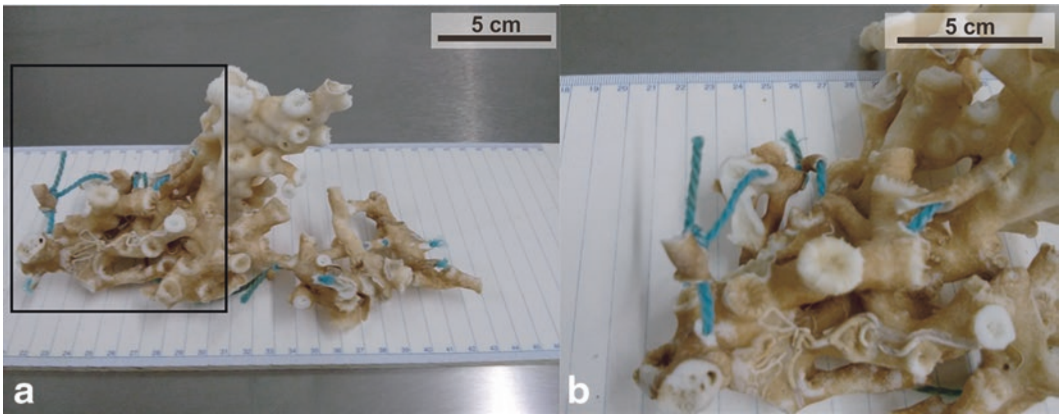


Fig. 26.6 (**a**) Fragments of a *Lophelia pertusa* colony growing on and surrounding nylon net cords retrieved from Agassiz trawl 7 (752–864 m depth) in the Blanes Canyon. (**b**) Detail of frame (approximate) in A (© GRC Geociències Marines, Universitat de Barcelona)

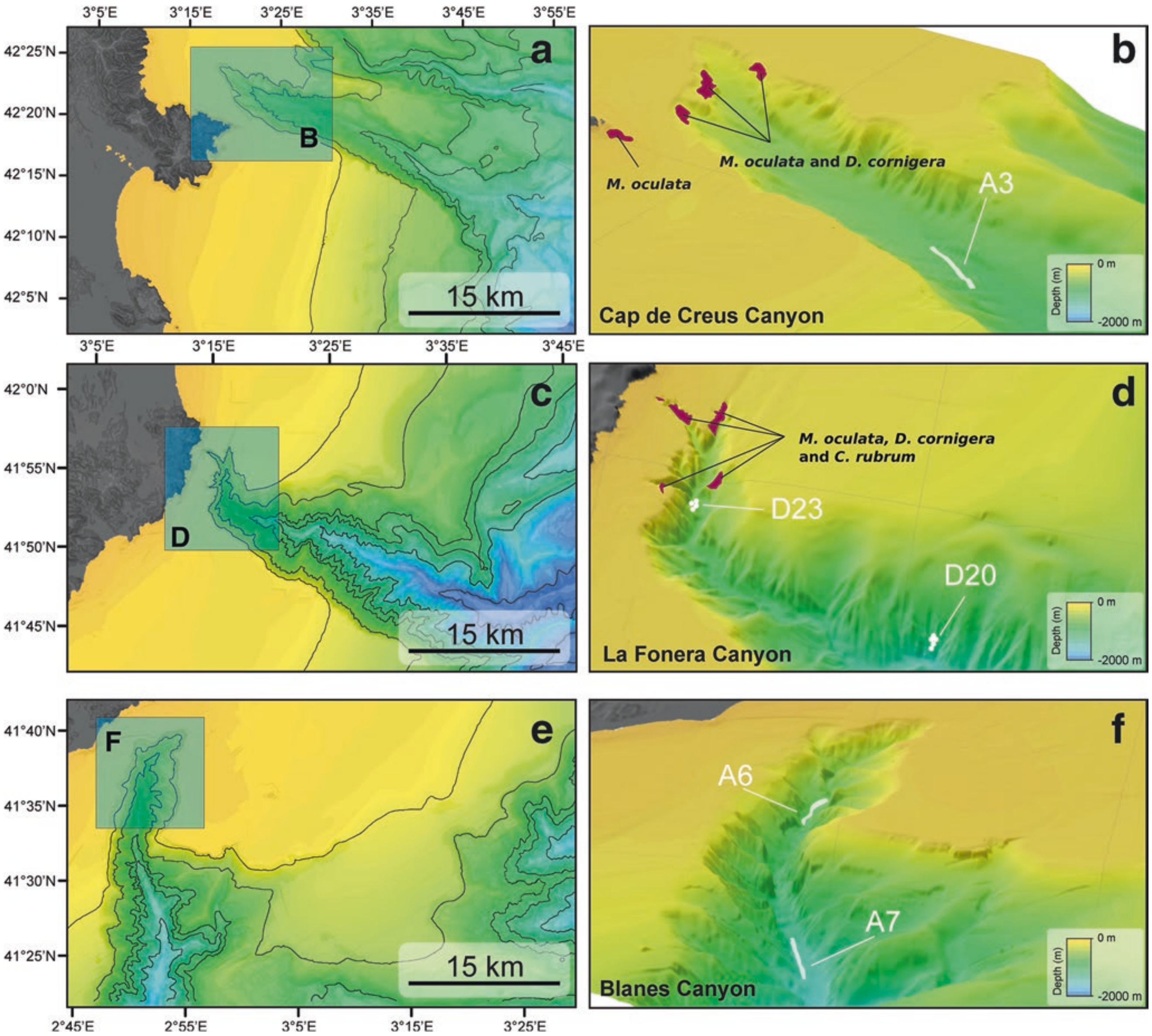


Fig. 26.7 Location of all CWCs species reported in the study area. (**a**) General bathymetry of Cap de Creus Canyon. (**b**) Zoom in of the head and upper course of Cap de Creus Canyon, and adjacent continental shelf, showing cold-water coral (CWC) occurrences. (**c**) General bathymetry of La Fonera Canyon. (**d**) Zoom in of the head and upper-middle course of La Fonera Canyon, and adjacent continental shelf, showing CWC occurrences. (**e**) General bathymetry of Blanes Canyon. (**f**) Zoom in of the head and upper-middle course of Blanes Canyon, and adjacent continental shelf, showing CWC occurrences. Magenta areas: *Madrepora oculata*, *Dendrophyllia cornigera* and *Corallium rubrum* occurrences reported by Rossi et al. (2008), Orejas et al. (2009), Lo Iacono et al. (2012), Gori et al. (2013), and Lastras et al. (2016). White areas: new locations of CWCs found in this study from ROV imaging. White lines: Agassiz trawling lines along which CWCs were sampled in this study. The new results obtained extend the range of CWC occurrences in the submarine canyons of the northwestern Mediterranean Sea and in the entire basin. (© GRC Geociències Marines, Universitat de Barcelona)

et al. 2017; Fanelli et al. 2017; Chimienti et al., this volume; D'Onghia, this volume). In these locations CWCs usually occur along the continental shelf edge, on sea knolls and seamounts, and within canyons. The deepest known occurrence of CWCs among all these locations is in Santa Maria di Leuca, where the framework-building species *M. oculata* and *L. pertusa*, commonly in association with solitary corals such as *D. dianthus*, have been detected at 1100 m (Tursi et al. 2004), a depth that is some hundreds of meters shallower than the deepest canyon reaches explored in our study.

The fauna associated to the CWC species here investigated belongs to different taxonomic groups, i.e. decapods (*Munida* sp.), holothurians (*Holothuria forskali*) and echinoderms (*Gracilechinus* sp.), with the most abundant specimens from classes Bivalvia and Polychaeta. A detailed study in Santa Maria di Leuca (Mastrototaro et al. 2010) identified more than 200 species living together with CWCs, where Bivalvia and Polychaeta, together with Crustacea and Echinodermata, were also among the most important groups contributing to local biodiversity. A rather small number of other studies in the Mediterranean have also considered CWCs' associated fauna, such as Tunesi et al. (2001), Schembri et al. (2007), Mastrototaro et al. (2010), Lastras et al. (2016), D'Onghia (this volume), and Rueda et al. (this volume).

Our data highlight the capability of CWCs to form aggregations and colonies at great depths under current environmental conditions in the northwestern Mediterranean Sea. In the three investigated submarine canyons, where we detected the presence of CWCs, a higher energy hydrodynamic regime occurs in comparison to open slopes at equivalent depths, especially during intense transport episodes driven by atmospheric forcing (Canals et al. 2006; Sanchez-Vidal et al. 2012; Durrieu de Madron et al. 2013). The funnelling of matter (and energy) from shallow to deep (Canals et al. 2004) along submarine canyons provides an above-threshold food flux for benthic resident species, in which flow velocity and food particle concentration look essential to the sustenance of the corals and associated species (Guinotte et al. 2006; Roberts et al. 2006, 2009; Cairns 2007; Davies et al. 2009; Purser et al. 2010; Puig and Gili, this volume). In parallel, the episodic high speed of near-bottom currents removes sediment that could eventually suffocate the organisms, thus easing coral growth. For instance, current speeds in the range of 20–85 cm s^{-1} are common during cascading events, with current peaks in excess of 1 m s^{-1} (Canals et al. 2006, 2009; Durrieu de Madron et al. 2013). CWC communities found at considerable depths in the three studied submarine canyons have been identified as vulnerable marine ecosystems (VME) by the General Fisheries Commission for the Mediterranean (2009). The North Catalan Sea, together with the adjacent Gulf of Lion, has also been classified as an *Ecologically or Biologically Significant Area* (EBSA) by the Regional Activity Center for Specially Protected Areas (Gabrie et al. 2012).

26.6 Conclusions

Our exploration of the deep-water reaches of three submarine canyons in the North Catalan margin expands current knowledge on CWC occurrence and distribution in the Mediterranean Sea. Our ROV video records on *Desmophyllum dianthus* demonstrates its presence at depths below 1400 m, thus representing the deepest confirmed record of living aggregations to date. Fragments of *Lophelia pertusa* and *Madrepora oculata* colonies were also collected with an AGT at 900 and 1200 m, although it was not possible to confirm if the sampled corals were alive. In any case, the growth of some of these colonies on nylon nets points to the existence of living colonies nearby and/or in very recent times. Our findings illustrate the relevance of CWC communities in the investigated canyon systems. Following previously published records of CWCs at generally shallower water depths, our study evidences how CWC occurrences can be extended deeper in submarine canyons of the northwestern Mediterranean Sea. Our results finally show the relevance of the North Catalan canyons in the frame of an improved knowledge of deep-sea benthic communities and particularly CWCs in the Mediterranean Sea. This added knowledge should be used to design future management and conservation strategies.

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References

Abelló P, Carbonell A, Torres P (2002) Biogeography of epibenthic crustaceans on the shelf and upper slope off the Iberian Peninsula Mediterranean coasts: implications for the establishment of natural management areas. Sci Mar 66:183–198

Aguzzi J, Company JB, Bahamon N, et al (2013) Seasonal bathymetric migrations of deep-sea fishes and decapod crustaceans in the NW Mediterranean Sea. Progr Oceanogr 118:210–221. https://doi.org/10.1016/j.pocean.2013.07.025

Álvarez-Pérez G, Busquets P, De Mol B, et al (2005) Deep-water coral occurrences in the strait of Gibraltar. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 207–221

Amblas D, Canals M, Urgeles R, et al (2006) Morphogenetic mesoscale analysis of the northeastern Iberian margin, NW Mediterranean Basin. Mar Geol 234:3–20. https://doi.org/10.1016/j.margeo.2006.09.009

Angeletti L, Mecho A, Doya C, et al (2015) First report of live deep-water cnidarian assemblages from the Malta Escarpment. Ital J Zool 82:1–7. https://doi.org/10.1080/11250003.2015.1026416

Borghini M, Bryden H, Schroeder K, et al (2014) The Mediterranean is becoming saltier. Ocean Sci 10:693–700. https://doi.org/10.5194/os-10-693-2014

Bouchet P, Taviani M (1992) The Mediterranean deep-sea fauna: pseudopopulations of Atlantic species? Deep-Sea Res Part 1 Oceanogr Res Pap 39:169–184. https://doi.org/10.1016/0198-0149(92)90103-Z

Bourcier M, Zibrowius H (1973) Les "boués rouges" deversées dans le canyon de la Cassidaigne (région de Marseille). Observations en soucoupe plongeante SP 350 (juin 1971) et résultats de dragages. Tethys 4:811–842

Cairns SD (1995) The marine fauna of New Zealand: Scleractinia (Cnidaria, Anthozoa) New Zealand Oceanogr. Inst Mem 103:210

Cairns SD (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. Bull Mar Sci 81:311–322

Cairns S, Stanley G (1982) Ahermatypic coral banks: living and fossil counterparts. Proceedings of the Fourth International Coral Reef Symposium, Manila (1981),1:611–618

Canals M, Casamor JL, Lastras G, et al (2004) The role of canyons in strata formation. Oceanography 17:80–91

Canals M, Puig P, Durrieu de Madron X, et al (2006) Flushing submarine canyons. Nature 444:354–357. https://doi.org/10.1038/nature05271

Canals M, Danovaro R, Heussner S, et al (2009) Cascades in Mediterranean submarine grand canyons. Oceanography 22:26–43. https://doi.org/10.5670/oceanog.2009.03

Canals M, Company JB, Martín D, et al (2013) Integrated study of Mediterranean deep canyons: novel results and future challenges. Progr Oceanogr 118:1–27. http://dx.doi.org/10.1016/j.pocean.2013.09.004

Carlier A, Le Guilloux E, Olu K, et al (2009) Trophic relationships in a deep Mediterranean cold-water coral bank (Santa Maria di Leuca, Ionian Sea). Mar Ecol Progr Ser 397:125–137. https://doi.org/10.3354/meps08361

Cartes JE, Sardà F (1989) Feeding ecology of the deep-water aristeid crustacean *Aristeus antennatus*. Mar Ecol Progr Ser 54:229–238. https://www.jstor.org/stable/24833757

Cartes JE, Sardà F, Company JB, et al (1993) Day-night migrations by deep-sea decapod crustaceans in experimental samplings in the Western Mediterranean Sea. J Exp Mar Biol 171:63–73. https://doi.org/10.1016/0022-0981(93)90140-J

Cartes JE, Company JB, Maynou F (1994) Deep-water decapod crustacean communities in the Northwestern Mediterranean: influence of submarine canyons and season. Mar Biol 120:221–229

Cartes JE, Maynou F, Fanelli E, et al (2009) The distribution of megabenthic, invertebrate epifauna in the Balearic Basin (western Mediterranean) between 400 and 2300 m: environmental gradients influencing assemblages composition and biomass trends. J Sea Res 61:244–257. http://hdl.handle.net/10261/15210

Company JB, Puig P, Sardà F, et al (2008) Climate influence on deep sea populations. PLoS One 3:e1431. https://doi.org/10.1371/journal.pone.0001431

Danovaro R, Company JB, Corinaldesi C, et al (2010) Deep-sea biodiversity in the Mediterranean Sea: the known, the unknown, and the unknowable. PLoS One 5:e11832. https://doi.org/10.1371/journalpone.0011832.

Davies AJ, Duineveld GCA, Lavaleye M, et al (2009) Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef complex. Limnol Oceanogr 54:620–629. https://doi.org/10.4319/lo.2009.54.2.0620

D'Onghia G, Politou CY, Bozzano A, et al (2004) Deep-water fish assemblages in the Mediterranean Sea. Sci Mar 68:87–99

D'Onghia G, Maiorano P, Sion L, et al (2010) Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:397–411. https://doi.org/10.1016/j.dsr2.2009.08.022

Dullo WC, Flögel S, Rüggeberg A (2008) Cold-water coral growth in relation to the hydrography of the Celtic and Nordic European continental margin. Mar Ecol Progr Ser 371:165–176. https://doi.org/10.3354/meps07623

Durrieu de Madron X, Houpert L, Puig P, et al (2013) Interaction of dense shelf water cascading and open-sea convection in the northwestern Mediterranean during winter 2012. Geophys Res Lett 40:1379–1385. https://doi.org/0094-8276/13/10.1002/grl.50331

Fabri MC, Pedel L, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207. http://dx.doi.org/10.1016/j.dsr2.2013.06.016

Fanelli E, Cartes JE, Papiol V, et al (2013) Environmental drivers of megafaunal assemblage composition and biomass distribution over mainland and insular slopes of the Balearic Basin (Western Mediterranean). Deep-Sea Res Part 1 Oceanogr Res Pap 78:79–94. https://doi.org/10.1016/j.dsr.2013.04.009

Fanelli E, Delbono I, Ivaldi R, et al (2017) Cold-water coral *Madrepora oculata* in the eastern Ligurian Sea (NW Mediterranean): historical and recent findings. Aquat Cons Mar Freshw Ecosyst 27:965–975. https://doi.org/10.1002/aqc.2751

Fiala-Medioni A, Madurell T, Romans P, et al (2012) ROV and submersible surveys on faunal assemblages in a deep-sea canyon (Rech Lacaze-Duthiers, Western Mediterranean Sea). Vie Milieu 62:173–190. http://hdl.handle.net/10261/91844

Font J, Salat J, Tintoré J (1988) Permanent features of the circulation in the Catalan Sea. Oceanol Acta 9:51–57

Försterra G, Beuck L, Häussermann V, et al (2005) Shallow-water *Desmophyllum dianthus* (Scleractinia) from Chile: characteristics of the biocoenoses, the bioeroding community, heterotrophic interactions and (paleo)-bathymetric implications. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 937–977

Försterra G, Häussermann V, Laudien J (2017) Animal forests in the Chilean fjords: discoveries, perspectives and threats in shallow and deep waters. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests. The ecology of benthic biodiversity hotspots. Springer, Cham, pp 277–314

Frederiksen R, Jensen A, Westerberg H (1992) The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing. Sarsia 77:157–171

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs. UNEP-WCMC, Cambridge, 84 p. http://www.unep-wcmc.org/resources/publications/UNEP_WCMC_bio_series/22.htm

Freiwald A, Beuck L, Rüggerberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:36–52. https://doi.org/10.5670/oceanog.2009.06

Gabrie C, Lagabrielle E, Crochelet E, et al (2012) The status of marine protected areas in the Mediterranean Sea. MedPAN & RAC/SPA. MedPAN Collection, 256 p

Galil BS (2004) The limit of the sea: the bathyal fauna of the Levantine Sea. Sci Mar 68:63–72. https://doi.org/10.3989/scimar.2004.68s363

General Fisheries Commission for the Mediterranean (GFCM, S.A.C.) (2009) Criteria for the identification of sensitive habitats of relevance for the management of priority species, General Fisheries Commission for the Mediterranean- Scientific Advisory Committee –Sub –Committee on Marine Environment and Ecosystems (SCMEE). http://www.gfcm.org

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060. https://doi.org/10.5194/bg-10-2049-2013

Guinotte JM, Orr J, Cairns D, et al (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? Front Ecol Environ 3:141–146

Hebbeln D, Wienberg C, Beuck L, et al (2009) Report and preliminary results of RV POSEIDON Cruise POS 385 "Cold-water corals of the Alboran Sea (western Mediterranean Sea)", Faro–Toulon, May

29–June 16, 2009. Ber Fachbereich Geowissenschaften Universität Bremen, 273 p

Heindel K, Titschack J, Dorschel B, et al (2010) The sediment composition and predictive mapping of facies on the Propeller Mound—a cold-water coral mound (Porcupine Seabight, NE Atlantic). Cont Shelf Res 30:1814–1829. https://doi.org/10.1016/j.csr.2010.08.007

Henry LA, Roberts JM (2007) Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. Deep-Sea Res Part 1 Oceanogr Res Pap 54:654–672. https://doi.org/10.1016/j.dsr.2007.01.005

Holme NA, McIntyre AD (1971) Methods for the study of marine benthos. IBP Handbook, Blackwell Oxford, 334 p

Husebø Å, Nøttestad L, Fossä JH, et al (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471:91–99

Jantzen C, Häussermann V, Försterra G, et al (2013) Occurrence of a cold-water coral along natural pH gradients (Patagonia, Chile). Mar Biol 160:2597–2607. https://doi.org/10.1007/s00227-013-2254-0

Kiriakoulakis K, Freiwald A, Fischer F, et al (2007) Organic matter quality and supply to deep-water coral/mound systems of the NW European Continental Margin. Int J Earth Sci 96:159–170. https://doi.org/10.1007/s00531-006-0078-6

Lartaud F, Pareige S, Rafaelis M, et al (2013) A new approach for assessing cold-water coral growth in situ using fluorescent calcein staining. Aquat Living Res 26:187–196. https://doi.org/10.1051/alr/2012029

Lastras G, Canals M, Amblas D, et al (2011) Understanding sediment dynamics of two large submarine valleys from seafloor data: Blanes and La Fonera canyons, northwestern Mediterranean Sea. Mar Geol 280:20–39. https://doi.org/10.1016/j.margeo.2010.11.005

Lastras G, Canals M, Ballesteros E, et al (2016) Cold-water corals and anthropogenic impacts in La Fonera submarine canyon head, Northwestern Mediterranean Sea. PLoS One 11:e0155729. https://doi.org/10.1371/journalpone.0155729

Lo Iacono C, Orejas C, Gori A, et al (2012) Habitats of the cap de Creus continental shelf and cap de Creus canyon, North-Western Mediterranean. In: Harris PT, Baker EK (eds) Seafloor geomorphology as benthic habitat: GeoHab atlas of seafloor geomorphic features and benthic habitats. Elsevier, London, pp 457–470

Martin J, Palanques A, Puig P (2006) Composition and variability of downward particulate matter fluxes in the Palamós submarine canyon (NW Mediterranean). J Mar Syst 60:75–97. https://doi.org/10.1016/j.jmarsys.2005.09.010

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430. https://doi.org/10.1016/j.dsr2.2009.08.021

Mecho A, Aguzzi J, Company JB, et al (2014a) First in situ observation of the deep-sea carnivorous ascidian *Dicopia antirrhinum* Monniot C. 1972 in the western Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 83:51–56. http://dx.doi.org/10.1016/j.dsr.2013.09.007

Mecho A, Billett DSM, Ramirez-Llodra E, et al (2014b) First records, rediscovery and compilation of deep-sea echinoderms in the middle and lower continental slope in the Mediterranean Sea. Sci Mar 78:281–302. https://doi.org/10.3989/scimar.03983.30C

Millot C (1999) Circulation in the Western Mediterranean Sea. J Mar Syst 20:423–442. https://doi.org/10.1016/S0924-7963(98)00078-5

Orejas C, Gori A, Lo Iacono C (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51. https://doi.org/10.3354/meps08314

Palanques A, García-Ladona E, Gomis D, et al (2005) General patterns of circulation, sediment fluxes and ecology of the Palamós (La Fonera) submarine canyon, northwestern Mediterranean. Progr Oceanogr 66:89–119. https://doi.org/10.1016/j.pocean.2004.07.016

Palanques A, Durrieu de Madron X, Puig P, et al (2006) Suspended sediment fluxes and transport processes in the Gulf of Lions submarine canyons. The role of storms and dense water cascading. Mar Geol 234:43–61. https://doi.org/10.1016/j.margeo.2006.09.002

Papiol V, Cartes JE, Fanelli E, et al (2012) Influence of environmental variables on the spatio-temporal dynamics of bentho-pelagic assemblages in the middle slope of the Balearic Basin (NW Mediterranean). Deep-Sea Res Part 1 Oceanogr Res Pap 61:84–99. https://doi.org/10.1016/j.dsr.2011.11.008

Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la Mer Méditerranée. Recueil des Travaux de la Station Marine d'Endoume, Marseille, 137 p

Purser A, Larsson AI, Thomsen L, et al (2010) The influence of flow velocity and food concentration on *Lophelia pertusa* (Scleractinia) zooplankton capture rates. J Exp Mar Biol 395:55–62.

Purser A, Orejas C, Gori A, et al (2013) Local variation in the distribution of benthic megafauna species associated with cold-water coral reefs on the Norwegian margin. Cont Shelf Res 54:37–51

Reveillaud J, Freiwald A, Van Rooij D, et al (2008) The distribution of scleractinian corals in the Bay of Biscay, NE Atlantic. Facies 54:317–331. https://doi.org/10.1007/s10347-008-0138-4

Reyss D (1970) Bionomie benthique de deux canyons sous-marins de la mer Catalane: le Rech du Cap et le Rech Lacaze-Duthiers. Université de Paris VI

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547. https://doi.org/10.1126/science.1119861

Roberts JM, Wheeler AJ, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334. https://doi.org/10.1017/CBO9780511581588

Rogers AD (2013) The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. Int Rev Hydrobiol 84:315–406. https://doi.org/10.1002/iroh.199900032

Rossi S, Tsounis G, Orejas C, et al (2008) Survey of deep-dwelling red coral (*Corallium rubrum*) populations at Cap de Creus (NW Mediterranean). Mar Biol 154:533–545. https://doi.org/10.1007/s00227-008-0947-6

Ryland JS (2000) European marine biology: past, present and future. Biol Mar Mediterr 7:1–27

Sanchez-Vidal A, Canals M, Calafat A, et al (2012) Impacts on the deep-sea ecosystem by a severe coastal storm. PLoS One 7:e30395. https://doi.org/10.1371/journalpone.0030395.

Sardà F, Cartes JE (1993) Distribution, abundance and selected biological aspects of *Aristeus Antennatus* in deep-water habitats in NW Mediterranean. Bios 1:59–73

Schembri P, Dimech M, Camilleri M, et al (2007) Living deep-water *Lophelia* and *Madrepora* corals in Maltese waters (Strait of Sicily, Mediterranean Sea). Cah Biol Mar 48:77

Sion L, Bozzano A, D'Onghia G, et al (2004) Chondrichthyes species in deep waters of the Mediterranean Sea. Sci Mar 68:153–162

Squires DF (1965) Neoplasia in a coral? Science 148:503–505. https://doi.org/10.1126/science.148.3669.503

Taviani M, Remia A, Corselli C, et al (2005) First geo-marine survey of living cold-water Lophelia reefs in the Ionian Sea (Mediterranean basin). Facies 50:409–417. https://doi.org/10.1007/s10347-004-0039-0

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78. https://doi.org/10.1016/j.dsr2.2015.12.008

Tecchio S, Ramirez-Llodra E, Aguzzi J, et al (2013) Seasonal fluctuations of deep megabenthos: finding evidence of standing stock accumulation in a flux-rich continental slope. Progr Oceanogr 118:188–198. https://doi.org/10.1016/j.pocean.2013.07.015

Thiem Ø, Ravagnan E, Fossä JH, et al (2006) Food supply mechanisms for cold-water corals along a continental shelf edge. J Mar Syst 60:207–219. https://doi.org/10.1016/j.jmarsys.2005.12.004

Tubau X, Canals M, Lastras G, et al (2015) Marine litter on the floor of deep submarine canyons of the Northwestern Mediterranean Sea: the role of hydrodynamic processes. Progr Oceanogr 134:379–403. https://doi.org/10.1016/j.pocean.2015.03.013

Tunesi L, Diviacco G, Mo G (2001) Observations by submersible on the biocoenosis of the deep-sea corals off Portofino promontory (Northwestern Mediterranean Sea). In: Proceedings of the first international symposium on deep-sea corals, Ecology Action Centre and Nova Scotia Museum, Halifax, Nova Scotia, pp 76–87

Tursi A, Mastrototaro F, Matarrese A, et al (2004) Biodiversity of the white coral reefs in the Ionian Sea (Central Mediterranean). Chem Ecol 20:107–116. https://doi.org/10.1080/02757540310001629170

Ulses C, Estournel C, Puig P, et al (2008) Dense shelf water cascading in the northwestern Mediterranean during the cold winter 2005. Quantification of the export through the Gulf of Lion and the Catalan margin. Geophys Res Lett 35:L07610. https://doi.org/10.1029/2008GL033257

White M, Mohn C, Stigter H, et al (2005) Deep-water coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall trough, NE Atlantic. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 503–514

Zibrowius H (1980) Les Scleractiniaires de la Mediterranee et de l'Atlantique nord-oriental. Mem Inst Océanogr 11:1–227

Zibrowius H (2003) The "White Coral Community", canyon and seamount faunas of the deep Mediterranean Sea. Project Report for the preparation of a Strategic Action Plan for the Conservation of Biological Diversity in the Mediterranean Region (SAP BIO), 39 p

Cross References

Addamo AM (this volume) *Desmophyllum dianthus* genetics and more

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

D'Onghia G (this volume) Cold-water corals as shelter, feeding and life-history critical habitats for fish species: ecological interactions and fishing impact

Fourt M, Goujard A, Chevaldonné P (this volume) Working with visual methods, comparison among the French deep-sea canyons

Puig P, Gili JM (this volume) Submarine canyons in the Mediterranean: a shelter for cold-water corals

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Drop Chapter Submarine Canyons in the Mediterranean: A Shelter for Cold-Water Corals

27

Pere Puig and Josep-Maria Gili

Abstract

In the Mediterranean Sea, many of the locations where cold-water coral communities have been reported and documented tend to be associated to submarine canyon environments. This contribution provides a summary of the Mediterranean canyons where, up to date, cold-water corals develop, describing the most common species, their water depth distribution and degree of preservation, and the prevalent hydrodynamic forcing at specific sites. Considering that the inventory, characterisation and detailed mapping of Mediterranean submarine canyons is far from complete, this compilation urges to focus new research and exploration efforts on these morphological features, as they appear to act as natural shelters of cold-water coral communities at present times.

Keywords

Shelf-slope exchange · Dense shelf water cascades · Internal waves · Canyon head · Rocky outcrop

The true extent of the cold-water coral (CWC) communities in the Mediterranean Sea is still poorly known, and the relatively few verified records of live colonies exhibit a scattered distribution pattern rather than a belt of occurrences, as is the case in the Northeast Atlantic (Zibrowius 1980; Freiwald et al. 2009; see Chimienti et al., this volume). Indeed, a common characteristic of Mediterranean CWC is that several of the reported sites are associated to submarine canyon environments, and therefore, their occurrence in some Mediterranean regions appears to be governed by the presence of such seafloor morphologies.

Submarine canyons are common geomorphic features that occur worldwide on passive and active continental margins, as single features or arranged in hierarchic tributary systems (Shepard and Dill 1966; Harris and Whiteway 2011; Harris et al. 2014). They evolve over geological timescales acting as preferential conduits of sediment from coastal and shelf environments to adjacent deep-sea basins, involving different sediment transport processes and triggering mechanisms operating at various time-scales (Shepard 1981; Piper and Normark 2009; Puig et al. 2014).

Submarine canyons, by dissecting continental margins, create a bathymetric steering of oceanic circulation and enhance shelf-slope exchange processes. The specific local circulation around canyon heads promote upwelling of cold, nutrient-rich waters to the sea surface that enhance surface productivity (Allen and Durrieu de Madron 2009), internal waves tend to be focused along canyon axis creating localised mixing and particle resuspension and advection (Shepard et al. 1979; Gardner 1989), and dense waters generated over shelves mainly cascade trough submarine canyons, delivering large amount of particulate and dissolved organic and inorganic matter from shallow to deep-sea environments (Canals et al. 2006).

In general, due to their specific hydrodynamics, submarine canyons exhibit larger particulate organic matter fluxes than the adjacent open slope areas and, therefore, act as hotspots of benthic biodiversity (Vetter 1994; Vetter and Dayton 1998; Bosley et al. 2004; De Leo et al. 2010). Additionally, shelf-incising canyons are characterised by steep terrains, containing vertical to overhanging bedrock exposures, which create important habitats for benthic ecosystems where biologically diverse communities, including CWC, may settle and develop (e.g. Orejas et al. 2009; De Mol et al. 2010; Huvenne et al. 2011; Gori et al. 2013; see Rueda et al., this volume). Nonetheless, submarine canyons also provide refuge to a number of species of commercial interest (Company et al. 2012) and, as they tend to be targets of intense fisheries, many of these benthic habitats are severely damaged or under threat (see Otero and Marin, this volume).

The Mediterranean Sea is characterised by some remarkably young submarine canyons (Pliocene-Quaternary),

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although several of them are much older and inherited from the lowering of sea level during the Messinian salinity crisis ca. 5.5 Ma (million years ago). In comparison to their oceanic counterparts, canyons in the Mediterranean Sea have been described as more dendritic and closely spaced, steeper, shorter and with a smaller depth range (Harris and Whiteway 2011). In particular, the northwestern Mediterranean (i.e., the Ligurian, Gulf of Lions and Catalan margins) is characterised by a dense network of submarine canyons (Canals et al. 2004; Migeon et al. 2012). It was in this region, specifically in the Cap de Creus and Lacaze-Duthiers submarine canyons, where the first occurrences of living CWC communities in the Mediterranean were reported (Pérès and Picard 1964; Reyss 1964a, b). More recent surveys in these two canyons using remotely operated vehicle (ROV) and manned submersible have provided more accurate and quantitative investigations of CWC distribution (Orejas et al. 2009; Watremez 2012; Gori et al. 2013; Fabri et al. 2014; Fourt et al. this volume). *Madrepora oculata* is the most abundant CWC in both canyons, while *Lophelia pertusa* and *Dendrophyllia cornigera* mostly occurs as isolated colonies or in small patches. An important exception was detected in a vertical cliff in Lacaze-Duthiers Canyon where a large *L. pertusa* framework has been documented (Gori et al. 2013; Fourt et al., this volume). In both canyons, coral populations are distributed in a depth range of 180–550 m, although deeper areas have not been explored yet, and are dominated by medium and large colonies. The frequent presence of small-sized colonies also indicates active recruitment (Gori et al. 2013). These submarine canyons are affected by the periodical arrival of dense shelf water cascades (Palanques et al. 2006; Canals et al. 2006; Puig et al. 2008), which contribute to create a favorable environment (i.e. exposed bedrocks and large organic particle fluxes) within the canyon heads for CWC settling and growing (Fig. 27.1).

Slightly towards the South, in the neighboring La Fonera Canyon (Catalan margin), an extensive ROV survey has recently documented the presence of CWC communities on different canyon-head tributaries and environments (Lastras et al. 2016; Lastras et al., this volume). In general, larger and healthier *M. oculata* colonies in this canyon are located in the rougher rocky areas of the canyon walls with higher slope gradients. They span over water depths of 130–370 m, being most frequent between 180 and 300 m depth. *D. cornigera* is found in a slightly similar water depth range, but preferentially settles on moderately sloping seafloor with rocky outcrops and also in areas partially covered with sediments. In contrast with the neighboring Cap de Creus and Lacaze-Duthiers canyons, *L. pertusa* appears to be absent in the explored areas of La Fonera Canyon. However, Agassiz trawl samples in the neighboring Blanes Canyon collected presumably living *M. oculata* and *L. pertusa* colonies at 1200 and 900 m depth, respectively (see Aymà et al., this volume). This fact may suggest the presence of these two species in the Catalan margin submarine canyons at deeper locations than those previously explored with ROV dives.

At the eastern sector of the Gulf of Lions canyoned margin, large colonies of *M. oculata* have been also reported in Cassidaigne Canyon (Bourcier and Zibrowius 1973; Watremez 2012; Fabri et al. 2014, 2016) and small patches of *M. oculata* have been recently reported in Bourcart (also hosting *D. cornigera*), Sicié and Var submarine canyons (Fabri et al. 2014), being all of those encounters at depths ranging from 200 to 350 m. A comprehensive list of submarine canyon locations in this Mediterranean region hosting CWC communities is provided by Fourt et al., this volume. Further East, in the Ligurian Sea, living *M. oculata* was also reported by Tunesi et al. (2001) at a 210 m water depth cliff off Portofino promontory, presumable in a canyon head region of a tributary of Levante Canyon (see Figure 2 in Migeon et al. 2012).

The southwestern Adriatic Sea is another Mediterranean region where dense shelf cascades occur (Zoccolotti and Salusti 1987; Trincardi et al. 2007). There, the Bari Canyon channelises most of the dense water flows (Turchetto et al. 2007) and it also harbors live CWC communities (Freiwald et al. 2009; Angeletti et al. 2014; Angeletti et al., this volume). Colonies of *L. pertusa, M. oculata* and *D. cornigera* (few isolated) have been reported in this canyon at slightly deeper locations (300–640 m water depth) than those in the northwestern Mediterranean canyon head regions. Further South along the western Adriatic margin, in a canyoned region off Otranto and Tricase, living specimens of *L. pertusa* and *M. oculata* where retrieved from blocks and thin hardgrounds at the canyon's base (720–790 m water depth) using grab sampling (Angeletti et al. 2014). These authors pointed out that these new findings suggest an almost uninterrupted, albeit patchy, belt of CWC sites all along the south-western Adriatic margin from Bari to Otranto, connecting the Adriatic populations to the well-known Ionian Santa Maria di Leuca CWC province (Freiwald et al. 2009), following the outflow of Adriatic Deep Water.

In the southeastern side of the Adriatic, Angeletti et al. (2014) also reported two CWC sites located in submarine canyons indenting the Montenegrin slope at depths between 420 and 490 m (see also Angeletti et al., this volume). ROV surveys revealed that rocky outcrops in this canyoned region are used as substrate for the settlement of large colonies (>1 m in height) of *M. oculata*, in addition to small colonies of *L. pertusa* and clusters of *D. cornigera*.

A new Mediterranean CWC province has been recently identified south of Sardinia Island after ROV dives in Nora Canyon (Taviani et al. 2016). This canyon harbor dense coral colonies of *M. oculata* that have been observed between 380 and 460 m depth, but also contains occasional presence of *L. pertusa* and *D. cornigera.* Large arborescent bushes of *M. oculata* growing of dead coral frames surrounded by muddy

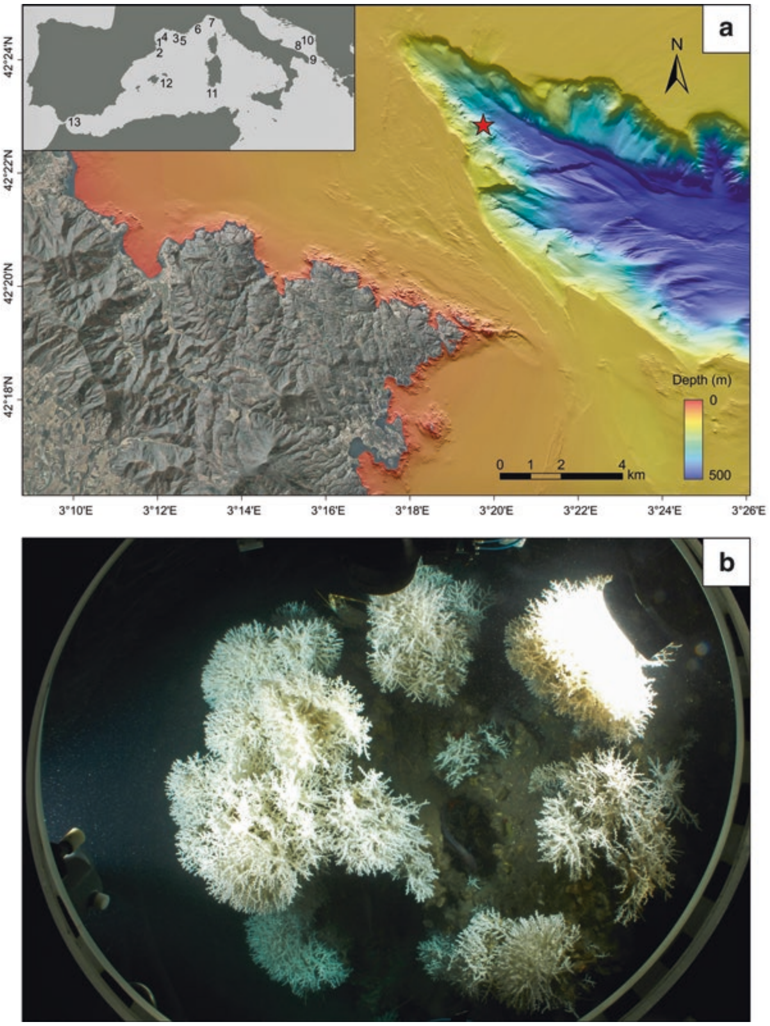

Fig. 27.1 (**a**) High-resolution bathymetric map (5 m grid) of the Cap de Creus continental shelf and submarine canyon head showing the rough terrain on its upper reaches where CWC communities develop. (**b**) Photography of *Madrepora oculata* colonies on the southern flank of the canyon at 250 m water depth obtained during a dive of the submersible JAGO (copyright: IFM-GEOMAR/ICM-CSIC). See location (red star) in (**a**). The inset map of the western Mediterranean in (**a**) also shows the locations of the submarine canyons mentioned in the text (ordered as they have been introduced): 1: Cap de Creus and Lacaze Duthiers; 2: La Fonera and Blanes; 3: Cassidaigne; 4: Bourcart; 5: Sicié; 6: Var; 7: Levante (off Portofino); 8: Bari; 9: canyons off Otranto and Tricase; 10: Montenegrin canyons; 11: Nora; 12: Minorca and canyons off Formentor; 13: La Linea and Guadiaro

sediments with abundant coral rubble are commonly found in this canyon environment.

The ROV dives conducted by *Oceana* in Minorca Canyon (Balearic Islands), also documented the presence of *D. cornigera* on several locations along the explored canyon head region (Marin and Aguilar 2012). More recent ROV surveys in the Balearic margin by Grinyó et al. (2018) confirmed the presence of numerous colonies of *D. cornigera* in Minorca Canyon as well in the upper reaches of the submarine canyons developed on the steep slope off Formentor Cape (Majorca Island), which were mainly found between 120 and 200 m water depth. ROV dives off Formentor Cape also found sparse colonies of *M. oculata* at 300 m water depth (Grinyó et al. 2018).

In the western Alborán Sea, close to the Strait of Gibraltar, Vázquez et al. (2015) reported the presence of colonies of *M.oculata* and *D. cornigera* in La Linea and Guadiaro submarine canyons. In this Mediterranean region, the hydrodynamics within the canyon is mostly dominated by semidiurnal internal tides (García Lafuente et al. 1999; Puig et al. 2004), which also seem to create favorable conditions for CWC communities' development.

So far, more than 800 examples of large canyon systems have been counted by Harris et al. (2014) for the Mediterranean Sea using Shuttle Radar Topography Mapping (SRTM30_PLUS) 30-arc second database. The inventory of Mediterranean submarine canyons is far from complete as it largely depends on the resolution of the available detailed bathymetry. In recent years, national and international programs have funded acquisitions of new higher-resolution morphological data allowing canyon systems never observed before to be identified (see examples in Würtz 2012; CIESM 2015). Given that several of the reported CWC sites in the Mediterranean Sea have been documented in steep and rough submarine canyon environments, it would be reasonable to focus the new research efforts on these morphological features once properly mapped, as they appear to act as natural refuges of Mediterranean CWC at present times. The distribution (density and aggregation of colonies) and demography of coral population could be a good indicator of the degradation or preservation of CWC communities in the canyons, parameters that should be used to propose appropriate measures for the protection and management of submarine canyons areas.

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References

Allen SE, Durrieu de Madron X (2009) A review of the role of submarine canyons in deep-ocean exchange with the shelf. Ocean Sci 5:607–620

Angeletti L, Taviani M, Canese S, et al (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Mediterr Mar Sci 15:263–273

Bosley KL, Lavelle JW, Brodeur RD, et al (2004) Biological and physical processes in and around Astoria submarine Canyon, Oregon, USA. J Mar Syst 50:21–37

Bourcier M, Zibrowius H (1973) Les "boues rouges" déversées dans le canyon de la Cassidaigne (région de Mareseille). Observations en soucoupe plongeante SP 350 (juin 1971) et résultats de dragages. Tethys 4:811–842

Canals M, Casamor JL, Lastras G, et al (2004) The role of canyons on strata formation. Oceanography 17:80–91

Canals M, Puig P, Durrieu de Madron X, et al (2006) Flushing submarine canyons. Nature 444:354–357

CIESM (2015) In: Briand F (ed) Submarine canyons dynamics in the Mediterranean and tributary seas – an integrated geological, oceanographic and biological perspective, CIESM Workshop Monograph n° 47. CIESM Publisher, Monaco

Company JB, Ramirez-Llodra E, Sardà F, et al (2012) Submarine canyons in the Catalan Sea (NW Mediterranean): megafaunal biodiversity patterns and anthropogenic threats. In: Würtz M (ed) Mediterranean submarine canyons: ecology and governance. IUCN, pp 133–144

De Leo FC, Smith CR, Rowden AA, et al (2010) Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. Proc R Soc B Biol Sci 277:2783–2792

De Mol L, Van Rooij D, Pirlet H, et al (2010) Cold-water coral habitats in the Penmarc'h and Guilvinec Canyons (Bay of Biscay): deep-water versus shallow-water settings. Mar Geol 282:40–52

Fabri MC, Pedel L, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207

Fabri MC, Bargain A, Pairaud I, et al (2016) Cold-water coral ecosystems in Cassidaigne Canyon: an assessment of their environmental living conditions. Deep-Sea Res Part 2 Top Stud Oceanogr. https://doi.org/10.1016/j.dsr2.2016.06.006

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

García Lafuente J, Sarhan T, Vargas M, et al (1999) Tidal motions and tidally induced fluxes through La Linea submarine canyon, western Alboran Sea. J Geophys Res 104:3109–3119

Gardner WD (1989) Periodic resuspension in Baltimore canyon focusing of internal waves. J Geophys Res 94:18185–18194

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Grinyó J, Gori A, Greenacre M, et al (2018) Megabenthic assemblages on the Mediterranean continental shelf edge and upper slope (Menorca Channel, Western Mediterranean Sea). Progr Oceanogr 162:40–51

Harris PT, Whiteway T (2011) Global distribution of large submarine canyons: geomorphic differences between active and passive continental margins. Mar Geol 285:69–86

Harris PT, Macmillan-Lawler M, Rupp J, et al (2014) Geomorphology of the oceans. Mar Geol 352:4–24

Huvenne VAI, Tyler PA, Masson DG, et al (2011) A picture on the wall: innovative mapping reveals cold-water coral refuge in submarine canyon. PLoS One 6:e28755

Lastras G, Canals M, Ballesteros E, et al (2016) Cold-water corals and anthropogenic impacts in La Fonera submarine canyon head, Northwestern Mediterranean Sea. PLoS One 11:e0155729

Marin P, Aguilar R (2012) Mediterranean submarine canyons 2012: pending protection. In: Würtz M (ed) Mediterranean submarine canyons: ecology and governance. IUCN, pp 191–205

Migeon S, Mascle J, Coste M, et al (2012) Mediterranean submarine canyons and channels: morphological and geological backgrounds. In: Würtz M (ed) Mediterranean submarine canyons: ecology and governance. IUCN, pp 27–39

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51

Palanques A, Durrieu de Madron X, Puig P, et al (2006) Suspended sediment fluxes and transport processes in the Gulf of Lions submarine canyons. The role of storms and dense water cascading. Mar Geol 234:43–61

Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la mer Mediterranée, vol 31. Extrait du Recueil des travaux de la Station Marine d'Endoume, pp 5–137

Piper DJW, Normark WR (2009) Processes that initiate turbidity currents and their influence on turbidites: a marine geology perspective. J Sediment Res 79:347–362

Puig P, Palanques A, Guillén J, et al (2004) Role of internal waves in the generation of nepheloid layers on the northwestern Alboran slope: implications for continental margin shaping. J Geophys Res 109:C09011

Puig P, Palanques A, Orange DL, et al (2008) Dense shelf water cascades and sedimentary furrow formation in the Cap de Creus Canyon, northwestern Mediterranean Sea. Cont Shelf Res 28:2017–2030

Puig P, Palanques A, Martín J (2014) Contemporary sediment-transport processes in submarine canyons. Annu Rev Mar Sci 6:53–77

Reyss D (1964a) Contribution à l'étude du rech Lacaze-Duthiers, vallée sous-marine des côtes du Roussillon. Vie Milieu 15:1–146

Reyss D (1964b) Observations faites en soucoupe plongeante dans deux vallées sous-marines de la mer Catalane: le rech du Cap et le rech Lacaze-Duthiers. Bull Inst Océanogr 63:1–8

Shepard FP (1981) Submarine canyons: multiple causes and long-time persistence. AAPG Bull 65:1062–1077

Shepard FP, Dill RF (1966) Submarine canyons and other sea valleys. Rand McNally & Company, Skokie, Chicago, 381 pp

Shepard FP, Marshall NF, McLoughlin PA, et al (1979) Currents in submarine canyons and other seavalleys, Studies in Geology No. 8. The American Association of Petroleum Geologists, Tulsa, 2 pp

Taviani M, Angeletti L, Canese S, et al (2016) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr. https://doi.org/10.1016/j.dsr2.2015.12.008

Trincardi F, Foglini F, Verdicchio G, et al (2007) The impact of cascading currents on the Bari Canyon System, SW-Adriatic Margin (Central Mediterranean). Mar Geol 246:208–230

Tunesi L, Diviacco G, Mo G (2001) Observations by submersible on the biocoenosis of the deep-sea corals off Portofino promontory (Northwestern Mediterranean Sea) In: Willison JHM, Hall J, Gass S, et al (eds) Proceedings of the first international symposium on deep-sea corals. Halifax, pp 76–87

Turchetto M, Boldrin A, Langone L, et al (2007) Particle transport in the Bari canyon (southern Adriatic Sea). Mar Geol 246:231–247

Vázquez JT, Ercilla G, Alonso B, et al (2015) Submarine canyons and related features in the Alboran Sea: continental margins and major isolated reliefs. In: Briand F (ed) Submarine canyons dynamics in the Mediterranean and tributary seas – an integrated geological, oceanographic and biological perspective, CIESM Workshop Monograph n° 47. CIESM Publisher, Monaco, pp 183–196

Vetter EW (1994) Hotspots of benthic production. Nature 372:47

Vetter EW, Dayton PK (1998) Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. Deep-Sea Res Part 2 Top Stud Oceanogr 45:25–54

Watremez P (2012) Canyon heads in the French Mediterranean overview of results from the MEDSEACAN and CORSEACAN campaings (2008–2010). In: Würtz M (ed) Mediterranean submarine canyons: ecology and governance. IUCN, pp 105–112

Würtz M (ed) (2012) Mediterranean submarine canyons: ecology and governance. IUCN, Gland, 192 pp

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mem l'Inst Oceanograph, Monaco 11:1–227

Zoccolotti L, Salusti E (1987) Observations of a vein of very dense marine water in the southern Adriatic Sea. Cont Shelf Res 7:535–551

Cross References

Angeletti L, Bargain A, Campiani E, et al (this volume) Cold-water coral habitat mapping in the Mediterranean Sea: methodologies and perspectives

Aymà A, Aguzzi J, Canals M, et al (this volume) Occurrence of living cold-water corals at large depths within submarine canyons of the northwestern Mediterranean Sea

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Fourt M, Goujard A, Chevaldonné P (this volume) Working with visual methods, comparison among the French deep-sea canyons

Lastras G, Sanchez-Vidal A, Canals M (this volume) A cold-water coral habitat in La Fonera submarine canyon, northwestern Mediterranean Sea

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Drop Chapter A Cold-Water Coral Habitat in La Fonera Submarine Canyon, Northwestern Mediterranean Sea

28

Galderic Lastras, Anna Sanchez-Vidal, and Miquel Canals

Abstract

Based on remotely operated vehicle video imaging, we describe a cold-water coral habitat in La Fonera canyon head (northwestern Mediterranean Sea) and the human impacts which threat this habitat. The dominant cold-water coral species is *Madrepora oculata* along with *Dendrophyllia cornigera*. The first occur on highly sloping rocky outcrops most frequently between 180 and 300 m water depth, being the largest colonies those protected by topographic overhangs. Predictive modelling accounting for terrain morphology and positive observations indicates that cold-water coral habitat extent should span over many areas of the canyon head, but *M. oculata* is mostly absent in the canyon branches incised closer to the coastline. This could be a consequence of an excess of sediment arrival during eastern storms. Daily trawling activity also results in enhanced sediment fluxes, which could account for some *M. oculata* colonies partially covered by fine mud in the eastern wall of the canyon. Recent physical damage is also observed at specific locations.

Keywords

Cold-water coral · *Madrepora oculata* · *Dendrophyllia cornigera* · Submarine canyon · Remotely operated vehicle · Anthropogenic impact

Cold-water corals (CWCs) have been observed in different canyons of the northwestern Mediterranean Sea, mainly by means of remotely operated vehicles (ROV) (see Puig and Gili, this volume). *Madrepora oculata*, *Lophelia pertusa* and *Dendrophyllia cornigera* have been reported at the head and upper flanks of Cap de Creus canyon (Orejas et al. 2009; Puig and Gili, this volume) at depths ranging between 200 and 300 m, and at deeper locations in the Lacaze-Duthiers canyon (250–530 m) and the Cassidaigne canyon (200–1000 m) (Gori et al. 2013; Fabri et al. 2014; Fourt et al., this volume). Recently, Lastras et al. (2016) revealed the extensive presence of CWCs in La Fonera canyon (Fig. 28.1), located immediately south of Lacaze-Duthiers and Cap de Creus canyons.

La Fonera canyon cuts through the North Catalan margin for 110 km from its head at 60–130 m depth down to 2550 m water depth. The head of the canyon incises 28 km into the shelf following a WNW-ESE trending course, with a N-S oriented shallowest part (Lastras et al. 2011). Pervasive networks of gullies carve its southern highly sloping wall (>25°), whereas daily trawling activity has smoothed the northern wall at depths shallower than 800 m (Puig et al. 2012). High resolution bathymetry data show that the head consists of three main branches (Fig. 28.1a): Cap de Begur branch, which runs in a N-S direction and has its tip at 135 m water depth; Illa Negra branch, which is NW-SE oriented and has its tip at 60 m water depth at a distance of barely 800 m from the coastline; and Sant Sebastià branch, which is W-E oriented and has its tip at 90 m water depth; as well as by many minor gullies. Contrasting terrain characteristics along the canyon walls are indicative of changing basement lithology, from rough, highly sloping outcropping granitoids along Illa Negra and Sant Sebastià branches, to smoother, layered sedimentary outcropping strata along the eastern wall of Cap de Begur branch.

A systematic exploration of the different environments within La Fonera canyon head aiming at detecting CWC communities and quantifying their extent was performed by means of 21 ROV dives in 2009 and 2010, using a Seaeye Lynx 1500 operated from Motor Vessel (*MV*) *Bon Pigall* owned by *Fundació Argomaris*. Dive transects summed up a total distance of 11.09 km, surveyed between 79 and 401 m depth. ROV images display a noticeable habitat variety, in terms of bottom topography and substrate types. These habi-

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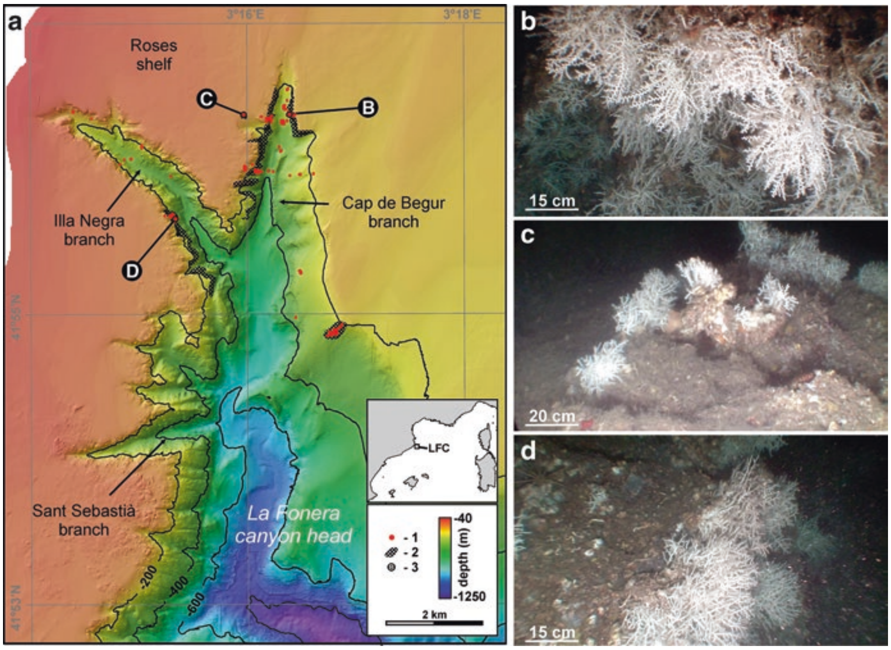

Fig. 28.1 Cold-water corals in La Fonera canyon head. (**a**) Bathymetric map of the canyon head with indication of (1) *M. oculata* observations, (2) possible lateral extension of observed CWC colonies according to maximum entropy modelling and negative observations, (3) location of selected ROV images in (**b**–**d**). See location in inset. *LFC* La Fonera canyon head. Scale bars are approximate. (© GRC Geociències Marines, Universitat de Barcelona)

tats mainly include rocky outcrops and large boulders, sandy (coarse sand to fine gravel mixture) bottoms and fine (clay to medium sand mixtures) sediment-covered bottoms, from flat, homogeneous sediment-covered seafloor to near-vertical and over-hanging rock walls with small holes and caves.

The dominant CWC species in La Fonera canyon head is *M. oculata* (Fig. 28.1b–d), often accompanied by other species including the gorgonians *Eunicella cavolinii* and *Corallium rubrum*, the scleractinian corals *D. cornigera* and *Caryophyllia smithii*, as well as sponges, hydrozoans, bryozoans and the bivalve *Neopycnodonte cochlear* frequently forming dense clusters. Mobile species roaming over or between the corals include the spiny lobster *Palinurus elephas*, the squad lobster *Munida* sp., hermit crabs, sea urchins, sea cucumbers and octopuses. Dense populations of the ophiurioid *Ophiothrix* sp. have been observed attached to coral branches.

The CWCs are not homogeneously distributed within the different La Fonera canyon environments (Lastras et al. 2016), but occur mainly on rocky outcrops and large boulders, as well as on fine sediment-covered bottoms where some objects act as substratum (e.g. pebbles, fishing lines). *M. oculata* colonies occur most frequently between 180 and 300 m water depth (mean 230 m) on highly sloping areas (mean 42.8°). They generally form apparently fragile small frameworks, although at some locations they build dense decimetre-sized clusters. They preferentially develop on the most abrupt parts of the canyon walls, and the largest colonies occur in protected overhangs, which represent the locations less exposed to sedimentation and impacts from commercial trawling. Colonies are most common along the first kilometre of the eastern wall of Cap de Begur branch, and on the opposite western wall where, although less densely, they extend further south (Fig. 28.1). Contrarily, *M. oculata* colonies are much scarcer, smaller and more isolated along the Illa Negra branch, and have not been observed at all along Sant Sebastià branch. Medium-sized highly-impacted living colonies develop along the middle and upper sections of the western wall of Illa Negra branch, nearby the confluence with Cap de Begur branch (Fig. 28.1).

Predictive modelling of CWCs occurrence in La Fonera canyon head by maximum entropy modelling results in an area of 0.36 km^2 having over 70% probability of *M. oculata* occurrence, with 0.10 km^2 exceeding 80% probability (Lastras et al. 2016). This modelling, based solely on terrain morphology and positive CWCs observations, clearly overestimates coral occurrence in Illa Negra and Sant Sebastià branches. This indicates that there are differences between the three branches that control the presence of CWCs which are not accounted for in the model. Such factors could be either limiting in Illa Negra and Sant Sebastià branches, or favouring in Cap de Begur branch, namely food (i.e. organic matter) availability, suspended sediment concentration and/or hydrodynamics. The dramatic incision of La Fonera canyon, with its head tip located at so short distance from the coastline, could explain, at least in part, this mismatch between what is predicted by the model and what is actually observed. On one hand its location favours capturing dense shelf water formed in the gulfs of Roses and Lion to the north (Canals et al. 2006; Ribó et al. 2011), which enhances downcanyon flows and food arrival favouring CWC development, even though water temperature is generally slightly beyond the species optimal conditions. Measurements in July 2011 at the exact locations where corals develop in Cap de Begur branch reveal bottom temperatures from 13.3 to

13.5 °C, and salinities from 38.18 to 38.36. On the other hand, coastline closeness can also involve an excess of sediment arrival during eastern storms (Martín et al. 2006), when the wave base attains larger depths over the shelf thus easing the transport of resuspended sediments into the canyon. This would be particularly relevant in Illa Negra and Sant Sebastià branches, while the Cap de Begur branch, and also the more distant sections of Illa Negra branch where corals grow, would be more protected from this increase in sediment arrival while still benefiting from such highly energetic processes.

The slopes surrounding La Fonera canyon are fishing grounds of the highly priced red shrimp *Aristeus antennatus*. Bottom trawling has been practiced there for decades, generating pervasive trawl marks, enhancing sediment-laden flows and producing dramatic large-scale effects over the seafloor morphology (Puig et al. 2012). Bottom trawling and other fishing techniques are also the direct source of large amounts of litter on the seafloor. Ropes, longlines and nets appear often entangled in coral patches. Dead coral branches are observed at the foot of colonies damaged by fishing gear. At specific locations, living branches are found on muddy bottoms, detached from the main colony, indicating recent impacts. Some coral colonies located on the eastern wall of La Fonera canyon are partially covered by fine mud, and only a few coral branches are partly visible, probably as a result of enhanced sediment fluxes due to daily resuspension by bottom trawling at shallower depths. Exposure to extreme or persistent suspended sediment results in CWC mortality increase (Brooke et al. 2009; Larsson and Purser 2011).

The absence of *L. pertusa*, at least in the uppermost reaches of La Fonera canyon, as well as the dominance of middle-sized, fragile *M. oculata* colonies, with poorly developed small-sized *D. cornigera* colonies, may indicate that La Fonera CWC habitat withstands a high environmental stress of both natural and human origin, and/or is close to the environmental limits where the structuring species can thrive (Lastras et al. 2016).

The results here reported, altogether with companion studies recently carried out along the North Catalan margin (e.g. Aymà et al., this volume), are continuously extending both the geographic spread and the depth range of the CWC habitat and their forming species in the Mediterranean Sea. The research work summarised here also addresses directly one of the main future challenges in submarine canyon research highlighted in Canals et al. (2013), which is the nature of the links between high-energy oceanographic processes and the deep ecosystem, as well as the subsequent action-response effects between such processes and deep ecosystem biodiversity and biological processes at both species and community levels.

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References

Brooke SD, Holmes MW, Young CM (2009) Sediment tolerance of two different morphotypes of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico. Mar Ecol Progr Ser 390:137–144

Canals M, Puig P, Durrieu de Madron X, et al (2006) Flushing submarine canyons. Nature 444:354–357

Canals M, Company JB, Martín D, et al (2013) Integrated study of Mediterranean deep canyons: novel results and future challenges. Progr Oceanogr 118:1–27

Fabri MC, Pedel L, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Larsson AI, Purser A (2011) Sedimentation on the cold-water coral *Lophelia pertusa*: Cleaning efficiency from natural sediments and drill cuttings. Mar Pollut Bull 62:1159–1168

Lastras G, Canals M, Amblas D, et al (2011) Understanding sediment dynamics of two large submarine valleys from seafloor data: Blanes and La Fonera canyons, northwest Mediterranean Sea. Mar Geol 280:20–39

Lastras G, Canals M, Ballesteros E, et al (2016) Occurrence and anthropogenic impacts on cold-water coral habitats in La Fonera submarine canyon head, northwestern Mediterranean Sea. PLoS One 11:e0155729

Martín J, Palanques A, Puig P (2006) Composition and variability of downward particulate matter fluxes in the Palamós submarine canyon (NW Mediterranean). J Mar Syst 60:75–97

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51

Puig P, Canals M, Company JB, et al (2012) Ploughing the deep sea floor. Nature 489:286–289

Ribó M, Puig P, Palanques A, et al (2011) Dense shelf water cascades in the Cap de Creus and Palamós submarine canyons during winters 2007 and 2008. Mar Geol 284:175–188

Cross References

Aymà A, Aguzzi J, Canals M, et al (this volume) Occurrence of living cold-water corals at large depths within submarine canyons of the northwestern Mediterranean sea

Fourt M, Goujard A, Chevaldonné P (this volume) Working with visual methods, comparison among the French deep-sea canyons

Puig P, Gili JM (this volume) Submarine canyons in the Mediterranean: a shelter for cold-water corals

Cold-Water Coral Associated Fauna in the Mediterranean Sea and Adjacent Areas

29

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Abstract

Cold-water corals are recognised as a key component of Mediterranean deep-sea ecosystems but the knowledge of their associated biodiversity is still limited. To date, the fauna associated to the Central Mediterranean cold-water coral habitats is the best known (e.g. the cold-water coral provinces of Santa Maria di Leuca, Bari canyon and Strait of Sicily) but such knowledge should be extended to the whole Mediterranean Basin. The combined biodiversity censed so far for Mediterranean cold-water coral habitats and those of adjacent areas (Strait of Gibraltar-Gulf of Cádiz) includes a conspicuous number of species (ca. 520 spp.) with a high representation of sponges (ca. 90 spp.), polychaetes (ca. 90 spp.), cnidarians (ca. 80 spp.), bryozoans (ca. 75 spp.), crustaceans (ca. 60 spp.), molluscs (ca. 50 spp.), fishes (ca. 50 spp.), echinoderms (ca. 20 spp.) and brachiopods (7 spp.). Most species are not univocally linked to cold-water corals, but they benefit from the complex and diverse microhabitats provided by them. There is a clear need to continue the investigation of Mediterranean cold-water coral habitats to fully document the faunistic inventory, biogeographic connections and functions of the many species connected to such emblematic ecoystems of the deep-sea.

Keywords

Biodiversity · Cold-water coral · Benthic community · Demersal fauna · Mediterranean Sea

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29.1 Historical Background on Cold-Water Coral Associated Fauna in the Mediterranean

The scientific attention on cold-water coral (CWC) grounds is steadily increasing worldwide leading to a better definition of such fundamental deep-sea habitats (hereafter CWC habitats) at regional and global scales, with respect to their biodiversity, ecological role, functioning and ecosystem services (Roberts et al. 2006). The demanding study of the benthic, suprabenthic and demersal biota taking advantage of such CWC habitats requires resources and time, with results, therefore, appearing only years after the discovery of these habitats. The Mediterranean is not an exception, and this explains why only limited, albeit growing, information is at present available on its CWC sites. Admitedly, most of the living CWC sites of the Mediterranean and adjacent areas have only been detected since the year 2000 onwards, with the likely expectation that more will be tracked in the future (Fig. 29.1).

Early observations on the presence of CWC in the Mediterranean Sea are accidental, mainly referring to *Madrepora oculata*, and based upon sea-cable recovery and fisheries, especially as by-catch of invasive tecnhiques for harvesting red coral (Zibrowius 1980, 2003). In the past, the occasional occurrence of CWC like *M. oculata* and *Lophelia pertusa* was reported from various Mediterranean locations (Zibrowius 1980), although generally deprived of information on its accompanying associated biota. A first turning point for the comprehensive appreciation of Mediterranean CWC must be credited to Pérès and Picard (1964) who described the CWC associated community as *Biocoenose des "coraux blancs"* (White-coral biocoenosis). Their study benefited from the pre-existing research carried out on Atlantic CWC associated fauna, from the experience gained through deep-sea dredging and trawling, as well as from the submergible surveys at different locations specifically in the Mediterranean Sea. Pérès and Picard (1964) detected some species which were later consistently found to be associated with CWC in the Mediterranean basin, such as the byssate *Asperarca nodulosa* and the cemented bivalve *Spondylus gussonii*, as well as the serpulid polychaete *Metavermilia multicristata*. These authors pointed out that most CWC in the Mediterranean were represented by dead subfossil findings, overall representing a low diversity assemblage with respect to Atlantic counterparts. Thus, it was postulated that Atlantic-type CWC flourished in the Mediterranean basin during the Pleistocene and then their prosperity declined drastically. This concept got direct support by extensive dating showing that, in fact, most CWC samples are late Pleistocene in age (Delibrias and Taviani 1984; Malinverno et al. 2010; McCulloch et al. 2010; Taviani et al., this volume; Vertino et al., this volume). Moreover, associated fauna to such Pleistocene CWC were also identified, mainly represented by scleractinians (Zibrowius 1980) and molluscs that included the large limid *Acesta excavata* and gastropods (Taviani and Colantoni 1979; Taviani and Taviani 1986).

A revolution in the knowledge of CWC habitats then took place due to the discovery of extensive live coral grounds with *L. pertusa* and *M. oculata* off Cape Santa Maria di Leuca (SML) in the northern Ionian Sea between 300 and 1100 m depth (Mastrototaro et al. 2002; Tursi et al. 2004; Taviani et al. 2005). This CWC province houses a diverse community of associated organisms (Mastrototaro et al. 2010; Rosso et al. 2010; D'Onghia et al. 2011; D'Onghia, this volume; Chimienti et al., this volume) and still represents the best case-study for the Mediterranean Sea in terms of research devoted to its various aspects such as habitat characterisation and mapping (Vertino et al. 2010; Savini et al. 2014; Angeletti et al., this volume; Lo Iacono et al., this volume), the diverging hard and soft-bottom thanatofacies (Rosso et al. 2010), assessment of its benthic and demersal fauna (Tursi et al. 2004; Mastrototaro et al. 2010; Vertino et al. 2010), taxonomical aspects of specific benthic groups (e.g. sponges, meiofauna, molluscs) (Longo et al. 2005; Bongiorni et al. 2010; Negri and Corselli 2016 respectively), the megafauna and commercial resources (D'Onghia et al. 2010, 2011; D'Onghia, this volume) and the evaluation of the trophic web (Carlier et al. 2009).

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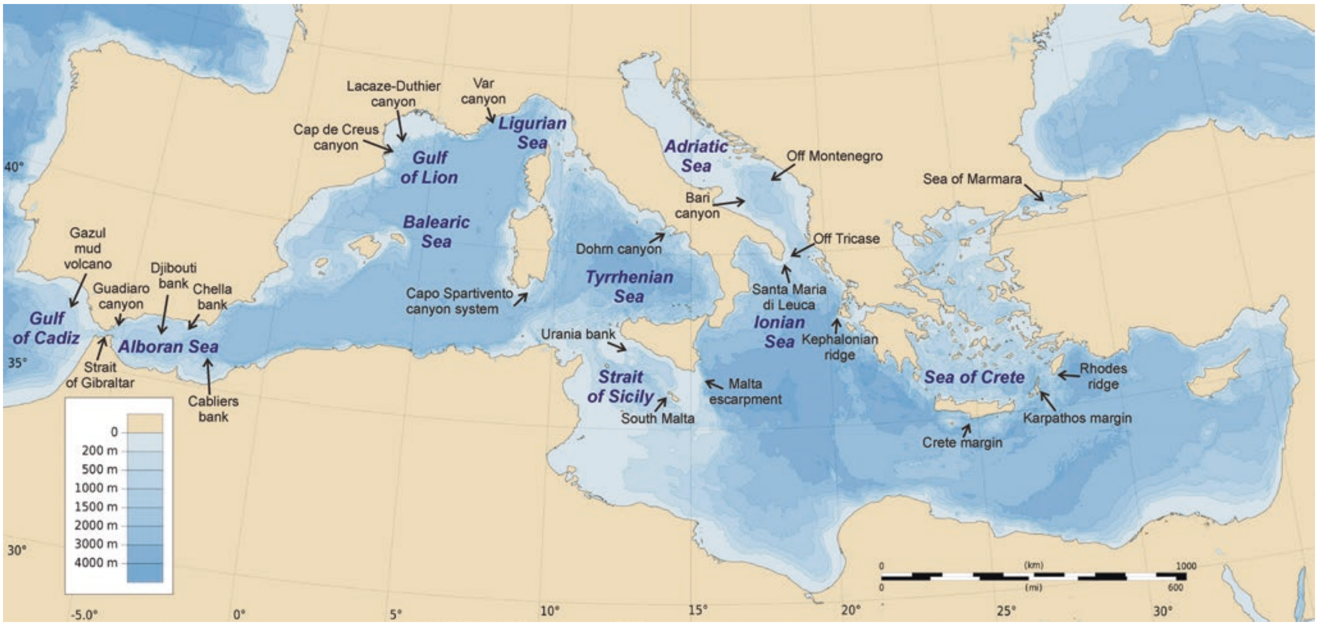

Fig. 29.1 Main areas with studies on associated fauna of cold-water coral habitats in the Mediterranean Sea and adjacent areas. Codes for references in Table 29.1: Gazul mud volcano (16, 46, 53, 54); Strait of Gibraltar (2); Guadiaro canyon (65); Djibouti bank (27, 32, 45); Chella bank (1, 13, 34, 45); Cabliers bank (45, 55); Cap de Creus canyon (28, 38, 44, 68); Lacaze-Duthiers canyon (22); Var canyon (22); Nora and Capo Spartivento canyons; Urania Bank (69); Dohrn canyon (24); Malta escarpment (4, 24); Santa Maria di Leuca (18, 19, 20, 35, 40, 43, 52, 66); Off Tricase (3, 61); Bari canyon (3, 21, 57, 61); Off Montenegro (3, 61); Kephalonian Ridge (42); Crete, Karpathos and Rhodes margins (Taviani et al. 2011b)

Further deep-sea exploration quickly detected CWCs in other areas of the Central Mediterranean, demonstrating that the SML coral province was not the only one in the Mediterranean (Freiwald et al. 2009). Some of these CWC sites were located on bedrock overhangs on steeply inclined submarine walls and escarpments that are difficult to sample, and most of the associated fauna is still to be characterised in the coming years (Schembri et al. 2007; Angeletti et al. 2015). In some seafloor structures of the Central Mediterranean (e.g. Bari Canyon in the southwestern Adriatic Sea), general studies on habitats and associated macro and megafauna communities documented the presence of living colonies of *M. oculata* (together with *Leiopathes glaberrima*, small colonies of *L. pertusa* and clusters of *Dendrophyllia cornigera*), and some of the associated species (especially serpulids, sponges, bryozoans and fishes) were then documented (Sanfilippo et al. 2013; D'Onghia et al. 2015; D'Onghia, this volume). In the Strait of Sicily (SoS) various CWC sites were detected (Zibrowius and Taviani 2005; Schembri et al. 2007; Freiwald et al. 2009) and their associated macrofauna is getting increasing attention for its richness (Schembri et al. 2007; Mifsud et al. 2009; Taviani et al. 2009, 2010, 2011b; Deidun et al. 2015). Remotely operated vehicle (ROV) surveys have also documented CWC in the southern Adriatic whose megabenthic fauna share many traits with the SML coral province (Freiwald et al. 2009; Angeletti et al. 2014; Taviani et al. 2016).

In other sectors of the Mediterranean Sea and adjacent areas (Strait of Gibraltar, Gulf of Cádiz) the knowledge on the CWC associated fauna is not as detailed as for SML. In the eastern Mediterranean, there is a scarce occurrence of CWC habitats (some of them dominated by living *Desmophyllum dianthus* and *Dendrophyllia ramea*, the latter observed off Cyprus at 125–170 m depth by Orejas et al. 2017a, this volume), and studies on the associated megafauna have only been carried out off the south western coasts of Kephalonia Island (Greece) (Mytilineou et al. 2014), along the margins of Crete, Karpathos and Rhodes as well as in the Sea of Marmara (Taviani et al. 2011b) and off Cyprus (Jiménez et al. 2016). In the western Mediterranean, recent findings of CWC were obtained using ROV in the Capo Spartivento canyon system, including the Nora canyon (South Sardinia CWC province) (Taviani et al. 2017), which has filled a gap not only in the known CWC geographic distribution within the Mediterranean Sea but also on the associated CWC fauna for western Mediterranean locations (Taviani et al. 2017). Further north, shallow buried subfossil deep-coral mounds were located in the Tuscan Archipielago, and their dominant sessile macrofauna described (Remia and Taviani 2005). Recent unpublished information confirms the occurrence of live *M. oculata* in this area (Taviani, pers. comm.). The Catalan-Provençal-Ligurian submarine canyons also represent an important Mediterranean area with CWC habitats (Domínguez-Carrió et al. 2014), however CWC studies have only dealt with the habitat-forming species (Orejas et al. 2009; Gori et al. 2013; Lastras et al. 2016, this volume; Aymà et al., this volume; Fourt et al., this volume; Puig and Gili, this volume), the fish community (de Lucia et al. 2008) or the megabenthic fauna, which only represent a small fraction of the associated biodiversity (Madurell et al. 2012b; Fabri et al. 2014, 2017; Fanelli et al. 2017). Nevertheless, the only study on the planktonic community of Mediterranean CWC habitats was performed in one of these canyons (Cap de Creus) (Madurell et al. 2012a). In the western Mediterranean, dense coral forests of the bamboo coral *Isidella elongata* have been discovered in the last decade, some of them apparently displaying very well-developed communities (Cartes et al. 2013; Bo et al. 2015; Mastrototaro et al. 2017; Pierdomenico et al. 2018). In the Alborán Sea, important CWC habitats have also been detected (Wienberg and Titschack 2017; Lo Iacono et al., this volume) and some studies have partially characterised the associated megabenthic community in the Chella (Seco de los Olivos) and Cabliers banks (Pardo et al. 2011; Sánchez-Gallego et al. 2014; de la Torriente et al. 2014), Djibouti banks (Hebbeln et al. 2009; Pardo et al. 2011), Melilla coral province (Hebbeln et al. 2009; Lo Iacono et al. 2014, this volume) and Guadiaro canyon (Vázquez et al. 2016). However, detailed studies on the biodiversity are still missing for any of the CWC habitats of the Alborán Sea which represents an important area, together with the Gulf of Cádiz (GoC), to better understand the distributional patterns of the associated fauna between the Mediterranean Sea and the Atlantic Ocean. This is also the case for the Strait of Gibraltar, where CWC habitats have also been detected and their scleractinian species identified, but no studies on other components of their associated fauna have ever been done (Álvarez-Pérez et al. 2005).

In the GoC, impinged by the Mediterranean Outflow Water current (MOW), there is a widespread occurrence of last glacial assemblages containing CWC (Taviani et al. 1991; Wienberg et al. 2009). Interestingly, extensive live CWC habitats have been detected during the last years in specific areas of the GoC (e.g. Gazul mud volcano), representing benthic and demersal biodiversity hotspots for the GoC (Díaz del Rio et al. 2014; Rueda et al. 2016; Orejas et al. 2017b).

29.2 Ecological Role of Mediterranean CWC Habitats for the Associated Fauna

Mediterranean CWC habitats are functionally and morphologically complex deep-sea habitats that form an intricate network of biogenic frames and interstices, providing niches, spawning, nursery or shelter ground for a large variety of organisms, including commercially important and threatened species (Table 29.1). Unlike the NE Atlantic, studies evaluating the ecological role of Mediterranean CWC habitats for the associated fauna are still scarce as commented on the previous section.

Primarily, CWC habitats provide a suitable substrate both for larval settlement and adult growth, adding to the number of hard substrates in the deep-sea which are scarcer than the prevailing soft bottoms (Zibrowius 2003). These habitats also increase the hard bottom complexity providing tridimensional structure and offering a complex network of biogenic interstices for many species in comparison to other types of hard and soft bottoms (Tursi et al. 2004; Longo et al. 2005; Mastrototaro et al. 2017). As detected in the NE Atlantic, the complexity of the CWC habitat in some Mediterranean areas (e.g. SML) is enhanced by other sessile species that develop on coral skeletons, such as sponges or polychaetes (e.g. serpulids, *Eunice norvegica*), that also create a complex living tridimensional structure for species of different taxa (Longo et al. 2005; Mastrototaro et al. 2010; Mueller et al. 2013). Bongiorni et al. (2010) detected higher meiofaunal diversity due to the effects on habitat heterogeneity/complexity in both living coral and coral rubble of SML than in surrounding slope sediments, concluding that the protection of dead corals, a so-far almost neglected habitat in terms of biological conservation, can further contribute to the maintenance of a high deep-sea biodiversity along continental margins (Henry and Roberts 2007; Rossi et al. 2017). The presence of soft bottoms in areas with coral rubble among live CWC colonies may also favor the occurrence of typical bathyal soft bottom fauna within the CWC habitats. Indeed, these areas with mixed bottoms can display a high biodiversity due to the higher microhabitat complexity (Rosso et al. 2010; Vertino et al. 2010). The comparisons at SML between different types of CWC related habitats, that were sampled with similar methods, disclosed a lower biodiversity for living coral colonies of *Madrepora oculata* and *Lophelia pertusa* (30 taxa), than for dead coral branches (83 taxa) and for coral rubble (59 taxa) (Mastrototaro et al. 2010). The authors indicated that this is probably due to the use of the exposed dead coral skeleton as attachment sites for a great number of sessile invertebrates because of the antifouling properties of the coral coenosarc or due to the instability of this living tissue (Jensen and Frederiksen 1992; Mortensen and Fosså

Table 29.1 Faunistic list of organisms found inhabiting cold-water coral (CWC) ecosystems and surrounding habitats in the Mediterranean Sea and Gulf of Cádiz, indicating whether they are strict (S; species displaying a strong relationship with CWC and predominantly found in CWC), dominant (D; species in high numbers at least at some studied locations), common (C; species frequently observed in some studied locations, although not strictly abundant) or occasional (O; species cited occasionally in any studied location)

Species	S	D	C	O	Habitats	Locations	References
PORIFERA Demospongiae							
Acantheurypon pilosella (Topsent, 1904)				+	Mo, Lp, Dd	CS	62
Alectona millari Carter, 1879				+	Mo, Lp, Dd	CS	62
Anisocrella hymedesmina Topsent, 1927				+	M-coral-R	CCa, GoC	46, 64
Antho signata (Topsent, 1904)				+	Mo, Lp, Dd	SML	35, 40
Antho involvens (Schmidt, 1864)				+	Mo	BCa	21
Axinella cannabina (Esper, 1794)				+	Mo, Lp, Dd	SML	35, 40
Axinella pumila Babiç, 1922				+	Mo	BCa	21
Biemna partenopea Pulitzer-Finali, 1978				+	Mo	BCa	21
Biemna tenuisigma Pulitzer-Finali, 1978				+	Mo	BCa	21
Bubaris carcisis Vacelet, 1969				+	M-coral-R	SCa	64
Bubaris subtyla Pulitzer-Finali, 1983				+	Mo	BCa	21
Bubaris vermiculata (Bowerbank, 1866)				+	Mo, M-coral-R	BCa, CCa	21, 64
Calthropella pathologica (Schmidt, 1868)				+	Mo, Lp, Dd, M-coral-R	SML, CCa	35, 40, 64
Characella pachastrelloides (Carter, 1876)				+	Lp, coral-R	Malta, GMV, GoC	10, 16
Chelonaplysilla psammophila (Topsent, 1928)				+	M-coral-R	CCa	64
Clathria anchorata (Carter, 1874)				+	Mo, Lp, Dd, M-coral-R	CS, CCa	62, 64
Clathria frogeti (Vacelet, 1969)				+	M-coral-R	CCa	64
Clathria gradalis Topsent, 1925				+	Mo	BCa	21
Cliona sp.				+	Mo, Lp	SML	35, 40
Crella alba (Vacelet, 1969)				+	M-coral-R	CCa	64
Crellastrina alecto (Topsent, 1898)				+	Mo, Lp, Dd	SML	35, 40
Damiria curvata (Vacelet, 1969)				+	M-coral-R	CCa	64
Dercitus plicatus (Schmidt, 1868)				+	Mo, Lp	SML	40
Desmacella annexa Schmidt, 1870				+	Mo, Lp, Dd	SML	35, 40
Desmacella inornata (Bowerbank, 1866)		+			Mo, Lp, Dd, M-coral-R	SML, BCa, CCa, CS, GMV	35, 40, 46, 21, 62, 64
Dragmatella aberrans (Topsent, 1890)				+	M-coral-R	CCa	64
Erylus discophorus (Schmidt, 1862)				+	Lp	Malta	10
Erylus papulifer Pulitzer-Finali, 1983			+		Mo, Lp, Dd	SML	35, 40
Esperiopsis strongylophora Vacelet, 1969				+	M-coral-R	CCa	64
Eurypon clavatum (Bowerbank, 1866)				+	Mo, Lp	SML	40
Eurypon cinctum Sarà, 1960				+	Mo	BCa	21
Eurypon denisae Vacelet, 1969				+	M-coral-R	CCa	64
Eurypon hispidulum (Topsent, 1904)				+	M-coral-R	CCa	64
Eurypon obtusum Vacelet, 1969				+	M-coral-R	SCa	64
Eurypon topsenti Pulitzer-Finali, 1983				+	Mo	BCa	21
Eurypon viride (Topsent, 1889)				+	Mo	BCa	21
Geodia nodastrella Carter, 1876				+	Mo, Lp, Dd	SML	35, 40
Geodia anceps (Vosmaer, 1894)				+	Mo, Lp, Dd	SML	35, 40
Haliclona arnesenae (Arndt, 1927)				+	M-coral-R	CCa	64
Haliclona magna (Vacelet, 1969)				+	M-coral-R	CCa	64
Haliclona mucosa (Griessinger, 1971)		+			Mo, Lp	GMV	54
Hamacantha azorica Topsent, 1904				+	Lp	Lis, GMV	10, 16
Hamacantha falcula (Bowerbank, 1874)				+	Mo, Lp, Dd, M-coral-R	CS, BSL	62, 64
Hamacantha johnsoni (Bowerbank, 1864)			+		Mo, Lp, Dd, M-coral-R	SML, BCa, CCa, CS	35, 40, 21, 62, 64
Hamacantha lundbecki Topsent, 1904				+	M-coral-R	CCa	64
Hamacantha papillata Vosmaer, 1885			+		Mo, Lp, Dd, M-coral-R	SML, BCa, PCa	35, 40, 21, 64

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Hexadella cf. *cripta* Reveillaud, Allewaert, Pérez, Vacelet, Banaigs & Vanreusel, 2012				+	Mo	CCa	23
Hexadella dedritifera Topsent, 1913				+	Mo, Lp, Dd	SML	35, 40
Hexadella pruvoti Topsent, 1896				+	Mo	BCa	21
Hymedesmia gracilisigma Topsent, 1928				+	M-coral-R	CCa	64
Hymedesmia inflata Vacelet, 1969				+	M-coral-R	CCa	64
Hymedesmia plicata Topsent, 1928				+	M-coral-R	PCa	64
Hymedesmia pugio Lundbeck, 1910				+	coral-R	Lis, GMV	10, 16
Hymedesmia mutabilis (Topsent, 1904)			+		Mo, Lp, Dd, M-coral-R	SML, CS, CCa	35, 40, 62, 64
Hymedesmia serrulata Vacelet, 1969				+	M-coral-R	CCa	64
Hymerhabdia oxytrunca Topsent, 1904				+	Mo, M-coral-R	BCa, CCa	21, 64
Hymerhabdia typica Topsent, 1892				+	Mo	BCa	21
Janulum spinispiculum (Carter, 1876)				+	Lp, M-coral-R	Lis, GMV, CCa	10, 16, 64
Jaspis incrustans (Topsent, 1890)			+		Mo, Lp	SML, LIs, BCa, GMV	35, 40, 10, 16, 21
Latrunculia rugosa (Vacelet, 1969)				+	M-coral-R	CCa	64
Leiodermatium cf. *lynceus* Schmidt, 1870				+	Mo, Lp	SML	35, 40
Lycopodina hypogea (Vacelet & Boury-Esnault, 1996)				+	Mo, Dc, Dd	ChBa, Urania bank, LIs	1
Melonanchora emphysema (Schmidt, 1875)				+	M-coral-R	CCa	64
Pachastrella monilifera Schmidt, 1868				+	Mo, Lp	SML, BCa, CS	35, 40, 21, 62
Penares euastrum (Schmidt, 1868)				+	coral-R	GoC	46
Petrosia sp.			+		Mo	GMV	54
Phakellia robusta Bowerbank, 1866				+	Mo, Lp	LIs, BCa, GMV	10, 16, 21
Plocamionida ambigua (Bowerbank, 1866)			+		Mo, Lp, Dd	SML	35, 40
Poecillastra compressa (Bowerbank, 1866)		+			Mo, Lp, M-coral-R	SML, BSL, Magaud bank, BCa, CS, GoC, CCCa	35, 40, 21, 62, 64, 17
Podospongia lovenii Barboza du Bocage, 1869				+	M-coral-R	BSL, CCa	64
Polymastia polytylota Vacelet, 1969				+	M-coral-R	BSL	64
Prosuberites longispinus Topsent, 1893				+	Mo	BCa	21
Pseudotrachya hystrix (Topsent, 1890)				+	M-coral-R	CCa	64
Rhabdeurypon spinosum Vacelet, 1969				+	M-coral-R	CCa	64
Rhizaxinella pyrifera (Delle Chiaje, 1828)				+	M-coral-R	EM, Cca, Corsica	32, 64
Sceptrella insignis (Topsent, 1890)		+			Mo, Lp, Dd, M-coral-R	SML, BCa, CCa, CS	35, 40, 21, 62, 64
Siphonidium ramosum (Schmidt, 1870)			+		Mo, Lp, Dd	SML	35, 40
Siphonodictyon infestum (Johnson, 1889)				+	Mo	SML, BCa	6, 2
Spiroxya levispira (Topsent, 1898)		+			Mo, Lp, Dd	SML, CS	35, 6, 40, 62
Spiroxya heteroclita Topsent, 1896				+	Mo, Lp, Dd	SML	35, 40
Stelligera rigida (Montagu, 1814)				+	M-coral-R	CCa	64
Stylocordyla pellita (Topsent, 1904)				+	M-coral-R	Cerigotto channel	64
Suberites sp. 1				+	Mo, Lp	SML	40
Suberites sp. 2				+	Mo, Lp	SML	40
Sulcastrella tenens (Vacelet, 1969)				+	M-coral-R	CCa	64
Thrombus abyssi (Carter, 1873)			+		Mo, Lp, Dd, coral-R	SML, GoC	35, 40
Timea chondrilloides (Topsent, 1904)				+	Mo, Lp, Dd, M-coral-R	SML, CCa	35, 40, 64
Vulcanella gracilis (Sollas, 1888)			+		Mo, Lp, coral-R, M-coral-R	LIs, Malta, SML, CS, CCa	35, 40, 10, 62, 64
PORIFERA Hexactinellida							
Asconema setubalense Kent, 1870			+		Mo, Lp	DBa, GMV	45, 16
Farrea sp.				+	Mo	CCa	23
Nodastrella nodastrella (Topsent, 1915)				+	coral-R	DBa	32
Oopsacas minuta Topsent, 1927				+	Mo	CCa	23

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Sympagella delauzei Boury-Esnault, Vacelet, Reiswig & Chevaldonné, 2015				+	Mo, Lp, coral-R	ChBa	13
Tretodictyum cf. *tubulosum* Schulze, 1886				+	Mo	CCa	23
PORIFERA Homoscleromorpha							
Plakina monolopha Schulze, 1880				+	Mo, Lp	SML	40
Plakortis simplex Schulze, 1880				+	Mo, Lp, Dd	SML, BCa	35, 40, 21
CNIDARIA Hydrozoa							
Acryptolaria conferta (Allman, 1877)			+		Mo, Lp, coral-R	SML, GdC, SoG, AS	37, 40, 47, 46
Acryptolaria crassicaulis (Allman, 1888)				+	Mo, Lp, coral-R	GMV	46
Aglaophenia tubulifera (Hincks, 1861)				+	coral-R	SoG	47
Antennella secundaria (Gmelin, 1791)				+	Mo, Lp, coral-R	SoG, GdC	47, 46
Bedotella armata (Pictet & Bedot, 1900)				+	Mo, Lp	GMV	46
Campanularia hincksii Alder, 1856				+	Mo, Lp, coral-R	GMV	46
Cladocarpus sinuosus Vervoort, 1966				+	Mo, Lp	GMV	46
Clytia gracilis (Sars, 1850)				+	coral-R	GMV	46
Clytia linearis (Thornely, 1900)				+	Mo, Lp	SML	40
Cryptolaria pectinata (Allman, 1888)			+		Mo, Lp, coral-R	SoG, GdC	47, 46
Diphasia margareta (Hassall, 1841)				+	Mo, Lp	GMV	16
Halecium labrosum Alder, 1859				+	Mo, Lp	SML	40
Halopteris catharina (Johnston, 1833)				+	coral-R	SoG	47
Hybocodon cf. *prolifer* Agassiz, 1860				+	Mo, Lp	SML	40
Lafoea dumosa (Fleming, 1820)				+	coral-R	GdC	47
Laodicea undulata (Forber & Goodsir, 1853)				+	Mo, Lp	SML	40
Lytocarpia myriophyllum (Linnaeus, 1758)				+	coral-R	GMV	46
Mitrocoma annae Haeckel, 1864				+	Mo, Lp	SML	40
Modeeria rotunda (Quoy & Gaimard, 1827)				+	coral-R	GMV	46
Nemertesia antennina (Linnaeus, 1758)				+	Mo, Lp	SML, GdC	40, 46
Nemertesia falcicula Ramil & Vervoort, 1992				+	Mo, Lp	GMV	46
Nemertesia ramosa (Lamarck, 1816)				+	Mo, Lp	SML	40
Polyplumaria flabellata Sars, 1874			+		Mo, Lp, coral-R	GdC, GMV	37, 16
Racemoramus panicula (G.O. Sars, 1874)				+	coral-R	GdC, GMV	47, 46
Schizotricha frutescens (Ellis & Solander, 1786)			+		Mo, Cr, Cs, Dc	FCa	33
Sertularella gayi (Lamouroux, 1821)			+		Mo, Cr, Cs, Dc, coral-R	GdC, GMV, FCa	33, 47, 46
Streptocaulus cf. *pectiniferus* Allman, 1883				+	coral-R	GMV	46
Tubiclavoides striatum Moura, Cunha & Schuchert, 2007				+	Mo, Lp	GdC	41
Turritopsis cf. *nutricula* McCrady, 1857				+	coral-R	GMV	46
Zygophylax biarmata Billard, 1905			+		Mo, Lp, coral-R	GdC, SoG	37, 47, 46
Zygophylax cf. *brownei* Billard, 1924				+	Mo, Lp	GMV	46
CNIDARIA Anthozoa, Hexacorallia							
Amphianthus dohrnii (Koch, 1878)			+		Mo, Lp	SML, EM	40, 66, 32
Antipathella subpinnata (Ellis & Solander, 1786)				+	RBB	GoL, GMV	22, 16
Antipathes dichotoma Pallas, 1766				+	coral-R, RBB	DBa, SML, GoL, CCa	66, 45, 22, 24
Caryophyllia calveri Duncan, 1873			+		Mo, Lp, RBB	SML	40, 66, 52
Caryophyllia cyathus (Ellis & Solander, 1786)				+	coral-R, RBB	SoG	2
Caryophyllia inornata (Duncan, 1878)				+	coral-R, RBB	SoG	2
Caryophyllia smithii Stokes & Broderip, 1828			+		coral-R	GMV	16

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Dendrophyllia cornigera (Lamarck, 1816)			+		Mo, Lp, coral-R, RBB	DBa, CaBa, ChBa, SML, SAS, SoG, GoL, GMV, CCCa, Malta, BCa, EM, FCa	2, 24, 44, 66, 52, 45, 28, 16, 3, 22, 33, 17, 18, 32
Desmophyllum dianthus (Esper, 1794)		+			Mo, Lp, RBB	NBa, SML, BCa, CCa, SAS, SoG, GoL, EM, CaBa, ChBa, CCCa	2, 69, 58, 24, 40, 52, 66 45, 8, 3, 22, 62, 32, 17
Edwardsiella loveni (Carlgren, 1892)	+				Mo, Lp, coral-R	LigurianSea, NBa, DBa	50, 69, 32
Eguchipsammia gaditana (Duncan, 1873)				+	Mo, coral-R	GMV	16
Epizoanthus sp.				+	Mo, Lp	SML	40, 66
Flabellum chunii Marenzeller, 1904			+		coral-R	GMV	16
Isozoanthus primnoidus Carreiro-Silva, Braga-Henriques, Sampaio, de Matos, Porteiro & Ocaña, 2010				+	Cv, Sv, lithistids	NWSicily, NBa, GoL	66, 9, 21
Kadophellia bathyalis Tur, 1991			+		coral-R, RBB	SML, SAS	40, 52, 3
Leiopathes glaberrima (Esper, 1788)			+		Mo, Lp, RBB, coral-R	CaBa, DBa, SML, SAS, GoL, GMV	66, 45, 3, 22, 16, 32
Lophelia pertusa (Linnaeus, 1758)		+			Lp, Mo, coral-R, RBB	DBa, ChBa, CaBa, SML, GMV, SoG, SoS, GoL, CS, FCa, CCCa, Malta, BCa, SAS, NBa, EM	2, 24, 44, 66, 52, 45, 28, 4, 22, 33, 17, 18, 62, 32, 16, 3
Madrepora oculata Linnaeus, 1758		+			Lp, Mo, coral-R, RBB	DBa, ChBa, CaBa, SML, GMV, SoS, GoL, CS, FCa, CCCa, NBa, Malta, BCa, SAS, Gca, EM, SoG	2, 24, 44, 66, 52, 45, 28, 22, 33, 17, 18, 62, 65, 32, 16, 3, 4
Parantipathes larix (Esper, 1788)			+		coral-R, RBB	CaBa, EM	45, 3
Parazoanthus anguicomus (Norman, 1868)				+	Spongesamongcoral-R	BCa	8
Peachia cylindrica (Reid, 1848)				+	SB	SML, BCa	40, 3
Protanthea simplex Carlgren, 1891				+	coral-R	NBa	69
Sagartia elegans (Dalyell, 1848)			+		Mo, Lp	SML	40, 66
Sagartia troglodytes (Price in Johnston, 1847)			+		Mo, Lp	SML	40, 66
Stenocyathus vermiformis (Pourtalès, 1868)		+			Mo, Lp, RBB	SML, SoS, SAS, SoG, NBa	2, 69, 24, 40, 52, 66, 3
Thalamophyllia gasti (Döderlein, 1913)				+	RBB	NBa	69
CNIDARIA Anthozoa, Octocorallia							
Acanthogorgia armata Verrill, 1878			+		coral-R, RBB	CaBa	45
Acanthogorgia hirsuta Gray, 1857			+		coral-R, RBB, Mo	SAS, SML, CaBa, GMV, EM, CCa	63, 40, 3, 45, 16, 32, 24
Anthomastus sp.				+	RBB	CaBa	45
Bebryce mollis Philippi, 1842			+		coral-R, RBB	SML	40, 66, 3
Callogorgia verticillata (Pallas, 1766)		+			coral-R, RBB, Mo	SAS, SML, DBa, CaBa, GoL, CCa	63, 45, 3, 22, 24
Cavernularia pusilla (Philippi, 1835)			+		coral-R	AS	45
Corallium rubrum (Linnaeus, 1758)			+		Mo, Lp, RBB	NBa, GoL, FCa	69, 11, 22, 33, 18
Dendrobrachia bonsai Lopez-Gonzales & Cunha, 2010			+		Mo, Lp	SML, NBa	40, 69
Eunicella cavolini (Koch, 1887)				+	Mo, Lp, RBB	GoL	22
Eunicella verrucosa (Pallas, 1766)				+	RBB	CaBa, ChBa	45
Funiculina quadrangularis (Pallas, 1766)			+		SB	DBa, ChBa	52, 45, 22
Isidella elongata (Esper, 1788)			+		SB	DBa, CaBa, ChBa, SML, SoS, NBa	69, 24, 40, 66, 52, 45
Kophobelemnon stelliferum (Müller, 1776)			+		SB	DBa, CaBa, ChBa	45
Paramuricea clavata (Risso, 1826)				+	Mo, Lp, RBB	GoL, ChBa	45, 22
Paramuricea macrospina (Koch, 1882)				+	coral-R, RBB	SML, SAS	40, 66, 3
Pennatula phosphorea Linnaeus, 1758			+		coral-R	AS	45

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Placogorgia spp.				+	Mo, Lp	GMV	16
Scleranthelia rugosa var. musiva Studer, 1878				+	coral-R	NBa	69
Plexauridae spp.				+	Mo	CCa	24
Swiftia pallida Madsen, 1970				+	coral-R, RBB	SML	40
Swiftia rosea (Grieg, 1887)			+		RBB	CaBa	45
Viminella flagellum (Johnson, 1863)				+	Mo, coral-R	GMV, CCa	16, 24
ANNELIDA Polychaeta							
Aglaophamus cf. *elamellatus* (Eliason, 1951)				+	M-coral-R	GoC	12
Ampharetidae				+	M-coral-R	GoC	12
Aricidea cf. *pseudoarticulata* Hobson, 1972				+	M-coral-R	GoC	12
Aricidea simonae Laubier & Ramos, 1974				+	M-coral-R	GoC	12
Bathyvermilia eliasoni (Zibrowius, 1970)			+		Mo, Lp, M-coral-R	SML, BCa	63, 40, 57, 16
Bispira sp.				+	BM	BCa	3
Bonellia sp.				+	BM	BCa	24
Bonellia viridis Rolando, 1822				+	BM, coral-R	CS, EM	62, 3
Capitellidae				+	M-coral-R	GoC	12
Cirratulidae				+	M-coral-R	GoC	12
Dodecaceria sp.				+	M-coral-R	GoC	12
Eclysippe sp.				+	M-coral-R	GoC	12
Eunice dubitata Fauchald, 1974				+	M-coral-R	GoC	12
Eunice norvegica (Linnaeus, 1767)		+	+		Mo, Lp, Pm, M-coral-R, BM	SML, Malta, GMV, BCa	63, 58, 12, 40, 66, 57, 16, 21, 62
Eunice sp.				+	BM	GoC	67
Exogone sp.				+	M-coral-R	GoC	12
Fauveliopsis sp.				+	M-coral-R	GoC	12
Filograna implexa Berkeley, 1835		+	+		Mo, Lp, Pm, M-coral-R, BM	SML, BCa	63, 40, 21
Filograna sp.		+	+		Mo, Lp, Dc, Pm, M-coral-R, Ant	NBa, Messina Strait, BCa, GMV	68, 7, 57, 16, 21, 69
Filogranula annulata (O.G. Costa, 1861)			+		Mo	SML	56
Filogranula gracilis Langerhans, 1884		+	+		Mo, Lp, Dc, M-coral-R, BM	SML, NBa, BCa	63, 68, 40, 57, 16, 21, 69
Filogranula stellata (Southward, 1963)		+	+		Mo, Lp, M-coral-R	SML, GoC	63, 40, 67
Flabelligeridae				+	M-coral-R	GoC	12
Galathowenia oculata (Zachs, 1923)				+	M-coral-R	GoC	12
Glycera tesselata Grube, 1840				+	M-coral-R	GoC	12
Goniadidae				+	M-coral-R	GoC	12
Haplosyllis chamaeleon Laubier, 1960	+			+	Pc	Chafarinas Islands	36
Haplosyllis spongicola (Grube, 1855)				+	M-coral-R	GoC	12
Harmothoe cf. *evei* Kirkegaard, 1980				+	M-coral-R	GoC	12
Harmothoe vesiculosa Ditlevsen, 1917	+				Mo, Lp	SML	40
Helmutneris flabellicola (Fage, 1936)			+		Fc	GMV	16
Hesionidae				+	M-coral-R	SML	40
Hyalopomatus madreporae Sanfilippo, 2009	+	+	+		Mo, Lp, Dc, Pm, BM	SML, BCa	56, 40, 57, 21
Hyalopomatus variorugosus Ben-Eliahu & Fiege, 1996		+	+		Mo, M-coral-R	NBa, SML	68, 56
Janita fimbriata (Delle Chiaje, 1822)			+		M-coral-R, BM	NBa, SML, BCa	68, 69, 40, 21
Lanice conchilega (Pallas, 1766)				+	BM	Cabliers Bank, GoC, FCa	45, 67, 33
Leiochrides sp.				+	M-coral-R	SML	40
Leitoscoloplos mammosus Mackie, 1987				+	M-coral-R	GoC	12
Leocrates atlanticus (McIntosh, 1885)			+		M-coral-R	GoC, SML	12, 40

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Lumbrineriopsis paradoxa (Saint-Joseph, 1888)				+	M-coral-R	GoC	12
Lumbrineris latreilli Audouin & Milne Edwards, 1834				+	M-coral-R	SML	40
Lumbrineris sp.				+	M-coral-R	SML	40
Lysidice ninetta Audouin & H Milne Edwards, 1833				+	M-coral-R	GoC	12
Lysippe cf. *fragilis* (Wollebaek, 1912)				+	M-coral-R	GoC	12
Magelona wilsoni Glémarec, 1966				+	M-coral-R	GoC	12
Maldanidae				+	M-coral-R	GoC	12
Metavermilia multicristata (Philippi, 1844)			+		Mo, Lp, Dc, M-coral-R, BM	SML, NBa, BCa	63, 68, 40, 57, 21, 69
Nephtys cf. *paradoxa* Malm, 1874				+	M-coral-R	SML	40
Nothria conchylega (Sars, 1835)				+	M-coral-R	SML	40
Notomastus sp.				+	M-coral-R	GoC	12
Oweniidae				+	M-coral-R	SML	40
Paradiopatra hispanica (Amoureux, 1972)				+	M-coral-R	GoC	12
Paraonidae				+	M-coral-R	GoC	12
Parasabella sp.				+	Encrusted calcareous sediments	BCa	3
Pareurythoe borealis (M. Sars, 1862)				+	M-coral-R	GoC	12
Phalacostemma sp.			+		M-coral-R	GoC,SML	12, 40
Pholoe sp.				+	M-coral-R	SML	40
Pholoides dorsipapillatus (Marenzeller, 1893)				+	M-coral-R	GoC	12
Phyllodoce cf. *maculata* (Linnaeus, 1767)				+	M-coral-R	GoC	12
Phyllodoce madeirensis Langerhans, 1880				+	M-coral-R	GoC	12
Phyllodoce mucosa Örsted, 1843				+	M-coral-R	SML	40
Pionosyllis nidrosiensis (Bidenkap, 1907)				+	M-coral-R	GoC	12
Placostegus tridentatus (Fabricius, 1779)		+	+		M-coral-R, BM	NBa, BCa	68, 69, 21
Poecilochaetus sp.				+	M-coral-R	GoC	12
Prionospio sp.				+	M-coral-R	GoC	12
Protula sp.				+	M-coral-R	NBa	68, 69
Protula tubularia (Montagu, 1803)				+	Mo, Dc	FCa	33
Sabella pavonina Savigny, 1822				+	Mo, Dc	FCa	33
Sabellidae				+	M-coral-R	GoC	12
Salmacina dysteri (Huxley, 1855)		+	+		Mo, Dc	FCa	33
Scolelepis sp.				+	M-coral-R	GoC	12
Semivermilia agglutinata (Marenzeller, 1893)			+		M-coral-R	NBa	68, 69
Serpula concharum Langerhans, 1880				+	BM	BCa	21
Serpula vermicularis Linnaeus, 1767		+	+		Mo, Lp, Dc, Dd, M-coral-R, BM	SML, NBa, BCa, CS	63, 68, 40, 3, 57, 21, 62, 69
Serpulidae				+	BM	GoC	67
Siboglinum sp.				+	M-coral-R	GoC	12
Sigalionidae				+	M-coral-R	GoC	12
Sphaerosyllis cf. *pirifera* Claparède, 1868				+	M-coral-R	GoC	12
Spiochaetopterus sp.				+	M-coral-R	GoC	12
Spiophanes sp.				+	M-coral-R	GoC	12
Subadyte pellucida (Ehlers, 1864)				+	Mo, Lp, M-coral-R	GoC, SML	12, 40
Synelmis sp.				+	M-coral-R	GoC	12
Terebellidae				+	M-coral-R	SML	40
Vermiliopsis monodiscus Zibrowius, 1968		+	+		Mo, Lp, Dc, M-coral-R, BM	NBa, SML, BCa	68, 40, 57, 21

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Vermiliopsis sp.			+		Mo, Dc, M-coral-R	NBa, SAS, FCa	68, 3, 33, 69
SIPUNCULA Sipunculidea							
Golfingiidae				+	M-coral-R	GoC	12
SIPUNCULA Phascolosomatidea							
Apionsoma murinae bilobatae (Cutler, 1969)				+	M-coral-R	SML	40
Aspidosiphon muelleri muelleri Diesing, 1851				+	M-coral-R	SML	40
MOLLUSCA Gastropoda							
Alvania cimicoides (Forbes, 1844)		+			coral-R	SML	52
Alvania testae (Aradas & Maggiore, 1844)				+	coral-R	SML	43
Anatoma tenuis (Jeffreys, 1877)				+	Mo, Lp, coral-R	SML	52
Anekes sculpturata Warén, 1992			+		coral-R	DBa	27
Babelomurex sentix Bayer, 1971				+	Mo, Lp, Dd, Cr	Malta	60
Callostracon thyrrenicum (Smriglio & Mariottini, 1996)				+	coral-R	SML	43
Cirsonella romettensis (Granata-Grillo, 1877)			+		coral-R	DBa	27
Coralliophila richardi (P. Fischer, 1882)	+				Mo, Lp	Malta	60
Coralliophila squamosa (Bivona Ant. in Bivona And., 1838)	+				Mo, Lp	Tuscan archip., NBa, GMV	60, 16
Danilia tinei (Calcara, 1839)			+		coral-R	SML, GMV	54, 16, 43
Emarginula adriatica (O.G. Costa, 1829)				+	Mo, Lp	SML, GMV	63, 54, 43
Emarginula multistriata Jeffreys, 1882				+	Mo, Lp, coral-R	SML, GMV	54, 16, 27, 43
Emarginula tenera Locard, 1892				+	Mo, Lp, coral-R	SML	43
Epitonium algerianum (Weinkauff, 1866)				+	Mo, Lp, coral-R	GMV	54, 16
Epitonium celesti (Aradas, 1854)			+		Mo, Lp, coral-R	GMV	54, 16
Fusinus rostratus (Olivi, 1792)				+	coral-R	SML	43
Iphitus tuberatus Jeffreys, 1883	+				Dc	Alboran Island, off Granada	39, 27
Lissotesta turrita (Gaglini, 1987)			+		Mo, Lp, coral-R	ChBa	27
Mitrella pallaryi (Dautzenberg, 1927)			+		Mo, Lp, coral-R	GMV	54, 16
Mathilda cochlaeformis Brugnone, 1873				+	coral-R	SML	43
Nassarius lima (Dillwyn, 1817)		+			coral-R	SML	52, 43
Pagodula echinata (Kiener, 1840)				+	coral-R	SML	52
Pleurotomella demosia (Dautz & Fischer, 1896)				+	coral-R	SML	43
Putzeysia wiseri (Calcara, 1842)			+		coral-R	SML	52, 43
Solatisonax bannocki (Melone & Taviani, 1980)			+		coral-R	SML	43
MOLLUSCA Bivalvia							
Abra longicallus (Scacchi, 1835)		+			coral-R	SML	52
Acesta excavata (Fabricius, 1779)	+				Mo, Lp	Dohrn canyon	Angeletti (comm. pers.)
Asperarca nodulosa (Müller, 1776)		+			Mo, Lp, HB, coral-R	SML, GMV	63, 40, 52, 54, 16, 43
Astarte sulcata (da Costa, 1778)			+		coral-R	GMV	54, 16
Bathyarca philippiana (Nyst, 1848)		+			Mo, Lp, coral-R	SML, GMV	63, 54, 43
Coralliophaga lithophagella (Lamarck, 1819)				+	Mo, Lp, coral-R	GMV	16
Cyclopecten hoskynsi (Forbes, 1844)			+		coral-R	SML	52
Delectopecten vitreus (Gmelin, 1791)			+		Mo, Lp	SML, BCa	63, 21, 43
Ennucula aegeensis (Forbes, 1844)			+		coral-R	SML	52, 43
Rocellaria dubia (Pennant, 1777)				+	Mo, Lp, coral-R	GMV	16
Heteranomia squamula (Linnaeus, 1758)		+			Mo, Lp, coral-R	SML	52, 43
Hiatella arctica (Linnaeus, 1767)				+	coral-R	SML	43
Karnecampia sulcata (Müller, 1776)			+		coral-R	SML	43
Kelliella miliaris (Philippi, 1844)				+	coral-R	SML	52

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Ledella messanensis (Jeffreys, 1870)			+		coral-R	SML	52
Lima marioni Fischer, 1882			+		Mo, Lp, coral-R	GMV	54, 16
Limopsis aurita (Brocchi, 1814)		+			coral-R	GMV	16
Limea crassa (Forbes, 1844)				+	coral-R	SML	52
Neopycnodonte cochlear (Poli, 1795)		+			Mo, Lp	Lacaze-Duthier	22
Neopycnodonte zibrowii Gofas, Salas & Taviani, 2009				+	Mo, Lp	Sicilian channel	24
Heteranomia squamula (Linnaeus, 1758)		+			Mo, Lp, coral-R	SML	52
Spondylus gussonii (O.G. Costa, 1829)			+		Mo, Lp	SML, Cassidaigne, GMV	63, 22, 27, 49, 43
Yoldiella lucida (Lovén, 1846)				+	coral-R	SML	52
MOLLUSCA Scaphopoda							
Antalis agilis (M. Sars in G.O. Sars, 1872)				+	coral-R	SML	52
MOLLUSCA Cephalopoda							
Onychoteuthis banksii (Leach, 1817)				+	Mo, Lp, HB	SML	19
Pteroctopus tetracirrhus (Delle Chiaje, 1830)				+	Mo, Lp, HB	SML	19
Todarodes sagittatus (Lamarck, 1798)				+	Mo, Lp	BCa	21
CRUSTACEA Amphipoda							
Amphipoda				+	Mo	CCCa	38
Harpinia dellavallei Chevreux, 1910				+	Mo	CCCa	38
Iphimedia obesa Rathke, 1843				+	Mo	CCCa	38
Melphidippella macra (Norman, 1869)				+	Mo	CCCa	38
Normanion ruffoi Diviacco & Vader, 1988				+	Mo	CCCa	38
Paraphoxus oculatus (G. O. Sars, 1879)				+	Mo	CCCa	38
Perrierella audouiniana (Bate, 1857)				+	Mo	CCCa	38
Platyscelus ovoides (Risso, 1816)				+	Mo	CCCa	38
Primno sp.				+	Mo	CCCa	38
Vibilia armata Bovallius, 1887				+	Mo	CCCa	38
CRUSTACEA Cirripedia							
Megabalanus tulipiformis (Ellis, 1758)				+	Mo, Lp	Sardinia, Sicily	48
Metaverruca recta (Aurivillius, 1898)			+		Mo, Lp	SML	15
Pachylasma giganteum (Philippi, 1836)			+		Mo, Lp, coral-R	Messina Strait, Malta	48, 58
Scalpellum scalpellum (Linnaeus, 1767)				+	Mo, Lp	SML	15
CRUSTACEA Copepoda							
Acartia sp.				+	Mo	CCCa	38
Calanus helgolandicus (Claus, 1863)			+		Mo	CCCa	38
Calanoida			+		Mo	CCCa	38
Centropages sp.				+	Mo	CCCa	38
Diaixis pygmaea (Scott T., 1894)		+			Mo	CCCa	38
Harparcticoida				+	Mo	CCCa	38
Oithonak sp.				+	Mo	CCCa	38
Pleuromamma sp.				+	Mo	CCCa	38
CRUSTACEA Decapoda							
Acanthephyra eximia Smith, 1884			+		Mo, Lp	SML	63
Anamathia rissoana (Roux, 1828)			+		Mo, Lp, Dd	SML, Malta, CS	58, 40, 62
Aristaeomorpha foliacea (Risso, 1827)			+		Mo, Lp	SML	63
Aristeus antennatus (Risso, 1816)			+		Mo, Lp	SML	63, 19
Bathynectes maravigna (Prestandrea, 1839)			+		Mo, Lp, coral-R	SML, DBa, EM	63, 3
Ebalia nux A. Milne-Edwards, 1883			+		coral-R	SML	52
Ebalia sp.			+		Mo, Lp, Dd	CS	62
Geryon longipes A. Milne-Edwards, 1882				+	Mo, Lp	SML	40
Homola barbata (Fabricius, 1793)			+		Mo, Lp, Dd	CS	62

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Inachus leptochirus Leach, 1817			+		Mo, Lp, HB	GMV	16
Jaxea nocturna Nardo, 1847				+	Mo	CCCa	38
Macropipus tuberculatus (Roux, 1830)				+	Mo, Lp	SML	40
Monodaeus couchii (Couch, 1851)			+		Mo, Lp	SML, GMV	63, 16
Munida intermedia A. Milne Edwards & Bouvier, 1899			+		Mo, Lp	SML, GMV	63, 16
Munida sp.			+		Mo, coral-R	ChBa, CCCa	45, 38
Munida tenuimana Sars, 1872			+		Mo, Lp	SML, CS	40, 62
Paguridae			+		Mo, Lp	SML, CCCa	40, 38
Palinurus mauritanicus Gruvel, 1911				+	Mo, Lp	DBa, EM	45, 3
Paromola cuvieri (Risso, 1816)			+		Mo, Lp, Dd	BCa, CS	21, 62
Philocheras bispinosus (Hailstone, 1835)				+	Mo	CCCa	38
Plesionika acanthonotus (Smith, 1882)			+		Mo, Lp	SML	63
Plesionika cf. *gigliolii* (Senna, 1902)				+	Mo, Lp, Dd	CS	62
Plesionika heterocarpus(A. Costa, 1871)			+		Mo, Lp	SAS	61
Plesionika martia (A. Milne-Edwards, 1883)			+		Mo, Lp, coral-R	SML	40, 19
Plesionika sp.			+		Mo, Lp, Dd	CS	62
Polycheles typhlops Heller, 1862			+		Mo, Lp	SML	40
Scyllarus arctus (Linnaeus, 1758)				+	Mo, Lp	AS	45
CRUSTACEA Euphausiacea							
Euphasiacea					Mo, Lp, Dd	CS	62
Nyctiphanes couchii (Bell, 1853)			+		Mo	CCCa	38
Stylocheiron suhmi G.O. Sars, 1883				+	Mo, Lp	SML	40
CRUSTACEA Isopoda							
Gnathia sp.				+	Mo	CCCa	38
CRUSTACEA Mysidacea							
Anchialina agilis (G.O. Sars, 1877)				+	Mo	CCCa	38
Leptomysis gracilis (G.O. Sars, 1864)				+	Mo	CCCa	38
Lophogaster typicus Sars, 1857				+	Mo	CCCa	38
Siriella sp.				+	Mo	CCCa	38
CRUSTACEA Ostracoda							
Bairdoppilata conformis (Terquem, 1878)			+		Mo, Lp, coral-R	SML	59
Bythocypris obtusata (Sars, 1866)			+		Mo, Lp, coral-R	SML	59
ECHINODERMATA Echinoidea							
Brissopsis atlantica mediterranea Mortensen, 1913				+	Mo, Lp	SML	40
Cidaris cidaris (Linnaeus, 1758)			+		Mo, Lp, Ant, Dc, Dd, Cr	SAS, BCa, SML, Malta, CS, GoL, DBa, CaBa, ChBa, GMV, EM	63, 58, 40, 66, 45, 3, 13, 22, 55, 33, 18, 54, 62, 32
Echinus melo Lamarck, 1816			+	+	Mo, Lp, Dd, Dc, Cr	BCa, SML, CS, GoL, FCa, ChBa, DBa	40, 3, 13, 22, 33, 62, 32
Gracilechinus acutus (Lamarck, 1816)			+	+	Mo, Lp, Dd, Dc, Cr	BCa, SML, GoL, FCa, ChBa, GMV	40, 13, 22, 21, 33, 54, 18
ECHINODERMATA Holothuroidea							
Holothuria forskali Delle Chiaje, 1823			+		Mo, Dc, Cr, Dd	FCa, ChBa	13, 33
Holothuria tubulosa Gmelin, 1791			+		Mo, Lp, Dd	ChBa	13
Mesothuria intestinalis (Ascanius, 1805)				+	Mo, Lp	SML	40
Parastichopus regalis (Cuvier, 1817)			+		Mo, Lp, Dd	SML, ChBa	63, 40, 13
Psolidium complanatum Cherbonnier, 1969	+				Mo, Lp, Dd	NBa	68
ECHINODERMATA Ophiuroidea							
Amphiura filiformis (O.F. Müller, 1776)			+		Mo, Lp	BCa, SML	63, 40, 21
Astrospartus mediterraneus (Risso, 1826)			+		Mo, Dc, Cr	GoL, FCa	22, 33
Ophiothrix fragilis (Abildgaard in O.F. Müller, 1789)			+		Mo, Lp, Dd	ChBa, EM	13, 3

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Ophiothrix quinquemaculata (Delle Chiaje, 1828)			+		Mo	BCa	21
Ophiothrix sp.			+		Mo, Lp, Dc, Cr	FCa, GMV, GCa	33, 54, 65
ECHINODERMATA Asteroidea							
Chaetaster longipes (Retzius, 1805)				+	Mo, Lp	GMV	16
Hacelia superba H.L. Clark, 1921		+			Mo, Lp, Dc	GMV	53, 54
Odontaster mediterraneus (Marenzeller, 1893)				+	Mo, Lp	SML	40, 66
Odontaster sp.				+	Mo, Lp, Ant, Dc	SAS	3
Peltaster placenta (Müller & Troschel, 1842)				+	Mo, Lp, Ant, Cv, Dc, Dd	BCa, Malta, CS	3, 14, 62
ECHINODERMATA Crinoidea							
Leptometra phalangium (Müller, 1841)			+		Mo, Lp, Ant	NWSicily, DBa, CaBa, GMV	45, 9, 16, 55
BRYOZOA Gymnolaemata							
Aetea sica (Couch, 1844)				+	Mo	SML	40
Aetea truncata (Landsborough, 1852)				+	Mo	BCa	21
Amphiblestrum ruggeroi Rosso, 1999			+		Mo, Lp	CM	68
Buskea dichotoma (Hincks, 1862)				+	Mo	CM	68
Callopora dumerilii (Audouin, 1826)				+	Mo, Lp	CM	68
Cellaria salicornioides Lamouroux, 1816				+	Mo, Lp	CM	68
Copidozoum exiguum (Barroso, 1920)				+	Mo, Lp	CM, IonianSea, SML, SoS	29, 68, 51, 40, 52
Copidozoum tenuirostre (Hincks, 1880)			+		Lp	CM	68
Copidozoum planum (Hincks, 1880)				+	Dd	WM	26
Copidozoum balgimae Reverter-Gil & Fernandez-Pulpeiro, 1999				+	Mo	AS	28
Coronellina fagei Gautier, 1962				+	Mo	SoS	29
Crassimarginatella crassimarginata (Hincks, 1880)				+	Mo	CM, WM	68, 26
Crepis harmelini Reverter-Gil, Souto & Fernández-Pulpeiro, 2011				+	Mo, Lp	SoG	29
Distansescharella alcicornis (Jullien, 1882)				+	Mo, Lp	SoG	31
Escharella acuta Zabala, Maluquer & Harmelin, 1993				+	Lp	CM	68
Escharella longicollis (Jullien, 1882)				+	Mo, Lp	SoG	31
Escharella octodentata (Hincks, 1880)				+	Lp	CM	68
Escharella ventricosa (Hassal, 1842)				+	Mo, Dc	WM, SML	25, 26
Escharina dutertrei protecta Zabala, Maluquer & Harmelin, 1993				+	Mo, Lp, Dc	CM, WM, Toulon	23, 24, 65
Escharina vulgaris (Moll, 1803)				+	Mo, Lp	CM, BCa	68, 2
Fenestrulina malusii (Audouin, 1826)				+	Mo, Lp	CM	68
Gregarinidra gregaria (Heller, 1867)				+	Mo, Lp	CM, BCa, WM	26, 68, 21
Haplopoma sciaphilum Silén & Harmelin, 1976				+	Mo	SoS	29
Herentia hyndmanni (Johnston, 1847)			+		Mo, Lp, Dc	CM, SML, BCa, WM, SoS	25, 26, 29, 68, 5, 40, 52, 21
Hincksina longispinosa Harmelin & d'Hondt, 1992a				+	Mo	SoG	30
Hippomenella mucronelliformis (Waters, 1899)				+	Mo	BCa	21
Hippothoa flagellum Manzoni, 1870				+	Mo, Lp	CM	68
Mollia patellaria (Moll, 1803)				+	Mo	WM	26
Myriapora truncata (Pallas, 1766)				+	Mo, Lp	BCa	24
Neolagenipora eximia (Hincks, 1860)			+		Mo, Lp	CM	68
Onychocella marioni (Jullien, 1882)				+	Mo	WM	26
Palmiskenea gautieri Madurell, Zabala, Domínguez-Carrió & Gili, 2013				+	Dc	WM	24

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Palmiskenea skenei (Ellis & Solander, 1786)				+	Lp	CM	68
Porella minuta (Norman, 1868)				+	Mo	WM	26
Cribrilaria hincksii (Friedl, 1917)				+	Lp	CM	68
Cribrilaria innominata (Couch, 1844)				+	Mo	CM	68
Cribrilaria radiata (Moll, 1803)				+	Mo, Lp	CM, BCa	68, 2
Cribrilaria pseudoradiata Harmelin & Aristegui, 1988				+	Mo	SML	40
Cribrilaria venusta (Canu & Bassler, 1925)				+	Mo, Dc	BCa, WM, SML	21, 25, 26
Puellina setosa (Waters, 1899)				+	Mo	SoS	29
Puellina scripta (Reuss, 1848)				+	Mo, Lp, Ca	AS	31
Glabrilaria pedunculata (Gautier, 1956)				+	Mo, Dc	BCa, Toulon, SoS, SML	25, 29, 40, 21
Reteporella sparteli (Calvet, 1906)				+	Mo, Lp	SML	52
Schizomavella cf. *discoidea* (Busk, 1859)				+	Mo	BCa	21
Schizomavella fischeri (Jullien, 1882)				+	Mo, Lp	SML	40, 5
Schizomavella linearis (Hassall, 1841)				+	Mo, Lp, Dc	CM, BCa	68, 2
Schizomavella neptuni (Jullien, 1882)				+	Mo, Lp	CM, SML, SoS	29, 68, 40, 52
Schizoretepora longisetae (Canu & Bassler, 1928)				+	Dc	WM	26
Scrupocellaria delilii (Audouin, 1826)				+	Mo, coral-R	CM, BCa, SML, CS	68, 52, 21, 62
Scrupocellaria incurvata Waters, 1896				+	Mo, Dc	CM, WM, SML	25, 26, 68
Setosella cavernicola Harmelin, 1978				+	Mo	SoS	29
Setosella vulnerata (Busk, 1860)				+	Mo, Lp	CM, SML	68, 40
Smittina cervicornis (Pallas, 1766)				+	Mo, Lp, Dc	SAS, BCa	57, 62
Smittina crystallina (Norman, 1867)			+		Mo, Lp	CM, BCa, SML, IonianSea	68, 51, 40, 52, 21
Smittoidea ophidiana (Waters, 1879)				+	Mo, Lp	CM, BCa	68, 2
Smittoidea reticulata (MacGillivray, 1842)				+	Mo, Lp	CM	68
Stephanollona armata (Hincks, 1862)				+	Mo	WM	26
Stephanotheca arrogata (Waters, 1879)				+	Mo	SoS, BCa, WM	26, 2
Stephanotheca watersi Reverter-Gil, Souto & Fernández-Pulpeiro, 2012				+	Mo	BCa	20
Tessaradoma boreale (Busk, 1860)		+			Mo, Lp	SML	40, 52
Teuchopora edwardsi (Jullien, 1882)				+	Mo, Lp	SoG	31
Turbicellepora coronopus (Wood, 1844)				+	Mo, Lp	CM, BCa	68, 2
BRYOZOA Stenolaemata							
Anguisia verrucosa Jullien, 1882				+	Mo	SML	40
Crisia ramosa Harmer, 1891				+	Mo	BCa	21
Crisia sigmoidea (Waters, 1916)				+	Mo	CM	68
Crisia tenella Calvet, 1906				+	Mo	SML, BCa	40, 52, 21
Entalophoroecia deflexa (Couch, 1844)				+	Mo, Lp	CM, BCa, SoS	29, 68, 21
Entalophoroecia robusta Harmelin, 1976				+	Lp	CM	68
Exidmonea coerulea (Harmelin, 1976)				+	Lp	CM	68
Exidmonea flexuosa (Pourtalès, 1867)				+	Mo, Lp	SoG	31
Plagioecia patina (Lamarck, 1816)			+		Mo, Lp	CM	68
Plagioecia inoedificata (Jullien, 1882)				+	Mo	SoS	29
Stomatopora gingrina Jullien, 1882				+	Mo	CM, SoS	29, 68
Tervia barrieri Rosso, 1998				+	Mo, Lp	SML	52
BRACHIOPODA Rhynchonellata							
Gryphus vitreus (Born, 1778)				+	Mo, Lp, coral-R, Lp, Dd, HB	NBa, SML, CS, CCCa, ChBa, DBa, GMV	34, 68, 40, 38, 16, 17, 62, 32
Megathiris detruncata (Gmelin, 1791)				+	coral-R, HB	NBa, ChBa	34, 68
Megerlia truncata (Linnaeus, 1767)			+		Mo, Lp, coral-R, HB	NBa, SML, CS, CCCa, ChBa	34, 68, 40, 1, 38, 62, 17
Platidia sp.				+	coral-R	NBa	68
Terebratulina retusa (Linnaeus, 1758)		+			coral-R, HB	CS, ChBa	34, 1, 62

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
BRACHIOPODA Craniata							
Novocrania anomala (O. F. Müller, 1776)				+	Mo, Lp, coral-R, HB	SAS, CS, ChBa, GMV	34, 3, 16, 62
Novocrania sp.				+	coral-R	NBa	68
FISH Actinopteri							
Acantholabrus palloni (Risso, 1810)				+	Mo	CS	62
Arctozenus risso (Bonaparte, 1840)				+	Mo, Lp	SML, DBa	19, 3
Aulopus filamentosus (Bloch, 1792)				+	Mo, Lp	SML	19
Bathypterois dubius Vaillant, 1888				+	Mo, Lp	SML	63
Benthocometes robustus (Goode and Bean, 1886)				+	Mo, Lp	SML, CS	63, 19, 62
Brama brama (Bonnaterre, 1788)				+	Mo, Lp	SML	18, 20
Capros aper (Linnaeus, 1758)				+	M-coral-R	EM	32
Chlorophthalmus agassizi Bonaparte, 1840				+	Mo, Lp	SML, CS	19, 62
Coelorinchus caelorhincus (Risso, 1810)			+		Mo, Lp	SML, CaBa, CS, EM	63, 19, 45, 62, 32
Conger conger (Linnaeus, 1758)			+		Mo, Lp, Ant	SML, CaBa, CIs	63, 18, 19, 20, 45, 42
Coryphaena hippurus Linnaeus, 1758				+	Mo, Lp	SML	18
Epigonus constanciae (Giglioli, 1880)				+	Mo	CS	62
Gadella maraldi (Risso, 1810)				+	Mo, coral-R	GMV	16
Helicolenus dactylopterus (Delaroche, 1809)			+		Mo, Lp, Ant	SML, CaBa, CIs, Malta, CS, GMV, EM	63, 18, 19, 20, 45, 42, 4, 62, 16, 32
Hoplostethus mediterraneus Cuvier, 1829				+	Mo, Lp	SML, CaBa	63, 45
Hymenocephalus italicus Giglioli, 1884				+	Mo, Lp	SML	63, 19
Lepidion lepidion (Risso, 1810)				+	Mo, Lp	SML	63, 19
Lepidopus caudatus (Euphrasen, 1788)			+		Mo, Lp, Ant	SML, Malta, CS, GMV	18, 19, 20, 4, 62, 16
Lepidorhombus whiffiagonis (Walbaum, 1792)				+	Mo	CS	62
Macroramphosus scolopax (Linnaeus, 1758)				+	Ant	Malta	4
Merluccius merluccius (Linnaeus, 1758)			+		Mo, Lp, Ant	SML, CIs	18, 19, 20, 42
Micromesistius poutassou (Risso, 1826)			+		Mo, Lp, Ant	SML, CaBa, DBa, CIs, GMV	18, 20, 45, 42, 16
Molva dipterygia (Pennant, 1784)				+	Mo, Lp	SML	18, 20
Mora moro (Risso, 1810)				+	Mo, Lp, Ant	SML, CIs	63, 18, 19, 20, 42
Nettastoma melanurum Rafinesque, 1810				+	Mo, Lp	SML	19
Nezumia aequalis (Günther, 1878)				+	Ie	GMV	16
Nezumia sclerorhynchus (Valenciennes, 1838)				+	Mo, Lp	SML	63, 19
Notacanthus bonaparte Risso, 1840				+	Mo, Lp	SML	63, 19
Pagellus bogaraveo (Brünnich, 1768)			+		Mo, Lp	SML, CaBa, ChBa, CS, EM	18, 19, 20, 45, 62, 32
Phycis blennoides (Brünnich, 1768)			+		Mo, Lp, Ant	SML, CIs, CS, GMV, EM	63, 18, 19, 20, 42, 62, 16, 32
Polyprion americanus (Bloch and Schneider, 1801)				+	Mo, Lp, Ant	SML, Malta, CS, DBa	20, 4, 62, 32
Ruvettus pretiosus Cocco, 1833				+	Mo, Lp	SML	18
Scorpaena elongata Cadenat, 1943				+	Mo	CS	62
Scorpaena scrofa Linnaeus, 1758				+	Mo, Lp	Dba, CaBa	45
Sudis hyalina Rafinesque, 1810				+	Mo, Lp	SML	19
FISH Elasmobranchii							
Centrophorus granulosus (Bloch and Schneider, 1801)				+	Mo, Lp	SML	18, 20
Chimaera monstrosa Linnaeus, 1758				+	Mo, Lp	SML	63, 19
Dalatias licha (Bonnaterre, 1788)				+	Mo, Lp	SML, CaBa	63, 45
Dipturus oxyrinchus (Linnaeus, 1758)				+	Mo, Lp	SML	63, 18, 20

(continued)

Table 29.1 (continued)

Species	S	D	C	O	Habitats	Locations	References
Etmopterus spinax (Linnaeus, 1758)			+		Mo, Lp	SML	63, 18, 19, 20
Galeus melastomus Rafinesque, 1810			+		Mo, Lp	SML, GMV, ChBa	63, 18, 19, 20, 16, 13
Hexanchus griseus (Bonnaterre, 1788)				+	Mo, Lp	SML	18
Leucoraja circularis (Couch, 1838)				+	Mo, Lp	SML	18, 20
Leucoraja fullonica (Linnaeus, 1758)				+	Mo, Lp	SML	20
Prionace glauca (Linnaeus, 1758)				+	Mo, Lp	SML	20
Pteroplatytrygon violacea (Bonaparte, 1832)				+	Mo, Lp	SML	20
Scyliorhinus canicula (Linnaeus, 1758)				+	M-coral-R	EM	32
Squalus blainville (Risso, 1827)				+	Ant	CIs	42

Codes for habitat-forming species and bottom types: *Mo Madrepora oculata*, *Lp Lophelia pertusa*, *Dd Desmophyllum dianthus*, *Dc Dendrophyllia cornigera*, *Cr Corallium rubrum*, *Cs Caryophyllia smithii*, *Ca Caryophyllia cyathus*, *Fc Flabellum chunii*, *Cv Callogorgia verticillata*, *Lg Leiopathes glaberrima*, *Ie Isidella elongata*, *Sv Stenocyathus vermiformis*, *Pc Paramuricea clavata*, *Ant* Anthipatarian banks, *Pm Pachastrella monilifera*, *SB* soft bottoms, *HB* hard bottoms, *RBB* rocky benches and boulders, *BM* bathyal mud, *coral-R* coral rubble, *M-coral-R* mud mixed with coral-R

Codes for locations: *SoG* Strait of Gibraltar, *SoS* Strait of Sicily, *GoC* Gulf of Cadiz, *GoL* Gulf of Lion, *WM* western Mediterranean, *AS* Alboran Sea, *SAS* South Adriatic Sea, *CM* Catalan margin, *CS* Capo Spartivento, *SML* Santa Maria di Leuca, *BCa* Bari canyon, *FCa* La Fonera canyon, *CCCa* Cap de Creus canyon, *GCa* Guadiaro canyon, *CCa* Cassidaigne canyon, *SCa* Sicié canyon, *PCa* Planier canyon, *CaBa* Cabliers bank, *DBa* Djinouti bank, *ChBa* Chella bank, *NBa* Nameless bank, *LIs*, Linosa island, *CIs*, Kephalonia island, *GMV* Gazul mud volcano, *EM* East Melilla

Codes for references: 1. Aguilar et al. (2011), 2. Álvarez-Pérez et al. (2005), 3. Angeletti et al. (2014), 4. Angeletti et al. (2015), 5. Berning et al. (2008), 6. Beuck et al. (2010), 7. Bo et al. (2009), 8. Bo et al. (2012), 9. Bo et al. (2014), 10. Calcinai et al. (2013), 11. Costantini et al. (2010), 12. Da Silva (2009), 13. de la Torriente et al. (2014), 14. Deidun et al. (2015), 15. Di Geronimo (2010), 16. Díaz del Rio et al. (2014), 17. Domínguez-Carrió et al. (2014), 18. D'Onghia et al. (2010), 19. D'Onghia et al. (2011), 20. D'Onghia et al. (2012), 21. D'Onghia et al. (2015), 22. Fabri et al. (2014), 23. Fabri et al. (2017), 24. Angeletti, Taviani pers. obs., 25. Gautier (1958), 26. Gautier (1962), 27. Gofas et al. (2011), 28. Gori et al. (2013), 29. Harmelin (1979), 30. Harmelin and d'Hondt (1992a), 31. Harmelin and d'Hondt (1992b), 32. Hebbeln et al. (2009), 33. Lastras et al. (2016), 34. Llompart (1988), 35. Longo et al. (2005), 36. López et al. (1996), 37. López-González and Cunha (2010), 38. Madurell et al. (2012b), 39. Margelli et al. (1995), 40. Mastrototaro et al. (2010), 41. Moura et al. (2007), 42. Mytilineou et al. (2014), 43. Negri and Corselli (2016), 44. Orejas et al. (2009), 45. Pardo et al. (2011), 46. present study (INDEMARES/CHICA project), 47. Ramil and Vervoort (1992), 48. Relini (1980), 49. Remia and Taviani (2005), 50. Rossi (1958), 51. Rosso (2003), 52. Rosso et al. (2010), 53. Rueda et al. (2011), 54. Rueda et al. (2016), 55. Sánchez-Gallego et al. (2014), 56. Sanfilippo (2009), 57. Sanfilippo et al. (2013), 58. Schembri et al. (2007), 59. Sciuto and Rosso (2015), 60. Taviani et al. (2009), 61. Taviani et al. (2016), 62. Taviani et al. (2017), 63. Tursi et al. (2004), 64. Vacelet (1969), 65. Vázquez et al. (2016), 66. Vertino et al. (2010), 67. Wienberg et al. (2009), 68. Zabala et al. (1993), 69. Zibrowius and Taviani (2005)

2006). In the western Mediterranean, Maynou and Cartes (2012) observed that areas with large stands of *Isidella elongata* support higher species richness, abundance and biomass of crustaceans compared to close muddy bottoms where *Isidella* was not present. These communities present an overall high invertebrate diversity, with a faunal assemblage comprising about 170 invertebrate taxa and 61 species of fish (Mastrototaro et al. 2017).

The CWC habitats generally provide a wide diversity of food sources due to the increased local biodiversity, as a result of the habitat complexity, and the large and wide variety of species that benefit from that (Mastrototaro et al. 2010, 2017). In general, sediments in areas occupied by CWCs display higher quantity and greater nutritional quality of organic matter (Bongiorni et al. 2010). Moreover, CWC habitats frequently occur in areas with high hydrodynamic conditions and food supply that favor the presence of other sessile suspensivores (e.g. sponges, gorgonians, black corals) (e.g. Domínguez-Carrió et al. 2014; Rueda et al. 2016). An increase of prey diversity and density is suggested to occur in both Atlantic and Mediterranean CWC habitats for some commercial species, such as *Helicolenus dactylopterus* which feeds on benthic crustaceans, fishes as well as planktonic organisms that generally occur in these habitats (Mortensen 2000; D'Onghia et al. 2012). Specific food sources of CWC habitats are CWC themselves, which are consumed by gastropods that are strictly associated with CWC (e.g. Muricidae-Coralliophilinae, Nystiellidae, Epitoniidae) (Taviani et al. 2009).

The CWC habitats may provide an important spawning, nursery and/or shelter area for mobile species from adjacent habitats (D'Onghia et al. 2010, 2012; Maynou and Cartes 2012; Mastrototaro et al. 2017; Chimienti et al., this volume; D'Onghia, this volume). Some species may occur at higher densities (*Pagellus bogaraveo, Conger conger, H. dactylopterus*) or display larger sizes (*Galeus melastomus, Etmopterus spinax, C. conger, H. dactylopterus*) in Mediterranean CWC habitats in comparison to adjacent bottoms (D'Onghia et al. 2012). Regarding invertebrate commercial species, Maynou and Cartes (2012) observed that some of them were more abundant or reached larger sizes in areas with high densitiy of *I. elongata*, particularly the red shrimp *Aristeus antennatus* and *Plesionika martia*. Nevertheless, it is difficult to demonstrate whether these species are less abundant in adjacent sedimentary habitats due to the fishing effects rather than more abundant in CWC habitats due to the increased habitat complexity and prey abundance and diversity (D'Onghia et al. 2012; Mastrototaro et al. 2017). Regarding this, D'Onghia et al. (2010) indicated that future research must address the importance of CWC habitats as an "essential fish habitat" (EFH) for creating "Deep-sea Fisheries Restricted Areas" (FRA) as implemented by the General Fisheries Commission for the Mediterranean (GFCM) (see also D'Onghia, this volume).

29.3 Spatial Differentiation of the CWC Associated Fauna in the Atlanto-Mediterranean Context

Studies on fauna associated with CWC have been done in different areas of the Mediterranean Sea and at different bathymetric ranges. Nevertheless, due to the difficulty of sampling CWC habitats, different methodological approaches were used and this creates difficulties when comparing spatial and bathymetric patterns of the CWC associated fauna. A high biodiversity has been found in CWC habitats of SML in comparison to other Mediterranean locations. This is surely the result of extensive multi-gear sampling and the collaboration of experts working on different taxonomic groups, therefore biodiversity comparisons with other studied coral provinces must take this into consideration (Mastrototaro et al. 2010; Chimienti et al., this volume). Similar detailed faunistic studies should be done in other newly discovered Mediterranean CWC habitats that are located in different environmental scenarios (e.g. hydrodynamics, depth, exposure to the Levantine Intermediate Water (LIW)), different seafloor geomorphic features (e.g. submarine canyons, seamounts) and levels of disturbance due to anthropogenic activities (e.g. bottom trawling). Nevertheless, it is clear that Mediterranean CWC habitats containing live and dead CWC seem to provide a higher biodiversity of different ecosystemic components (e.g. meiofauna, macrofauna) than surrounding soft bottoms because these complex habitats act like "oases in the desert" in deep-sea Mediterranean areas (Bongiorni et al. 2010; Mastrototaro et al. 2010).

It has been suggested that Mediterranean CWC habitats are less diverse than their NE Atlantic counterparts, in response to a variety of historical, oceanographic and climatic factors which conspired in shaping the deep-sea Mediterranean benthic and demersal fauna (Zibrowius 1980; Fredj and Laubier 1983; Fredj and Maurin 1987; Bouchet and Taviani 1992; Vertino et al. 2014, this volume). As documented for Atlantic CWC habitats, important components of the Mediterranean CWC associated fauna seem to also include sponges, molluscs, bryozoans and cnidarians (Jensen and Frederiksen 1992; Mastrototaro et al. 2010; Chimienti et al., this volume). Some of the common and dominant associated taxa are similar in both basins (e.g. *Eunice norvegica, Coralliophila richardi, Asperarca nodulosa, Delectopecten vitreus*, *Heteranomia squamula,* etc.), but some of the typical associated species in Atlantic CWC habitats are generally absent or uncommon in Mediterranean ones (Jensen and Frederiksen 1992; Tursi et al. 2004; López-Correa et al. 2005; Mortensen and Fosså 2006; Mastrototaro et al. 2010). Nevertheless, recent surveys using ROV are providing new data on Atlantic species occurring on Mediterranean CWC habitats (Mastrototaro et al. 2017). One of the typical components on Atlantic CWC habitats is the bivalve *Acesta excavata* which seems to be very rare in CWC habitats of the Mediterranean Sea and the GoC (López-Correa et al. 2005). This mollusc is the largest known bivalve associated with CWC and was widespread throughout the Mediterranean Sea during the last glacial period, and live-individuals still occur in different parts of the western Mediterranean, for instance in the Var and Dohrn canyons (North Tyrrhenian Sea) (López-Correa et al. 2005) (Fig. 29.2).

As reported for the Atlantic banks (Jensen and Frederiksen 1992; Mortensen and Fosså 2006), there is generally not a specific fauna associated with CWC habitats (Mastrototaro et al. 2010). In agreement with Roberts et al. (2009), species recorded within or around CWC banks are drawn from the regional species pool and could be found in other habitats rather than being restricted to the CWC habitat in an obligate sense. There are over 1300 known species living on *Lophelia pertusa* reefs in the NE Atlantic (Roberts et al. 2006), and less than a half of the species (ca 520 taxa listed in this study) have been recorded in Mediterranean CWC habitats so far (mostly from biodiversity studies of SML) (Bongiorni et al. 2010; Mastrototaro et al. 2010; Vertino et al. 2010; Negri and Corselli 2016) (Table 29.1). Consequently, it is reasonable to assume that the Mediterranean CWC community is potentially less rich in species, although additional biodiversity studies on the benthic and demersal assemblages on different CWC sites (e.g. Alborán Sea, Catalan-Provençal-Ligurian canyons, SoS) are still needed for detailed and faithful Atlanto-Mediterranean comparisons. In line with this, several authors have highlighted that the biodiversity of the deep benthic Mediterranean fauna, including that of CWC habitats, is lower compared to that of coastal areas where highly diverse benthic communities have been generally reported in threedimensionally complex habitats (Pérès 1985; Boudouresque 2004; Emig and Geistdoerfer 2004; Templado 2014). Regarding CWC habitats, the associated communities seem to be less biodiverse than those from the Atlantic Ocean.

29.4 Associated Fauna of CWC Habitats in the Mediterranean Sea and Adjacent Areas

29.4.1 Poriferans

Sponges are common components of Atlantic and Mediterranean CWC habitats, displaying high species richness and biomass that increase in turn the benthic heterogeneity and the number of available microhabitats (Longo et al. 2005; Freiwald et al. 2009). Likewise, it cannot be discarded that the participation of the sponge fauna in the benthic-pelagic coupling of local fluxes of dissolved inorganic nutrients (N, Si, C, P) and particulate suspended food (organic Carbon) may significantly contribute to fuel the basal steps of the trophic web in CWC habitats, as it is known to occur in other marine environments (Maldonado et al. 2012).

If the functional role of sponges in Mediterranean CWC habitats is far from being fully understood, the knowledge on the taxonomic composition of the associated or co-occuring sponge fauna is not much better known for most of the CWC provinces in the Mediterranean. One of the earliest studies specifically on the sponge fauna was addressed by Vacelet (1969), who documented the sponge assemblages from bathyal hard bottoms with CWCs in the Gulf of Lion (NW Mediterranean Sea). Currently, most of the available information about the sponge fauna of CWC habitats comes from SML and Bari canyon CWC provinces. There, sponges become the second most abundant component (i.e. number of individuals) of the benthic assemblages (Longo et al. 2005; Anonymous 2009; Freiwald et al. 2009; Mastrototaro et al. 2010; Calcinai et al. 2013; Angeletti et al. 2014; D'Onghia et al. 2015; Taviani et al. 2016), and the encrusting desmosponges of the order Poecilosclerida are the most common taxonomic group (Longo et al. 2005; Calcinai et al. 2013) (Table 29.1). Studies by Longo et al. (2005) and Mastrototaro et al. (2010) reported the occurrence of 36 species in SML, overgrowing in many cases dead branches of CWC colonies. The assemblage was dominated by small and encrusting sponges including *Desmacella inornata* and *Sceptrella insignis*, and ocassional larger massive species such as *Calthropella pathologica*, *Erylus papulifer* as well as the flabellates *Poecillastra compressa* and *Pachastrella monilifera*. Seven species previously known from other deep-sea habitats, but previously not detected in CWC habitats, such as *E. papulifer*, *Geodia anceps*, *Spiroxya heteroclita*, *Antho signata*, *Crellastrina alecto*, *Axinella cannabina* and *Hexadella dedritifera*, were also described for the first time in that CWC province (Longo et al. 2005). Two boring sponges able to excavate the calcareous framework of CWC (*Spiroxya levispira* and *Siphonodictyon infestum*) were also found. The latter, occurring exclusively in *Madrepora oculata* colonies (Beuck et al. 2010), appears to have an important role in the bioerosion of the CWC biocoenosis (Calcinai et al. 2001). The sponge assemblages of SML display a distinct bathymetric pattern with marked decrease in species richness with depth (Longo et al. 2005). For instance, *S. insignis* was preferentially found from 600 to 800 m, while *Hamacantha implicans* (= *H. papillata*) from 800 to 1100 m. In the Bari canyon (southwestern Adriatic Sea), more than 20 sponge species have been found growing within *M. oculata* banks (D'Onghia et al. 2015), being the massive *P. monilifera* one of the top-dominant sponges (Freiwald et al. 2009; Bo et al. 2012). Furthermore, D'Onghia et al. (2015) also reported *S. infestum* heavily attacking the basal portion of CWC colonies, along with another 11 species that had never been found before in Mediterranean CWC habitats, namely *Prosuberites longispinus*, *Antho involvens*, *Eurypon cinctum*, *E. topsenti*, *Biemna partenopea, B. tenuisigma, Axinella pumila*, *Bubaris subtyla*, *Cerbaris curvispiculifer*, *Hymerhabdia typica* and *Hexadella pruvoti*. In CWC habitats of the SoS, Calcinai et al. (2013) listed ten sponges, mostly encrusting ones and some typical of bathyal environments (e.g. *Janulum spinispiculum*, *Thrombus abyssi*). Two new records for the Mediterranean Sea such as *Characella pachastrelloides* and *Hamacantha azorica* were also detected in that area.

Regarding the western Mediterranean, Fabri et al. (2017) reported *Tretodyctum* cf *tubulosum*, *Oopsacas* cf *minuta*, *Hexadella* cf *crypta* and *Farrea* sp. from the CWC habitat in the Cassidaigne submarine canyon. In the Sardinian CWC province, Taviani et al. (2017) reported a striking paucity of large demosponges which are characteristic and often dominant components of other Mediterranean CWC banks and many slope and seamount hard-bottom habitats (e.g. *P. compressa*, *P. monilifera*), noticing that most species were established on dead coral. These authors also documented the occurrence of some so far uncommon species such as *Clathria anchorata* and *Acantheurypon pilosella* and, all together the Sardinian CWC province is interpreted as a putative Mediterranean biodiversity hotspot. The information relative to the Alborán Sea is limited, based on occasional sampling at Chella bank. There, among other species, the carnivorous sponge *Asbestopluma hypogea* (= *Lycopodina hypogea*) has been documented growing on *Dendrophyllia cornigera* colonies (Aguilar et al. 2011), and the hexactinellids *Asconema setubalense* and *Sympagella delauzei* associated with *Lophelia pertusa* and *M. oculata* banks (Pardo et al. 2011; de la Torriente et al. 2014) (Fig. 29.2). In the adjacent GoC, ten large sponges have been listed in CWC habitats of Gazul MV, where *Phakellia* sp., *Haliclona mucosa, A. setubalense* and *Petrosia* sp. dominate (Díaz del Rio et al. 2014; Rueda et al. 2016). A study still in progress on the sponge fauna of MVs in the GoC (Sitjá et al. 2018) has identified six additional species growing directly on branches of dead coral, namely *Desmacella inornata, Poecillastra compressa, Anisocrella hymedesmina, Penares euastrum,*

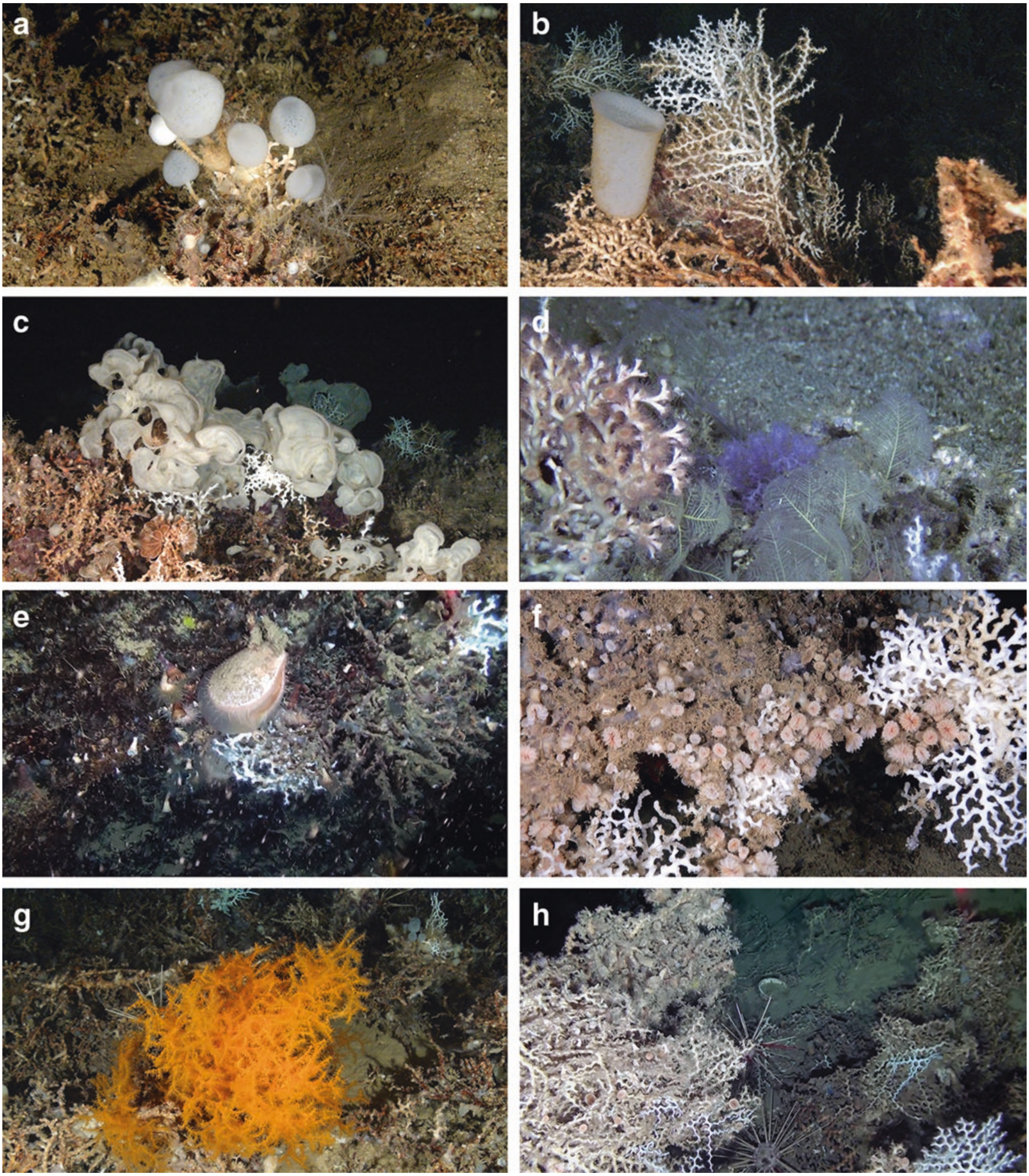

Fig. 29.2 Sponges, cnidarians and other invertebrates in cold-water coral (CWC) habitats of the Mediterranean Sea and adjacent areas (Gulf of Cadiz): (**a**) Lollipop-like sponges (*Sympagella delauzei*) on a dead coral ground (Cabliers bank, 400 m depth); (**b**) A small specimen of the sponge *Asconema setubalense* growing on a coral ground represented by degraded and living *Madrepora oculata* colonies (Cabliers bank, 350 m); (**c**) Dense aggregate of fan-shaped unknown sponges growing on a coral framework of dead and living *Lophelia pertusa* and *M. oculata*, note the presence of several specimens of undetermined crinoids at the base (Catifas bank, 390 m); (**d**) Colonies of *L. pertusa* and *M. oculata* together with the hydroid *Polyplumaria flabellata* at a CWC bank of the Gulf of Cadiz (Gazul mud volcano, 440 m); (**e**) The bivalve *Acesta excavata* together with colonial and solitary scleractinians (mainly *M. oculata* and *Desmophyllum dianthus*) (Dohrn submarine canyon, 420 m); (**f**) High density of *D. dianthus* on a *M. oculata* framework (Malta trough, 750 m); (**g**) A colony of *Leiopathes glaberrima* on a dead *M. oculata* framework with the echinoid *Cidaris cidaris* and lollipop-like sponges (Cabliers bank, 400 m). (**h**) Large *M. oculata* colonies colonised by *D. dianthus* polyps and *C. cidaris*. (Pictures from © Oceana (a–c, g), Oceana©LIFE BaĦAR for N2K (f), © Instituto Español de Oceanografía (d), and © ISMAR-CNR (e, h))

Characella pachastrelloides and *Thrombus abyssi*, as well as several individuals of *L. hypogea* growing on boulders located in the Gazul MV.

Summarising, ca. 90 sponge species have been detected so far in Mediterranean CWC habitats, but only three species (*D. inornata*, *Jaspis incrustans* and *P. compressa*) are common to most of these sites (e.g. Catalan-Provençal-Ligurian canyons, SML, SoS, Bari Canyon). Nevertheless, none of them is specific to CWC, since these species are common in a large variety of deep-sea habitats. The causes for the poor diversity and low abundance of coral excavating sponges in Mediterranean CWC habitats remain elusive. It has been conjectured that it could derive from the difficulty of larvae to reach these calcareous substrates separated by bottoms not suitable for skeleton boring fauna (Beaulieu 2001), but it is not a strong argument, as calcareous shells are common everywhere in deep-sea and they would serve as stepping-stones between CWC habitats. Regarding biogeographical affinities, most of the sponges found in CWC habitats of the Central Mediterranean Sea show an Atlantic-Mediterranean distribution, with a higher affinity with Boreal fauna, and a very low percentage of Mediterranean endemic species (13–14%) (Longo et al. 2005; D'Onghia et al. 2015). Moreover, a strong taxonomic differentiation in the composition of the deep sponge fauna inhabiting soft or hard substrates (e.g. coral banks) has been reported, with less than ten species (e.g. *P. compressa*, *Siphonidium ramosum*, *Leiodermatium* cf. *lynceus*, *Desmacella annexa*, *Haliclona flagellifera*) shared between a CWC habitat off SML and Mediterranean muddy bathyal bottoms (Pansini and Musso 1991; Longo et al. 2005).

29.4.2 Cnidarians

Deep-sea anthozoans occurring in Mediterranean CWC habitats are mainly represented by structuring scleractinians, antipatharians, pennatulaceans and gorgonians (Carpine and Grasshoff 1975; Zibrowius 1980; Mastrototaro et al. 2013, 2017; Bo et al. 2015; Altuna and Poliseno, this volume; Chimienti et al., this volume) showing no strict endemism and, frequently, with an Atlanto-Mediterranean distribution (Taviani et al. 2005; Vertino et al. 2014) (Table 29.1). The scleractinians *M. oculata* and *L. pertusa* are the main frame-building species of the deep Mediterranean CWC habitats (Fig. 29.2). Nonetheless, approximately 50 anthozoans have been recorded so far associated with these bioconstructions (Zibrowius and Taviani 2005; Freiwald et al. 2009; Mastrototaro et al. 2010; Pardo et al. 2011; Angeletti et al. 2014; Bo et al. 2014; Fabri et al. 2014; Lastras et al. 2016; see also Altuna and Poliseno, this volume). Different groups of anthozoans can be identified based on their role in the benthic community, their degree of intimacy with the structuring coral framework and their habitat preferences (Vertino et al. 2010). Within the CWC framework, the solitary polyps of the scleractinian *Desmophyllum dianthus* typically settle on the tissue-barren basal portions of *M. oculata* and *L. pertusa* playing an important secondary structuring role, especially in some areas (e.g. La Fonera submarine canyons) together with the less abundant *Stenocyathus vermiformis* and *Caryophyllia calveri* (Mastrototaro et al. 2010; Aymà et al., this volume; Lastras et al., this volume) (Fig. 29.2). Among the most intimate relationships is that of the actinian *Edwardsiella loveni* boring dead branches of *L. pertusa* (Zibrowius and Taviani 2005). Black corals (e.g. *Leiopathes glaberrima*) and gorgonians are also common components of these biocoenoses and are found both on dead coral ramifications and among colonies (Tursi et al. 2004; Zibrowius and Taviani 2005; Angeletti et al. 2014; Bo and Bavestrello, this volume; see Gori et al., this volume). Noticeably, the calcitic *Corallium rubrum* (precious or red coral), a gorgonian mostly distributed in shallow waters, has been found to occur at bathyal depths mixed with CWC in the Strait of Sicily from ca 400 down to 1000 m (Freiwald et al. 2009; Costantini et al. 2010; Taviani et al. 2010; Knittweis et al. 2016), and in the Cassidaigne Canyon (Fabri et al. 2017). Three actinians (*Amphianthus dohrnii, Sagartia elegans* and *S. troglodytes*) are known to occur as commensal on living portions of *M. oculata* and other anthozoans, similarly to some zoanthids associated with the living coral matrix or with sponges (Mastrototaro et al. 2010; Bo et al. 2012).

Aside from hydrozoans and anthozoans, the CWC framework is known to host benthic stages of scyphozoan *Coronatae medusae* (Jarms et al. 2003; Mastrototaro et al. 2010), whereas loose to cemented CWC rubble and other biogenic hard bottoms generally occurring around CWC banks host numerous gorgonian species (e.g. *Acanthogorgia hirsuta*, *Bebryce mollis*), scleractinians (*D. cornigera*) and antipatharians (*Antipathes dichotoma*, *Parantipathes larix*) (Mastrototaro et al. 2010; Pardo et al. 2011; Angeletti et al. 2014; Fabri et al. 2017). Abundant populations of the stoloniferan *Scleranthelia rugosa* have been reported on giant oyster shells (likely *Neopycnodonte zibrowii*) while the rare actinian *Kadophellia bathyalis* has been found on dead coral fragments together with the sea anemone *Protanthea simplex* (Zibrowius and Taviani 2005; Mastrototaro et al. 2010). The adjacent soft bottoms surrounding coral banks usually host a very peculiar community dominated by pennatulaceans (such as *Kophobelemnon stelliferum* and *Funiculina quadrangularis*) and actinians, such as *Peachia cylindrica* (Mastrototaro et al. 2010; Pardo et al. 2011). Among gorgonians, the only representative in this soft bottoms habitat is *Isidella elongata* (Freiwald et al. 2009; Pardo et al. 2011; Fabri et al. 2014) and some solitary scleractinians can also occur such as *Flabellum chunii* (Díaz del Rio et al. 2014) (Fig. 29.3). Sparse rocky hardgrounds within CWC habitats host numerous anthozoans, including

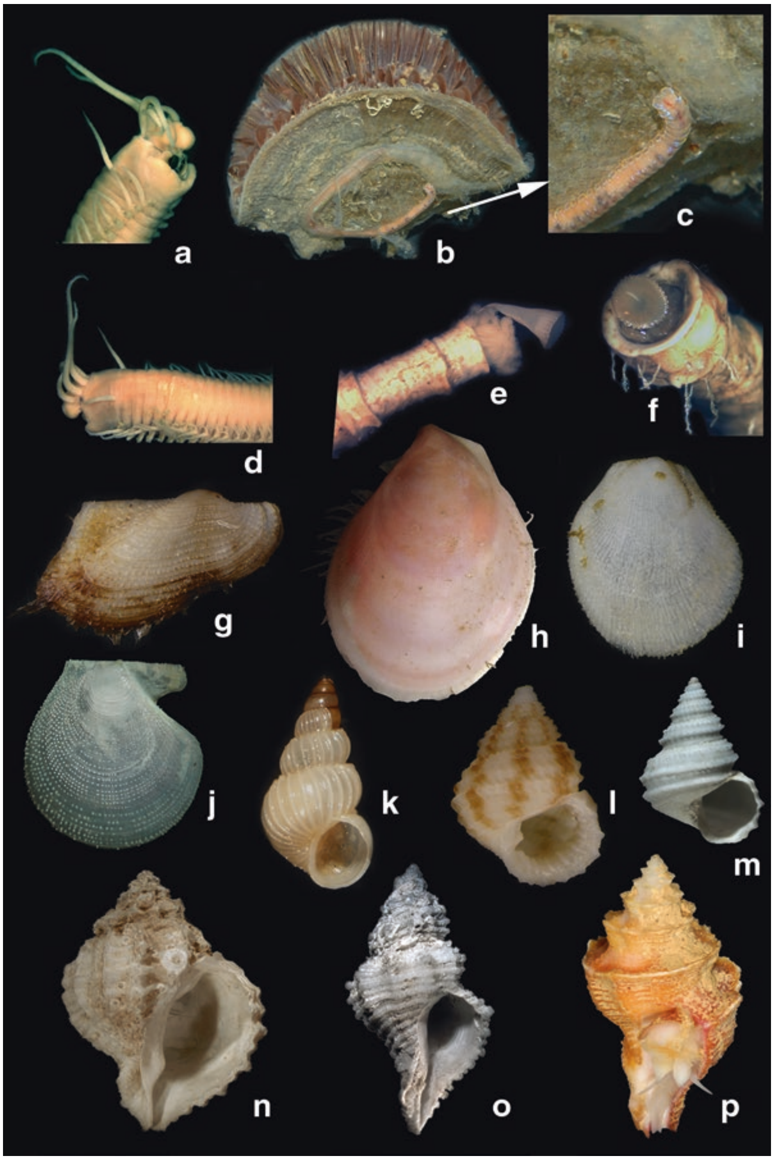

Fig. 29.3 Common polychaetes and molluscs of CWC habitats in the Mediterrranean Sea and adjacent areas. (**a** and **d**) *Eunice norvegica*; (**b** and **c**) *Helmutneris flabellicola* on *Flabellum chunii*; (**e** and **f**) *Serpula vermicularis*; (**g**) *Asperarca nodulosa*; (**h**) *Acesta excavata*; (**i**) *Spondylus gussonii*; (**j**) *Delectopecten vitreus*; (**k**) *Epitonium algerianum*; (**l**) *Danilia tinei*; (**m**) *Iphitus tuberatus*; (**n**) *Coralliophila richardi*; (**o**) *Coralliophila squamosa*; (**p**) *Babelomurex sentix*. (Pictures from © Instituto Español de Oceanografía (a–g, i, k, l), © ISMAR-CNR (h, m–p) and © Serge Gofas – Universidad de Málaga (j))

scleractinians (such as *C. calveri*, *D. cornigera*, *D. dianthus*, *Thalamophyllia gasti*), black corals (*L. glaberrima*), alcyonarians (*Anthomastus* sp.) and those gorgonians that also occur on the coral rubble (Álvarez-Pérez et al. 2005; Mastrototaro et al. 2010; Pardo et al. 2011; Lastras et al. 2016) as well as the bioluminescent and parasitic zoanthid *Isozoanthus primnoidus* (Zibrowius and Taviani 2005; Bo et al. 2014). Black corals and gorgonians are known to form "animal forests" (*sensu* Rossi et al. 2017) with high-density aggregations along the Mediterranean continental margin usually confining coral banks in the deepest bathyal ranges (Bo et al. 2012, 2015; Bo and Bavestrello, this volume; Angeletti et al. 2014; Mytilineou et al. 2014; Cau et al. 2015; Deidun et al. 2015; Taviani et al. 2017; Grinyó et al. 2016; Gori et al., this volume). Other deep-sea gorgonians such as *I. elongata* can form facies with a high density of colonies growing on bathyal muddy environments and a high diverse associated community, including some cnidarians such as *D. dianthus*, *F. quadrangularis* and *A. dohrnii* (Maynou and Cartes 2012; Mastrototaro et al. 2017; Pierdomenico et al. 2018).

Although the hydroid fauna of the Mediterranean Sea is one of the best known in the world (Boero and Bouillon 1993; Bouillon et al. 2004), the deep-sea hydroids have received little attention and the information is mainly restricted to the western Mediterranean and adjacent GoC (Gili and Ros 1981; Ramil and Vervoort 1992; Moura et al. 2007). The information about CWC associated hydroids is still very scarce worldwide (Fosså and Mortensen 1998; Henry 2001; Buhl-Mortensen and Mortensen 2005; Henry and Roberts 2007) and the same applies in the Mediterranean Sea and adjacent areas, where around 30 species have been found so far (Mastrototaro et al. 2010; Lastras et al. 2016) (Table 29.1). This may stem from the fact that most published information on Mediterranean CWC habitats derives from ROV observations, that is a useful deep-sea exploration and sampling method but not ideal for characterising an important part of the associated biodiversity of CWCs, for example the hydroids among other groups of inconspicuous or cryptic organisms. For this reason and/or because of the increasing loss of taxonomical expertise, hydroids occurring in Mediterranean CWC habitats are often reported in a general way as "hydroids", without identification at species level (Schembri et al. 2007; Bongiorni et al. 2010; Rosso et al. 2010; Vertino et al. 2010; Angeletti et al. 2014). In addition, most of these and other studies on Mediterranean deep-sea hydrozoan fauna do not include accurate data about the species abundance and their substrate (often also recorded in a general form such as "corals"). Thus, the real number of hydroid species known to be associated with Mediterranean CWC habitats is probably still underestimated (Table 29.1). The scant available information does not allow to confidently asses whether some hydrozoans are common, rare or specific to CWC habitats because further detailed studies are needed. In SML, the most common hydroids seem to be *Acryptolaria conferta, Clytia linearis, Halecium labrosum, Hybocodon* cf. *prolifer, Laodeicea undulata, Mitrocoma annae, Nemertesia antennina* and *N. ramosa* (Mastrototaro et al. 2010). In the CWC habitats of Gazul MV (GoC), the most common hydroids are *Acryptolaria crassicaulis, A. conferta*, *Bedotella armata, Campanularia hincksii, C. gracilis*, *Streptocaulus* cf. *pectiniferus*, *Cladocarpus sinuosus*, *Cryptolaria pectinata*, *Diphasia margareta*, *Lytocarpia myriophyllum*, *Modeeria rotunda*, *Nemertesia falcicula*, *N. antennina*, *Polyplumaria flabellata, Zygophylax biarmata* and *Zygophylax* cf. *brownie* (Díaz del Rio et al. 2014; Megina and Gónzalez-Duarte unpublished results) (Fig. 29.2). Other studies have indicated the presence of a lower number of species (e.g. *Aglaophenia tubulifera, C. pectinata, Halopteris catharina*, etc.) in coral rubble bottoms and CWC habitats of the Strait of Gibraltar (Ramil and Vervoort 1992) and of La Fonera submarine canyon (Lastras et al. 2016).

An important feature of some mentioned hydrozoa is that they are generally non-specific (with a few exceptions) with regard to the substrate selection (Cornelius 1982; Calder 1991; González-Duarte et al. 2014) and they typically exhibit a wide bathymetric range, sometimes inhabiting both shallow and deep-sea habitats (Altuna 2007). Actually, among the 31 species detected so far in Mediterranean CWC habitats, only 14 can be considered more common of deep-sea habitats, with the family Aglaopheniidae and Lafoeidae showing the highest number of those species (3 and 5, respectively). A particular case is *Tubiclavoides striatum*; a species described in deep-waters of GoC, associated with mud breccia bottoms, carbonate chimneys and *M. oculata* and *L. pertusa* banks. Although it was reported as very frequent in this zone, there are no other records for this species in the world.

29.4.3 Annelids and Phyllogenetically Related Groups

Few papers are specifically related to polychaetes associated with CWC habitats in the Mediterranean Sea (Sanfilippo 2009; Sanfilippo et al. 2013), however substantial information on this group is found in those contributions listing the benthic biodiversity of Mediterranean CWC habitats (Tursi et al. 2004; Zibrowius and Taviani 2005; Da Silva 2009; Freiwald et al. 2009; Mastrototaro et al. 2010; Angeletti et al. 2014; D'Onghia et al. 2015; Taviani et al. 2017; Lastras et al. 2016) (Table 29.1). In total, ca. 80 species have been recorded so far from living CWC grounds but also subfossil ones (Remia and Taviani 2005; Taviani et al. 2011b), of which Serpulidae accounts for 11 taxa. The occurrence of the polychaete species in CWC habitats is very variable, but the eunicid *Eunice norvegica* is an ubiquitous inhabitant of Mediterranean CWC as detected in the Atlantic ones (Tursi et al. 2004; Schembri et al. 2007; Da Silva 2009; Sanfilippo et al. 2013; D'Onghia et al. 2015; Taviani et al. 2017) (Fig. 29.3). Other common serpulids in CWC are typical components of bathyal hard bottoms, including *Serpula vermicularis*, *Filogranula gracilis*, *Metavermilia multicristata* and *Hyalopomatus madreporae* (Tursi et al. 2004; Zibrowius and Taviani 2005; Mastrototaro et al. 2010; Rosso et al. 2010; Sanfilippo et al. 2013; Angeletti et al. 2014; D'Onghia et al. 2015; Taviani et al. 2017) (Fig. 29.3). Because of their abundance and diversity, serpulids, therefore, play a role as secondary builders in CWC habitats by filling gaps and adding encrusting material with the calcareous tubes they secrete. Nevertheless, the extent of this effect is quite variable, and it mostly depends on the locality and the species involved. Thus, serpulid species found in SML are very abundant, but in turn they are usually small-sized and scarcely supply carbonate to the biological framework (Mastrototaro et al. 2010; Rosso et al. 2010). On the other hand, in the CWC communities of the Bari canyon, the dominant serpulid is the large size *S. vermicularis*, which is closely associated with *M. oculata* (and more subordinately with *L. pertusa* and *D. cornigera*) in building massive and very compact aggregates (Sanfilippo et al. 2013).

The interpretation of the errantiate polychaete *E. norvegica* is emblematic because of the difficulty to assess with confidence the ecological role of deep-sea organisms within CWC habitats. The worm was firstly interpreted as a coral bioeroder by using its strong jaws to pierce galleries (Glynn 1997), or as kleptoparasite of CWC polyps (Mortensen 2001). Further studies on NE Atlantic CWC banks unveiled a completely different and positive function documenting that *E. norvegica* contributes to strengthen the CWC structure by stimulating the encalcification of their parchment-like tubes into the coral frames (Freiwald et al. 1997; Roberts 2005). Furthermore, *E. norvegica* enhances coral calcification (up to four times in the case of *L. pertusa*) resulting in branch thickening and anastomosis and facilitating reef growth and framework strength (Mueller et al. 2013). This phenomenon is also commonly observed in the Mediterranean CWC habitats (Tursi et al. 2004; Mastrototaro et al. 2010). The remaining epibionthic polychaetes likely act as opportunistic commensals or kleptoparasites of CWC (Buhl-Mortensen and Mortensen 2004), although some strict symbionts such as *Haplosyllis chamaeleon* (mainly with gorgonians) or *Helmutneris flabellicolla* (mainly with *Caryophyllia* sp. and *Flabellum* sp.) can be mentioned (Zibrowius et al. 1975; López et al. 1996) (Fig. 29.3). Another striking characteristic of the polychaete assemblages inhabiting Mediterranean CWC habitats is the very few records of Polynoidae, especially when taking into account that it is the most common family of CWC symbiotic polychaetes worldwide with 12 recorded species (Buhl-Mortensen and Mortensen 2004). Nevertheless, just two Polynoidae species were recorded in Mediterranean CWC habitats, namely *Subadyte pellucida* and *Harmothoe vesiculosa* (Mastrototaro et al. 2010), and only the latter seems to be a strict symbiont of cnidarians (Núñez et al. 2015).

The polychaete fauna seems to be more diverse in the biogenic carbonate rubble around CWC colonies, where ca. 70 species belonging to 32 families have been recorded (Mastrototaro et al. 2010), with only 13% of the total invertebrate species dwelling on living branches. Again, Serpulidae is the most speciose family and is represented by 12 species. The assemblages in the calcareous rubble bottoms are apparently formed of a mixture of species that are also found in the living colonies such as *S. vermicularis*, *Filograna implexa* or *E. norvegica* and species commonly found in other detritic bathyal bottoms as well. The number of species recorded from soft bottoms in surrounding areas is comparatively low with 18 species belonging to five families (Mastrototaro et al. 2010). Contrary to the CWC colonies, in which a number of species were very frequently detected in several localities, no constant species can be mentioned for sedimentary environments.

Other related taxa are by far less known than Polychaeta in Mediterranean CWC habitats. The presence of Oligochaeta in these environments is unknown, although this group can be abundant in bathyal soft bottoms in the Mediterranean basin (Baldrighi et al. 2014). Sipunculans were recorded only occasionally, always within the sediment surrounding CWC colonies (Da Silva 2009; Mastrototaro et al. 2010) but never among the branches, whereas the echiurid *Bonellia viridis* is often seen in muddy coral rubble facies (Hebbeln et al. 2009).

29.4.4 Molluscs

Molluscs represent a diverse component of benthic habitats, including those conformed by CWC in the Mediterranean Sea and adjacent areas (e.g. GoC). With few exceptions (Negri and Corselli 2016), most information on molluscs associated with CWC habitats is part of more extensive lists on benthic fauna (Tursi et al. 2004; Mastrototaro et al. 2010; Angeletti et al. 2014; Díaz del Rio et al. 2014; Rueda et al. 2016), benthopelagic fauna (D'Onghia et al. 2011) or thanatofacies of CWC habitats (Taviani and Colantoni 1979, 1984; Bonfitto et al. 1994a, b; Remia and Taviani 2005; Rosso et al. 2010; Angeletti and Taviani 2011; Taviani et al. 2011b; Panetta et al. 2013) (Table 29.1). The overall Mediterranean deep-sea mollusc fauna is notoriously impoverished with respect to the Atlantic Ocean (Bouchet and Taviani 1992; Sabelli and Taviani 2014), and this obviously extends to the CWC habitats, which are quite diverse in the Atlantic (Mortensen and Fosså 2006). At the basin scale, the Central Mediterranean is much better known than the eastern and western areas (Gofas et al. 2011; Taviani et al. 2011a; Angeletti et al. 2014; de la Torriente et al. 2014; Negri and Corselli 2016). The number of censed species is higher when based upon extensive bottom sampling (Tursi et al. 2004; Rosso et al. 2010; Díaz del Rio et al. 2014; Negri and Corselli 2016) than that derived of underwater images which fails to spot small-sized and cryptic elements (D'Onghia et al. 2011; Fabri et al. 2014; Angeletti et al. 2014; Taviani et al. 2017).

Over 50 species of molluscs have been reported from Mediterranean CWC habitats, including coral rubble and taphocoenoses (Table 29.1). Nevertheless, most of them are not strictly associated with CWC and some benefit from the hard substrate and tridimensional complexity provided. Some of these species are able to become common and dominant in CWC habitats such as the bivalves *Bathyarca philippiana, Asperarca nodulosa*, *Delectopecten vitreus*, *Spondylus gussonii* and *Heteranomia squamula* and the gastropods *Danilia tinei, Putzeysia wiseri* and *Mitrella pallaryi* (Tursi et al. 2004; Rosso et al. 2010; Taviani et al. 2011b; Angeletti et al. 2014; Díaz del Rio et al. 2014; Negri and Corselli 2016) (Fig. 29.3). Some common bathyal molluscs inhabiting soft bottoms, such as the bivalves *Abra longicallus, Karnecampia sulcata, Ledella messanensis* and *Ennucula aegeensis*, the gastropods *Pagodula echinata,* or the scaphopod *Antalis agilis* could be consistently detected in mobile sediment within CWC sites (Mastrototaro et al. 2010; Rosso et al. 2010; Díaz del Rio et al. 2014; Negri and Corselli 2016). Although not exclusive of such habitats, the epifaunal bivalve *D. vitreus* often occurs at CWC sites (Mastrototaro et al. 2010; Panetta et al. 2010; Taviani et al. 2011a; Negri and Corselli 2016). Large limid bivalves such as *Lima marioni* and *A. excavata* are ocasionally found associated with CWC habitats (Taviani and Colantoni 1979; López Correa et al. 2005; Freiwald et al. 2009; Díaz del Rio et al. 2014) (Figs. 29.2 and 29.3). The giant deep-sea oyster *Neopycnodonte zibrowii* preferentially settles on hard substrates next to CWC banks and sometimes on coral frames themselves (Taviani et al. 2017). Although not at all exclusive to CWC habitats, the bivalves

Rocellaria dubia and *Coralliophaga lithophagella* can be found boring or nestling in CWC rubble (Remia and Taviani 2005; Díaz del Rio et al. 2014). The Solenogastre *Anamenia gorgonophila* has been identified from the gorgonacean *Paramuricea macrospina* from the South Malta CWC province (Mifsud et al. 2008), whilst an undetermined nudibranch has been observed on CWC associated cnidarians in the southeastern Adriatic Sea (Angeletti et al. 2014). Demersal molluscs have been scarcely investigated in Mediterranean CWC habitats, but the species *Onychoteuthis banksi* and *Pteroctopus tetracirrhus* have been identified around coral frameworks and hard bottoms at SML (D'Onghia et al. 2011). In general, mollusc assemblages associated with CWC host a wider number of species than adjacent bathyal muddy bottoms. This holds particularly true when coral rubble, soft sediment patches and hard bottoms co-occur (Mastrototaro et al. 2010; Rosso et al. 2010).

Only a few molluscs are obligatorially associated with CWC, and those are all microcarnivores, mostly in the families Epitoniidae, Nystiellidae and Muricidae-Coralliophilinae (Oliverio 1989; Taviani et al. 2009). One of the very few species strictly related to the 'white corals' in the Mediterranean and Atlantic alike is the Coralliophilinae *Coralliophila richardi* (Fig. 29.3), possibly feeding on both *L. pertusa* and *M. oculata* (Taviani and Taviani 1986). As for the nystiellid *Iphitus tuberatus*, this amphiatlantic taxon has been documented in the CWC habitats of the Central and western Mediterranean and also from submerged Pleistocene CWC taphocoenoses (Taviani and Colantoni 1979; Taviani and Taviani 1986), but not reported thus far from the eastern basin. The elusive Atlantic nystiellid *Iphitus marshalli*, reported from the Alborán Sea (Templado and Villanueva 2010; Gofas et al. 2011), is also probably related to deep scleractinian corals. The gastropods *Babelomurex sentix* and *Coralliophila squamosa* (mainly its form *ruderatus*) have also been reported from both recent (Oliverio 1989; Taviani et al. 2009) and subfossil Mediterranean CWC sites (Taviani and Colantoni 1979; Remia and Taviani 2005; Angeletti and Taviani 2011), although their cnidarian hosts are still unknown and possibly exclude white corals *sensu stricto* (Fig. 29.3). *Iphitus tuberatus* is a cnidarian-predatory gastropod relatively common on living *L. pertusa* banks in the NE Atlantic and as CWC associated Pleistocene fossil in the Mediterranean Sea (Taviani and Sabelli 1982). Rather interestingly, it has been reported living associated with *D. cornigera* in the Alborán Sea (Rubio Salazar 1987; Gofas et al. 2011) suggesting a more generalistic trophic habit encompassing multiple scleractinian corals. With respect to epitoniid gastropods, *Epitonium dendrophylliae* has been collected adhering to *Dendrophyllia* spp. (Margelli et al. 1995; Gofas et al. 2011), whose polyps are in all likeness its prey; *E. algerianum* has been reported to occur from CWC habitats of the GoC (Díaz del Rio et al. 2014; Rueda et al. 2016), and *E. celesti* also from the GoC and SML (Díaz del Rio et al. 2014; Negri and Corselli 2016), but their trophic relationships are presently unknown. Species of fissurellid gastropods of the genus *Emarginula* and architectonicids are also recurrent components in Atlantic and Mediterranean CWC banks, including subfossil occurrences (Remia and Taviani 2005), and possibly feeding on associated sponges and cnidarians, respectively (Gofas et al. 2011). Some small gastropods such as *Lissotesta turrita, Anekes sculpturata* and *Cirsonella romettensis* are sometimes found in bottoms with CWC and coral rubble but their ethology is unknown (Gofas et al. 2011).

29.4.5 Crustaceans

Crustaceans of Mediterranean CWC habitats have been addressed in general research on benthic communities (Tursi et al. 2004; Schembri et al. 2007; Mastrotaro et al. 2010; Rosso et al. 2010) or megafauna assemblages (D'Onghia et al. 2010, 2011, 2015; Angeletti et al. 2014; Taviani et al. 2016, 2017; Fabri et al. 2017). A few papers dealt with the suprabenthic and planktonic associated community (Madurell et al. 2012a) or listed some balanids occurring in CWC (Relini 1980; Di Geronimo 2010) (Table 29.1). Most attention has been given to the Central Mediterranean and to large crustaceans such as decapods, although some research included detailed information on small size crustaceans such as ostracods and copepods (Rosso et al. 2010; Madurell et al. 2012a; Sciuto and Rosso 2015). Small size crustaceans seem to represent an important contribution of the crustacean assemblage, with dominance of copepods (mainly *Calanus helgolandicus* and *Diaxis pygmaea*), euphausiids (mainly *Nyctiphanes couchii*), and decapoda larvae (*Munida* sp.) in the planctonic component of CWC habitats (Madurell et al. 2012a). Amphipods (mainly *Melphidippella macra* and *Normanion ruffoi*), and mysidacea (*Lophogaster typicus*) also occur but not as dominant components. Only two living ostracod species, namely *Bairdoppilata conformis* and *Bythocypris obtusata*, have been found living in Mediterranean CWC habitats but nearly 30 additional species were found in the associated thanatocoenoses (Sciuto and Rosso 2015). Most of these small crustaceans are not exclusive of CWC habitats and can be common and dominant in different Mediterranean bathyal and pelagic habitats.

Decapods are probably one of the best studied crustacean groups in Mediterranean CWC habitats, with several studies providing faunistic lists and underwater images (Tursi et al. 2004; Schembri et al. 2007; Freiwald et al. 2009; Mastrototaro et al. 2010; D'Onghia et al. 2011; Maynou and Cartes 2012; Angeletti et al. 2014; Taviani et al. 2016, 2017). More than 20 species have been listed so far, especially for the Central Mediterranean CWC habitats (Table 29.1). Nevertheless, in some of these works, some decapods could not be identified at species level, so the decapod diversity is expected to be higher (D'Onghia et al. 2011; Fabri et al. 2014). Most of the decapod species are not linked specifically to CWC, but they benefit from the complex and diverse microhabitats provided by corals (Purser et al. 2013a; Maynou and Cartes 2012). The exception is *Munidopsis serricornis* which is a comensal seemingly obligate to cnidarians mainly occurring on *L. pertusa*, but also found on *Paramuricea* or *Acanthogorgia* in NE Atlantic as well as in NW Mediterranean (Mortensen 2001; Macpherson and Segonzac 2005). The most common species associated with Mediterranean CWC habitats are the pandalids *P. martia* and *P. heterocarpus*, the crab *Anamathia rissoana*, the anomurans *Munida intermedia* and *M. tenuimana* or the xanthiid *Monadaeus couchii* (Fig. 29.4). Other species such as *Ebalia nux*, *Paramola cuvieri* and *Homola barbata* usually occur in CWC habitats because of the shelter provided among the coral rubble or the presence of sessile species (sponges and cnidarians) that are picked up for camouflage. Species of commercial interest such as the giant red shrimp *Aristaeomorpha foliacea*, the blue and red shrimp *Aristeus antennatus,* the crab *Geryon longipes* or the pink spiny lobster *Palinurus mauritanicus* also occur, indicating the importance of CWC habitats for fisheries in adjacent bottoms (Tursi et al. 2004; Mastrototaro et al. 2010; D'Onghia et al. 2011; Pardo et al. 2011; Maynou and Cartes 2012) (Fig. 29.4).

Decapod assemblages associated with Mediterranean CWC habitats seem to be less diverse that in the Atlantic, with some associated species occurring in both basins (e.g. *M. tenuimana*, *Bathynectes maravigna*, *Polycheles typhlops*) and several species only found on Atlantic CWC habitats (e.g. *Chaceon affinis*, *Eumunida picta*, *Uroptychus rubrovitattus*, *Gastroptychus formosus*, *Pandalus propinquus*, *Caridion gordoni*, *Synalpheus townsendi*) (Buhl-Mortensen and Mortensen 2004; Cartes et al. 2014). Although the occurrence of CWC is not always linked to a high decapod diversity (Metaxas and Davis 2005), the number of decapod species is usually higher in CWC habitats than in adjacent soft bottoms (D'Onghia et al. 2010; Maynou and Cartes 2012; Cartes et al. 2014; Mastrototaro et al. 2017). D'Onghia et al. (2010) showed that most decapods, including some of commercial interest (e.g. *P. martia, Parapenaeus longirostris*), displayed higher densities and biomasses nearby CWC habitats in SML than further out, because CWC may provide a refuge area for many species often exploited in surrounding muddy bottoms (Krieger and Wing 2002). Maynou and Cartes (2012) documented 54 species of decapods crustaceans in *Isidella elongata* facies of the northwestern Mediterranean, with higher abundance and biomass of crustaceans than in adjacent areas, and including species of commercial interest such as *A. antennatus* and *P. martia*. Similarly, Mastrototaro et al. (2017) reported a higher biodiversity of different taxa, including crustaceans, in *I. elongata* facies located in the Balearic Promontory (western Mediterranean) in comparison to similar bathyal muddy bottoms lacking *I. elongata*.

Regarding Cirripedia, barnacles benefit from the hard substrate provided by CWC and some studies have given evidence of their occurrence on both CWC colonies (Schembri et al. 2007) and on coral rubble (Di Geronimo 2010), whereas others added information on the linkage to some CWC species (Relini 1980; Young 2001). Although some balanids are often attached to CWC, their strict association with CWC is still unclear, unlike that of some balanids with shallow water scleractinians (e.g. *Adna anglica* with *Astroides calycularis* and other species) (Relini 1980). Some of these balanids are amongst the largest ones occurring in the Mediterranean such as *Pachylasma giganteum*, documented in the South Malta coral province in the SoS (Schembri et al. 2007; Angeletti et al. 2011; Deidun et al. 2015), or *Megabalanus tulipiformis* in association with different CWC (Relini 1980). Other species that have been previously found are *Metaverruca recta* on CWC and *Scalpellum scalpellum* on antipatharians (Di Geronimo 2010). The balanid assemblages inhabiting Atlantic deep-sea corals show a higher number of species, including the deep species found in the Mediterranean Sea (Henry and Mc Laughlin 1986; Young 2001; Buhl-Mortensen and Mortensen 2004).

29.4.6 Echinoderms

Most information available on echinoderms of Mediterranean CWC habitats, including dead subfossil grounds, concerns SML, southern Adriatic sites, and the SoS (Tursi et al. 2004; Taviani et al. 2005, 2011a; Freiwald et al. 2009; Mifsud et al. 2009; Mastrotaro et al. 2010; Vertino et al. 2010; Angeletti et al. 2014) (Table 29.1). Eight echinoderm species have been detected so far in SML, including the holothuroid *Parastichopus regalis* and the echinoid *Cidaris cidaris*, the latter a common grazer on both live and dead coral branches and generally found between CWC colonies on the smooth crusts of the subhorizontal and subvertical substrates as reported in Atlantic CWC habitats (Stevenson and Rocha 2013) (Figs. 29.2 and 29.4). On adjacent soft bottoms, the brittle star *Amphiura filiformis* forms a true facies and the echinoids *Brissopsis atlantica mediterranea*, *Echinus melo* and *Gracilechinus acutus*, the asteroid *Odontaster mediterraneus* and the holothuria *Mesothuria intestinalis* are common components in SML. In the Adriatic Sea (Bari submarine canyon) *C. cidaris* seems to be also a common echinoderm of the CWC habitats, together with *E. melo* as well as the widespread *A. filiformis* in coral rubble bottoms and *Ophiothrix quinquemaculata* generally inhabiting *M. oculata* colonies and other hard substrates (Angeletti et al. 2014; D'Onghia et al. 2015).

In the SoS, Zibrowius and Taviani (2005) recorded the sessile suspension feeding holothurian *Psolidium complanatum* firmly attached to substrates embedding subfossil skel-

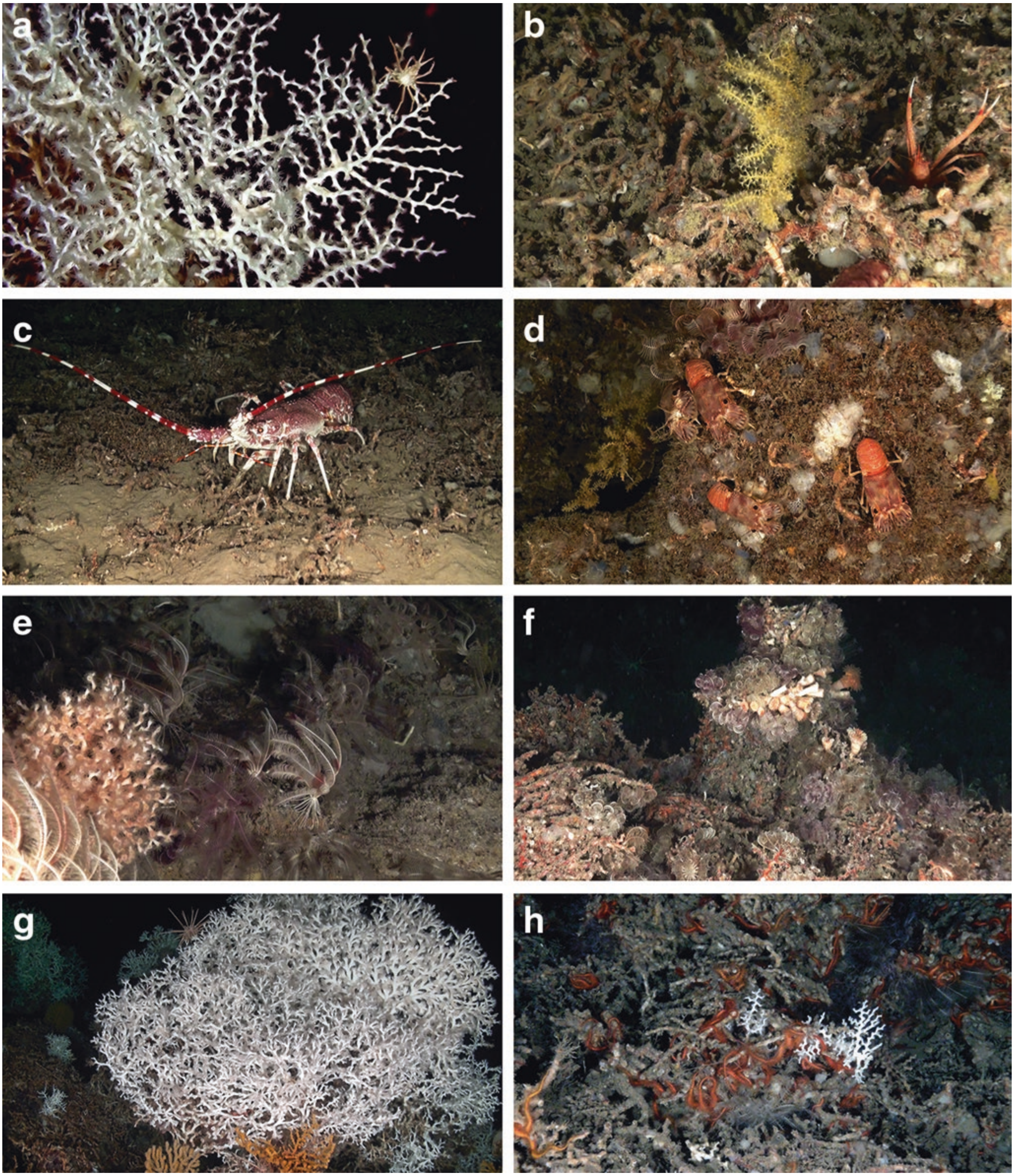

Fig. 29.4 Common decapods and echinoderms of Mediterranean cold-water coral (CWC) habitats. (**a**) The decapod *Anamathia rissoana* on a *Madrepora oculata* colony (Nora canyon, 420 m depth); (**b**) The decapod *Munida* sp. in CWC rubble colonised by *Acanthogorgia hirsuta* (Avempace bank, 370 m); (**c**) The deep-water lobster *Palinurus mauritanicus* in partially buried CWC remains (Avempace bank, 400 m); (**d**) *Scyllarus arctus* inhabiting a dead CWC framework with *Acanthogorgia hirsuta* and unidentified crinoids (Chella bank, 250 m); (**e**) High density of the crinoid *Leptometra phalangium* in a CWC habitat with *Lophelia pertusa* (Gulf of Cadiz in front of Faro, 495 m); (**f**) Dead *M. oculata* framework with living *Desmophyllum dianthus* and a high density of unidentified crinoids (Chella bank, 400 m); (**g**) A large *L. pertusa* colony with the echinoid *Cidaris cidaris* and the gorgonian *A. hirsuta* (Cabliers bank, 360 m); (**h**) *M. oculata* framework with a few scattered living colonies and high densities of *Ophiothrix* sp. and unidentified crinoids (Chella bank, 420 m). (Pictures from © ISMAR-CNR (a) and © Oceana (b–h))

etal remains of *Desmophyllum*, *Lophelia* and *Madrepora,* subfossil giant oyster shells and micriticised sponges. Other echinoderms have been reported from the south Malta coral province, i.e., the almost ubiquitous *C. cidaris*, and the asteroidea *Peltaster placenta* and *Coronaster briareus* (Schembri et al. 2007; Mifsud et al. 2009; Deidun et al. 2015; Evans et al. 2016). The crinoid *Leptometra phalangium* and cidarid sea urchins were recorded in habitats dominated by the black coral *L. glaberrima* and coral rubble (mainly of *D. cornigera*) at St. Vito Promontory, offshore the northwestern coast of Sicily (Bo et al. 2014).

In the western Mediterranean, similar echinoderms have been detected in CWC habitats of the submarine canyons of the southern margin of Sardinia as well as of those of the Catalan-Provençal-Ligurian Canyons region, including the species *C. cidaris*, *E. melo* and *G. acutus* (Fabri et al. 2014, 2017; Taviani et al. 2017; Lastras et al. 2016). In some of these canyons (e.g. La Fonera), the ofiuroid *Astrospartus mediterraneus* and dense populations of *Ophiothrix* sp. were documented attached to CWC branches (mainly of *M. oculata*) (Lastras et al. 2016). At places, *P. placenta* was occasionally found within or around CWC banks of these areas and the sea cucumber *Holothuria forskali* was observed roaming over or between the CWC (Taviani et al. 2017; Lastras et al. 2016). Some ophiuroids and crinoids have also been detected in underwater images taken in CWC habitats of southwestern Sardinia, nevertheless these specimens could not be identified (Bo et al. 2015).

In the Alborán Sea CWC habitats of Avempace, Catifas and Cablier banks, *C. cidaris* and *L. phalangium* were detected in coral rubble bottoms, together with large densities of *Ophiothrix* sp. (Pardo et al. 2011; Sánchez-Gallego et al. 2014) (Fig. 29.4). The CWC associated echinoderms of Chella bank have been studied with more detail, and the assemblage includes *C. cidaris* and *Ophiothrix* sp. within the coral banks, as well as *C. cidaris*, *E. melo, G. acutus* and *H. forskali* in adjacent hard bottoms, while *Holothuria tubulosa* and *P. regalis* are common components of the soft sediments (de la Torriente et al. 2014). Along the Moroccan margin, CWC habitats of the Melilla Coral Province were studied by Hebbeln et al. (2009) but generally most echinoderms (except *C. cidaris*) could not be identified to species level. In the GoC, the echinoderm assemblage occurring in CWC habitats at Gazul MV was similar as those for the Alborán Sea, but also included one of the very few European populations of the amphiatlantic asteroid *Hacelia superba* (Rueda et al. 2011).

In conclusion, ca. 20 echinoderms have been censed thus far for Mediterranean CWC habitats, including a high proportion of suspension and filter feeding species (*L. phalangium*, *Psolidium complanatum*, *P. placenta*, *O. fragilis*, *O. quinquemaculata*, *A. filiformis* and *A. mediterraneus*) which may take advantage from organic matter inputs arriving from the water column in areas with strong hydrodynamisms where CWC generally occur. Sedimentivorous (holothurians and irregular echinoids) and grazing (echinoids) echinoderms are also common components of the Mediterranean CWC habitats. As previously mentioned for the Atlantic CWC habitats (Mortensen and Fosså 2006), there is no specific echinoderm fauna associated with Mediterranean CWC, and most of the associated species are facultative and common in other deep-sea habitats, with some of them being very widespread species (e.g. *A. filiformis*) or displaying an aggregation behavior that leads to the formation of dense beds (e.g. *Ophiothrix* spp.). Most of these echinoderms have an Atlantic-Mediterranean distribution or even a cosmopolitan one (e.g. *A. mediterraneus*), except *O. quinquemaculata* (mainly Mediterranean) and *P. complanatum* (Atlantic and previously unknown in the Mediterranean).

29.4.7 Bryozoans

Bryozoans from deep waters, including those associated with CWC, have been poorly and occasionally investigated, both in the Atlantic Ocean and the Mediterranean Sea. Most papers usually dealt with taxonomical aspects, and the biogeographic information is often restricted to the geographic locality (often including latitude and longitude) and depth of occurrence (Harmelin and d'Hondt 1982, 1992a, b). Ecological and environmental data including habitat/substratum where colonies lived are usually missing, as well as information about other species forming the community. Furthermore, only selected CWC areas have been investigated in the Mediterranean and mostly in the last decade. Focusing exclusively on bryozoans occurring in Mediterranean "white coral" habitats, Rosso and Di Martino (2016) listed 61 species (12 cyclostomes, 1 ctenostome and 48 cheilostomes) associated with deep water corals, whereas Jiménez et al. (2016) reported 36 species on *D. ramea* colonies from deep circalitoral sedimentary bottoms off Cyprus and Menorca Channel. These data show that CWC habitats support a lower bryozoan diversity within the Mediterranean basin, at present knowledge, in comparison to shallow-water habitats conformed by cnidarians such as coralligenous bottoms (Table 29.1).

Nevertheless, no assessment hitherto relates to bryozoans associated with other CWC habitats in the area, although some studies were devoted to bryozoans associated with Dendrophyllids from the shelf break (Biocoenosis of Offshore Rocky Bottoms (RL) of Pérès and Picard 1964) and/or mentioned the association of some species with particular CWC habitats. One of the first studies that included information on bryozoans associated with Mediterranean CWC habitats was published by Gautier (1958), who recorded 6 species (*Scrupocellaria incurvata*, *Puellina venusta* and *Herentia hyndmanni*, among others) colonising Dendrophylliid coral skeletons from the Gulf of Genoa (Fig. 29.5). Gautier (1962) listed a total of 222 species from

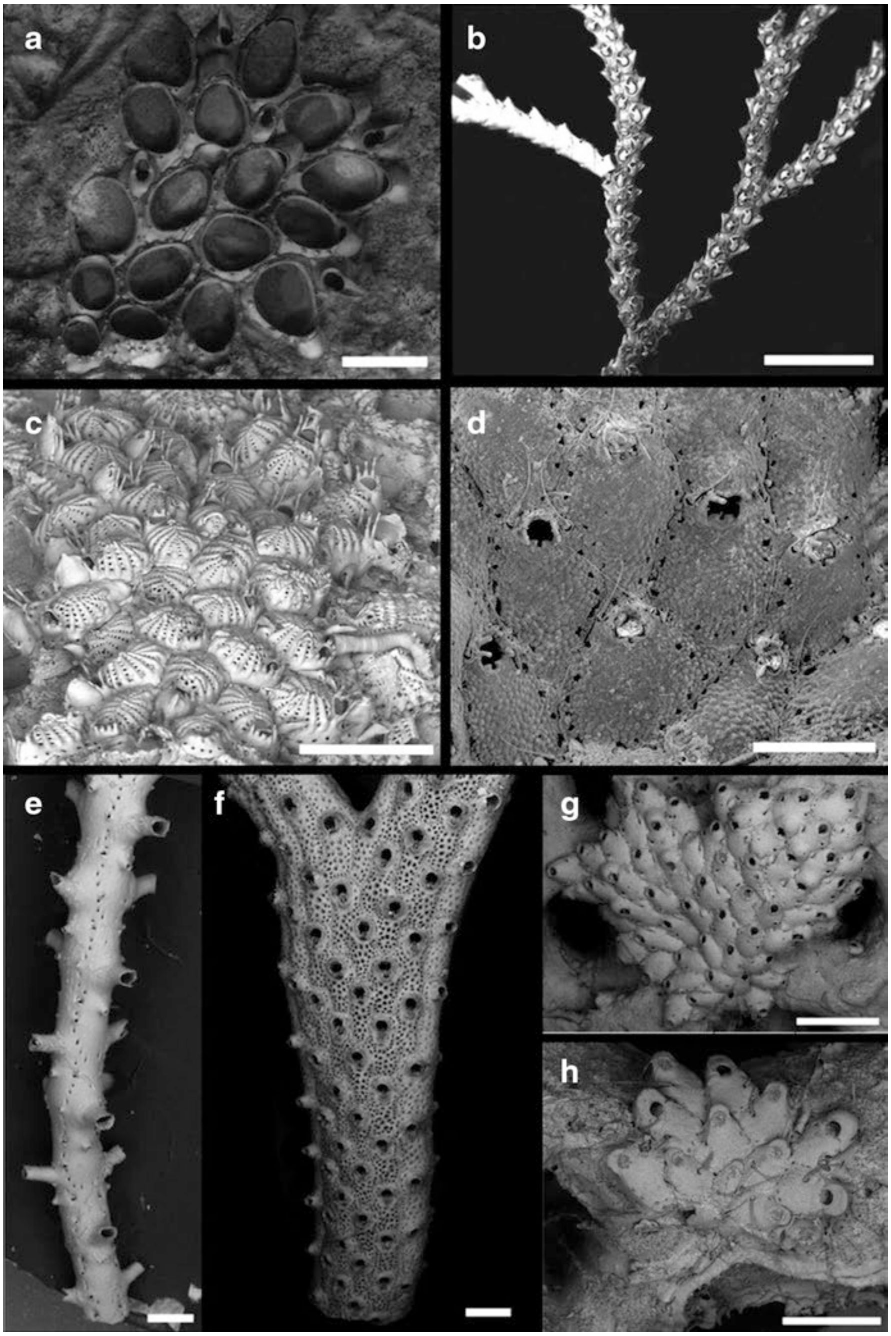

Fig. 29.5 Bryozoans occurring in CWC habitats of the Mediterranean Sea. (**a**) *Copidozoum exiguum* (Menorca Channel, 240 m depth); (**b**) *Scrupocellaria delilli* (Menorca Channel, 190 m); (**c**) *Puellina* (*G.*) *pedunculata* (Menorca Channel, 190 m); (**d**) *Escharina dutertrei protecta* (Menorca Channel, 190 m); (**e**) *Tessaradoma boreale* (Sicily Strait, 690 m); (**f**) *Smittina cervicornis* (Bari Canyon, 306 m); (**g**) *Escharina vulgaris* (Bari Canyon, 277 m); (**h**) *Herentia hyndmanni* (Santa Maria di Leuca, 513 m). Scale bars 500 µm (a, c–f, h), 1 mm (g), 1.5 mm (b). (Pictures from © Teresa Madurell and © Mikel Zabala and deposited at Museu de Ciències Naturals de Barcelona (a–d) and © Antonietta Rosso (University of Catania) (e–h))

the western Mediterranean but only 16 species (among which *Escharella ventricosa*, *Porella minuta* and *Stephanollona armata*) occurred on coral skeletons. Harmelin (1979) recorded 19 taxa (13 cheilostomes and 6 cyclostomes, seven of which left in open nomenclature but no ctenostomes) colonising rock fragments and dead *M. oculata* colonies in the SoS (250–750 m depth). Harmelin and d'Hondt (1992a, b) recorded 152 bryozoans from the Balgim Expedition (1984) through the Strait of Gibraltar and nearby areas but, unfortunately, almost no information on the habitat or substrate was given, except for three cheilostome species that occurred on CWC skeletons (*Lophelia*, *Desmophyllum*). Nevertheless, Harmelin and d'Hondt (1992c) mentioned species occurring on CWC skeletons, such as *Haplopoma sciaphilum* and *Crepis harmelini* on *M. oculata* and *Desmophyllum* in the SoS and *Puellina scripta* on *M. oculata, L. pertusa* and *Caryophyllia cyathus* in the Alborán Sea.

The first study aimed at identifying and describing bryozoans associated with CWC was published by Zabala et al. (1993) from samples of submarine canyons carving the northern Catalan margin (180–350 m depth), from where 36 species (7 cyclostomes and 29 cheilostomes) were reported to colonise living and dead *Madrepora* and *Lophelia* exposed skeletons. Recently, the discovery of CWC habitats in different sectors of Italian waters enhanced the knowledge of their associated bryozoans. Surveys in the SML coral province (Rosso 2003; Taviani et al. 2005; Mastrototaro et al. 2010; Rosso et al. 2010) and along the Bari submarine canyon (Freiwald et al. 2009; Sanfilippo et al. 2013; D'Onghia et al. 2015), allowed the record of 33 bryozoans in deep water coral bioconstructions and neighboring habitats. From these studies, 19 species (4 cyclostomes, 14 cheilostomes and an undetermined ctenostome) were reported for SML and the same number for the Bari submarine canyon (3 cyclostomes and 16 cheilostomes), with 5 species shared by these two relatively closely spaced localities. Further knowledge on bryozoans is sparse in general papers dealing with CWC habitats (Taviani et al. 2011a, b, 2016, 2017).

A total of 74 species (62 cheilostomes and 12 cyclostomes) have been reported so far from CWC habitats in the Mediterranean Sea and nearby waters subjected to Mediterranean influx (GoC) (Table 29.1). Information primarily refers to white coral bioconstructions, covering all the CWC provinces presently recognised in the Mediterranean following Taviani et al. (2011a) and also to a few dead coral bioconstructions, although with some areas investigated in more detail than others.

Regardless of the number of collected samples and published papers, some areas seem to be species richer than others. The Iberian-Provençal Basin, with a total of 46 species (Gautier 1958, 1962; Zabala et al. 1993) includes a large part of the biodiversity of bryozoans associated with CWC habitats. A relatively high number of living species (21) has been also reported from the southern Adriatic Sea (Freiwald et al. 2009; Sanfilippo et al. 2013; D'Onghia et al. 2015). In contrast, lower species diversity pertain to the northern Ionian Sea (Rosso 2003; Mastrototaro et al. 2010; Rosso et al. 2010) and the SoS area (Harmelin 1979), from where 15 and 12 species have been reported, respectively. Only seven species are known from the GoC (Harmelin and d'Hondt 1992a, b, c). Finally, occasional records from other areas include two species from the Alborán Sea (Harmelin and d'Hondt 1992a, b), one species from localities in isolated sectors of the Tyhrrenian Sea (Taviani et al. 2016) and one species from the Aegean Sea (Taviani et al. 2011a, b). It is remarkable that the higher values of biodiversity belong to CWC located within submarine canyons, where general environmental conditions presumably favor the settlement and thriving of bryozoans.

The most recorded species are *Herentia hyndmanni*, *Scrupocellaria delilii* and *Glabrilaria pedunculata* followed by *Smittina crystallina, Copidozoum exiguum* and *Stephanotheca arrogata*, occurring all throughout the Mediterranean (Fig. 29.5). Several species, although widely distributed in other habitats of the Mediterranean Sea, have been so far recorded in just one CWC province, whereas few species have only been found in restricted areas as *Hincksina longispinosa*, reported from the Strait of Gibraltar-GoC area and Alborán Sea and never recorded eastwards.

Bryozoans occurring in Mediterranean CWC habitats usually grow as small sized encrusters, often developing spot colonies or small patches (Zabala et al. 1993; Rosso et al. 2010; D'Onghia et al. 2015). Uniserial runners are rare and erect species are not common and usually consist of large sized flexible colonies belonging to candiids, whereas erect rigid species are particularly rare. *Tessaradoma boreale* and *Idmidronea* species are small sized and the only known large colonies belong to *Smittina cervicornis* (Fig. 29.5). Most of them have been reported as associated with *M. oculata* and *L. pertusa* (73 species) and only few with *D. cornigera* (11 species), and occasionally with other corals (one species on *Caryophyllia* spp.), but none of them seems to be restricted to CWC habitats. Indeed, these species have also been reported from a variety of habitats (some in the neighborhood of CWC) and substrate types (D'Onghia et al. 2015). Most of the CWC associated bryozoans have wide bathymetric distributions, being also widespread to mid-outer shelf habitats. Only *H. hyndmanni* and *G. pedunculata* seem restricted to the very outer shelf and the upper slope (Berning et al. 2008; Mastrototaro et al. 2010) although extending to some shallow submarine caves (Rosso et al. 2013; Sanfilippo et al. 2013) (Fig. 29.5).

29.4.8 Brachiopods

The information on this group is practically limited to some punctual records from the Central Mediterranean. In the SML province, Mastrototaro et al. (2010) reported *Gryphus vitreus* as a very abundant species on *M. oculata* and *L. pertusa* coral colonies, and *Megerlia truncata* on dead *Madrepora* colonies. Close to SML, Angeletti et al. (2014) revealed the existence of cnidarian-rich deep-sea habitats in the southern Adriatic Sea (Apulian and Montenegrin margins), with the presence of *Novocrania anomala* among the associated benthic fauna. In the SoS, Zibrowius and Taviani (2005) listed five brachiopod species found on coral ruble bottoms of solitary *D.dianthus* and colonial *L. pertusa* and *M. oculata*, at times embedded in packstones and framestones. These brachiopods were represented by *Megathiris detruncata*, *G. vitreus*, *M. truncata*, *Novocrania* sp. and *Platidia* sp.

Regarding the western Mediterranean, Taviani et al. (2017) documented in the Nora canyon (Capo Spartivento canyon system, Sardinian coral province) a high density of *Terebratulina retusa* (up to 50 specimens per 0.2 m^2) on dead *M. oculata* and *L. pertusa* frameworks and *D. dianthus* specimens, as well as abundant *N. anomala* and occasional individuals of *M. truncata*. On the other hand, *G. vitreus* was rarely observed, except on soft inter-coral sediment or associated with dead coral frames. In the Cap de Creus submarine canyon (northwestern Mediterranean Sea), the most common brachiopods in CWC communities (dominated by *M. oculata*) were also *G. vitreus* and *M. truncata* (Madurell et al.

2012b; Domínguez-Carrió et al. 2014). In the Alborán Sea, *M. truncata* and *T. retusa* commonly settle at CWC and hard bottoms of the Chella bank, where a total of 6 different species co-occur (Llompart 1988; Aguilar et al. 2011; de la Torriente et al. 2014). Most of the reported brachiopod species are widespread in different circalittoral and bathyal habitats so they are not specific of CWC habitats, but it is unknown if they may reach higher densities than in hard bottoms at similar depths.

29.4.9 Fishes

As mentioned previously, Mediterranean CWC habitats may serve as a feeding area, shelter in front of predators and/or breeding and nursery habitats for fishes, where they generally display higher density and diversity values than in adjacent bottoms (Husebø et al. 2002; Costello et al. 2005; D'Onghia et al. 2011; Biber et al. 2014). Nevertheless, the functional role of the CWC on fish diversity and abundance is still not fully understood (Milligan et al. 2016) and data assessing the linkage between CWC and fish are still scarce (Purser et al. 2013b; Biber et al. 2014). Milligan et al. (2016) suggested that the importance of Atlantic CWC for fish is species-specific and depends on the broader spatial context in which the substratum is found, so this could also apply to the Mediterranean CWC communities.

Most previous studies on fish communities associated to CWCs in the Mediterranean have been done at SML, where Tursi et al. (2004) identified 17 fishes (5 Chondroichthyes and 12 Osteichthyes) classified as co-occurrent species including the frequent *Etmopterux spinax, Galeus melastomus, Benthocometes robustus* and *Nezumia sclerorhynchus* (Table 29.1). In this area, D'Onghia et al. (2010, 2011, 2012) found that the most abundant fishes were the teleosts *Pagellus bogaraveo, Helicolenus dactylopterus* and *Conger conger*, as well as the cartilagineous *G. melastomus* (Fig. 29.6). A remarkable abundance of small sized fishes was detected due to the recruitment of *E. spinax*, *Merluccius merluccius, Micromesistius poutassou, Phycis blennoides* and *H. dactylopterus.* This suggests that SML CWC habitats act as nursery areas, provinding suitable environmental conditions for early life stages of those fishes (D'Onghia et al. 2010; D'Onghia, this volume). Considering the repeated observations of occurrence in CWC habitats, adult individuals of *P. bogaraveo* seem to be energetically dependent on the hydrographically mediated food production in these habitats (D'Onghia et al. 2012). The significantly high abundance recorded for *C. conger* seems to indicate a preferential distribution of the species in structurally complex three-dimensional habitats like those built by CWC (D'Onghia et al. 2012), as detected for its congener *C. oceanicus* in western Atlantic CWC habitats (Ross and Quattrini 2007 in Linley et al. 2015). Although *H. dactylopterus* uses a wide range of habitats and seems to be closely associated with the seabed, it is also common in CWC habitats, also in the Atlantic (see for instance Purser et al. 2013b) probably due to trophic reasons because zooplankton and small shrimps can be more abundant among the colonies (D'Onghia et al. 2012). This fish is also very common in CWC habitats (dominated by *M. oculata*) at the Nora canyon (Sardinian coral province), together with *Polyprion americanus*, large *Scorpaena elongata* specimens, *Acantholabrus palloni* and *Benthocometes robustus* (Taviani et al. 2017), as well as in black coral habitats (dominated by *L. glaberrima*) at the Malta Escarpment (310–315 m) together with *Macroramphosus scolopax*, *Lepidopus caudatus* and *P. americanus* (Angeletti et al. 2015) (Fig. 29.6). Close to the Eastern Mediterranean, the information on fish assemblages is limited to the study by Mytilineou et al. (2014) who characterised them in CWC habitats at Kephalonia Island (300–850 m). *H. dactylopterus* and *G. melastomus* were the most commonly caught fishes close to CWC. According to Mytilineou et al. (2014), no clear relationship for diet or reproduction was detected between *H. dactylopterus* and CWC and therefore the only suggestion, if any, could be related to the shelter provided by CWC. Regarding *G. melastomus*, its preference for CWC habitats in relation to hard/mixed bottoms could be due to feeding, as CWC related bottoms are generally inhabited by higher amounts of small crustaceans.

In western Mediterranean CWC habitats, information on fishes is also scarce and no detailed studies have been done to date (Reyss 1971; de Lucia et al. 2008; Hebbeln et al. 2009; Pardo et al. 2011; de la Torriente et al. 2014). At Lacaze-Duthiers submarine canyon, the most common fishes in CWC habitats are Scorpaenids (*Scorpaena* spp.) and Serranids (*Polyprion americanus*) (Reyss 1971), whereas *H. dactylopterus*, *Trisopterus luscus* and *Trachurus mediterraneus* are the most abundant fishes within an assemblage including 23 fish species at Cap de Creus canyon (de Lucia et al. 2008). Mastrototaro et al. (2017) reported a total of 15 fishes in aggregations of *I. elongata* of the Balearic Promontory, documenting interesting behaviour patterns for some species including *B. robustus*, which was observed camouflaging itself swimming vertically behind the branches of *I. elongata*. At Alborán Sea CWC habitats and coral rubble bottoms from Chella, Djibouti and Cabliers banks, the most common species are *H. dactylopterus*, *Scorpaena scrofa, M. poutassou, Hoplostethus mediterraneus* and *P. bogaraveo* (Hebbeln et al. 2009; Pardo et al. 2011; de la Torriente et al. 2014) (Fig. 29.6). In CWC habitats at Gazul MV (GoC), the fish assemblages are dominated by similar species than those of the Alborán Sea (Díaz del Rio et al. 2014).

These studies reported, in most cases, fish species that are common at similar depths and in different habitat types (from soft to hard bottoms), thus the fish fauna occurring in CWC habitats is not exclusive to this habitat type. For instance, *H. dactylopterus* is widespread in the whole

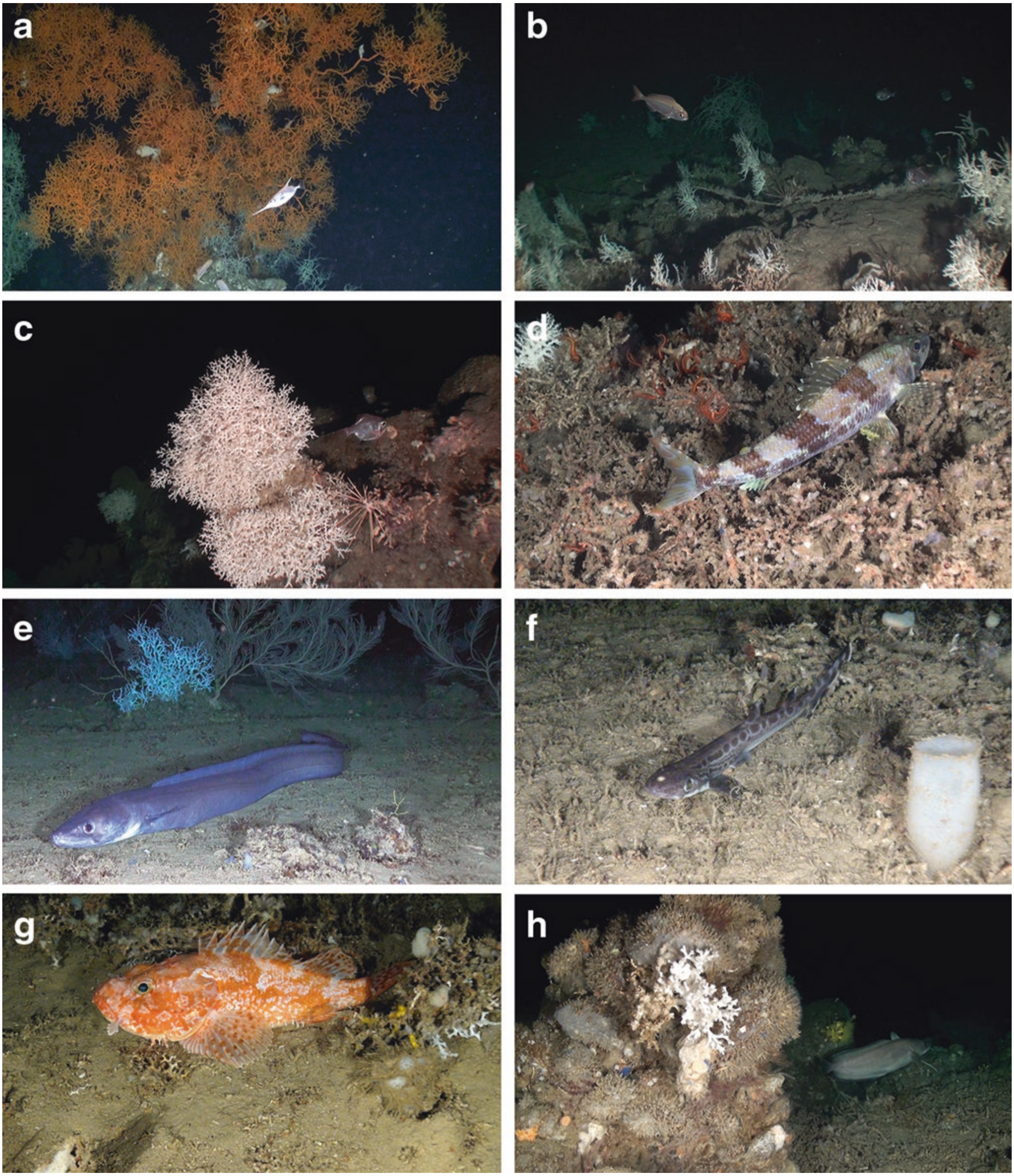

Fig. 29.6 Some fishes frequently observed in Mediterranean CWC habitats. (**a**) *Macroramphosus scolopax* in front of a large colony of the black coral *Leiopathes glaberrima* (Chella bank, 360 m depth); (**b**) *Pagellus bogaraveo* on a *Madrepora oculata* dominated bank, together with several individuals of *Hoplostethus mediterraneus* (right) and a *Cidaris cidaris* (center) over a lost fishing longline (Chella bank, 320 m); (**c**) The fish *H. mediterraneus* close to a large *M. oculata* colony, with several *C. cidaris* in the foreground and background (Chella bank, 340 m); (**d**) An individual of *Aulopus filamentosus* lying on a dead coral framework with a high density of *Ophiothrix* sp. (Chella bank, 250 m); (**e**) A large specimen of *Conger conger* close to several colonies of *M. oculata* and the large gorgonian *Callogorgia verticillata* (Malta trough, 550 m); (**f**) *Galeus melastomus* on a buried dead coral framework together with a small *Asconema setubalense* (Catifas bank, 400 m); (**g**) *Scorpaena elongata* on a *M. oculata* framework (Cabliers bank, 370 m); (**h**) *Phycis blennoides* moving on coral rubble bottoms, with colonies of *Lophelia pertusa* (front) and *Dendrophyllia cornigera* (background) (Chella bank, 430 m). (Pictures from © Oceana (a–d, f–h) and from © Oceana©LIFE BaĦAR for N2K (e))

Mediterranean basin covering a large range of depths (between 40 and 1100 m) and bottom types (Lloris 2015). A better understanding of the interactions of CWC with the associated fish species, biological and ecological processes and environmental regulating factors is of crucial importance as the effects of CWC on fish diversity and/or abundance varies across CWC habitats (Linley et al. 2015). Nevertheless, interpreting apparent species-habitat associations must be done with care taking into account that any assessment of a fish species preference will require detailed study on the organism over appropriate temporal and spatial scales (Milligan et al. 2016).

29.5 Future Research

Although many studies on Mediterranean CWC banks have been published in recent years, the information about their associated faunistic communities and the relationships between CWC and that fauna is very scarce, especially in the western and eastern basins, as well as in the adjacent areas influenced by the MOW (e.g. Strait of Gibraltar, GoC) (Zibrowius 2003; Tursi et al. 2004; Taviani et al. 2005, 2017; Freiwald et al. 2009; Mastrototaro et al. 2010; D'Onghia et al. 2015). Preliminary investigations on biodiversity of CWC habitats from the Alborán Sea and other Mediterranean areas (e.g. Malta escarpment, off South Creta) as well as from the GoC under the framework of different ongoing projects will provide new and needed information on the spatial distribution and linkage of associated species across CWC habitats of this part of the world (see Knittweiss et al., this volume). Future directions should also include the analysis of large scale spatial and temporal patterns as well as the environmental linkage of the CWC associated fauna, as this type of information is completely absent for the Mediterranean Sea.

The available faunistic information on the CWC associated communities is still partial as most of the studies did not combine sampling methods targetting endofauna, epifauna and demersal fauna in order to obtain a comprehensive and detailed biological characterisation of each "compartment" of the CWC ecosystem. Nowadays, ROVs are widely used to study the characteristics of the CWC habitats. However, although they are very useful and non-invasive deep-sea exploration methods, these methods are not ideal for characterising an important part of the associated biodiversity occurring in these complex habitats. Hence, to our mind, studies sampling benthic, planktonic and demersal samples are needed in order to collect the small sized species (mainly for highly biodiverse groups such as molluscs, bryozoans, polychaetes and crustaceans) and those species that can not be fully identified using external morphological characters (e.g. sponges).

To date, there are only few studies that focused on specific species or faunistic groups inhabiting CWC banks in the Mediterranean Sea (mainly in the central basin) (e.g. poriferans: Longo et al. 2005; Calcinai et al. 2013; molluscs: López-Correa et al. 2005; Negri and Corselli 2016; bryozoans: Zabala et al. 1993; Rosso 2003; fishes: D'Onghia et al. 2012; meiofauna: Bongiorni et al. 2010; Sandulli et al. 2015; decapods: Capezzuto et al. 2012). Regarding cnidarians, the scarce available information on CWC associated hydroids hinders our understanding of whether some species are common, rare or specific of this habitat within the Mediterranean Sea, and thus accurate data about assemblage composition, species abundance and hydroid preferential substrate is needed. With respect to deep anthozoans, there are still many knowledge gaps regarding some taxa, such as stoloniferans, alcyonarians, corallimorpharians, actinarians, ceriantharians and zoantharians, due both to sampling constrains because of their small size, fragility or burrowing habits and to significative taxonomic issues that have led to an underestimation of their importance in deep-sea communities (see Altuna and Poliseno, this volume). Regarding polychaetes, future research should include the study of those inhabiting live CWC colonies in order to identify potential symbiotic relationships (especially Polynoidae), as well as to assess the role of Serpulidae species as binders or secondary builders in CWC habitats across the Mediterranean basin. To date, neither Platyhelminthes nor Nemerteans have been recorded from Mediterranean CWC habitats, although further studies devoted to the infauna inhabiting sediments around these structures might shed some light on the presence of both groups. There is also scarce information on the relationships of bryozoans and brachiopods with CWC habitats, moreover there are no studies on their preferential substrate and microhabitats within the CWC habitat in order to determine how strong is their association with CWC species. The functional role of CWC habitats in fish diversity and abundance is still not fully understood and data assessing the linkage between CWC and fish species are also needed to detect species-specific patterns (Biber et al. 2014; Milligan et al. 2016; D'Onghia, this volume).

In general, some groups (peracarid crustaceans, echiurans, sipunculids, nemerteans, platyhelminths, etc.) have hardly been considered in previous studies on associated CWC biota and the information is nearly absent for the whole Mediterranean CWC habitats. Moreover, there is also limited knowledge on prokaryotes that occur in CWC for the Mediterranean and no information on protozoans and meiofaunal metazoans for mediterranean CWC (for prokaryotes check Weinbauer et al., this volume). Consequently, detailed studies on them are still needed. The ethology of CWC strictly or preferentially associated taxa (e.g. the gastropods *Coralliophila richardi* and other Coralliophilinae, *Iphitus tuberatus,* and the polychaete *Eunice norvegica*) should be explored in-depth to better define their trophic relationships with the coral host.

To complement research efforts addressing these gaps in knowledge of CWC associated fauna, priority should also be given to the investigation of the occurrence and quality of CWC dominated communities along the Mediterranean basin and to support the establishment of measures to enhance conservation at large-scale for both the habitat and all associated biota, as suggested for other vulnerable deep-water habitats (Hogg et al. 2010; see Otero and Marin, this volume).

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References

Aguilar R, Correa ML, Calcinai B, et al (2011) First records of *Asbestopluma hypogea* Vacelet and Boury-Esnault, 1996 (Porifera, Demospongiae Cladorhizidae) on seamounts and in bathyal settings of the Mediterranean Sea. Zootaxa 2925:33–40

Altuna A (2007) Bathymetric distribution patterns and biodiversity of benthic Medusozoa (Cnidaria) in the Bay of Biscay (north-eastern Atlantic). J Mar Biol Assoc UK 87:681–694

Álvarez-Pérez G, Busquets P, De Mol B, et al (2005) Deep-water coral occurrences in the Strait of Gibraltar. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 207–221

Angeletti L, Taviani M (2011) Entrapment, preservation and incipient fossilization of benthic predatory molluscs within deep-water coral frames in the Mediterranean Sea. Geobios 44:543–548

Angeletti L, Montagna P, Schembri PJ, et al (2011) Giant sessile barnacles contribute to the construction of cold-water coral habitats south of Malta (Mediterranean Sea). HERMIONE, 2nd annual meeting, Malaga (Spain), April 2011, pp 11–15

Angeletti L, Taviani M, Canese S, et al (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Mediterr Mar Sci 15:225–238

Angeletti L, Mecho A, Doya C, et al (2015) First report of live deep-water cnidarian assemblages from the Malta escarpment. Ital J Zool 82:291–297

Anonymous (2009) Deep-water coral ecosystems in the Central Mediterranean Sea. Cruise No. 70, Leg 1, September 24–October 18, 2006, La Valetta (Malta)-Heraklion (Greece), Supplement to the Meteor Cruise Report M70/1, Meteor-Berichte, pp 11–5

Baldrighi E, Lavaleye E, Allani S, et al (2014) Large spatial scale variability in bathyal macrobenthos abundance, biomass, and diversity along the Mediterranean continental margin. PLoS One 9:e107261

Beaulieu SE (2001) Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks. Deep-Sea Res Part 2 Top Stud Oceanogr 48:1121–1137

Berning B, Tilbrook KJ, Rosso A (2008) Revision of the north-eastern Atlantic and Mediterranean species of the genera *Herentia* and *Therenia* (Bryozoa: Cheilostomata). J Nat Hist 42:1509–1547

Beuck L, Freiwald A, Taviani M (2010) Spatio-temporal bioerosion patterns in deep-water scleractinians from off Santa Maria di Leuca (Apulia, Ionian Sea). Deep-Sea Res Part 2 Top Stud Oceanogr 57:458–470

Biber MF, Duineveld GC, Lavaleye MS, et al (2014) Investigating the association of fish abundance and biomass with cold-water corals in the deep Northeast Atlantic Ocean using a generalised linear modelling approach. Deep-Sea Res Part 2 Top Stud Oceanogr 99:134–145

Bo M, Bavestrello G, Canese S, et al (2009) Characteristics of a black coral meadow in the twilight zone of the Central Mediterranean Sea. Mar Ecol Prog Ser 397:53–61

Bo M, Canese S, Spaggiari C, et al (2012) Deep coral oases in the South Tyrrhenian Sea. PLoS One 7:e49870

Bo M, Cerrano C, Canese S, et al (2014) The coral assemblages of an off-shore deep Mediterranean rocky bank (NW Sicily, Italy). Mar Ecol 35:332–342

Bo M, Bavestrello G, Angiolillo M, et al (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS One 10:e0119393

Boero F, Bouillon J (1993) Zoogeography and life cycle patterns of Mediterranean hydromedusae (Cnidaria). Biol J Linn Soc 48:239–266

Bonfitto A, Oliverio M, Sabelli B, et al (1994a) A Quaternary deep-sea marine molluscan assemblage from East Sardinia (Western Tyrrhenian Sea). Boll Malacol 30:141–157

Bonfitto A, Bigazzi M, Fellegara I, et al (1994b) Rapporto scientifico sulla crociera DP'91 (Margine orientale della Sardegna, Mar Mediterraneo). Boll Malacol 30:129–140

Bongiorni L, Mea M, Gambi C, et al (2010) Deep-water scleractinian corals promote higher biodiversity in deep-sea meiofaunal assemblages along continental margins. Biol Conserv 143:1687–1700

Bouchet P, Taviani M (1992) The Mediterranean deep-sea fauna: pseudopopulations of Atlantic species? Deep-Sea Res Part 1 Oceanogr Res Pap 39:169–184

Bouderesque CF (2004) Marine biodiversity in the Mediterranean: status of species, populations and communities. Sci Rep Port-Cross Nat Park, France 20:97–146

Bouillon J, Medel M, Pagès F, et al (2004) Fauna of the Mediterranean Hydrozoa. Sci Mar 68:5–438

Buhl-Mortensen L, Mortensen PB (2004) Symbiosis in deep-water corals. Symbiosis 37:33–61

Buhl-Mortensen L, Mortensen PB (2005) Distribution and diversity of species associated with deep-sea gorgonain corals off Atlantic Canada. In: Freiwald A, Roberts JM (eds) Cold-water corals ecosystems. Springer, Berlin, Heidelberg, pp 849–879

Calcinai B, Bavestrello G, Cattaneo-Vietti R, et al (2001) Il ruolo dei poriferi nei processi bioerosivi dei substrati organogeni. Biol Mar Med 8:181–190

Calcinai B, Moratti V, Martinelli M, et al (2013) Uncommon sponges associated with deep coral bank and maerl habitats in the Strait of Sicily (Mediterranean Sea). Ital J Zool 80:412–423

Calder DR (1991) Associations between hydroid species assemblages and substrate types in the mangal at Twin Cays, Belize. Can J Zool 69:2067–2074

Capezzuto F, Maiorano P, Panza M, et al (2012) Occurrence and behaviour of *Paromola cuvieri* (Crustacea, Decapoda) in the Santa Maria di Leuca cold-water coral community (Mediterranean Sea). Deep-Sea Res Part 1 Oceanogr Res Pap 59:1–7

Carlier A, Le Guilloux E, Olu K, et al (2009) Trophic relationships in a deep Mediterranean cold-water coral bank (Santa Maria di Leuca, Ionian Sea). Mar Ecol Prog Ser 397:125–137

Carpine C, Grasshoff M (1975) Les gorgonaires de la Mediterranee. Bull Inst Oceanogr 71:1–140

Cartes JE, Lo Iacono C, Mamouridis V, et al (2013) Geomorphological, trophic and human influences on the bamboo coral *Isidella elongata* assemblages in the deep Mediterranean: to what extent does *Isidella* form habitat for fish and invertebrates? Deep-Sea Res Part 1 Oceanogr Res Pap 76:52–65

Cartes JE, Papiol V, Frutos I, et al (2014) Distribution and biogeographic trends of decapod assemblages from Galicia Bank (NE Atlantic) at depths between 700 and 1800 m, with connections to regional water masses. Deep-Sea Res Part 2 Top Stud Oceanogr 106:165–178

Cau A, Follesa MC, Moccia D, et al (2015) Deep water corals biodiversity along roche du large ecosystems with different habitat complexity along the south Sardinia continental margin (CW Mediterranean Sea). Mar Biol 162:1865–1878

Cornelius P (1982) Hydroids and medusae of the family Campanulariidae recorded from the eastern North Atlantic, with a world synopsis of genera. Bull Br Mus Nat Hist Zool 42:37–148

Costantini F, Taviani M, Remia A, et al (2010) Deep-water *Corallium rubrum* (L., 1758) from the Mediterranean Sea: preliminary genetic characterisation. Mar Ecol 31:261–269

Costello MJ, McCrea M, Freiwald A, et al (2005) Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 771–805

D'Onghia G, Maiorano P, Sion L, et al (2010) Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:397–411

D'Onghia G, Indennidate A, Giove A, et al (2011) Distribution and behaviour of the deep-sea benthopelagic fauna observed using towed cameras in the Santa Maria di Leuca cold water coral province. Mar Ecol Prog Ser 443:95–110

D'Onghia G, Maiorano P, Carlucci, et al (2012) Comparing deep-sea fish fauna between coral and non-coral "megahabitats" in the Santa Maria di Leuca cold-water coral Province (Mediterranean Sea). PLoS One 7:e44509

D'Onghia G, Capezzuto F, Cardone F, et al (2015) Macro- and megafauna recorded in the submarine Bari canyon (southern Adriatic, Mediterranean Sea) using different tools. Mediterr Mar Sci 16:180–196

Da Silva FM (2009) Biodiversity of cold-water coral reefs in the Gulf of Cadiz (NE Atlantic). Master Thesis Dissertation, Universidade de Aveiro

Deidun A, Andaloro F, Bavestrello G, et al (2015) First characterisation of a *Leiopathes glaberrima* (Cnidaria: Anthozoa: Antipatharia) forest in Maltese exploited fishing grounds. Ital J Zool 82:271–280

de la Torriente A, Aguilar R, Serrano A, et al (2014) Sur de Almería-Seco de los Olivos. Proyecto LIFE+ INDEMARES. Fundación biodiversidad, Ministerio de Agricultura, Alimentación y Medio Ambiente, p 102

Delibrias G, Taviani M (1984) Dating the death of Mediterranean deep-sea scleractinian corals. Mar Geol 62:175–180

de Lucia AG, Gori A, Orejas C, et al (2008) Ichtyofauna diversity and distribution in the Cap de Creus Canyon (Northwestern Mediterranean) from video transects. In: Neil H, Tracey D (eds) Proceedings of the Fourth Deep Sea Coral Symposium (ISDSC), Wellington (New Zealand), December 2008, p 210

Di Geronimo R (2010) Cirripeds from deep-water coral mounds off S. Maria di Leuca, Apulian Plateau Bank (Mediterranean Sea). Deep-Sea Res Part 2 Top Stud Oceanogr 57:487–492

Díaz del Rio V, Bruque G, Fernández-Salas LM, et al (2014) Volcanes de fango del golfo de Cádiz, Proyecto LIFE + INDEMARES. Fundación Biodiversidad, Ministerio de Agricultura, Alimentación y Medio Ambiente, p 128

Domínguez-Carrió C, Requena S, Gili JM (2014) Sistema de Cañones Submarinos Occidentales del Golfo de León, Proyecto LIFE + INDEMARES. Fundación Biodiversidad, Ministerio de Agricultura, Alimentación y Medio Ambiente, p 100

Emig C, Geistdoerfer P (2004) The Mediterranean deep-sea fauna: historical evolution, bathymetric variations and geographical changes. Carnets Géol 1:1–10

Evans J, Knittweis L, Aguilar R, et al (2016) On the occurrence of *Coronaster briareus* (Echinodermata, Forcipulatida, Asteriidae) in the Mediterranean Sea. Mar Biodivers 48: 1381–1390

Fabri MC, Pedel L, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207

Fabri MC, Bargain A, Pairaud I, et al (2017) Cold-water coral ecosystems in Cassidaigne Canyon: an assessment of their environmental living conditions. Deep-Sea Res Part 2 Top Stud Oceanogr 137:436–453

Fanelli E, Delbono I, Ivaldi R, et al (2017) Cold-water coral *Madrepora oculata* in the eastern Ligurian Sea (NW Mediterranean): historical and recent findings. Aquat Conserv Mar Freshw Ecosyst 27:965–975

Fosså JH, Mortensen PB (1998) Artsmangfoldet på *Lophelia*-korallrev og metoder for kartlegging og overvåkning. Fisken Havet 17:95

Fredj G, Laubier L (1983) The Deep Mediterranean Benthos. Ecology 8:109–145

Fredj G, Maurin C (1987) Les poissons dans la banque de données MEDIFAUNE. Application à l'étude des caractéristiques de la faune ichtyologique méditerranéenne. Cybium 11:31–139

Freiwald A, Heinrich R, Pätzold J (1997) Anatomy of a deep-water coral reef mound from Stjernsun, west Finnmark, Northern Norway. In: Jame NP, Clarke JAD (eds) Cool-water carbonates. Society of Sedimentary Geologist, Special Publication 56, pp 140–161

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Gautier YV (1958) Sur quelques Bryozoaires de la zone à coraux profonds du golfe de Gênes. Bull Inst Oceanogr 1123:1–11

Gautier YV (1962) Recherches écologiques sur les Bryozoaires chilostomes en Méditerranée occidentale. Rec Travel St Mar Endoume 38(24):1–434

Gili JM, Ros JD (1981) Types of bottoms and benthic Cnidaria from the trawling grounds (littoral and bathyal) off Catalonia (NE Spain). Vie Milieu 37:85–98

Glynn PW (1997) Bioerosion and coral reef growth: a dynamic balance. In: Birkeland C (ed) Life and death of coral reefs. Chapman and Hall, New York, pp 68–95

Gofas S, Moreno D, Salas C (2011) Moluscos marinos de Andalucía. Universidad de Málaga, Junta de Andalucía, Málaga, p 200

González-Duarte MM, Megina C, Piraino S (2014) Looking for long-term changes in hydroid assemblages (Cnidaria, Hydrozoa) in Alboran Sea (South-Western Mediterranean): a proposal of a monitoring point for the global warming. Helgol Mar Res 68:511–521

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Grinyó J, Gori A, Ambroso S, et al (2016) Diversity, distribution and population size structure of deep Mediterranean gorgonian assemblages (Menorca Channel, Western Mediterranean Sea). Prog Oceanogr 145:42–56

Harmelin JG (1979) Aperçu de la faune bryozoologique bathyale du détroit Siculo-Tunisien. Rapp Comm Int Mer Médit 25–26: 171–172

Harmelin JG, d'Hondt JL (1982) Bryozoaires cyclostomes bathyaux des campagnes océanographiques del "Atlantis II" du "Chain" et du "Knorr" 1967–1972. Bull Mus Nat Hist Nat (A) 4:3–16

Harmelin JG, d'Hondt JL (1992a) Bryozoaires des parages de Gibraltar (campagne océanographique BALGIM, 1984). 1-Chéilostomes. Bull Mus Nat Hist Nat 14:23–67

Harmelin JG, d'Hondt JL (1992b) Bryozoaires des parages de Gibraltar (campagne océanographique BALGIM, 1984). 2-Cténostomes et cyclostomes. Bull Mus Nat Hist Nat 14:605–621

Harmelin JG, d'Hondt JL (1992c) Transfers of bryozoan species between the Atlantic Ocean and the Mediterranean Sea via the Strait of Gibraltar. Oceanol Acta 16:63–72

Hebbeln DC, Wienberg C, Beuck L, et al (2009) Report and preliminary results of RV Poseidon cruise POS 385 "cold-water corals of the Alboran Sea (Western Mediterranean Sea)", Faro-Toulon, May–June 2009. Berichte, Fachbereich Geowissenschaften, Universität Bremen, No. 273

Henry LA (2001) Hydroids associated with deep-sea corals in the boreal north-west Atlantic. J Mar Biol Assoc UK 81:163–164

Henry DP, McLaughlin PA (1986) The recent species of *Megabalanus* (Cirripedia: Balanomorpha) with special emphasis on *Balanus tintinnabulum* (Linnaeus) senso lato. Zool Verhandel 235:3–60

Henry LA, Roberts JM (2007) Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. Deep-Sea Res Part 1 Oceanogr Res Pap 54:654–672

Hogg MM, Tendal OS, Conway KW, et al (2010) Deep-sea sponge grounds: reservoirs of biodiversity, UNEP-WCMC Biodiversity Series 32. UNEP-WCMC, Cambridge

Husebø Å, Nøttestad L, Fosså J, et al (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471:91–99

Jarms G, Tiemann H, Padros AA (2003) A new bathybenthic coronate polyp, *Nausithoe sorbei* sp. nov. (Scyphozoa, Coronatae) from the Bay of Biscay and off Azores. Mitten Hamburg Zool Mus Inst 100:1–11

Jensen A, Frederiksen R (1992) The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractiniaria) on the Faroe shelf. Sarsia 77:53–69

Jiménez C, Achilleos K, Abu Alhaija R, et al (2016) Living in close quarters: epibionts on *Dendrophyllia ramea* deep-water corals (Cyprus and Menorca channel). Rapp Comm Int Mer Médit 41:466

Knittweis L, Aguilar R, Alvarez H, et al (2016) New depth record of the precious red coral *Corallium rubrum* for the Mediterranean. Rapp Comm Int Mer Médit 41:467

Krieger KJ, Wing B (2002) Megafauna associations with deep-water corals (*Primnoa* spp.) in the Gulf of Alaska. Hydrobiologia 471:83–90

Lastras G, Canals M, Ballesteros E, et al (2016) Cold-water corals and anthropogenic impacts in La Fonera Submarine canyon head, Northwestern Mediterranean Sea. PLoS One 11:e0155729

Linley TD, Lavaleye M, Maiorano P, et al (2015) Effects of cold-water corals on fish diversity and density (European Continental Margin: Artic, NE Atlantic and Mediterranean Sea): data from three baited lander systems. Deep-Sea Res Part 2 Top Stud Oceanogr.

Llompart C (1988) Braquiópodos del Banco de Chella (Mar de Alborán, Mediterráneo Occidental). Act Geol Hisp 23:311–319

Lloris D (2015) Ictiofauna marina. Manual de identificación de los peces marinos de la Península Ibérica y Baleares. Ediciones Omega, Barcelona

Lo Iacono C, Gràcia E, Ranero CR, et al (2014) The West Melilla cold water coral mounds, Eastern Alboran Sea: morphological characterization and environmental context. Deep-Sea Res Part 2 Top Stud Oceanogr 99:316–326

Longo C, Mastrototaro F, Corriero G (2005) Sponge fauna associated with a Mediterranean deep-sea coral bank. J Mar Biol Assoc UK 85:1341–1352

López Correa M, Freiwald A, Hall-Spencer J, et al (2005) Distribution and habitats of *Acesta excavata* (Bivalvia: Limidae) with new data on its shell ultrastructure. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 173–205

López E, San Martín G, Jiménez M (1996) Syllinae (Syllidae, Annelida, Polychaeta) from Chafarinas Islands (Alborán Sea, Western Mediterranean). Misc Zool 19:105–118

López-González PJ, Cunha MR (2010) Two new species of *Dendrobrachia* Brook, 1889 (Cnidaria: Octocorallia: Dendrobrachiidae) from the north-eastern Atlantic and western Mediterranean. Sci Mar 74:423–434

Macpherson E, Segonzac M (2005) Species of the genus *Munidopsis* (Crustacea, Decapoda, Galatheidae) from the deep Atlantic Ocean, including cold-seep and hydrothermal vent areas. Zootaxa 1095:1–60

Madurell T, Olariaga A, Gili JM (2012a) Submarine coupled with multi-filtration pump. J Plankton Res 34:1078–1085

Madurell T, Orejas C, Requena S, et al (2012b) The benthic communities of the Cap de Creus canyon. In: Würtz M (ed) Mediterranean submarine canyons: ecology and governance. IUCN, Gland/Málaga, pp 123–132

Maldonado M, Ribes M, Van Duyl F (2012) Nutrient fluxes through sponges: biology, budgets, and ecological implications. Adv Mar Biol 62:114–182

Malinverno E, Taviani M, Rosso A, et al (2010) Stratigraphic framework of the Apulian deep-water coral province, Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:345–359

Margelli A, Coppini M, Bogi C (1995) Remarks on some poorly known Mediterranean mollusks. La Conchiglia 275:42–44

Mastrototaro F, Matarrese A, Tursi A (2002) Un mare di coralli nel Mar Ionio. Biol Mar Mediterr 9:616–619

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral ecosystem off cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

Mastrototaro F, Maiorano P, Vertino A, et al (2013) A facies of *Kophobelemnon* (Cnidaria, Octocorallia) from Santa Maria di Leuca coral province (Mediterranean Sea). Mar Ecol 34:313–320

Mastrototaro F, Chimienti G, Acosta J, et al (2017) *Isidella elongata* (Cnidaria: Alcyonacea) facies in the western Mediterranean Sea: visual surveys and descriptions of its ecological role. Eur Zool J 84:209–225

Maynou F, Cartes JE (2012) Effects of trawling on fish and invertebrates from deep-sea coral facies of *Isidella elongata* in the western Mediterranean. J Mar Biol Ass UK 92:1501–1507

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the Younger Dryas. Earth Plan Sci Lett 298:143–152

Metaxas A, Davis JE (2005) Megafauna associated with assemblages of deep- water corals on the Scotian slope. J Mar Biol Assoc UK 85:1381–1390

Mifsud C, Mastrototaro F, Taviani M (2008) On the occurrence of *Anamenia gorgonophila* (Kowalevsky, 1880) (Solenogastres: Strophomeniidae) and its host *Paramuricea macrospina* in the Maltese waters (Mediterranean Sea). Boll Malacol 4485–8: 109–112

Mifsud C, Taviani M, Stohr S (2009) Remarks on Echinodermata from the South Central Mediterranean Sea based upon collections made during the MARCOS cruise (10 to 20th April, 2007). Mediterr Mar Sci 10:63–72

Milligan RJ, Spence G, Roberts JM, et al (2016) Fish communities associated with cold-water corals vary with depth and substratum type. Deep-Sea Res Part 1 Oceanogr Res Pap 114:43–54

Mortensen PB (2000) *Lophelia pertusa* (Scleractinia) in Norwegian waters: distribution, growth and associated fauna. Dissertation, University of Bergen, Norway

Mortensen PB (2001) Aquarium observation on the deep-water coral *Lophelia pertusa* (L., 1758) (Scleractinia) and selected associated invertebrates. Ophelia 54:83–104

Mortensen PB, Fosså JH (2006) Species diversity and spatial distribution of invertebrates on deep-water *Lophelia* reefs in Norway. In: Glynn PM, Pichon M (eds) Proceedings of the 10th international coral reefs symposium, Okinawa (Japan), June–July 2004, pp 1849–1868

Moura CJ, Cunha MR, Schuchert P (2007) *Tubiclavoides striatum* gen. nov et sp nov (Cnidaria: Hydrozoa) a new bathyal hydroid from the Gulf of Cadiz, north-east Atlantic Ocean. J Mar Biol Assoc UK 87:421–428

Mueller CE, Lundälv T, Middelburg JJ, et al (2013) The symbiosis between *Lophelia pertusa* and *Eunice norvegica* stimulates coral calcification and worm assimilation. PLoS One 8:e58660

Mytilineou C, Smith CJ, Anastasopoulou A, et al (2014) New cold-water coral occurrences in the Eastern Ionian Sea: results from experimental long line fishing. Deep-Sea Res Part 2 Top Stud Oceanogr 99:146–157

Negri MP, Corselli C (2016) Bathyal Mollusca from the cold-water coral biotope of Santa Maria di Leuca (Apulian margin, southern Italy). Zootaxa 4186:1–97

Núñez J, Barnich R, Brito MC, et al (2015) Familia Polynoidae Kinberg, 1855. In: Parapar J, et al (eds) Fauna Ibérica, Annelida, Polychaeta IV, vol 41. Museo Nacional de Historia Natural/CSIC, Madrid, pp 104–216

Oliverio M (1989) Famiglia Coralliophilidae Chenu, 1869 in Mediterraneo. La Conchiglia 246–249:48–55

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Prog Ser 397:37–51

Orejas C, Gori A, Jiménez C, et al (2017a) First in situ documentation of a population of the coral *Dendrophyllia ramea* off Cyprus (Levantine Sea) and evidence of human impacts. Galaxea, J Coral Reef Stud 19:15–16

Orejas C, Addamo A, Álvarez M, et al (2017b) Cruise report MEDWAVES survey. (MEDiterranean out flow WAter and Vulnerable Eco systemS) ATLAS Project H2020. 211 pp and Appendixes. https://zenodo.org/badge/DOI/10.5281/zenodo.556516.svg

Panetta P, Mastrototaro F, Capezzuto F, et al (2010) Size evaluation of *Delectopecten vitreus* (Mollusca Bivalvia) from Santa Maria di Leuca deep-water-coral site (Ionian Sea). Biol Mar Mediterr 17:308–309

Panetta P, Mastrototaro F, Chimienti G, et al (2013) Tanatocenosi Würmiana nel Canyon di Bari (Mar Adriatico). Biol Mar Mediterr 20:148–149

Pansini M, Musso B (1991) Sponges from trawl-exploitable bottoms of Ligurian and Tyrrhenian seas: distribution andecology. Mar Ecol 12:317–329

Pardo E, Aguilar R, García S, et al (2011) Documentación de arrecifes de corales de agua fría en el Mediterráneo occidental (Mar de Alborán). Chron Nat 1:20–34

Pérès JM (1985) History of the Mediterranean biota and the colonization of the depths. In: Margalef R (ed) Key environments: western Mediterranean. Pergamon Press, Oxford, pp 198–232

Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la Mer Méditerranée. Rec Trav St Mar Endoume 31:1–137

Pierdomenico M, Russo T, Ambroso S, et al (2018) Effects of trawling activity on the bamboo-coral *Isidella elongata* and the sea pen *Funiculina quadrangularis* along the Gioia Canyon (Western Mediterranean, southern Tyrrhenian Sea). Prog Oceanogr 169:214–226

Purser A, Ontrup J, Schoening T, et al (2013a) Microhabitat and shrimp abundance within a Norwegian cold-water coral ecosystem. Biogeosciences 10:5779–5791

Purser A, Orejas C, Gori A, et al (2013b) Local variation in the distribution of benthic megafauna species associated with cold-water coral reefs on the Norwegian margin. Cont Shelf Res 54:37–51

Ramil F, Vervoort W (1992) Report on the Hydroida collected by the'BALGIM' expedition in and around the Strait of Gibraltar. Zool Verh 277:1–262

Relini G (1980) Guide per il riconoscimento delle specie animali delle acque lagunari e costiere italiane. Cirripedi Toracici. Consiglio Nazionale delle Ricerche

Remia A, Taviani M (2005) Shallow-buried pleistocene *Madrepora*-dominated coral mounds on a muddy continental slope, Tuscan archipielago NE Tyrrhenian Sea. Facies 50:419–425

Reyss D (1971) Les canyons sous-marins de la mer catalane, le rech du Cap et le rech Lacaze-Duthiers. 3. Les peuplements de macrofaune benthique. Vie Milieu 22:529–613

Roberts JM (2005) Reef-aggregation behavior by symbiotic eunicid polychaetes from cold-water corals: do worms assemble reefs? J Mar Biol Assoc UK 85:813–819

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Roberts JM, Wheeler AJ, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, Cambridge, New York, p 334

Rossi L (1958) Contributo allo studio della fauna di profondità vivente presso la Riviera lugure di Levante. Ann Mus Civ St Nat Genova 2:1–13

Rossi S, Bramanti L, Gori A, et al (2017) An overview of the animal forests of the world. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests. The ecology of benthic biodiversity hotspots. Springer, Cham, pp 1–26

Rosso A (2003) Bryozoans on deep-water scleractinians from the Mediterranean: a first sight. In: Abstracts of the 2nd international symposium on deep-sea corals, Erlangen geol Abh Sonder, 9–12 September 2003

Rosso A, Di Martino E (2016) Bryozoan diversity in the Mediterranean Sea: an update. Mediterr Mar Sci 17:567–607

Rosso A, Vertino A, Di Geronimo I, et al (2010) Hard- and soft-bottom thanatofacies from the Santa Maria di Leuca deep-water coral province, recent Mediterranean. Deep-Sea Res Part 2 Top Stud Oceanogr 57:360–379

Rosso A, Sanfilippo R, Taddei Ruggiero E, et al (2013) Serpuloidean, bryozoan and brachiopod faunas from submarine caves in Sicily. Boll Soc Pal Ital 52:167–176

Rosso A, Beuck L, Vertino A, Sanfilippo R, Freiwald A (2018) Cribrilinids (Bryozoa, Cheilostomata) associated with deep-water coral habitats in the great Bahama Bank slope (NW Atlantic), with description of new taxa. Zootaxa 4524(4):401–439. https://doi.org/10.11646/zootaxa.4524.4.1

Rubio Salazar F (1987) Presencia de *Iphitus tuberatus* Jeffreys, 1883 (Gastropoda: Epitoniidae) en las costas españolas del mar de Alboran. Iberus 7:111–113

Rueda JL, Gil J, González-García E, et al (2011) First record of *Hacelia superba* (Echinodermata: Asteroidea) on the European continental margin. Mar Biodivers Rec 4e96:1–5

Rueda JL, González-García E, Krutzky C, et al (2016) From chemosynthesis-based communities to cold-water corals: vulnerable deep-sea habitats of the Gulf of Cádiz. Mar Biodivers 46:473–482

Sabelli B, Taviani M (2014) The making of the Mediterranean molluscan biodiversity. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 285–306

Sánchez-Gallego A, Orejas C, Lo Iacono C, et al (2014) Descripción de la megafauna en los fondos profundos del banco de Cabliers en el mar de Alborán. In: Ríos P, Suárez LA, Cristobo J (eds) XVIII Simposio Ibérico de Estudios de Biologia Marina, Gijón (Spain), September 2014, p 182

Sandulli R, Miljutin D, Angeletti L, et al (2015) Meiobenthos and nematode assemblages from different deep-sea habitats of the Strait of Sicily (Central Mediterranean Sea). Mediterr Mar Sci 16:402–412

Sanfilippo R (2009) New species of *Hyalopomatus* Marenzeller, 1878 (Annelida, Polychaeta, Serpulidae) from recent Mediterranean deep-water coral mounds and comments on some congeners. Zoosystema 3:147–161

Sanfilippo R, Vertino A, Rosso A, et al (2013) *Serpula* aggregates and their role in deep-sea coral communities in the southern Adriatic Sea. Facies 59:663–677

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the Northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108

Schembri PJ, Dimech M, Camilleri M, et al (2007) Living deep water *Lophelia* and *Madrepora* corals in Maltese waters (Strait of Sicily, Mediterranean Sea). Cah Biol Mar 48:77–83

Sciuto F, Rosso A (2015) Bathyal ostracods from the Santa Maria di Leuca deep–water coral province (northern Ionian Sea). Paleo Electron 18.2:1–17

Sitjá C, Maldonado M, Farias C, et al (2018) Deep-water sponge fauna from the mud volcanoes of the gulf of Cadiz (North Atlantic, Spain). J Mar Biol Assoc UK 1–25. https://doi.org/10.1017/

Stalder C, Vertino A, Rosso A et al (2015) Microfossils, a key to unravel cold-water carbonate mound evolution through time: evidence from the eastern Alboran Sea. PlosOne 10(10):e0140223

Stevenson A, Rocha C (2013) Evidence for the bioerosion of deep-water corals by echinoids in the Northeast Atlantic. Deep-Sea Res Part 1 Oceanogr Res Pap I 71:73–78

Taviani M, Colantoni P (1979) Thanatocoenoses wurmienses associees aux coraux blancs. Rapp Comm Int Mer Médit 25/26:141–142

Taviani M, Colantoni P (1984) Paléobiocoenoses profondes à scléractiniaires sur l'escarpement de Malte-Syracuse (Mer Méditerranée): leur structure, leur âge et leur signification. Oil Gas Sci Technol – Revue del IFP 39:547–559

Taviani M, Sabelli B (1982) *Iphitus* (Mollusca, Gastropoda) a deep-water genus new to the Mediterranean Sea. Lavori SIM 5:103–107

Taviani M, Taviani N (1986) Remarks on *Coralliophila richardi* (P. Fischer, 1882) (Gastropoda, Prosobranchia). Boll Malacol 22:65–72

Taviani M, Bouchet P, Metivier B, et al (1991) Intermediate steps of southwards faunal shifts testified by last glacial submerged thanatocoenoses in the Atlantic Ocean. Palaeogeogr Palaeoclimatol Palaeoecol 86:331–338

Taviani M, Remia A, Corselli C, et al (2005) First geo-marine survey of living cold-water *Lophelia* reefs in the Ionian Sea (Mediterranean basin). Facies 50:409–417

Taviani M, Angeletti L, Dimech M, et al (2009) Coralliophilinae (Mollusca: Gastropoda) associated with deep-water coral banks in the Mediterranean. Nautilus 123:106–112

Taviani M, Freiwald A, Beuck L (2010) The deepest known occurrence of the precious red coral *Corallium rubrum* (L. 1758) in the Mediterranean Sea. In: Bussoletti E, Cottingham D, Bruckner A, et al (eds) Proceedings of the international workshop on red coral science, management, trade: lessons from the Mediterranean, NOAA Technical Memorandum CRCP-13. NOAA, Silver Spring, pp 87–93

Taviani M, Angeletti L, Antolini B, et al (2011a) Geo-biology of Mediterranean deep-water coral ecosystems. In: Brugnoli E, Cavaretta G, et al (eds) Marine research at CNR. Dipartamento Terra e Ambiente, Consiglio Nazionale delle Ricerche, Roma, pp 705–720

Taviani M, Vertino A, López Correa M, et al (2011b) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603

Taviani M, Angeletti L, Beuck L, et al (2016) On and off the beaten track: megafaunal sessile life and Adriatic cascading processes. Mar Geol 369:273–287

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr.

Templado J (2014) Future trends of Mediterranean biodiversity. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea. Its history and present challenges. Springer, New York, pp 479–498

Templado J, Villanueva R (2010) Checklist of Phylum Mollusca. In: Coll M, Piroddi C, Steenbeek J, et al (eds) The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PLoS One 5:148–198

Tursi A, Mastrototaro F, Matarrese A, et al (2004) Biodiversity of the white coral reefs in the Ionian Sea (central Mediterranean). Chem Ecol 20:107–116

Vacelet J (1969) Éponges de la roche du large et de l'étage bathyal de Méditerranée (Récoltes de la soucoupe plongeante Cousteau et dragages). Mus Nat d'Historie Nat, Paris

Vázquez JT, Ercilla G, Alonso B, et al (2016). Submarine Canyons and related features in the Alboran Sea: continental margins and major isolated reliefs. In: Commission Internationale pour l'Exploration Scientifique de la mer Méditerranée (eds) Submarine Canyon Dynamics in the Mediterranean and Tributary Seas-An integrated geological, oceanographic and biological perspective. CIESM Workshop Monographs 47: 183–196

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML coral province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396

Vertino A, Stolarski J, Bosellini F, et al (2014) Mediterranean corals through time: from miocene to present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean sea: its history and present challenges. Springer, Dordrecht, pp 257–274

Wienberg C, Titschack J (2017) Framework-forming scleractinian cold-water corals through space and time: a late quaternary North Atlantic perspective. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests. The ecology of benthic biodiversity hotspots, Springer, Cham, pp 699–732

Wienberg C, Hebbeln D, Fink HG, et al (2009) Scleractinian cold-water corals in the Gulf of Cádiz-first clues about their spatial and temporal distribution. Deep-Sea Res Part 2 Top Stud Oceanogr 56:1873–1893

Young PS (2001) Deep-sea Cirripedia Thoracica (Crustacea) from the northeastern Atlantic collected by French expeditions. Zoosystema 23:705–756

Zabala M, Maluquer P, Harmelin JG (1993) Epibiotic bryozoans on deep-water scleractinian corals from the Catalonia slope (western Mediterranean, Spain, France). Sci Mar 57:65–78

Zibrowius H (1980) Les scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mém Inst Océanogr Monaco 11:1–284

Zibrowius H (2003) The "White Coral Community", canyon and seamount faunas of the deep Mediterranean Sea. Project Report for the preparation of a Strategic Action Plan for the Conservation of Biological Diversity in the Mediterranean Region (SAP BIO). p 39

Zibrowius H, Taviani M (2005) Remarkable sessile fauna associated with deep coral and other calcareus substrastes in the Strait of Sicily, Mediterranean Sea. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 807–819

Zibrowius H, Southward EC, Day JH (1975) New observations on a little-known species of *Lumbrineris* (Polychaeta) living on various Cnidarians, with notes on its recent and fossil Scleractinian hosts. J Mar Biol Assoc UK 55:83–108

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Angeletti L, Bargain A, Campiani E, et al (this volume) Cold-water coral habitat mapping in the Mediterranean: methodologies and perspectives

Aymà A, Aguzzi J, Canals M, et al (this volume) Occurrence of living cold-water corals at large depths within submarine canyons of the northwestern Mediterranean Sea

Bo M, Bavestrello G (this volume) Mediterranean black coral communities

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

D'Onghia G (this volume) Cold-water coral as shelter, feeding and life-history critical habitats for fish species: ecological interactions and fishing impact

Fourt M, Goujard A, Chevaldonné P (this volume) Working with visual methods, comparison among the French deep-sea canyons

Gori A, Grinyó J, Dominguez-Carrió C, et al (this volume) Gorgonian and black coral assemblages in deep coastal bottoms and continental shelves of the Mediterranean Sea

Knittweis L, Evans J, Aguilar R, et al (this volume) Recent discoveries of extensive cold-water coral assemblages in Maltese waters

Lastras G, Sanchez-Vidal A, Canals M (this volume) A cold-water coral habitat in La Fonera submarine canyon, northwestern Mediterranean Sea

Lo Iacono C, Savini A, Huvenne VAI, et al (this volume) Habitat mapping of cold-water corals in the Mediterranean Sea

Orejas C, Jiménez C, Gori A, et al (this volume) Corals of Aphrodite: *Dendrophyllia ramea* populations of Cyprus

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Puig P, Gili JM (this volume) Submarine canyons in the Mediterranean: a shelter for cold-water corals

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Weinbauer MG, Oregioni D, Großkurth A, et al (this volume) Diversity of bacteria associated with the cold water corals *Lophelia pertusa* and *Madrepora oculata*

Cold-Water Corals as Shelter, Feeding and Life-History Critical Habitats for Fish Species: Ecological Interactions and Fishing Impact

30

Gianfranco D'Onghia

Abstract

This chapter is a review of studies that present the role of cold-water corals as shelter, feeding and life-history critical habitats for fish species in the Mediterranean Sea and world oceans. Studies in the Mediterranean have been carried out both in *Madrepora-Lophelia* dominated communities and in coral areas characterised by octocorals and black corals. Most studies in the northeast Atlantic regard *Lophelia pertusa* reefs, while those in the northwest Atlantic refer to *Oculina varicosa*, *L. pertusa* and octocoral species. Octocorals and black corals dominated in the studies from the northeast Pacific. Most studies show that the cold-water coral habitats are important for fish species. In fact, a variety of fish species have been observed and suggested to benefit from shelter and productive feeding in the complex heterogeneous habitats built by corals. This is due to the enhanced density of zooplankton as potential prey for planktivorous fish and high density of invertebrates between and around corals as food for benthos feeders and scavengers. Moreover, several fish species use cold-water coral habitats as a spawning area and nursery. The occurrence of gravid individuals frequently observed in the coral habitats, as well as the presence of egg masses found deposited on coral stalks and egg cases attached to corals or found nested in coral colonies are clear evidence that several fish species rely on coral habitats as a place to spawn and protect offspring. The fish species of families Scyliorhinidae, Sebastidae, Serranidae, Berycidae, Zoarcidae, Lotidae, Moridae, Congridae, Liparidae seem to be more tightly associated to cold-water coral habitats. Some fish species of these families obtain multiple benefits from their association with cold-water coral habitats, despite being facultative inhabitants. Regarding the occurrence of many commercial fish species in cold-water coral habitats, it should be take into consideration that these habitats are highly impacted in the Mediterranean and throughout the oceans in general. Studies on this topic have been reviewed shortly focusing on the Mediterranean Sea where longlining and trawling are the main causes of fishing impact.

Keywords

Cold-water coral · Habitat · Fish · Megafauna · Fishing · Impact · Mediterranean

30.1 Introduction

The habitat can be considered as the structural and functional component of the environment that attracts organisms and where biological and ecological activities take place (Ricklefs 1979; Hayes et al. 1996). The habitat offer to the organisms suitable physical and chemical features, food and spatial resources, places for courtship, mating and spawning, breeding sites and nurseries, places to hide from predators and refuges to escape from adverse environmental conditions (e.g. Ricklefs 1979 and references therein; Orth et al. 1984; Rozas and Odum 1988; Lindberg and Stanton 1989; Hixon and Beets 1993; Beck 1995; Tupper and Boutilier 1995; Langton et al. 1996; Auster et al. 1997; Harvey and Bourget 1997; Lipcius et al. 1998; Sale 2002; Ryer et al. 2004; Caddy 2007, 2008; Juanes 2007; Wirsing and Ripple 2010; Ryer et al. 2015).

Many studies have demonstrated that the structural complexity of the marine habitat plays a very important role in the life history of invertebrate species and fishes, both in shallow (e.g. Orth et al. 1984; Tupper and Boutilier 1997; Sale 2002; Caddy 2007 and references therein; Juanes 2007 and references therein) and deep waters (e.g. Pearcy et al. 1989; Stein et al. 1992; Caddy 2007 and references therein; Juanes 2007 and references therein; Buhl-Mortensen et al.

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2010 and references therein; Miller et al. 2012; Porteiro et al. 2013; Ross et al. 2015). The structural complexity of the marine habitat can be related to the complexity of the geomorphology and substrate: from small-medium scale heterogeneity due to pits, cobbles, boulders, rocky outcrops, vertical reliefs (Stein et al. 1992; Tupper and Boutilier 1995; Caddy 2007) to large seafloor features, such as seamounts and canyons (Porteiro et al. 2013; Fabri et al. 2014; Ross et al. 2015). In addition, habitat complexity can be enhanced by the architecture of biological structures which range from natural shell detritus (Caddy 2007), sabellariid worm reefs (Gore et al. 1978), amphipod tubes (Auster et al. 1997), pen shells (Kuhlmann 1998), cerianthid anemones (Auster et al. 2003), polychete tubes (Diaz et al. 2003), to seagrass beds (Orth et al. 1984; Stoner and Waite 1990), kelp forests (Tegner 1993), sponge fields and coral reefs in shallow (Sale 2002 and references therein) and deep waters (e.g. Freese and Wing 2003; Buhl-Mortensen et al. 2010 and references therein; Miller et al. 2012).

The framework-forming cold-water corals (CWCs) represent complex heterogeneous habitats that occur worldwide, from shallow (from a depth of 40 m in some Norwegian fjords) to deep waters, in environments otherwise dominated by soft sediments (e.g. Reed 2002; Freiwald et al. 2004; Roberts et al. 2009; Buhl-Mortensen et al. 2010, 2017a). In the last two decades many studies have investigated the megafauna distribution in relation to CWC habitats in northeast Atlantic (e.g. Fosså et al. 2002; Husebo et al. 2002; Costello et al. 2005; Roberts et al. 2005; Söffker et al. 2011; Purser et al. 2013; Biber et al. 2014; Kutti et al. 2014; Milligan 2016; Linley et al. 2017), northwest Atlantic (e.g. Reed 2002; Reed et al. 2006; Edinger et al. 2007; Ross and Quattrini 2007; Sulak et al. 2007; Baker et al. 2012; Quattrini et al. 2012), northeast Pacific (e.g. Heifetz 2002; Krieger and Wing 2002; Stone 2006; Du Preez and Tunnicliffe 2011), and in the Mediterranean Sea (e.g. Tursi et al. 2004; D'Onghia et al. 2010, 2011, 2012, 2016; Bo et al. 2015; Mastrototaro et al. 2010, 2017; Chimienti et al., this volume; Rueda et al., this volume). Although most of the studies have not demonstrated whether CWCs themselves or only their structural complexity are the attracting factors for different life stages of the fish fauna (e.g. Auster 2005, 2007; Du Preez and Tunnicliffe 2011; Söffker et al. 2011; Quattrini et al. 2012; Biber et al. 2014; Kutti et al. 2014; Milligan et al. 2016), several investigations have proved a significant role of CWCs as functional habitats for different fish species or a significant relationship between fish presence and CWC framework (e.g. Koenig et al. 2000; Husebo et al. 2002; Krieger and Wing 2002; Etnoyer and Warrenchuk 2007; Ross and Quattrini 2007; D'Onghia et al. 2010; Baillon et al. 2012; Henry et al. 2013; Purser et al. 2013; Bo et al. 2015; Cau et al. 2017; Henry and Roberts 2017 and references therein).

The first data on fishes associated with CWC in the Mediterranean Sea were reported in Reyss (1964) for the Lacaze-Duthiers canyon and Bourcier and Zibrowius (1973) for the Cassidaigne canyon. Observations of fish species distributed in coral habitats were also reported in Tunesi and Diviacco (1997), Tunesi et al. (2001), Tursi et al. (2004), Hebbeln et al. (2009) and Mastrototaro et al. (2010). However, the first quantitative data on the effects of CWC habitat on the abundance and size of fishes were provided by D'Onghia et al. (2010). Successively, further studies were carried out in the Mediterranean CWC habitats at different depths and locations, including canyons, providing new insights into the role of CWC as critical habitats for fish species (e.g. D'Onghia et al. 2011, 2012, 2015a, b, 2016; Bo et al. 2011a, 2012, 2015; Fabri et al. 2014; Mytilineou et al. 2014; Cau et al. 2017; Mastrototaro et al. 2017).

Irrespective of the mechanistic linkage between CWCs and associated fish fauna, a review of the studies that show a role of CWCs as shelter, feeding and critical life-history habitats for fish species in the Mediterranean Sea and the world's oceans is presented here. In addition, information on the fishing impact on these sensitive habitats has also been provided, focusing on the Mediterranean Sea.

30.1.1 Structure of This Chapter

This review regards fish species and CWCs, the latter mostly represented by colonial species which live in cold waters, have a complex branching morphology and form a habitat on the seafloor and hard substrata. A literature search was carried out in online libraries, primarily Google Scholar, using a combination of keywords: (1) deep-sea corals, (2) cold-water corals, (3) fish, (4) megafauna, (5) habitat, (6) nursery, and in addition (7) fishing/fisheries and (8) impact, mostly for the Mediterranean Sea. Unpublished papers and those from the so called "grey literature" have not been included because these are difficult to obtain and generally not available to most readers. Apart from some particular case studies which document a clear link between coral presence and fish habitat use, papers regarding canyons and seamounts with the presence of CWCs were also not examined due to the confounding effect related to these topographic features and CWCs. Relevant studies that detail CWC habitat association and use by fish species are presented according to the topic of the ecological interaction in two main groups: (1) CWCs as shelter and feeding habitats and (2) CWCs as spawning and nursery habitats. In each of these two groups the results of the different studies have been analysed for the Mediterranean Sea and for the world's oceans. The scientific and common names of the fish species are reported according to FishBase (Froese and Pauly 2000).

30.1.2 Terminology

The term "shelter" refers to a place within the normal range of species distribution which allows the protection of individuals, irrespective of whether they are juveniles or adults, elsewhere subject to high mortality, mostly due to predation and/or fishing.

The term "feeding habitat" refers to a place within the normal range of species distribution which provides food resources to individuals, irrespective of whether they are juveniles or adults.

A "life-history critical habitat" can be defined as a part of a fish habitat related to breeding, spawning and nursery. This does not imply the exclusive or obligate use of the habitat, but the absence of this habitat may lead to lower reproduction and growth, affecting the renewal of populations.

No distinction has been made between "juvenile concentration" and "nursery habitat" or "mature individual concentration" and "spawning habitat" due to the insufficient data available to make such distinctions possible.

30.2 Ecological Interactions Between Fishes and Cold-Water Corals in the Mediterranean Sea

30.2.1 CWCs as Shelter and Feeding Habitats

The first clear evidence of the role of CWC habitats as shelter for fish species is reported in Hebbeln et al. (2009). These authors document the presence of the blackbelly rosefish (*Helicolenus dactylopterus*) seek shelter close and underneath the coral frameworks, using a remotely operated vehicle (ROV) in an area of the Alborán Sea (western Mediterranean), at about 320 m in depth, characterised by dead coral frameworks with live colonies of *Madrepora oculata* and *Lophelia pertusa,* several *Desmophyllum dianthus*, abundant *Acanthogorgia hirsuta*, white gorgonians, black corals and sponges. Several other fish species, such as the lesser spotted dogfish (*Scyliorhinus canicula*), the greater forkbeard (*Phycis blennoides*), the boarfish (*Capros aper*), the blackspot seabream (*Pagellus bogaraveo*) and macrourids, were also observed close to hardgrounds and coral frameworks with a quite diverse epibenthic organisms (Hebbeln et al. 2009).

In the Santa Maria di Leuca (SML) *Madrepora-Lophelia* CWC province (northern Ionian Sea, central Mediterranean), at depths between 300 and 800 m, D'Onghia et al. (2010) used modified experimental fishing gears and recorded greater biomass, densities and sizes inside the coral area than outside, indicating refuge effects. Outside the CWC province, fishing effects were evident due to lower biomass and densities and smaller sizes. Large specimens of *H. dactylopterus* and *P. bogaraveo* were exclusively collected in the coral habitat using longline. The blackmouth catshark (*Galeus melastomus*) was captured both inside and outside the CWC area but with large individuals mostly captured in the coral area. Greater abundances in the coral area were also obtained for the European hake (*Merluccius merluccius*), the blue whiting (*Micromesistius poutassou*), *P. blennoides*, the hollowsnout grenadier (*Coelorinchus caelorhincus*), the Mediterranean slimehead (*Hoplostethus mediterraneus*) and the velvet belly shark (*Etmopterus spinax*) (D'Onghia et al. 2010).

The presence of coral mounds mostly in the north-eastern sector of the SML CWC province seems to influence the large scale distribution of the deep-sea benthopelagic fauna due to higher food availability and a high heterogeneity of substrates (D'Onghia et al. 2011). In fact, the greater presence of corals and sponges in the north-eastern part of the SML coral area might create a refuge for small planktonic and benthic invertebrates, which in turn may be preyed upon by the mobile fauna observed in the area. Although not quantified, the high concentration of small invertebrates observed using towed cameras on the north-eastern side of SML, most probably represents the attracting factor for the benthopelagic fauna (D'Onghia et al. 2011). Among fish species, *H. dactylopterus* exhibited a clear behavioural pattern of resting on the seabed in different macrohabitats while *P. bogaraveo* seemed to be significantly associated with the presence of corals (D'Onghia et al. 2011). Further evidence of a tight relationship between the blackspot seabream and CWC communities is reported in D'Onghia et al. (2012) and Carluccio et al. (2014). In addition, the preferential distribution of the European conger (*Conger conger*), the wreckfish (*Polyprion americanus*), *H. dactylopterus*, *G. melastomus* and *E. spinax* in structurally complex habitats like those built by deep-sea corals has been suggested to be related to their feeding habits linked to need for shelter (D'Onghia et al. 2012). A close association of *C. conger* and *H. dactylopterus* with CWC communities was subsequently observed (Capezzuto et al. 2012; Sion et al. 2012; Maiorano et al. 2013). The occurrence and behaviour of the sharks, such as *E. spinax*, the gulper (*Centrophorus granulosus*), the kitefin (*Dalatias licha*) and the bluntnose sixgill (*Hexanchus griseus*) in the SML CWC province were also recorded using a benthic lander (Sion et al. 2013).

The consistent abundance of *G. melastomus*, *C. conger*, *H. dactylopterus*, *M. merluccius*, *P. blennoides* and *P. bogaraveo* was also recorded in five different CWC habitats of the central Mediterranean, along the continental slope of the southern Italy, between the southern Adriatic and northern Ionian (D'Onghia et al. 2016). The species *G. melastomus* and *H. dactylopterus* were the most common fish species caught close to the black coral *Leiopathes glaberrima* and the gorgonian *Isidella elongata* in the eastern Ionian Sea (Mytilineou et al. 2014). Feeding and protection relationships with coral habitat have been suggested for *G. melastomus* and *H. dactylopterus*, respectively (Mytilineou et al. 2014). *H. dactylopterus* was also found together with the longspine snipefish (*Macroramphosus scolopax*), silver scabbardfish (*Lepidopus caudatus*) and *P. americanus* in black coral habitats dominated by *L. glaberrima* at the Malta Escarpment (310–315 m) (Angeletti et al. 2015).

Linley et al. (2017), using baited cameras on autonomous benthic landers on coral mounds and off the mounds in the immediate surrounding area in the SML CWC province, revealed fish abundance higher within the coral stations but no significant difference in fish diversity between coral and non coral areas. However, *C. conger* was observed with much higher density within the coral areas. Faster arrival and higher peak numbers also indicate a greater abundance of *H. dactylopterus* in the coral habitat than in the reference area. Although *P. bogaraveo* was often observed in both coral and non coral habitat, its abundance estimation could be largely biased due to the fast swimming of the different individuals.

In the south Tyrrhenian Sea, in a rocky area characterised by the presence of the black coral *Antipathes dichotoma*, at depths between 90 and 132 m, the labrid *Lappanella fasciata* was observed hidden between the coral ramifications (Bo et al. 2011a). In the same geographic area, in a coral garden made up of arborescent colonies of gorgonians (*Callogorgia verticillata*, *Paramuricea clavata*, *Paramuricea macrospina*, *Bebryce mollis*, *Villogorgia bebrycoides*, *Corallium rubrum*, and *Leptogorgia sarmentosa*) and antipatharians (*A. dichotoma, Antipathella subpinnata* and *Parantipathes larix*), between 70 and 130 m depth, in the Gulf of St. Eufemia, the occurrence of *L. fasciata*, John dory (*Zeus faber*), *M. scolopax*, red bandfish (*Cepola macrophthalma*), *H. dactylopterus*, forkbeard (*Phycis phycis*) and the shark nursehound (*Scyliorhinus stellaris*) was recorded (Bo et al. 2012).

A school of *C. aper* (erroneously reported as *M. scolopax*) was observed among the coral colonies of *P. larix*, between 100 and 200 m, on rocky outcrops located southeast of the Island of Montecristo (Tuscan Archipelago, Tyrrhenian Sea) (Bo et al. 2014b).

Various fish species were observed hiding among the black coral *L. glaberrima* on a rocky bank with presence of other coral species (*C. verticillata*, *B. mollis*, *A. hirsuta*, *P. larix* and *A. dichotoma*), at depths between 186 and 210 m, off the south-western coasts of Sardinia (western Mediterranean): *S. canicula*, the swallowtail seaperch (*Anthias anthias*), *M. scolopax*, *Z. faber*, *L. fasciata*, *Trachurus* sp., and *Benthocometes robustus*, the latter being one of the most commonly associated fish species (Bo et al. 2015; Cau et al. 2017). *B. robustus* was only observed in the close vicinity of large colonies of gorgonians *C. verticillata* and antipatharians *L. glaberrima* and *A. dichotoma* up to 1 m long in the Bourcart and Cassidaigne canyons (Fabri et al. 2014). In particular, three individuals were observed hiding in *C. verticillata* fans with their heads pointing downwards (Fabri et al. 2014). *Benthocometes robustus* that camouflages itself among the branches of *I. elongata* swimming vertically was also observed on the muddy bottoms between two seamounts east of Ibiza (Balearic Sea) (Mastrototaro et al. 2017). According to these authors *I. elongata* forests also act as trophic areas where many species, such as *G. melastomus*, *E. spinax*, *M. merluccius*, *M. poutassou*, *P. blennoides, H. dactylopterus, H. mediterraneus* and the four-spot megrim (*Lepidorhombus boscii*), find preys swimming among the colonies or climbing on them. Contrary to these observations, Cartes et al. (2013) pointed out a rather low capacity of *I. elongata* facies in forming habitat for megafauna on muddy bottoms of the Mediterranean slope.

30.2.2 CWC as Spawning and Nursery Habitats

Fish species observed using the coral habitat for reproduction have been recorded in the Mediterranean Sea. Hebbeln et al. (2009) observed egg capsules of *Scyliorhinus* (most probably *S. canicula*) on colonies of *L. glaberrima* at 647 m and 452 m on El Idrissi Bank (Alborán Sea).

D'Onghia et al. (2010) collected gravid and near-gravid individuals of *H. dactylopterus* in the SML CWC province, suggesting the presence of a spawning area. The shark *E. spinax* was almost exclusively caught inside the coral area with a noteworthy number of small individuals. The remarkable abundance of juveniles both in *E. spinax* and the teleost fish *M. merluccius*, *M. poutassou*, *P. blennoides* and *H. dactylopterus* would suggest that the SML CWC province acts as a nursery area for these deep-water species which find suitable environmental conditions and refuge from fishing in their early life stages (D'Onghia et al. 2010). The presence of maturing and mature individuals, both females and males, as well as post-reproductive individuals of *G. melastomus*, *C. conger*, *H. dactylopterus*, *M. merluccius*, *P. blennoides, P. bogaraveo,* although with different percentages, in five CWC sites along the continental slope between the southern Adriatic and northern Ionian, indicates that these sites act as spawning areas, representing a potential "renewal network" for the fish populations (D'Onghia et al. 2016).

On a rocky bank dominated by the antipatharian *L. glaberrima*, off the south-western coasts of Sardinia (western Mediterranean), at depths between 186 and 210 m, eight specimens of the shark *S. canicula* were observed moving on the muddy bottom near the rocky elevations and within the coral branches (Bo et al. 2015). A total of 743 egg cases of this shark were observed, at different stages of maturation, on the colonies with some corals lacking eggs. In particular, among 244 colonies of *L. glaberrima* examined, 148 (61%) hosted egg cases (five capsules per colony, on average), and one, 2 m tall, hosting 44 capsules of *S. canicula* and one egg case of skate (Bo et al. 2015; Cau et al. 2017). The presence of egg capsules at different stages of development (i.e from capsules hosting embryos to apparently degraded and old capsules), provide support that the coral forest from SW Sardinia can serve as nursery grounds for *S. canicula* as it has been repeatedly used by this shark (Cau et al. 2017).

Egg capsules of *Scyliorhinus* sp. (erroneously reported as *G. melastomus*) have been recorded anchored to the branches of the bamboo coral *I. elongata* in the Balearic Sea (Mastrototaro et al. 2017). Images of fish species and ecological interactions in Mediterranean CWC habitats are reported in the Fig. 30.1.

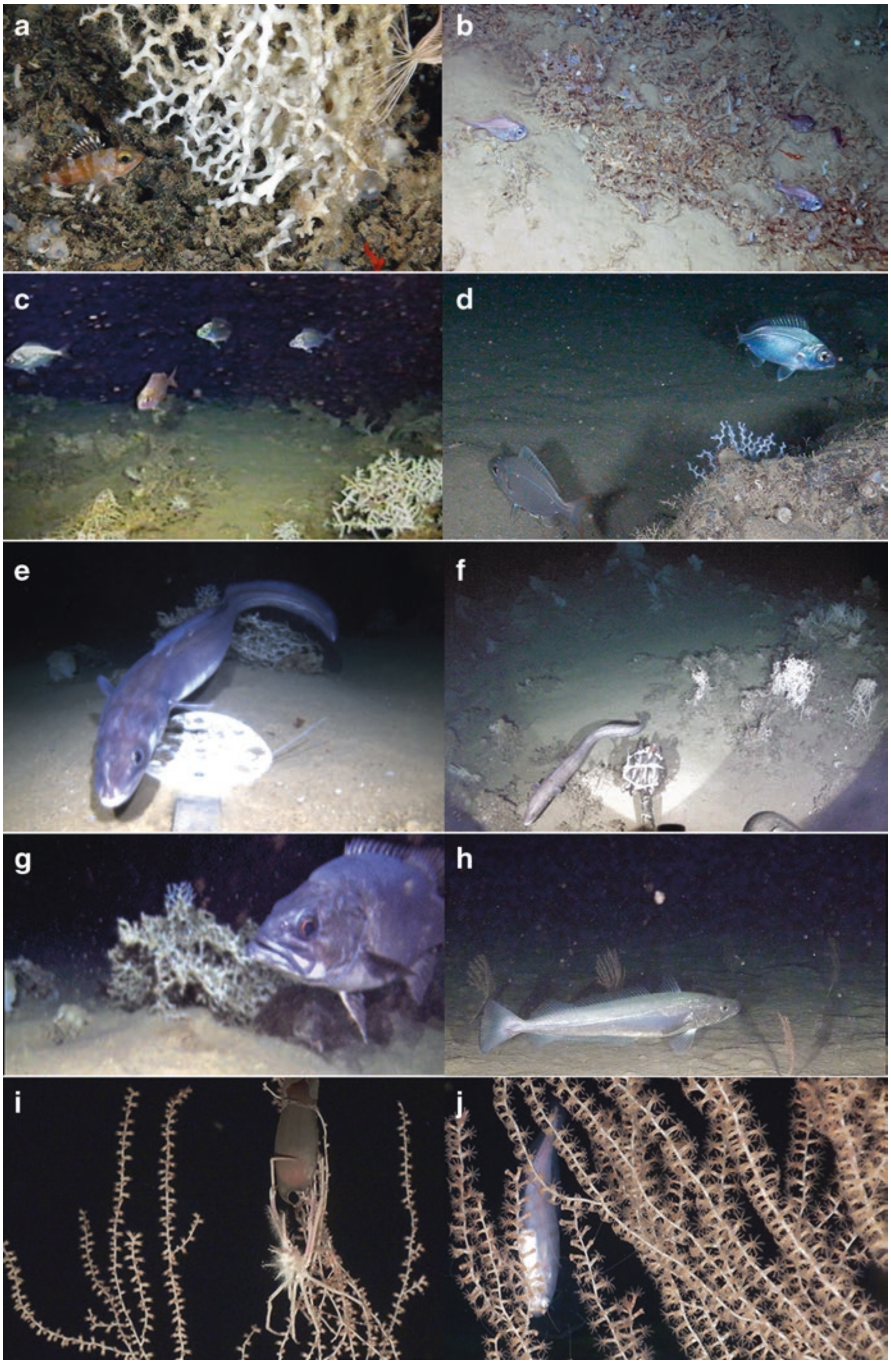

Fig. 30.1 Fish species and ecological interactions in the Mediterranean CWC habitats: (**a**) *Helicolenus dactylopterus* in coral framework habitats close to *Madrepora oculata* colonies; (**b**) Some specimens of *Hoplostethus mediterraneus* in coral rubble; (**c**) *Pagellus bogaraveo* in the SML CWC *Madrepora-Lophelia* province; (**d**) *P. bogaraveo* near to hardground with *M. oculata* colonies; (**e**) *Concer conger* in the SML CWC *Madrepora-Lophelia* province; (**f**) *C. conger* in *Madrepora-Lophelia* habitat off Tricase (central Mediterranean)*;* (**g**) *Polyprion americanus* in the SML CWC *Madrepora-Lophelia* province; (**h**) *Merluccius merluccius* in *Isidella elongata* habitat; (**i**) an egg capsule of *Scyliorhinus* sp. and *Anamathia rissoana* on *I. elongata*; (**j**) *Benthocometes robustus* among the branches of *I. elongata*. (**a**, **d**) Photo copyright and courtesy by © OCEANA ©LIFE BaĦAR for N2K; (**b**) From C. Orejas © MEDWAVES/ATLAS project; (**c**, **e–g**) Photo © by Department of Biology, University of Bari (CoNISMa ULR); (**h–j**) Photo copyright and courtesy by © OCEANA

30.3 Ecological Interactions Between Fish and CWCs in the Oceans

30.3.1 CWCs as Shelter and Feeding Habitats

30.3.1.1 Northeast Atlantic

Data on the presence of the fauna associated with CWC habitats dates back to studies carried out in the first half of the twentieth century as reported in Jensen and Frederiksen (1992). In particular, these authors collected a small specimen (80 mm) of the Norway redfish *Sebastes viviparus* trapped in a coral block recovered from *Lophelia pertusa* reefs on the Faroe shelf. Off Norway, Mortensen et al. (1995) identified five fish species from *Lophelia* reefs: the saithe *Pollachius virens* (mostly observed feeding), the tusk *Brosme brosme*, *S. viviparus* and the golden redfish *Sebastes marinus* as the most common fish in the living *Lophelia* zone, and the Atlantic cod *Gadus morhua*. *Sebastes* spp., ling (*Molva molva*) and tusk were mostly captured on the *Lophelia* reefs compared to non-reef areas (Furevik et al. 1999 in Fosså et al. 2002; Husebo et al. 2002). The presence of tusk and Atlantic wolffish (*Anarhichas lupus*) among the dead coral framework was also recorded at the Sula Reef Complex (Norwegian Shelf) (Freiwald et al. 2002). *G. morhua* and vahl's eelpout (*Lycodes vahli*) were preferentially associated to *Lophelia reef* in the Kosterfjord (between Norwegian and Swedish waters) (Jonsson et al. 2004). Costello et al. (2005), using video systems, identified *S. viviparus* (hovering, hiding, resting on the seabed, feeding) as the most abundant fish on top of the reef at Sula Ridge and *P. virens* (actively swimming, feeding) as the dominant fish at the Tautra Reef; *G. morhua* as the dominant species at Säcken Reef (Kosterfjord), over the transitional and coral debris areas; the poor cod *Trisopterus minutus* (hiding), *B. brosme* (resting on the seabed, feeding) and *A. lupus* (resting on the seabed) were most frequently recorded in association with the coral reef habitat (Costello et al. 2005). Redfish (*Sebastes* sp.) sheltering near sponges was also observed using a benthic photo-lander at the Sula Ridge reef complex (Roberts et al. 2005). Using longline in the Træna Deep marine protected area and adjacent areas of the Norwegian continental shelf, Kutti et al. (2014) found higher abundances of *B. brosme*, *Galeus melastomus* and *Chimaera monstrosa* in coral habitats than in non coral ones, most probably due to shelter and feeding reasons. Subsequently, Kutti et al. (2015), using a towed video system in the same study areas, observed *S. viviparus* and *B. brosme* associated with the CWC and sponge habitats at all the spatial scales examined. However, none of the species examined were confined to a single habitat. Linley et al. (2017), using baited cameras on autonomous benthic landers on coral mounds and off the mounds in the immediate surrounding area, detected fish abundance higher within CWC areas than in surrounding areas. *P. virens* was unique to the coral area, whereas *S. viviparus* and *B. brosme* were observed both in coral and reference habitat. This latter was the most numerous species attending the bait with much higher density within the coral areas.

In relation to the abundant presence of benthic invertebrates (mostly *Munida* spp.) and plankton, several authors suggested that the reefs act as sites of increased food availability, providing fishes with refuge from predators and habitat from which to ambush prey (Mortensen et al. 1995; Husebo et al. 2002; Jonsson et al. 2004; Costello et al. 2005; Kutti et al. 2014). The benthic fish species, such as tusk, preyed predominantly on epibenthic decapods, such as *Munida* spp. and *Lithodes maja* (Husebo et al. 2002; Kutti et al. 2014), while redfish are known to be planktotrophic predators and the bioherms may enhance the amount of zooplankton available to these fishes (Mortensen et al. 1995; Buhl-Mortensen et al. 2017a).

In *Lophelia* coral reefs explored from the Faroe-Shetland Channel to Porcupine Seabight, *Sebastes* sp. and *M. molva*, followed by *B. brosme*, dominated the fish fauna at Hurtside wreck (Costello et al. 2005). *Brosme brosme* was also observed at Hatton Bank, where it solely occurred in the coral framework habitats resulting in a highly significant relationship (Biber et al. 2014). The presence of the North Atlantic codling (*Lepidion eques*), hiding beneath colonies of *L. pertusa*, *M. oculata*, and Antipatharia, was recorded using an ROV in the deep-water coral province of Porcupine Bank, on the Irish continental margin (Wheeler et al. 2005a). The fish *L. eques*, *H. dactylopterus*, *C. monstrosa* and *G. melastomus*, were observed in different types of macrohabitat, including coral rubble, coral framework and rock macro-habitats on Hatton Bank (Roberts et al. 2008). *Lepidion eques* was also the most common species recorded using an ROV on Twin Mounds and Giant Mounds, which are situated 9 km apart on Porcupine Bank (Söffker et al. 2011). It always occurred a few cm above bottom and was significantly more active on the reefs than on sedimentary habitats. In this study area, two fish species were particularly associated with coral habitats: *Guttigadus latifrons* and the false boarfish *Neocyttus helgae*. The former was mainly found amongst dense living coral thickets and was not observed in non coral habitats, the latter was found predominantly on structural habitats provided by dead corals (Söffker et al. 2011). *Lepidion eques* showed a significantly higher abundance at coral framework patches in Belgica Mound Province where individuals were observed hiding underneath the coral framework but also frequently occurred in non coral areas, where they were particularly associated with boulders (Biber et al. 2014). The species feeds mainly on crustaceans and polychaetes, which might explain its frequent occurrence near CWC reefs as these supports a higher macrofaunal biomass than surrounding soft sediments (Biber et al. 2014). *Helicolenus dactylopterus* was also commonly observed at Rockall Bank sitting relatively motionless on top of corals. The association of this fish with coral framework was explained by the fact that it is considered a protection seeker (Biber et al. 2014).

Using bottom trawl, the capture of the birdbeak dogfish *Deania calcea*, *G. melastomus*, *C. monstrosa* and the angler *Lophius piscatorious* from areas characterised by the presence of *L. pertusa*, *M. oculata* and other CWC on Hatton Bank was also reported by Durán-Muñoz et al. (2009). Along the rugged bottom of the rocky outcrop, high catches per unit effort of the adult fraction of vulnerable deep-water sharks and Lotidae fish were obtained using longline in coral areas (Durán-Muñoz et al. 2011). On the Mingulay Reef Complex, a seascape of *Lophelia* reefs off western Scotland, the mean abundance of *G. melastomus* was significantly higher in trawl sets located nearer a coral reef than those located further away, suggesting that this shark is locally enhanced near coral habitats (Henry et al. 2013). *Scyliorhinus canicula* was also observed resting among *Lophelia* colonies on the Mingulay Reef Complex (Henry et al. 2013).

Video footage on demersal fish and substratum types was taken from Logachev Mounds, Rockall Bank and Hebrides Terrace Seamount (Milligan et al. 2016). Significant differences in community composition between all regions, within each region at scales of 20–3500 m, and between CWC and non CWC substrata were detected. *Sebastes* sp. (mainly *S. viviparus*) was closely associated with CWC reef substrata at Rockall Bank. *N. helgae* was significantly more likely to occur in coral areas at the Hebrides Terrace Seamount. The species *L. eques*, *C. caelorhincus* and *H. dactylopterus* occurred on coral reefs and transitional substrata and their relative abundances were significantly affected by depth. The results of this study suggest that the importance of CWCs to fish is species-specific and is related to the broader spatial context in which this type of substratum is present (Milligan et al. 2016).

From *in situ* observations using baited cameras, fish species diversity was higher within the coral habitats than in reference habitats of the Belgica Mound Province and the Bay of Biscay (Linley et al. 2017). The majority of sightings in the former region were of five dominant species that were present in both habitat types: the bluntnose sixgill shark *Hexanchus griseus*, *Synaphobranchus kaupii*, *L. eques*, the common mora *Mora moro* and *Phycis blennoides*. Deployments in the latter region were dominated by the same actinopyterygian species as the former: *S. kaupii*, *L. eques*, *M. moro* and *P. blennoides*. The authors report that while CWC reefs have a positive effect on fish diversity and/or abundance, this effect varies across Europe's reefs mainly as a consequence of the different time of year, depth and topography. Temporal variations in the abundance of several species were also observed in the CWC community on Galway Mound (Belgica Mound Province) where *L. eques* was by far the most common fish, followed by *P. blennoides* (Lavaleye et al. 2017).

Video surveys carried out from the Azores to the Canary Islands revealed the circalittoral *Lappanella fasciata* and the upper bathyal *Benthocometes robustus* closely associated to biogenic habitats made up of CWC (e.g. *Antipathella* spp., *Acanthogorgia armata*, *Callogorgia verticillata*, *Dendrophyllia alternata*, *Leiopathes* spp.) and large hydrozoans (Gomes-Pereira et al. 2017). Individuals of these two fish species were shown swimming inside or close to CWC, moving in and out of corals three-dimensional structures, as well as maintaining position in relation to the corals or hydroids. The swimming position indicates behavioral adaptations to coral-cryptic behavior, suggesting that CWCs and large hydrozoans provide shelter from predators, current avoidance and preys for both fish species (Gomes-Pereira et al. 2017).

30.3.1.2 Northwest Atlantic

In this geographic region, off the south-eastern United States, two types of deep-water coral reefs are formed by the scleractinian corals *Oculina varicosa*, on the shelf, and *L. pertusa*, on the slope (Reed et al. 2005). Schools of thousands of small individuals of the red barbier (*Baldwinella vivanus*) were observed to swim among the branches of *O. varicosa* corals for shelter and/or for feeding on the invertebrates living within (Reed 2002). *Oculina* reefs were observed as feeding grounds for gag (*Mycteroperca microlepis*), scamp (*Mycteroperca phenax*), snowy grouper (*Hyporthodus niveatus*) and other fish including black seabass (*Centropristis striata*), red grouper (*Epinephelus morio*), speckled hind (*Epinephelus drummondhayi*), warsaw grouper (*Hyporthodus nigritus*), Atlantic goliath grouper (*Epinephelus itajara*), longfin yellowtail (*Seriola rivoliana*), greater amberjack (*Seriola dumerili*), red porgy (*Pagrus pagrus*), Northern red snapper (*Lutjanus campechanus*), grey snapper (*L. griseus*), little tunny (*Euthynnus alletteratus*), ocean sunfish (*Mola mola*), giant manta (*Manta birostris*), tiger shark (*Galeocerdo cuvieri*) and scalloped hammerhead (*Sphyrna lewini*) (Reed 2002). The most common larger grouper observed in 2003 were *E. morio* and *M. phenax*, although a few individuals of *H. niveatus* and *M. microlepis* were also present (Reed et al. 2005). A large male of *M. phenax* was photographed on *O. varicosa* bioherm at 80 m (Reed and Ross 2005). The ROV surveys on fish assemblages and benthic habitat inside and outside the *Oculina* Habitat Area of Particular Concern (OHAPC) off eastern Florida revealed grouper densities (mainly *Mycteroperca* spp., *Epinephelus* spp., *Serranus* spp.) significantly higher on the most structurally complex habitats (live *O. varicosa*, standing dead *O. varicosa* and rock outcrops) compared to the less complex ones (pavement and rubble) (Harter et al. 2009).

In the regions of *Lophelia* reef habitats off the south-eastern United States (Blake Plateau, the Straits of Florida and eastern Gulf of Mexico), surveyed using submersibles and ROV, the most abundant fish species were *H. dactylopterus* and the morid cod (*Laemonema melanurum*), followed by the alfonsino (*Beryx decadactylus*), the western roughy (*Hoplostethus occidentalis*), the American conger (*Conger oceanicus*) and the wreckfish (*Polyprion americanus*) (Reed and Ross 2005; Reed et al. 2006). *H. dactylopterus* and *L. melanurum* were also found to be common in sinkhole and bioherms on the southern edge of the Pourtalès Terrace (south Florida), even though these sites are mainly characterised by stylasterid corals, octocorals, sponges, ascidians and lack the scleractinian corals *L. pertusa* and *M. oculata* (Reed et al. 2005). Schools of ~ 50–100 *P. americanus*, were observed on several submersible dives in May 2004 and again at the same site in April 2005 (Reed et al. 2006). Wenner and Barans (2001) (in Reed et al. 2006) noted that wreckfish individuals were frequently seen on these reefs. Specimens of anglerfish *Chaunax stigmaeus*, *Lophiodes beroe*, *Lophiodes monodi*, and a single specimen of *Sladenia shaefersi* sitting on beds of dead coral *L. pertusa* rubble were observed in dives performed by submersible in the same geographic area (Caruso et al. 2007).

The demersal fish fauna from hard substrate and *Lophelia* coral biotope in the northern Gulf of Mexico (Vioska Knoll) was investigated by submersible (Sulak et al. 2007). Large mobile schooling fishes dominated at 325 m in depth (the barrelfish *Hyperoglyphe perciformis,* the Darwin's slimehead *Gephyroberyx darwini* and *H. niveatus*) together with sit-and-wait ambush mesocarnivores *H. dactylopterus* and the ambush predator *C. oceanicus*. On the 500 depth horizon *C. oceanicus, Laemonema goodebeanorum, H. dactylopterus, H. occidentalis,* the Atlantic thornyhead *Trachyscorpia cristulata,* the thorny tinsel fish *Grammicolepis brachiusculus* were most frequently observed. *G. brachiusculus,* a morphologically very specialised epifaunal picker, appears to be highly associated with *Lophelia* reefs.

Ross and Quattrini (2007) used a submersible to describe the degree of habitat specificity of the fishes in prime *Lophelia* reef habitat, transition reef and off reef in eight areas on the south-eastern United States. They found distinct fish assemblages in prime reef and transition reef habitats compared to off-reef habitats, suggesting that deep reefs host unique fish communities. The prime reef fish assemblage was characterised by *L. melanurum*, the rough tip grenadier *Nezumia sclerorhynchus*, *B. decadactylus* and *H. dactylopterus*. Some species, such as the swallowtail bass *Anthias woodsi*, *B. decadactylus*, *C. oceanicus* and the cutthroat eel *Dysommina rugosa*, showed specificity to reef habitats. In addition, they found three new fish species (McCosker and Ross 2007; Fernholm and Quattrini 2008; Nielsen et al. 2009). Among the characteristic fishes associated with the deep reefs of the south-eastern U.S., the new species of myxinid fish *Eptatretus lopheliae* was videotaped and caught in close association with *Lophelia* reef habitat (Fernholm and Quattrini 2008). Successively, Ross and Quattrini (2009) surveyed fishes in nine deep reef study areas along the south-eastern U.S. slope. Fish assemblages at the North Carolina sites were different from the sites to the south and there was a large amount of variability in species abundance and distribution patterns among the different sites. *Laemonema barbatulum*, *L. melanurum* and *H. dactylopterus* were abundant and consistently observed during the majority of North Carolina dives. *C. oceanicus* and *B. decadactylus* were also abundant indicator species. Other species that contributed to fish assemblage differences included *H. occidentalis*, *D. rugosa* and *Idiastion kyphos* and the chain catshark *Scyliorhinus retifer*. In the Cape Fear area, *N. sclerorhynchus* and *P. americanus* were abundant, contributing to the dissimilarities between this site and others. Ross and Quattrini (2009) suggested that fish community structures were associated with the size, profile and complexity of the deep reefs. Among the fish species examined by Quattrini et al. (2012), *B. decadactylus* and *C. oceanicus* were most frequently observed near the top of the coral mound in the presence of high vertical profile, live coral coverage and topographic complexity, most probably in relation to their enhanced feeding and refuge opportunities. *L. melanurum* was often observed in moderate profile habitats and not often in live coral habitats. Transient species, such as *H. dactylopterus* and *L. barbatulum* were most observed on the mound slope and base with moderate complexity. *P. americanus* and *N. sclerorhynchus* exhibited the least affinities for a particular type of habitat. Quattrini et al. (2012) concluded that certain reef-associated species seem to be habitat specialists whereas others are habitat generalists.

Northward, the deep-water gorgonian corals *Primnoa resedaeformis* and *Paragorgia arborea* in the north-east Channel (Nova Scotia, Canada) were considered as preferred habitats of redfish (*Sebastes* spp.) providing shelter against strong near-bottom currents and predators (Mortensen et al. 2005).

30.3.1.3 Central Eastern Atlantic

In this geographic region, during the ROV video surveys carried out on coral mounds, along the Angola margin (West Africa), high abundance of Zoarcidae fish was observed in the living and dead *Lophelia* coral framework (Le Guilloux et al. 2009). Their absence in the surrounding sediments and observed hiding behaviour indicated potential habitat selectivity. Other species associated with corals were *Chaunax* sp., *Lophius* sp., *H. dactylopterus* and *G. darwini* (Le Guilloux et al. 2009).

Among the six fish species observed in the *Lophelia* reef on the Ghanaian shelf (Gulf of Guinea), the most common were *H. dactylopterus*, the western softhead grenadier *Malacocephalus occidentalis* and the blackfin sorcerer *Nettastoma melanorum*. These fish were often found hiding among blocks of dead coral (Buhl-Mortensen et al. 2017b). Images of fish species and ecological interactions in Atlantic CWC habitats are reported in the Fig. 30.2.

30.3.1.4 Northeast Pacific

In a photograph taken by a submersible, an aggregation of adult Pacific ocean perch (*Sebastes alutus*) was observed near several sea whips in the Gulf of Alaska (Krieger 1993). Hundreds of rockfish individuals, mainly Pacific ocean perch, were observed inhabiting a "forest'" of attached sea whips, *Halipteris willemoesi*, during night deployments of the ROV in Pribilof Canyon (Bering Sea) (Brodeur 2001). During the day, individuals of *S. alutus* were seen above the "forest", where they were apparently feeding on dense swarms of euphausiids, indicating that these fish utilise food resources in the canyon during the day and are associated with the sea whip habitat at night during periods of inactivity.

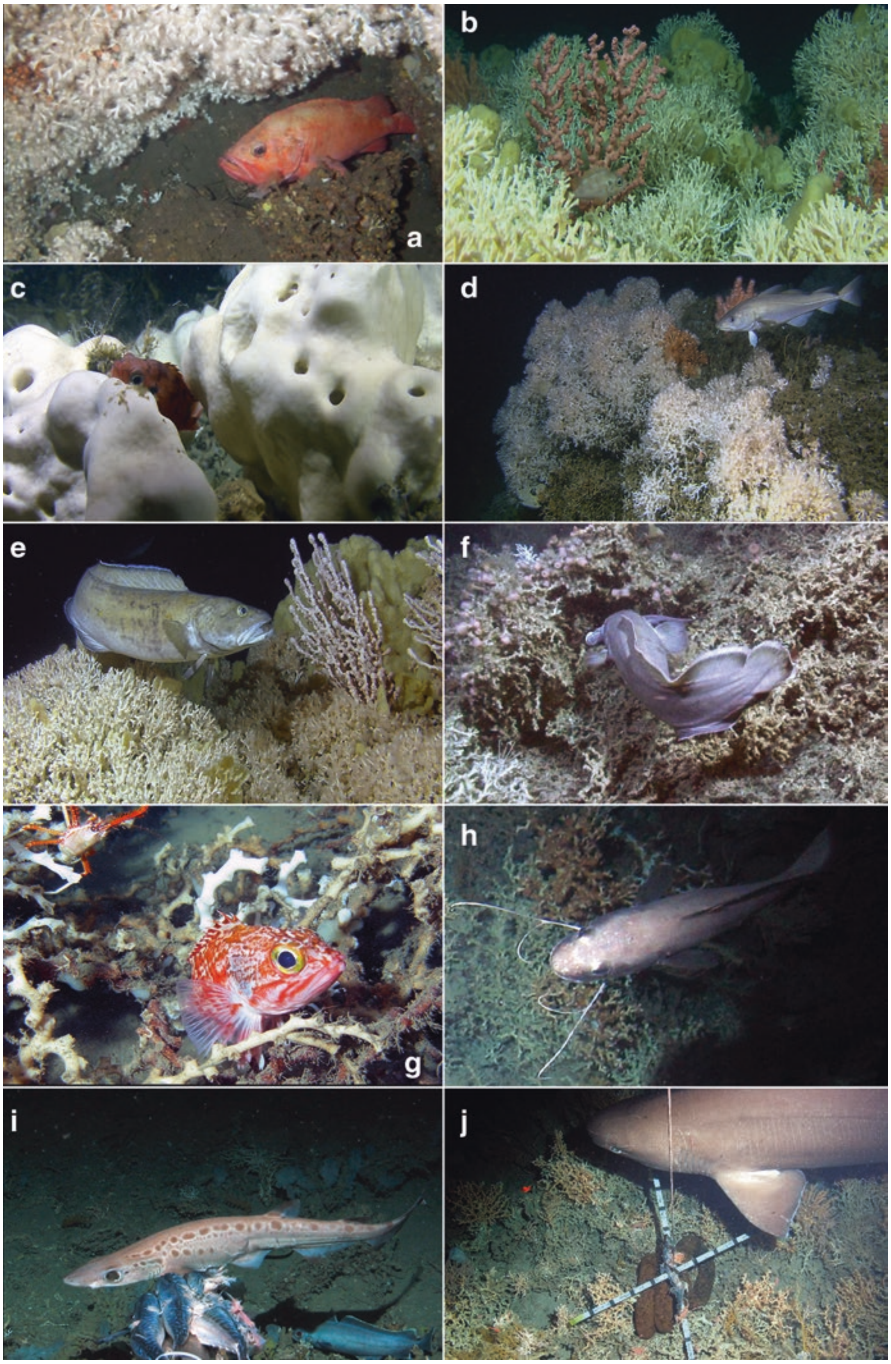

Fig. 30.2 Fish species and ecological interactions in Atlantic CWC habitats: (**a**) Redfish (*Sebastes marinus*) in the *L. pertusa* reef; (**b**, **c**) *Sebastes* spp. in *Lophelia* reef and sponge ground; (**d**) *Gadus morhua* in *Lophelia* reef; (**e**) *Brosme brosme* in *Lophelia* reef; (**f**) *Brosme brosme* feeding on a smaller fish caught on the reef (probably a *Lepidion* sp.); (**g**) *Helicolenus* and *Eumunida picta* in *Lophelia* habitat; (**h**) *Phycis blennoides* in *Lophelia* habitat*;* (**i**) *Galeus melastomus* and *Mora moro* close to CWC habitat*;* (**j**) *Hexanchus griseus* in *Lophelia* habitat. (**a**) Photo © Marine Research Institute of Iceland, courtesy of Stefán Áki Ragnarsson and Steinunn Hilma Ólafsdóttir (from CoralFISH Gallery); (**b–e**) Photo © Institute of Marine Research (Norway), courtesy of Jan Helge Fosså and Tina Kutty; (**f**) Photo © National University of Ireland (Galway), courtesy of Anthony Grehan (from CoralFISH Gallery); (**g**) Photo © and courtesy of the U.S. Geological Survey; (**h, j**) Photo © and courtesy of OceanLab (University of Aberdeen) and NIOZ (Royal Netherlands Institute of Sea Research) (from CoralFISH Gallery); (**i**) Photo © and courtesy of OceanLab (University of Aberdeen) (from CoralFISH Gallery)

In fact, areas with damaged *H. willemoesi* had far fewer individuals and areas without sea whips had no individuals. In addition, other fishes were occasionally seen within the sea whip habitat, including arrow tooth flounders (*Atheresthes stomias*), saw back poachers (*Sarritor frenatus*) and big skate (*Beringraja binoculata*), but none seemed to be as consistently associated with this habitat as the rockfish (Brodeur 2001). Successively, Miller et al. (2012) reported that rockfishes, including *S. alutus*, preferentially utilise corals for habitat in Pribilof Canyon.

Using submersible, six species of rockfish (rougheye rockfish *Sebastes aleutianus*, redbanded rockfish *S. babcocki*, shortraker rockfish *S. borealis*, sharpchin rockfish *S. zacentrus*, dusky rockfish *S. ciliatus* and yelloweye rockfish *S. ruberrimus*) were found associated with *Primnoa* in the Gulf of Alaska (Krieger and Wing 2002). These fishes have been considered as protection seekers and were observed either beneath, among or above the corals. Shrimps were not identified, but hundreds of them were observed among the branches of large colonies. Krieger and Wing (2002) suggested that the large rockfish (*S. borealis* and *S. aleutianus*) associate with corals for feeding since shrimps are their main prey. Off Alaska, the rockfish, *Sebastes* spp. and the shortspine thornyhead (*Sebastolobus alascanus*), and Atka mackerel (*Pleurogrammus monopterygius*) were among the most common fish captured with gorgonians (*Callogorgia*, *Primnoa*, *Paragorgia*, *Thouarella* and *Arthrogorgia*), cup corals (*Caryophyllia* sp.) and hydrocorals, whereas flatfish (Bothidae and Pleuronectidae) and gadids (mostly the Alaska pollock *Gadus chalcogrammus*) and the Pacific cod (*Gadus macrocephalus*) were the most common species associated with the soft coral *Gersemia* sp. (Heifetz 2002). Roberts et al. (2006) reported photos of rockfish (*Sebastes* sp.) among gorgonian corals (*Primnoa* sp.) in the Gulf of Alaska.

Stone (2006) observed many species exhibiting a strong association with corals and emergent epifauna in the Aleutian Islands of Alaska. Habitats that had the highest densities of corals also supported the highest densities of several commercial species. The association with emergent epifauna ranged from 100% for prowfish (*Zaprora silenus*), followed by sharpchin rockfish (*S. zacentrus)*, rockfish juveniles (97%), rougheye rockfish (*S. aleutianus)*, dusky rockfish (*S. ciliates)*, northern rockfish (*S. polyspinis*), Pacific ocean perch (*S. alutus)*, shortraker rockfish (*S. borealis)*, "other" rockfish (*Sebastes* spp.), skate (Rajidae), Pacific cod, sculpins, Atka mackerel, shortspine thornyhead (*S. alascanus)*, giant grenadier (*Albatrossia pectoralis*), up to 31% in righteye flounders (Pleuronectidae), indicating that these habitats appear to be more frequently used within the region (Stone 2006).

In situ images were used to examine which variables of the seafloor, including epifauna cover, might influence scorpaenid fish abundance patterns on Learmonth Bank off northern British Columbia (Du Preez and Tunnicliffe 2011). The most abundant scorpaenid fish were *S. alascanus* and the rockfish *Sebastes* spp., mostly *S. zacentrus.* Thornyhead abundance did not vary with substratum type while rockfish abundance increased significantly with higher substratum and epifauna relief. Over 50% of *Primnoa pacifica* taller than 30 cm had at least one associated rockfish and often several while, in comparison, no rockfish were observed with *P. pacifica* under 30 cm in height.

Association of fish with sponges, black corals and gorgonians was also examined, using submersible, in continental shelf and slope ecosystems off southern California (Tissot et al. 2006). Six species were found at significantly higher frequencies than predicted by their density along transects: cowcod (*Sebastes levis*), bank rockfish (*Sebastes rufus*), swordspine rockfish (*Sebastes ensifer*), shortbelly rockfish (*Sebastes jordani*), pinkrose rockfish (*Sebastes simulator*), and members of the rockfish subgenus *Sebastomus.* Tissot et al. (2006) concluded that there is not necessarily a functional relationship between these groups of organisms. However, the authors also recognised the relatively low number and size of individual sponges, black corals and gorgonians observed in their study.

30.3.1.5 Central Pacific

A study carried out in the north-western Hawaiian Islands with submersibles revealed that the deep-sea coral colonies may aggregate individuals of *C. oceanicus* and attract foraging monk seals to *Gerardia* sp. and *Corallium* sp. reefs at depths over 500 m (Parrish et al. 2000). Notably, the seals searched for prey in low-relief bottom habitat. This uniform habitat was probably selected over the complex coral reef habitat in relation to the differences in accessibility of prey. In fact, fish species of the coral reef use available shelter to avoid predators while the foraging technique of the seal is best suited for uniform habitats where the amount of territory covered can be maximised. Exploiting a much higher probability of capture in an area of lower prey density on the deep slope may yield more than a low probability of capture at high prey densities in the coral shallows (Parrish et al. 2000). This is a clear case study of a refuge effect of coral habitat for a fish species.

30.3.2 CWC as Spawning and Nursery Habitats

30.3.2.1 Northeast Atlantic

Lophelia reefs in Norwegian waters were observed to support dense aggregations of *Sebastes* spp. which in May-June were dominated by gravid females with distended bellies, indicating that CWCs may play a role in the reproductive cycle of redfish species and that both spawning females and juveniles can find protection from predators in the coral habitat (Furevik et al. 1999, in Fosså et al. 2002). The small specimen of *S. viviparus* trapped in a coral block recovered from *L. pertusa* reefs on the Faroe shelf might be considered as a first proof of juveniles in coral habitat (Jensen and Frederiksen 1992).

Costello et al. (2005) hypothesised that *Lophelia* reefs conceal juveniles and thus they might act as a nursery habitat. These authors observed the presence of gravid redfish (*S. viviparus*) as well as egg cases of skates (*Raja* sp.) at Sula Ridge indicating that the reefs are also spawning sites for some fish species. More recently, the occurrence of some gravid individuals of *Sebastes* sp. (mainly *S. viviparus*) was reported associated with the CWC reef at Rockall Bank (Milligan et al. 2016). On the Mingulay Reef Complex, video surveys revealed spawning grounds of *G. melastomus* (Henry et al. 2013). Shark egg cases were always found nested in live corals at a narrow depth range (165–172 m) on slightly inclined sites colonised by live corals. Henry et al. (2013) suggested that *G. melastomus* targets coral colonies because of multiple benefits. The hard colonial skeleton of *Lophelia* provides a framework of branches that could deter egg predators while reducing the risk of eggs drifting away. A coral framework also elevates capsules into water currents that ventilate the eggs, with coral polyps helping to remove sediments that could otherwise accumulate and smother the egg cases.

30.3.2.2 Northwest Atlantic

Using a submersible, Reed and Gilmore (1981) observed a male and a female of rough tail stingray, *Dasyatis centroura,* in an apparent courtship or mating ritual near the base of a coral bank of *O. varicosa* at a depth of 80 m, off central eastern Florida. Successively, schools of thousands of small individuals of *B. vivanus* swimming among the branches of *O. varicosa* were observed (Reed 1985 and Reed and Hoskin (1987), in Reed 2002). Moreover, *Oculina* reefs were observed as breeding grounds for commercially important populations of *M. microlepis*, *M. phenax*, *C. striata*, *H. niveatus* and *E. drummondhayi* as well as nursery grounds for *H. niveatus* and *E. drummondhayi* (Gilmore and Jones 1992; Coleman et al. 1996; Koenig et al. 2000; Reed 2002; Koenig et al. 2005; Reed et al. 2005).

Castro et al. (1998) collected two egg cases of the chain catshark *S. retifer* attached to corals accidentally entangled in long line used in rough bottom areas off South Carolina, at depths of 230–450 m. Another egg case attached to a coral was obtained by submersible at 240 m depth in the Gulf of Mexico (Castro et al. 1998). In this geographic area, Etnoyer and Warrenchuk (2007), using an ROV, recorded 296 egg cases attached to 117 colonies of *Callogorgia americana delta* with a maximum of 17 cases observed on a single colony. The egg cases were suggested to be of the chain catshark *S. retifer*, but they belong to another species (Ross et al. 2015). However, this occurrence demonstrated that large monotypic fields of gorgonian octocorals on low relief mounds can provide a nursery area for fish species in the Gulf of Mexico, although it was insufficient to define whether the catshark nursery area is substrate-specific, taxon-specific or site-specific (Etnoyer and Warrenchuk 2007). Living eggs of an unidentified Liparidae fish were collected and observed in the octocorals *Anthothela* sp. and *Acanthogorgia* sp. from the U.S. middle Atlantic slope (Ross et al. 2015).

Specimens of the Pluto skate *Fenestraja plutonia* were collected using otter trawl off North Carolina; three egg-bearing females, newly hatched juveniles and deposited egg cases were collected near the Cape Lookout deep coral banks (Quattrini et al. 2009). These data and those of Ross and Quattrini (2007), who observed this fish near deep coral banks off the south-eastern U.S., suggested that *Lophelia* coral bank area off Cape Lookout represents an important egg-laying area and possibly a nursery area for this skate species.

Fish larvae, mainly belonging to the Acadian redfish *Sebastes fasciatus* and beaked redfish *Sebastes mentella*, were found on deep-water sea pens (mostly *Anthoptilum grandiflorum, Pennatula aculeata, Halipteris finmarchica*) by Baillon et al. (2012, 2014). The closeness of the association between these fish and CWCs suggests that the viviparous redfish release their progeny near corals, where they remain during early ontogeny. It seems that the calcified parts (sclerites) and/or toxic chemicals produced by soft corals deter potential predators. Therefore, fish may release larvae among corals to provide them with shelter and protection. The number of fish larvae harboured was positively correlated to the size of the sea pen colony. Eggs or larvae of the lantern fish (*Benthosema glaciale*) and the eelpout (*Lycodes esmarkii*) were also found (Baillon et al. 2012, 2014). Buhl-Mortensen et al. (2017a) reported a figure of a colony of *P. arborea* with 26 eggs of deep-sea catshark (*Apristurus profundorum*) collected with bottom trawl at around 500 m depth in the northeast Channel, Nova Scotia.

30.3.2.3 Northeast Pacific

In situ evidence of habitat functions for deep-sea corals was derived from video and photographic observations (e.g. an egg case attached to a *Paragorgia*) (Etnoyer and Morgan 2005). Evidence of egg masses of the goldeneye snailfish *Allocareproctus unangas* found deposited surrounding stalks of the octocoral *Primnoa* sp. from the Aleutian Islands was provided by Busby et al. (2006). These eggs contained embryos in the flexion stage of development. Another stalk of *Primnoa* sp. collected in the same area had three attached masses of eggs belonging to other unidentified Liparidae fishes (Busby et al. 2006).

The egg cases of the brown catshark *Apristurus brunneus* were observed attached to filter-feeding invertebrates such as gorgonians (e.g. *Euplexaura marki*), sponges and anemones, while those of the filetail catshark *Parmaturus xaniurus* were found attached by their long tendrils to substrates, such as corals (e.g. *Antipathes* sp.), hydroids, ascidians and other egg cases (Flammang et al. 2007, 2011).

30.3.2.4 Southeast Pacific

Concha et al. (2010) collected eighteen capsules from nine gravid females of the dusky catshark *Bythaelurus canescens* and four capsules were attached to the deep-sea coral *Antipathes speciosa*. All females and corals were caught off southern Chile as by-catch of bottom longline fisheries.

30.4 Fishing Impact to Cold-Water Coral Habitats

The CWC habitats are considered valuable fishing areas due to the distribution and abundance of fish species of commercial interest (e.g. Fosså et al. 2002; Morgan et al. 2005; Reed et al. 2005; D'Onghia et al. 2017; Hinz 2017). The impact of fishing to CWC communities has been documented both in the Atlantic and Pacific Oceans in relation to the exhaustion of commercial fish stocks in readily accessible inshore waters (e.g. Rogers 1999; Koenig et al. 2000; Roberts et al. 2000; Duncan 2001; Fosså et al. 2002; Grehan et al. 2005; Mortensen et al. 2005; Reed et al. 2005; Wheeler et al. 2005b; Stone 2006; Hourigan et al. 2007; Lumsden et al. 2007; Hourigan 2009; Durán-Muñoz et al. 2011; Sampaio et al. 2012; Pham et al. 2014).

Although different types of fishing gears impact the seafloor and pose potential threats to CWC communities, otter trawls and dredges are the most destructive gears (e.g. Hall-Spencer et al. 2002; Roberts 2002; Morgan et al. 2005; Lumsden et al. 2007; Hourigan 2009; Pham et al. 2014; Hinz 2017). The main impact of trawling and dredging on CWC habitats is the mechanical damage caused by otter boards, nets and iron/steel structures that destroy the three-dimensional (3D) coral colonies and reduce habitat complexity that provide shelter for fishes and invertebrates (Hinz 2017 and references therein). The impacts of bottom trawling on the benthos have been compared to clear-cutting techniques in old growth forests (Watling and Norse 1998). The morphology of the upper continental slope could be altered and the habitat complexity could be markedly reduced by intensive bottom trawling, producing comparable effects on the deep sea floor to those generated by agricultural ploughing on land (Puig et al. 2012).

Since trawling and dredging can often be carried out on muddy bottoms near to coral areas, they have an indirect impact due to the alterations of the hydrodynamic and sedimentary conditions (e.g. Piskaln et al. 1998; Watling and Norse 1998; Purser 2015). In addition, an increase in sediment suspension from trawling activities could affect corals and associated benthic species in neighbouring coral mounds. In fact, coral species, like all suspension feeders, are particularly vulnerable to the effects of increased sedimentation (e.g. Rogers 1999; Buhl-Mortensen et al. 2010; Purser 2015).

Other fishing gears, such as longlines, gillnets, pots and traps, can also cause impact to CWC communities since they cause breakage of the coral colonies from rocks and boulders (e.g. Butler 2005; Reed et al. 2005; Morgan et al. 2005; Stone 2006; Lumsden et al. 2007; Mortensen et al. 2008; Hourigan 2009; Durán-Muñoz et al. 2011; D'Onghia et al. 2012; Sampaio et al. 2012; Pham et al. 2014; Hinz 2017). Longlining is often used in deep waters with hard untrawlable substrates that can be suitable habitats for CWCs, which increases the probability of coral by-catch. Disturbance caused by longlines is not well defined and can be easily masked by natural events or disturbance created by other gear types (Heifetz et al. 2009; Hourigan 2009; Sampaio et al. 2012). Longlines, gillnets, pots and traps can also cause: (i) "ghost fishing", since discarded or lost gear may continue to catch different organisms for a long time; (ii) mechanical injuries on benthic species if drifting on the sea floor; (iii) accumulation of debris on the bottoms from lost gear, altering habitats (e.g. Reed et al. 2005; Matsuoka et al. 2005; Brown and Macfadyen 2007; Bo et al. 2014a; Hinz 2017).

Other indirect effects of the different fishing gears include increased vulnerability to epibiosis, parasitism and predation, especially for corals damaged and detached from the seafloor, as well as interruption of reproduction in damaged corals due to a reallocation of energy reserves for tissue repair and regeneration (e.g. Mortensen et al. 2005; Stone and Shotwell 2007; Bo et al. 2009).

30.4.1 Mediterranean Observations

The Mediterranean CWC communities are subject to fishing impacts (e.g. Orejas et al. 2009; Maynou and Cartes 2011; Bo et al. 2011b, 2012, 2014a; Madurell et al. 2012; Cartes et al. 2013; Fabri et al. 2014; Mytilineou et al. 2014; Savini et al. 2014; D'Onghia et al. 2017; Mastrototaro et al. 2017; Taviani et al. 2017; Otero and Marin, this volume).

Explorations in the SML CWC province have provided images of trawling traces, fishing line remains and solid waste in the coral community (Taviani et al. 2005; Freiwald et al. 2009; Vertino et al. 2010). Savini et al. (2014) recorded lost or discarded long lines and nets in association with coral rubble, boulder fields and loosely packed coral habitats. These authors identified trawling traces within mud-dominated sediments in the vicinity or at the base of coral mounds or in between coral mounds. More recently, D'Onghia et al. (2017), using towed cameras, observed remains of long lines on the bottoms and/or entangled in corals as well as trawl door scars on the sea floor around the coral mounds in the Fisheries Restricted Area (FRA), within the SML CWC province. These authors also examined the geographic distribution of fishing effort through an observers' program of longline and trawl fishing activities during 2009 and 2010 and Vessel

Monitoring by satellite System (VMS) data from 2008 to 2013. The longliners mainly fished on the shelf in the north of the SML CWC province and off the FRA whereas the trawlers generally fished on the muddy bottoms of the upper and middle slope within the SML CWC province as well as near and inside the northward limit of the FRA. These results indicate a greater impact of trawling than longlining and that conservation and effective management of this vulnerable marine ecosystems (VMEs) (FAO 2009) remain difficult. Coral by-catch was observed in the Ionian (Vafidis et al. 2006; Mytilineou et al. 2014; D'Onghia et al. 2017) and along the southern Adriatic Sea (D'Onghia et al. 2016).

A total of 197 bottom longlines were recorded in the Cap de Creus canyon (western Mediterranean) (Orejas et al. 2009). Although the statistical analysis related to this finding did not show a clear pattern in the relationship between benthic longline distribution on the seabed and coral density, coral occurrence correlated with bottom longlines in two video transects. The large quantity of benthic longlines found within this canyon indicates that the seabed is periodically exposed to dragging lines (Orejas et al. 2009). The seafloor disturbance due to trawling on soft bottoms and to longlines on rocky substrates was also recorded in the Gulf of Lion (Fabri et al. 2014). The colonies of scleractinian corals (*Lophelia pertusa* and *Madrepora oculata*) were often observed entangled in fishing lines in both the Lacaze-Duthiers and Cassidaigne canyons. The alcyonacean *Callogorgia verticillata* was also severely affected by bottom fishing gears since many colonies were entangled in bottom lines and fishing nets. The high diversity sheltered by the structure-forming gorgonians is attractive for local fisheries even if the examined area is located far from the coast (60 km). Lost fishing gears, lead weights and ropes, damaging structure-forming fauna and breaking cnidarian colonies were observed in most canyons off the French coast (Fabri et al. 2014). Recently, discarded fishing gears, including entangled nets and lines, have been observed in the Sardinian *Madrepora* CWC province (western Mediterranean) (Taviani et al. 2017). Longline and trawling impacts have also been observed on *Isidella elongata* facies in Balearic Sea, including a canyon southwest of Formentera (Mastrototaro et al. 2017).

The occurrence of lost fishing gears, anchor and rope, entangled and damaged colonies of different species, together with a significant degradation of the habitat and the communities, were recorded in several rocky areas in the southern Tyrrhenian Sea (Bo et al. 2011a, 2012, 2014a). The majority of the debris was due to longlines, for which a significant inverse relationship between the presence of these lost gears and the distance from the coast was detected. Other obvious factors, such as the depth of the site, topography and the occurrence of commercial target stocks may influence the fishing effort and, in turn, the impact on benthic communities (Bo et al. 2014a). Lost nets and longlines were observed on rocky shoals located southeast of the Island of Montecristo (Tuscan Archipelago, Tyrrhenian Sea) where *Eunicella cavolinii* and *Parantipathes larix* were clearly entangled in lost lines (Bo et al. 2014b). The area of the Marco Bank (northwest coasts of Sicily, south Tyrrhenian Sea) appeared strongly affected by fishing activities mainly focused on the blackspot seabream *Pagellus bogaraveo*. Ghost longlines were present everywhere entangled in the branches of the largest coral colonies of *Leiopathes glaberrima* and *C. verticillata*, this latter severely damaged by lost lines (Bo et al. 2014c). Lost longlines and lines entangled in the colonies of these two species were also observed on a rocky bank off the southwest coasts of Sardinia (western Mediterranean) (Bo et al. 2015).

30.5 Discussion and Conclusions

30.5.1 Ecological Interactions

Most studies examined in this review show that the CWC habitats are important habitats for fish species. Greater abundance and positive effects related to CWCs have been detected in many fish species both throughout the Mediterranean and world's oceans. With this regard, several authors suggested that CWCs can be functionally equivalent to other hard-bottom structurally complex habitats and that the association with CWCs varies largely according to the different coral and fish species, depth, time of the year and spatial scale (e.g. Auster et al. 2005; Stone 2006; Harter et al. 2009; Ross and Quattrini 2009; Du Preez and Tunnicliffe 2011; D'Onghia et al. 2012; Quattrini et al. 2012; Biber et al. 2014; Kutti et al. 2015; Milligan et al. 2016; Linley et al. 2017). However, several studies have provided evidence of the role of CWCs as critical habitats for fish since:

1. Several species have been observed and suggested to benefit from shelter and productive feeding in the complex heterogeneous habitats built by corals (e.g. Mortensen et al. 1995; Brodeur 2001; Fosså et al. 2002; Husebo et al. 2002; Krieger and Wing 2002; Jonsson et al. 2004; Costello et al. 2005; Sulak et al. 2007; Buhl-Mortensen et al. 2010; D'Onghia et al. 2010, 2011, 2012; Quattrini et al. 2012; Biber et al. 2014; Kutti et al. 2014; Gomes-Pereira et al. 2017) (Table 30.1);
2. A variety of cartilaginous and teleost fishes use CWC habitats for reproduction and as nursery areas (e.g. Reed and Gilmore 1981; Gilmore and Jones 1992; Koenig et al. 2000; Fosså et al. 2002; Reed 2002; Etnoyer and Morgan 2005; Busby et al. 2006; Stone 2006; Etnoyer and Warrenchuk 2007; Quattrini et al. 2009; Concha et al. 2010; D'Onghia et al. 2010, 2016; Flammang et al. 2011; Baillon et al. 2012; Henry et al. 2013; Bo et al. 2015; Cau et al. 2017; Mastrototaro et al. 2017) (Table 30.2).

Table 30.1 Most common fish species observed and suggested to use cold-water coral (CWC) habitats for shelter and/or feeding

Geographic area	CWC species	Fish species	Authors
Mediterranean Sea	*Madrepora oculata, Lophelia pertusa* (with presence of other CWCs)	**Cartilaginous fish**: *Etmopterus spinax. Galeus melastomus, Scyliorhinus canicula* **Teleost fish**: *Coelorinchus caelorhincus, Conger conger, Helicolenus dactylopterus, Hoplostethus mediterraneus, Merluccius merluccius, Micromesistius poutassou, Phycis blennoides, Pagellus bogaraveo, Polyprion americanus*	Hebbeln et al. (2009), D'Onghia et al. (2010, 2011, 2012), Capezzuto et al. (2012), Sion et al. (2012), Maiorano et al. (2013), Carluccio et al. (2014), D'Onghia et al. (2016), and Linley et al. (2017)
Mediterranean Sea	*Leiopathes glaberrima, Isidella elongata*	**Cartilaginous fish**: *G. melastomus, E. spinax* **Teleost fish**: *Benthocometes robustus, H. dactylopterus, H. mediterraneus, Lepidorhombus boscii, M. merluccius, M. poutassou, P. americanus, P. blennoides*	Mytilineou et al. (2014), Angeletti et al. (2015), and Mastrototaro et al. (2017)
Mediterranean Sea	Gorgonians (mostly *Callogorgia verticillata*) and antipatharians (mostly *Leiopathes glaberrima, Antipathes dichotoma, Parantipathes larix*)	**Cartilaginous fish**: *Scyliorhinus canicula, S. stellaris* **Teleost fish**: *Anthias anthias, B. robustus, Capros aper, Cepola macrophthalma, H. dactylopterus, Lappanella fasciata, Macroramphosus scolopax, Phycis phycis, Zeus faber*	Bo et al. (2011a, 2012, 2014b), Fabri et al. (2014), Bo et al. (2015), and Cau et al. (2017)
Northeast Atlantic (Faroe shelf, Norwegian and Swedish waters)	*Lophelia pertusa*	**Cartilaginous fish**: *Galeus melastomus* **Teleost fish**: *Anarhichas lupus, Brosme brosme, Gadus morhua, Lycodes vahli, Molva molva, Pollachius virens, Sebastes viviparus, Sebastes marinus, Trisopterus minutus*	Jensen and Frederiksen (1992), Mortensen et al. (1995), Furevik et al. (1999) in Fosså et al. (2002), Freiwald et al. (2002), Husebo et al. (2002), Jonsson et al. (2004), Costello et al. (2005), Roberts et al. (2005), Kutti et al. (2014, 2015), and Linley et al. (2017)
Northeast Atlantic (from Faroe-Shetland Channel to Porcupine Seabight, Bay of Biscay and Azores)	*Lophelia pertusa* (some studies with presence of *Madrepora oculata*, black corals, octocorals and hydrocorals)	**Cartilaginous fish**: *Galeus melastomus, Hexanchus griseus, Scyliorhinus canicula* **Teleost fish**: *Benthocometes robustus, Brosme brosme, Guttigadus latifrons, Helicolenus dactylopterus, Lappanella fasciata, Lepidion eques, Molva molva, Mora moro, Neocyttus helgae, Phycis blennoides, Sebastes viviparus*	Costello et al. (2005), Wheeler et al. (2005a), Roberts et al. (2008), Durán-Muñoz et al. (2009), Söffker et al. (2011), Henry et al. (2013), Biber et al. (2014), Milligan et al. (2016), Gomes-Pereira et al. (2017), Lavaleye et al. (2017), Linley et al. (2017)
Northwest Atlantic (south-eastern United States, eastern Florida)	*Oculina varicosa*	**Teleost fish**: *Baldwinella vivanus, Centropristis striata, Epinephelus drummondhayi, E. itajara, E. morio, Hyporthodus niveatus, H. nigritus, Lutjanus campechanus, L. griseus, Mycteroperca microlepis, M. phenax*	Reed (2002), Reed et al. (2005), Reed and Ross (2005), and Harter et al. (2009)
Northwest Atlantic (south-eastern United States, eastern Florida, Gulf of Mexico)	*Lophelia pertusa* (some studies with presence of other CWCs)	**Cartilaginous fish**: *Scyliorhinus retifer* **Teleost fish**: *Anthias woodsi, Beryx decadactylus, Conger oceanicus, Dysommina rugosa, Eptatretus lopheliae, Gephyroberyx darwini, Grammicolepis brachiusculus, Helicolenus dactylopterus, Hoplostethus occidentalis, Hyperoglyphe perciformis, Hyporthodus niveatus, Idiastion kyphos, Laemonema barbatulum, L. melanurum, L. goodebeanorum, Nezumia sclerorhynchus, Polyprion americanus, Trachyscorpia cristulata*	Wenner and Baran (2001) in Reed et al. (2006); Reed and Ross (2005), Reed et al. (2006), Sulak et al. (2007), Ross and Quattrini (2007, 2009), Fernholm and Quattrini (2008), and Quattrini et al. (2012)
Central eastern Atlantic	*Lophelia pertusa*	**Teleost fish**: *Gephyroberyx darwini, Helicolenus dactylopterus, Malacocephalus occidentalis, Nettastoma melanorum*	Le Guilloux et al. (2009) and Buhl-Mortensen et al. (2017b)
Northeast Pacific (Gulf of Alaska, Bering Sea)	Sea whips, *Halipteris willemoesi*	**Teleost fish**: *Sebastes alutus*	Krieger (1993), Brodeur (2001) and Miller et al. (2012)

(continued)

Table 30.1 (continued)

Geographic area	CWC species	Fish species	Authors
Northeast Pacific (Gulf of Alaska, Aleutian Islands, British Columbia, off California)	*Primnoa* spp., *Callogorgia* sp., *Gersemia* sp., other gorgonians, black corals, sea pens, hydrocorals and other epifauna	**Teleost fish**: *Albatrossia pectoralis, Gadus chalcogrammus, G. macrocephalus, Sebastes aleutianus, S. alutus, S. babcocki, S. borealis, S. ciliatus, S. ensifer, S. jordani, S. levis, S. polyspinis, S. ruberrimus, S. rufus, S. simulator, S. zacentrus, Sebastolobus alascanus, Pleurogrammus monopterygius, Zaprora silenus*	Heifetz (2002), Krieger and Wing (2002), Roberts et al. (2006), Stone (2006), Tissot et al. (2006), and Du Preez and Tunnicliffe (2011)
Central Pacific	*Gerardia* sp., *Corallium* sp.	**Teleost fish**: *Conger oceanicus*	Parrish et al. (2000)

Table 30.2 Fish species observed to use cold-water coral (CWC) habitats for spawning and/or nursery

Geographic area	CWC species	Fish species	Authors
Mediterranean Sea	*Madrepora oculata, Lophelia pertusa* (with presence of other CWCs)	**Cartilaginous fish**: *Etmopterus spinax, Galeus melastomus* **Teleost fish**: *Conger conger, Helicolenus dactylopterus, Merluccius merluccius, Micromesistius poutassou, Pagellus bogaraveo, Phycis blennoides*	D'Onghia et al. (2010, 2016)
Mediterranean Sea	*Leiopathes glaberrima*	**Cartilaginous fish**: *Scyliorhinus canicula*	Hebbeln et al. (2009), Bo et al. (2015), and Cau et al. (2017)
Mediterranean Sea	*Isidella elongata*	**Cartilaginous fish**: *Scyliorhinus* sp.	D'Onghia (this chapter, ref. Mastrototaro et al. 2017)
Northeast Atlantic (from Norwegian waters to Rockall Bank)	*Lophelia pertusa*	**Cartilaginous fish**: *Galeus melastomus* **Teleost fish**: *Sebastes viviparus*	Jensen and Frederiksen (1992), Furevik et al. (1999) in Fosså et al. (2002), Costello et al. (2005), Henry et al. (2013), and Milligan et al. (2016)
Northwest Atlantic (south-eastern United States, eastern Florida, Gulf of Mexico)	*Oculina varicosa* (and other deep-water corals)	**Cartilaginous fish**: *Dasyatis centroura, Scyliorhinus retifer* **Teleost fish**: *Baldwinella vivanus, Mycteroperca microlepis, M. phenax, Centropristis striata, Hyporthodus niveatus, Epinephelus drummondhayi*	Reed and Gilmore (1981), Gilmore and Jones (1992), Coleman et al. (1996), Castro et al. (1998), Koenig et al. (2000), (2005), Reed (2002), and Reed et al. (2005)
Northwest Atlantic (Gulf of Mexico)	*Callogorgia americana delta*	**Cartilaginous fish**: *Scyliorhinus retifer* (confuted by Ross et al. 2015)	Etnoyer and Warrenchuk (2007)
Northwest Atlantic (off north Carolina)	*Lophelia pertusa*	**Cartilaginous fish**: *Fenestraja plutonia*	Ross and Quattrini (2007) and Quattrini et al. (2009)
Northwest Atlantic (off eastern Canada, Nova Scotia)	*Paragorgia arborea*, deep-water sea pens (mostly *Anthoptilum grandiflorum, Pennatula aculeata, Halipteris finmarchica*)	**Cartilaginous fish**: *Apristurus profundorum* **Teleost fish**: *Benthosema glaciale, Lycodes esmarkii, Sebastes fasciatus, S. mentella*	Baillon et al. (2012, 2014) and Buhl-Mortensen et al. (2017a)
Northeast Pacific (Aleutian Islands)	*Primnoa* sp.	**Teleost fish**: *Allocareproctus unangas*	Busby et al. (2006)
Northeast Pacific (from Washington to California)	Gorgonians (e.g. *Euplexaura marki*), black corals (e.g. *Antipathes* sp.), hydroids	**Cartilaginous fish**: *Apristurus brunneus, Parmaturus xaniurus*	Flammang et al. (2007, 2011)
Southeast Pacific (off southern Chile)	*Antipathes speciosa*	**Cartilaginous fish**: *Bythaelurus canescens*	Concha et al. (2010)

With regard to the first point, the 3D CWC framework can provide habitats not present in the surrounding areas and firm substrates within extended areas of soft homogeneous bottoms. The topography and hydrography of the sites where corals thrive can favour a greater food supply for the corals themselves and the associated fauna. CWCs act as a biological filter that intercept and trap organic matter from the water column and can be a hot spot of zooplankton, macrofaunal biomass and carbon cycling along continental margins (Van Oevelen et al. 2009; Mienis et al. 2014; Soetaert et al. 2016; Buhl-Mortensen et al. 2017a). Several works report enhanced density of zooplankton as potential prey for planktivorous fish and high density of invertebrates between and around corals as potential food for benthos feeders and scavengers (e.g. Reed et al. 1982; Mortensen et al. 1995; Husebo et al. 2002; Costello et al. 2005; Sulak et al. 2007; D'Onghia et al. 2011; Biber et al. 2014). In addition, fishes may use CWC habitats as refuges to maintain position in an optimal feeding location, reducing the metabolic cost of actively swimming in strong currents between feeding periods (Mortensen et al. 2005; Quattrini et al. 2012). The high biodiversity associated with CWCs attract fishes with different feeding strategies and behaviours (e.g. Buhl-Mortensen and Mortensen 2004a, b, c, 2005; Lumsden et al. 2007; Edinger et al. 2007; Sulak et al. 2007; Buhl-Mortensen et al. 2010 and references therein; D'Onghia et al. 2011; Quattrini et al. 2012; Girard et al. 2016). The 3D CWC structure may function in a very similar way to their tropical counterparts, providing feeding sites for aggregating fish species, hiding places from predators and ambush sites for predators (e.g. Hourigan et al. 2007). Most tropical reef fish do not have an obligate relationship with individual coral species, but they do depend on the reef environment (Sale 2002).

With regard to the second topic (spawning and nursery), particular case studies and observations reported here reveal a clear, probably obligate, relationship between fishes and corals (Castro et al. 1998; Busby et al. 2006; Etnoyer and Warrenchuk 2007; Concha et al. 2010; Flammang et al. 2011; Baillon et al. 2012, 2014; Henry et al. 2013; Bo et al. 2015; Cau et al. 2017). In addition, some deep-sea skates and rays are not tightly associated with corals (Costello et al. 2005; Ross and Quattrini 2007; Sulak et al. 2007), but their egg cases co-occur with these benthic organisms (e.g. Costello et al. 2005; Etnoyer and Morgan 2005; Quattrini et al. 2009; Buhl-Mortensen et al. 2017a), suggesting changes in habitat use over time and CWCs as an important habitat for reproduction and for the early life stages. CWCs also seem to be used by a variety of teleost fishes, such as *Sebastes* spp. (Fosså et al. 2002; Costello et al. 2005; Milligan et al. 2016), *Mycteroperca microlepis*, *M. phenax*, *Centropristis striata*, *Hyporthodus niveatus* and *Epinephelus drummondhayi* (Gilmore and Jones 1992; Coleman et al. 1996; Koenig et al. 2000; Reed 2002; Koenig et al. 2005; Reed et al. 2005), *Galeus melastomus*, *Conger conger*, *Helicolenus dactylopterus*, *Merluccius merluccius*, *Phycis blennoides, Pagellus bogaraveo* (D'Onghia et al. 2010, 2016) since adult reproductive individuals were often reported associated with the coral habitats.

The papers examined in this review show that the potential benefits provided by CWCs for several fish species are not only related to food supply, but concurrently as spawning sites, nursery grounds, and protection refuges from predators, bottom currents and fishing activities (e.g. *Sebastes* spp., *Mycteroperca* spp., *Conger oceanicus*, *C. conger*, *B. brosme*, *H. dactylopterus*, *P. bogaraveo*, *B. decadactylus*, *G. melastomus*, *S. canicula*) (e.g. Mortensen et al. 1995; Koenig et al. 2000; Fosså et al. 2002; Husebo et al. 2002; Krieger and Wing 2002; Costello et al. 2005; Koenig et al. 2005; Etnoyer and Warrenchuk 2007; Ross and Quattrini 2007; D'Onghia et al. 2010, 2011, 2016; Du Preez and Tunnicliffe 2011; Baillon et al. 2012; Quattrini et al. 2012; Henry et al. 2013; Bo et al. 2015; Cau et al. 2017).

Some fish species (i.e. those of the Scyliorhinidae, Sebastidae, Serranidae, Berycidae, Zoarcidae, Lotidae, Moridae, Congridae and Liparidae families) seem to be more tightly associated to CWC habitats. However, from the available knowledge, they cannot be considered as habitat specialists. In fact, most of these species (e.g. *Sebastes* spp., *H. dactylopterus*, *B. decadactylus, C. oceanicus, C. conger, P. bogaraveo, G. melastomus*), which obtain benefits from CWC habitats, could be facultative inhabitants since they have also been found in other types of habitats (e.g. Uiblein et al. 2003; Reed et al. 2006; Ross and Quattrini 2007; Roberts et al. 2008; D'Onghia et al. 2012, 2016; Quattrini et al. 2012; Biber et al. 2014; Kutti et al. 2014; Milligan et al. 2016). In this respect, species that display ontogenetic migration as well as those that cover larger areas during foraging activity, may visit both coral and non coral habitats. For example, *H. dactylopterus* and *P. bogaraveo* generally show ontogenetic migration, with juveniles distributed in the shallower waters on muddy bottoms and adults at greater depths often containing CWCs, outcrops, banks and habitats less accessible to trawling (Uiblein et al. 2003; Reed et al. 2006; Ross and Quattrini 2007; Roberts et al. 2008; D'Onghia et al. 2010, 2016; Mytilineou et al. 2013; Milligan et al. 2016); *G. melastomus* is a very mobile shark which swims over different habitats searching for food based on benthic crustaceans, among which *Munida* sp., and a mixture of benthopelagic and mesopelagic species (euphausiids, *Pasiphaea multidentata*, fishes and cephalopods) (e.g. Carrassón et al. 1992; Roberts et al. 2008; Durán-Muñoz et al. 2009; D'Onghia et al. 2012; Kutti et al. 2014; Mastrototaro et al. 2017). Contrary to all these facultative inhabitants, *Eptatretus lopheliae*, which was videotaped and caught in close association with a *Lophelia* reef habitat (Fernholm and Quattrini 2008), might be a specialist inhabitant, but also in this case the knowledge is very scant.

Based on a variety of studies, a consensus has emerged that environmental variables, such as physical structures, food availability, predator occurrence, depth, current speed and temperature, can all influence the distribution of the species and their association with CWCs (e.g. Harter et al. 2009; Buhl-Mortensen et al. 2010; Du Preez and Tunnicliffe 2011; Söffker et al. 2011; Quattrini et al. 2012; Biber et al. 2014; Milligan et al. 2016; Buhl-Mortensen et al. 2017a; Henry and Roberts 2017). Often the potential importance of CWCs remains unclear because studies do not coincide with the period when fish might use this habitat (e.g. Auster 2007;

Baillon et al. 2012; Milligan et al. 2016; Linley et al. 2017). Moreover, there are currently many methodological difficulties in sampling deep-sea species and studying coral-associated fish density and diversity that need to be addressed and improved (e.g. Ross and Quattrini 2007; Roberts et al. 2009; Buhl-Mortensen et al. 2010; Milligan et al. 2016). Despite these uncertainties and difficulties, from all the above reported, there are several sources of evidence that CWCs play an important role as life-history critical habitats for fish species. Considering that an Essential Fish Habitat (EFH) can be defined as "those waters and substrates necessary to fish for spawning, breeding, feeding, or growth to maturity" (Rosenberg et al. 2000), there is enough evidence of the role of CWCs as EFHs.

30.5.2 Fishing Impact

The CWC habitats are valuable fishing areas as large sizes and high abundances of commercial fish species often occur in these habitats. Thus, CWC habitats are often impacted by commercial fishing (e.g. Roberts et al. 2000; Fosså et al. 2002; Hall-Spencer et al. 2002; Reed 2002; Roberts 2002; Grehan et al. 2005; Wheeler et al. 2005b; Buhl-Mortensen et al. 2010; Bo et al. 2014a; D'Onghia et al. 2017; Hinz 2017; Otero and Marin this volume). The fishing activity in CWC areas can cause both direct effects of fishing on the stocks and direct and indirect effects of fishing on the habitat, which can then further impact stocks (Armstrong and Falk-Petersen 2008; Armstrong et al. 2009, 2014). Clear examples of coral degradation and consequent reduction in economically important species have been reported in some studies (e.g. Koenig et al. 2000; Reed et al. 2005; Du Preez and Tunnicliffe 2011). In relation to trawling activity carried out on Learmonth Bank off northern British Columbia and the consequent reduction of rockfish, Du Preez and Tunnicliffe (2011) concluded that the degradation of biogenic structures is a long-term detriment to rockfish species and, although the mechanism remains unclear, their observations suggest that it occurs through the destruction of a habitat that is more effective for shelter than rough inert seafloor.

Foley et al. (2010) used a production function approach to capture the functional values provided by CWC communities, such as habitat, spawning grounds, nursery and refuge to commercial species of redfish (*Sebastes* spp.). They found that both the carrying capacity and growth rate of redfish are functions of a CWC habitat and thus CWCs can be considered an EFH. Application of the EFH model indicated an approximate annual loss in harvest of between 11% and 29% for the range of coral decline proposed by scientists. The results of this study demonstrate that a decline in CWCs can explain some of the changes in the harvest of Norwegian redfish (Foley et al. 2010). No studies of this type have been conducted in the Mediterranean, but longlining and trawling as well as lost fishing gears are among the major causes of degradation of CWC habitats in the Mediterranean (e.g. Bo et al. 2014a; Savini et al. 2014; D'Onghia et al. 2017; Taviani et al. 2017).

Despite this evidence and the different conservation initiatives proposed for the Mediterranean CWCs (e.g. de Juan and Lleonart 2010; Oceana 2011; Micheli et al. 2013; Otero and Marin, this volume), conservation and effective management of this VME remain challenging due to the difficulties in controlling the fishing activities in the international Mediterranean waters (beyond 12 nautical miles of the coast). In the SML CWC province, a refuge effect from fishing has been shown for some commercial species distributed in the coral areas (D'Onghia et al. 2010, 2012), but trawlers still often fish inside the FRA with the aim of obtaining greater catches and larger sizes of commercial species (D'Onghia et al. 2017).

Due to the slow recovery rates of CWCs, the habitats that they build are highly vulnerable and may take many decades or centuries to recover from damage (e.g. Roberts 2002; Freiwald et al. 2004; Shester and Ayers 2005). Considering that fishing activity is carried out using different fishing techniques and targeting different species both on muddy and rocky bottoms, knowledge of CWC habitat location and their relative use by fish species is of utmost importance for the development of effective management and conservation measures. In this regard, in order to increase the knowledge and promote an effective ecosystem-based fishery management of the deep sea (Rosenberg et al. 2000; Grehan et al. 2009, 2017), a large-scale monitoring of the fishing impact on CWCs needs to be properly implemented as part of Marine Strategy Framework Directive.

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References

Angeletti L, Mecho A, Doya C, et al (2015) First report of live deep-water cnidarian assemblages from the Malta escarpment. Ital J Zool 82:291–297

Armstrong CW, Falk-Petersen J (2008) Habitat fisheries interactions: a missing link? ICES J Mar Sci 65:817–821

Armstrong CW, Grehan AJ, Kahui V, et al (2009) Bioeconomic modeling and the management of cold-water coral resources. Oceanography 22:86–91

Armstrong CW, Foley N, Kahui V, et al (2014) Cold water coral reef management from an ecosystem service perspective. Mar Policy 50:126–134

Auster PJ (2005) Are deep-water corals important habitats for fishes? In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 747–760

Auster PJ (2007) Linking deep-water corals and fish populations. In: George RY, Cairns SD (eds) Conservation and adaptive management of seamount and deep-sea coral ecosystems. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, pp 93–99

Auster PJ, Watling L, Rieser A (1997) Response: the interface between fisheries research and habitat management. N Am J Fish Manag 17:596–598

Auster PJ, Lindholm J, Valentine PC (2003) Variation in habitat used by juvenile Acadian redfish, *Sebastes fasciatus*. Environ Biol Fish 68:381–389

Auster PJ, Moore J, Heinonen KB, et al (2005) A habitat classification scheme for seamount landscapes: assessing the functional role of deep-water corals as fish habitat. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 761–769

Baillon S, Hamel J-F, Wareham VE, et al (2012) Deep cold-water corals as nurseries for fish larvae. Front Ecol Environ 10:351–356

Baillon S, Hamel J-F, Mercier A (2014) Diversity, distribution and nature of faunal associations with deep-sea Pennatulacean corals in the Northwest Atlantic. PLoS One 9:e111519

Baker KD, Haedrich RL, Snelgrove PVR, et al (2012) Small-scale patterns of deep-sea fish distributions and assemblages of the Grand Banks, Newfoundland continental slope. Deep-Sea Res Part 1 Oceanogr Res Pap 65:171–188

Beck MW (1995) Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. Ecology 76:968–980

Biber MF, Duineveld GCA, Lavaleye MSS, et al (2014) Investigating the association of fish abundance and biomass with cold-water corals in the deep Northeast Atlantic Ocean using a generalised linear modelling approach. Deep-Sea Res Part 2 Top Stud Oceanogr 99:134–145

Bo M, Bavestrello G, Canese S, et al (2009) Characteristics of a black coral meadow in the twilight zone of the central Mediterranean Sea. Mar Ecol Progr Ser 397:53–61

Bo M, Bavestrello G, Canese S, et al (2011a) Coral assemblages off the Calabrian Coast (South Italy) with new observations on living colonies of *Antipathes dichotoma*. Ital J Zool 78:231–242

Bo M, Bertolino M, Borghini M, et al (2011b) Characteristics of the mesophotic megabenthic assemblage of the Vercelli Seamount (North Tyrrhenian Sea). PLoS One 6:e16357

Bo M, Canese S, Spaggiari C, et al (2012) Deep coral oases in the South Tyrrhenian Sea. PLoS One 7:e49870

Bo M, Bava S, Canese S, et al (2014a) Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. Biol Conserv 171:167–176

Bo M, Canese S, Bavestrello G (2014b) Discovering Mediterranean black coral forests: *Parantipathes larix* (Anthozoa: Hexacorallia) in the Tuscan Archipelago, Italy. Ital J Zool 81:112–125

Bo M, Cerrano C, Canese S, et al (2014c) The coral assemblages of an off-shore deep Mediterranean rocky bank (NW Sicily, Italy). Mar Ecol 35:332–342

Bo M, Bavestrello G, Angiolillo M, et al (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS One 10:e0119393

Bourcier M, Zibrowius H (1973) Les "boues rouges" déversées dans le canyon de la Cassidaigne (région de Marseille). Observations en soucoupe plongeante SP 350 (juin 1971) et résultats de dragages. Tethys 4:811–842

Brodeur RD (2001) Habitat-specific distribution of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. Cont Shelf Res 21:207–224

Brown J, Macfadyen G (2007) Ghost fishing in European waters: impacts and management responses. Mar Policy 31:488–504

Buhl-Mortensen L, Mortensen PB (2004a) Symbiosis in deep-water corals. Symbiosis 37:33–61

Buhl-Mortensen L, Mortensen PB (2004b) Crustacean fauna associated with the deep-water corals *Paragorgia arborea* and *Primnoa resedaeformis*. J Nat Hist 38:1233–1247

Buhl-Mortensen L, Mortensen PB (2004c) *Gorgonophilus canadensis* n. gen., n. sp. (Copepoda: Lamippidae), a gall forming endoparasite in the octocoral *Paragorgia arborea* (L., 1758) from the Northwest Atlantic. Symbiosis 37:155–268

Buhl-Mortensen L, Mortensen PB (2005) Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 849–879

Buhl-Mortensen L, Vanreusel A, Gooday AJ, et al (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Mar Ecol 31:21–50

Buhl-Mortensen P, Buhl-Mortensen L, Purser A (2017a) Trophic ecology and habitat provision in cold-water coral ecosystems. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 919–944

Buhl-Mortensen L, Serigstad B, Buhl-Mortensen P, et al (2017b) First observations of the structure and megafaunal community of a large *Lophelia* reef on the Ghanaian shelf (the Gulf of Guinea). Deep-Sea Res Part 2 Top Stud Oceanogr 137:148–156

Busby MS, Orr JW, Blood DM (2006) Eggs and late-stage embryos of *Allocareproctus unangas* (family Liparidae) from the Aleutian Islands. Ichthyol Res 53:423–426

Butler M (2005) Conservation corals in Atlantic Canada: a historical perspective. In: Freiwald A, Roberts MJ (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 1199–1209

Caddy JF (2007) Marine habitat and cover: their importance for productive coastal fishery resources. UNESCO Publishing, Paris, 249 pp

Caddy JF (2008) The importance of "cover" in the life histories of demersal and benthic marine resources: a neglected issue in fisheries assessment and management. Bull Mar Sci 83:7–52

Capezzuto F, Maiorano P, Panza M, et al (2012) Occurrence and behaviour of *Paromola cuvieri* (Crustacea, Decapoda) in the Santa Maria di Leuca cold-water coral community (Mediterranean Sea). Deep-Sea Res Part 1 Oceanogr Res Pap 59:1–7

Carluccio A, Capezzuto F, Lionetti A, et al (2014) Refuge areas of *Pagellus bogaraveo* (Brünnich, 1768) in the central Mediterranean Sea: Santa Maria di Leuca cold-water coral province and Bari canyon. Biol Mar Mediterr 21:214–215

Carrassón C, Stefanescu C, Cartes JE (1992) Diets and bathymetric distributions of the two bathyal sharks of the Catalan deep sea (western Mediterranean). Mar Ecol Progr Ser 82:21–30

Cartes JE, Lo Iacono C, Mamouridis V, et al (2013) Geomorphological, trophic and human influences on the bamboo coral *Isidella elongata* assemblages in the deep Mediterranean: to what extent does *Isidella* form habitat for fish and invertebrates? Deep-Sea Res Part 1 Oceanogr Res Pap 76:52–65

Caruso JH, Ross SW, Sulak KJ, et al (2007) Deep-water chaunacid and lophiid anglerfishes (Pisces: Lophiiformes) off the south-eastern United States. J Fish Biol 70:1015–1026

Castro JI, Bubucis PM, Overstrom NA (1998) The reproductive biology of the chain dogfish, *Scyliorhinus retifer*. Copeia 3:740–746

Cau A, Follesa MC, Moccia D, et al (2017) *Leiopathes glaberrima* millennial forest from SW Sardinia as nursery ground for the small spotted catshark *Scyliorhinus canicula*. Aquat Conserv 27:731–735

Coleman FC, Koenig CC, Collins LA (1996) Reproductive styles of shallow-water grouper (Pisces: Serranidae) in the eastern Gulf of

Mexico and the consequences of fishing spawning aggregations. Environ Biol Fish 47:129–141

Concha F, Bustamante C, Oddone MC, et al (2010) Egg capsules of the dusky catshark *Bythaelurus canescens* (Carcharhiniformes, Scyliorhinidae) from the south-eastern Pacific Ocean. J Fish Biol 77:963–971

Costello MJ, McCrea M, Freiwald A, et al (2005) Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: Freiwald A, Roberts MJ (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 771–805

D'Onghia G, Maiorano P, Sion L, et al (2010) Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:397–411

D'Onghia G, Indennidate A, Giove A, et al (2011) Distribution and behaviour of the deep-sea benthopelagic fauna observed using towed cameras in the Santa Maria di Leuca cold water coral province. Mar Ecol Progr Ser 443:95–110

D'Onghia G, Maiorano P, Carlucci R, et al (2012) Comparing deep-sea fish fauna between coral and non-coral "megahabitat" in the Santa Maria di Leuca cold-water coral province (Mediterranean Sea). PLoS One 7:e44509

D'Onghia G, Capezzuto F, Cardone F, et al (2015a) Macro- and megafauna recorded in the submarine Bari Canyon (southern Adriatic Sea, Mediterranean Sea) using different tools. Mediterr Mar Sci 16:180–196

D'Onghia G, Capezzuto F, Carluccio A, et al (2015b) Exploring composition and behaviour of fish fauna by in situ observations in the Bari Canyon (Southern Adriatic Sea, Central Mediterranean). Mar Ecol 36:541–556

D'Onghia G, Calculli E, Capezzuto F, et al (2016) New records of cold-water coral sites and fish fauna characterization of a potential network existing in the Mediterranean Sea. Mar Ecol 37:1398–1422

D'Onghia G, Calculli C, Capezzuto F, et al (2017) Anthropogenic impact in the Santa Maria di Leuca cold-water coral province (Mediterranean Sea): observations and conservation straits. Deep-Sea Res Part 2 Top Stud Oceanogr 145:87–101

de Juan S, Lleonart J (2010) A conceptual framework for the protection of vulnerable habitats impacted by fishing activities in the Mediterranean high seas. Ocean Coast Manag 53:717–723

Diaz RJ, Cutter GR Jr, Able KW (2003) The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries 26:12–20

Du Preez C, Tunnicliffe V (2011) Shortspine thornyhead and rockfish (Scorpaenidae) distribution in response to substratum, biogenic structures and trawling. Mar Ecol Progr Ser 425:217–231

Duncan C (2001) Off shore marine conservation, 'Darwin Mounds' and beyond. Mar Conserv 5:14–15

Durán-Muñoz P, Sayago-Gil M, Cristobo J, et al (2009) Seabed mapping for selecting cold-water coral protection areas on Hatton Bank, Northeast Atlantic. ICES J Mar Sci 66:2013–2025

Durán-Muñoz P, Murillo FJ, Sayago-Gil M, et al (2011) Effects of deep-sea bottom longlining on the Hatton Bank communities and benthic ecosystem, north-east Atlantic. J Mar Biol Assoc UK 91:939–952

Edinger EN, Wareham VE, Haedrich RL (2007) Patterns of ground fish diversity and abundance in relation to deep-sea coral distributions in Newfoundland and Labrador waters. In: George RY, Cairns SD (eds) Conservation and adaptive management of seamount and deep-sea coral ecosystems. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, pp 101–122

Etnoyer P, Morgan LE (2005) Habitat-forming deep-sea corals in the Northeast Pacific Ocean. In: Freiwald A, Roberts MJ (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 331–343

Etnoyer P, Warrenchuk J (2007) A catshark nursery in a deep Gorgonian field in the Mississippi Canyon, Gulf of Mexico. Bull Mar Sci 8:553–559

Fabri MC, Pedel L, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207

FAO (2009) Report of the technical consultation on international guidelines for the management of deep-sea fisheries in the high seas, Rome, 4–8 February and 25–29 August 2008. FAO Fish Aquac Rep 881:86

Fernholm B, Quattrini AM (2008) A new species of Hagfish (Myxinidae: *Eptatretus*) associated with deep-sea coral habitat in the Western North Atlantic. Copeia 2008:126–132

Flammang BE, Ebert DA, Cailliet GM (2007) Egg cases of the genus *Apristurus* (Chondrichthyes: Scyliorhinidae): phylogenetic and ecological implications. Zoology 110:308–317

Flammang BE, Ebert DA, Cailliet GM (2011) Intraspecific and interspecific spatial distribution of three eastern north pacific catshark species and their egg cases (Chondrichthyes: Scyliorhinidae). Breviora Mus Comp Zool 525:1–18

Foley NS, Armstrong CW, Rensburg van TM (2010) Estimating linkages between redfish and cold water coral on the Norwegian coast. Mar Resour Econ 25:105–120

Fosså JH, Mortensen PB, Furevik DM (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471:1–12

Freese JL, Wing BL (2003) Juvenile red rockfish, *Sebastes* sp., associations with sponges in the Gulf of Alaska. Mar Fish Rev 65:38–42

Freiwald A, Hühnerbach V, Lindberg B, et al (2002) The Sula reef complex, Norwegian shelf. Facies 47:179–200

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs. UNEP-WCMC, Cambridge, 86 pp

Freiwald A, Beuck L, Rüggerberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:36–52

Froese R, Pauly D (2000) FishBase 2000: concepts, design and data sources. ICLARM, Los Baños

Gilmore R, Jones RJ (1992) Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. Bull Mar Sci 51:83–103

Girard F, Fu B, Fisher CR (2016) Mutualistic symbiosis with ophiuroids limited the impact of the deepwater horizon oil spill on deep-sea octocorals. Mar Ecol Progr Ser 549:89–98

Gomes-Pereira JN, Carmo V, Catarino D, et al (2017) Cold-water corals and large hydrozoans provide essential fish habitat for *Lappanella fasciata* and *Benthocometes robustus*. Deep-Sea Res Part 2 Top Stud Oceanogr 145:33–48

Gore RH, Scotto LE, Becker LJ (1978) Community composition, stability and trophic partitioning in decapod crustaceans inhabiting some subtropical sabellariid worm reefs. Studies on decapod crustacea from the Indian River Lagoon region of Florida. IV. Bull Mar Sci 28:221–248

Grehan AJ, Unnithan V, Olu K, et al (2005) Fishing impacts on Irish deep-water coral reefs: making a case for coral conservation. Am Fish Soc Symp 41:819–832

Grehan AJ, van Den Hove S, Armstrong CW, et al (2009) HERMES promoting ecosystem-based management and the sustainable use and governance of deep-water resources. Oceanography 22:154–166

Grehan AJ, Arnaud-Haond S, D'Onghia G, et al (2017) Towards ecosystem based management and monitoring of the deep Mediterranean, North-East Atlantic and beyond. Deep-Sea Res Part 2 Top Stud Oceanogr 145:1–7

Hall-Spencer J, Allain V, Fosså JH (2002) Trawling damage to north-east Atlantic ancient coral reefs. Proc R Soc Lond Ser B Biol Sci 269:507–511

Harter SL, Ribera MM, Shepard AN, et al (2009) Assessment of fish populations and habitat on *Oculina* Bank, a deep-sea coral marine protected area off eastern Florida. Fish Bull 107:195–206

Harvey M, Bourget E (1997) Recruitment of marine invertebrates onto arborescent epibenthic structures: active and passive processes acting at different spatial scales. Mar Ecol Progr Ser 153:203–215

Hayes DB, Ferreri CP, Taylor WW (1996) Linking fish habitat to their population dynamics. Can J Fish Aquat Sci 53:383–390

Hebbeln D, Wienberg C, Beuck L, et al (2009) Report and preliminary results of RV POSEIDON Cruise POS 385 "Cold-Water Corals of the Alboran Sea (western Mediterranean Sea)". Universität Bremen, Berichte, Fachbereich Geowissenschaften 273:79

Heifetz J (2002) Coral in Alaska: distribution, abundance, and species associations. Hydrobiologia 471:19–28

Heifetz J, Stone RP, Shotwell SW (2009) Damage and disturbance to coral and sponge habitat of the Aleutian Archipelago. Mar Ecol Progr Ser 397:305–308

Henry LA, Roberts JM (2017) Global biodiversity in cold-water coral reef ecosystems. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 235–256

Henry LA, Navas JM, Hennige SJ, et al (2013) Cold-water coral reef habitats benefit recreationally valuable sharks. Biol Conserv 161:67–70

Hinz H (2017) Impact of bottom fishing on animal forests: science, conservation, and fisheries management. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1041–1059

Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol Monogr 63:77–101

Hourigan TF (2009) Managing fishery impacts on deep-water coral ecosystems of the USA: emerging best practices. Mar Ecol Progr Ser 397:333–340

Hourigan TF, Lumsden SE, Dorr G, et al (2007) Deep coral ecosystems of the United States: introduction and national overview. In: Lumsden SE, Hourigan TF, Bruckner AW, et al (eds) The state of deep coral ecosystems of the United States, NOAA Tech Memo CRCP-3. NOAA, Silver Spring, pp 1–64

Husebø A, Nøttestad L, Fosså JH, et al (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471:91–99

Jensen A, Frederiksen R (1992) The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe shelf. Sarsia 77:53–69

Jonsson LG, Nilsson PG, Floruta F, et al (2004) Distributional patterns of macro- and megafauna associated with a reef of the cold-water coral *Lophelia pertusa* on the Swedish west coast. Mar Ecol Progr Ser 284:163–171

Juanes F (2007) Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. J Fish Biol 70:661–677

Koenig CC, Coleman FC, Grimes CB, et al (2000) Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf edge reefs of Florida. Bull Mar Sci 66:593–616

Koenig CC, Shepard AN, Reed JK, et al (2005) Habitat and fish populations in the *Oculina* coral ecosystem of the Western Atlantic. Am Fish Soc Symp 41:795–805

Krieger KJ (1993) Distribution and abundance of rockfish determined from a submersible and by bottom trawling. Fish Bull 91:87–96

Krieger KJ, Wing BL (2002) Megafauna associations with deep-water corals (*Primnoa* spp.) in the Gulf of Alaska. Hydrobiologia 471:83–90

Kuhlmann KL (1998) Spatial and temporal patterns in the dynamics and use of pen shells (*Atrina rigida*) as shelters in St. Joseph Bay, Florida. Bull Mar Sci 62:157–179

Kutti T, Bergstad OA, Fosså JH, et al (2014) Cold-water corals mound and sponge-beds as habitats for demersal fish on the Norwegian shelf. Deep-Sea Res Part 2 Top Stud Oceanogr 99:122–133

Kutti T, Fosså JH, Bergstad OA (2015) Influence of structurally complex benthic habitats on fish distribution. Mar Ecol Progr Ser 520:175–190

Langton RW, Steneck RS, Gotceitas V, et al (1996) The interface between fisheries research and habitat management. N Am J Fish Manag 16:1–7

Lavaleye M, Duineveld G, Bergman M, et al (2017) Long-term baited lander experiments at a cold-water coral community on Galway Mound (Belgica Mound Province, NE Atlantic). Deep-Sea Res Part 2 Top Stud Oceanogr 145:22–32

Le Guilloux E, Olu K, Bourillet JF, et al (2009) First observations of deep-sea coral reefs along the Angola margin. Deep-Sea Res Part 2 Top Stud Oceanogr 56:2394–2403

Lindberg WJ, Stanton GR (1989) Resource quality, dispersion and mating prospects for crabs occupying bryozoan colonies. J Exp Mar Biol Ecol 128:257–282

Linley TD, Lavaleye M, Maiorano P, et al (2017) Interaction of cold-water corals with fish diversity and density across differing European regions: data from three baited lander systems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:8–21

Lipcius RN, Eggleston DB, Miller DL, et al (1998) The habitat-survival function for Caribbean spiny lobsters: an inverted size effect and non-linearity in mixed algal and seagrass habitats. Mar Freshw Res 49:807–816

Lumsden SE, Hourigan TF, Bruckner AW, et al (2007) The state of deep coral ecosystems of the United States. NOAA Technical Memorandum CRCP-3, Silver Spring, 365 pp

Madurell T, Orejas C, Requena S, et al (2012) The benthic communities of the Cap de Creus canyon. In: Würtz M (ed) Mediterranean submarine canyons: ecology and governance. IUCN, Gland, pp 123–132

Maiorano P, Sion L, Capezzuto F, et al (2013) Exploring deep-sea benthopelagic fauna using a baited lander in the Santa Maria di Leuca cold-water coral province. Rapp Comm Int Mer Mediterr 40:719

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

Mastrototaro F, Chimienti G, Acosta J, et al (2017) *Isidella elongata* (Cnidaria: Alcyonacea) *facies* in the western Mediterranean Sea: visual surveys and descriptions of its ecological role. Eur Zool J 84:209–225

Matsuoka T, Nakashima T, Nagasawa N (2005) A review of ghost fishing: scientific approaches to evaluation and solutions. Fish Sci 71:691–702

Maynou F, Cartes JE (2011) Effects of trawling on fish and invertebrates from deep-sea coral *facies* of *Isidella elongata* in the western Mediterranean. J Mar Biol Assoc 92:1501–1507

McCosker JE, Ross SW (2007) A new deep water species of the snake eel genus *Ophichthus* (Anguilliformes: Ophichthidae) from North Carolina. Copeia 2007:783–787

Micheli F, Levin N, Giakoumi S, et al (2013) Setting priorities for regional conservation planning in the Mediterranean Sea. PLoS One 8:e59038

Mienis F, Duineveld G, Davies AJ, et al (2014) Cold-water coral growth under extreme environmental conditions, the Cape Lookout area, NW Atlantic. Biogeosciences 11:2543–2560

Miller RJ, Hocevar J, Stone RP, et al (2012) Structure-forming corals and sponges and their use as fish habitat in Bering Sea submarine canyons. PLoS One 7:e33885

Milligan RJ, Spence G, Roberts JM, et al (2016) Fish communities associated with cold-water corals vary with depth and substratum type. Deep-Sea Res Part 1 Oceanogr Res Pap 14:43–54

Morgan LE, Etnoyer P, Scholz A, et al (2005) Conservation and management implications of deep-sea coral and fishing effort distributions in the Northeast Pacific Ocean. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 1171–1187

Mortensen PB, Hovland M, Brattegard T, et al (1995) Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64° N on the Norwegian shelf: structure and associated megafauna. Sarsia 80:145–158

Mortensen PB, Buhl-Mortensen L, Gordon Jr DC, et al (2005) Effects of fisheries on deep-water gorgonian corals in the Northeast Channel, Nova Scotia (Canada). In: Barnes PW, Thomas JP (eds) Benthic habitats and the effects of fishing. Am Fish Soc Symp 41:369–382

Mortensen PB, Buhl-Mortensen L, Gebruk AV, et al (2008) Occurrence of deep-water corals on the Mid-Atlantic Ridge based on MAR-ECO data. Deep-Sea Res Part 2 Top Stud Oceanogr 55:142–152

Mytilineou CH, Tsagarakis K, Bekas P, et al (2013) Spatial distribution and life-history aspects of blackspot seabream *Pagellus bogaraveo* (Osteichthyes: Sparidae). J Fish Biol 83:1551–1575

Mytilineou CH, Smith CJ, Anastasopoulou A, et al (2014) New cold-water coral occurrences in the Eastern Ionian Sea: results from experimental long line fishing. Deep-Sea Res Part 2 Top Stud Oceanogr 99:146–157

Nielsen JG, Ross SW, Cohen DM (2009) Atlantic occurrence of the genus *Bellottia* (Teleostei, Bythitidae) with two new species from the Western North Atlantic. Zootaxa 2018:45–57

Oceana (2011) Oceana MedNet, MPA proposal for the Mediterranean Sea. 100 reasons to reach 10%. Oceana, Madrid, 96 pp

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51

Orth RJ, Heck KL, van Montfrans J (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7:339–350

Parrish FA, Craig MP, Ragen TJ, et al (2000) Identifying diurnal foraging habitat of endangered Hawaiian monk seals using a seal-mounted video camera. Mar Mamm Sci 16:392–412

Pearcy WG, Stein DL, Hixon MA, et al (1989) Submersible observations of deep-reef fish of Heceta Bank, Oregon. Fish Bull 87:955–965

Pham CK, Diogo H, Menezes G, et al (2014) Deep-water longline fishing has reduced impact on vulnerable marine ecosystems. Sci Rep 4:4837

Piskaln CH, Churchill JH, Mayer LM (1998) Resuspension of sediment by bottom trawling in the Gulf of Maine and potential geochemical consequences. Conserv Biol 12:1223–1229

Porteiro FM, Gomes-Pereira JN, Pham CK, et al (2013) Distribution and habitat association of benthic fish on the Condor seamount (NE Atlantic, Azores) from in situ observations. Deep-Sea Res Part 2 Top Stud Oceanogr 98:114–128

Puig P, Canals M, Company JB, et al (2012) Ploughing the deep sea floor. Nature 489:286–289

Purser A (2015) A time series study of *Lophelia pertusa* and reef megafauna responses to drill cuttings exposure on the Norwegian margin. PLoS One 10:e0134076

Purser A, Orejas C, Gori A, et al (2013) Local variation in the distribution of benthic megafauna species associated with cold-water coral reefs on the Norwegian margin. Cont Shelf Res 54:37–51

Quattrini AM, Partyka ML, Ross SW (2009) Aspects of the reproductive biology of the skate *Fenestraja plutonia* (Garman) off North Carolina. Southeast Nat 8:55–70

Quattrini AM, Ross SW, Carlson MCT, et al (2012) Megafaunal-habitat associations at a deep-sea coral mound off North Carolina, USA. Mar Biol 159:1079–1094

Reed JK (2002) Deep-water *Oculina* coral reefs of Florida: biology, impacts, and management. Hydrobiologia 471:43–55

Reed JK, Gilmore RG (1981) Inshore occurrence and nuptial behavior of the roughtail stingray, *Dasyatis centroura* (Dasyatidae), on the continental shelf, east central Florida. Northeast Gulf Sci 5:1–4

Reed JK, Ross SW (2005) Deep-water reefs off the Southeastern U.S.: recent discoveries and research. J Mar Educ 21:33–37

Reed JK, Gore RH, Scotto LE, et al (1982) Community composition, structure, areal and trophic relationships of decapods associated with shallow- and deep-water *Oculina varicosa* coral reefs: studies on decapod Crustacea from the Indian River region of Florida, XXIV. Bull Mar Sci 32:761–786

Reed JK, Shepard AN, Koenig CC, et al (2005) Mapping, habitat characterization, and fish surveys of the deep-water *Oculina* coral reef marine protected area: a review of historical and current research. In: Freiwald A, Roberts MJ (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 443–465

Reed JK, Weaver DC, Pomponi SA (2006) Habitat and fauna of deep-water *Lophelia pertusa* coral reefs off the southeastern U.S.: Blake plateau, Straits of Florida, and Gulf of Mexico. Bull Mar Sci 78:343–475

Reyss D (1964) Observations faites en Soucoupe Plongeante dans deux vallees sous-marines de la mer catalane; le rech du Cap et le rech Lacaze-Duthiers. Bulletin de l'Institut Oceanographique de Monaco 63:1–8

Ricklefs RE (1979) Ecology, 3rd edn. Chiron, Portland, p 849

Roberts CM (2002) Deep impact: the rising toll of fishing in the deep sea. Trends Ecol Evol 17:242–245

Roberts JM, Harvey SM, Lamont PA, et al (2000) Seabed photography, environmental assessment and evidence for deep-water trawling on the continental margin west of the Hebrides. Hydrobiologia 44:173–183

Roberts JM, Peppe OC, Dodds LA, et al (2005) Monitoring environmental variability around cold-water coral reefs: the use of a benthic photolander and the potential of seafloor observatories. In: Freiwald A, Roberts MJ (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 483–502

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Roberts JM, Henry LA, Long D, et al (2008) Cold-water coral reef frameworks, megafaunal communities and evidence for coral carbonate mounds on the Hatton Bank, north east Atlantic. Facies 54:297–316

Roberts JM, Wheeler A, Freiwald A, Cairns SD (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334

Rogers AD (1999) The biology of *Lophelia pertusa* (Linnaeus, 1758) and other deep-water reef-forming corals and impacts from human activities. Int Rev Hydrobiol 84:315–406

Rosenberg A, Bigford TE, Leathery S, et al (2000) Ecosystem approaches to fishery management through essential fish habitat. Bull Mar Sci 66:535–542

Ross SW, Quattrini AM (2007) The fish fauna associated with deep coral banks off the southeastern United States. Deep-Sea Res Part 1 Oceanogr Res Pap 54:975–1007

Ross SW, Quattrini AM (2009) Deep-sea reef fish assemblage patterns on the Blake Plateau (Western North Atlantic Ocean). Mar Ecol 30:74–92

Ross SW, Rhode M, Quattrini AM (2015) Demersal fish distribution and habitat use within and near Baltimore and Norfolk Canyons, U.S. middle Atlantic slope. Deep-Sea Res Part 1 Oceanogr Res Pap 103:137–154

Rozas LP, Odum WE (1988) Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77:101–106

Ryer CH, Stoner AW, Titgen RH (2004) Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. Mar Ecol Progr Ser 268:231–243

Ryer CH, Long WC, Spencer ML, et al (2015) Depth distribution, habitat associations, and differential growth of newly settled southern

Tanner crab (*Chionoecetes bairdi*) in embayments around Kodiak Island, Alaska. Fish Bull 113:256–269

Sale PF (2002) Coral reef fishes, dynamics and diversity in a complex ecosystem. Academic, San Diego, 487pp

Sampaio I, Braga-Henriques A, Pham C, et al (2012) Cold-water corals landed by bottom longline fisheries in the Azores (north-eastern Atlantic). J Mar Biol Assoc UK 92:1547–1555

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the northern Ionian Sea (central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108

Shester G, Ayers J (2005) A cost effective approach to protecting deep-sea coral and sponge ecosystems with an application to Alaska's Aleutian Islands region. In: Freiwald A, Roberts MJ (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 1151–1169

Sion L, Maiorano P, Carlucci R, et al (2012) Comparing distribution of *Helicolenus dactylopterus* (Delaroche, 1809) between coral and non coral habitats in the Santa Maria di Leuca coral province. Biol Mar Mediterr 19:229–230

Sion L, Capezzuto F, Carlucci R, et al (2013) Behaviour of deep-sea sharks observed in the Santa Maria di Leuca cold-water coral province. Rapp Comm Int Mer Mediterr 40:494

Soetaert K, Mohn C, Rengstorf A, et al (2016) Ecosystem engineering creates a direct nutritional link between 600-m deep cold-water coral mounds and surface productivity. Sci Rep 6:35057

Söffker M, Sloman KA, Hall-Spencer JM (2011) In situ observations of fish associated with coral reefs off Ireland. Deep-Sea Res Part 1 Oceanogr Res Pap 58:818–825

Stein DL, Tissot BN, Hixon MA, et al (1992) Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. Fish Bull 90:540–551

Stone RP (2006) Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. Coral Reefs 25:229–238

Stone RP, Shotwell SK (2007) State of deep coral ecosystems in the Alaska Region: Gulf of Alaska, Bering Sea and the Aleutian Islands. In: Lumsden SE, Hourigan TF, Bruckner AW, et al (eds) The state of deep coral ecosystems of the United States, NOAA Technical Memorandum CRCP-3. NOAA, Silver Spring, pp 65–108

Stoner AW, Waite JM (1990) Distribution and behaviour of queen conch, *Strombus gigas*, relative to seagrass standing crop. Fish Bull 88:573–585

Sulak KJ, Brooks RA, Luke KE, et al (2007) Demersal fishes associated with *Lophelia pertusa* coral and hard-substrate biotopes on the Continental Slope, Northern Gulf of Mexico. In: George RY, Cairns SD (eds) Conservation and adaptive management of seamount and deep-sea coral ecosystems. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, pp 65–92

Taviani M, Remia A, Corselli C, et al (2005) First geo-marine survey of living cold-water *Lophelia* reefs in the Ionian Sea (Mediterranean basin). Facies 50:409–417

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78

Tegner MJ (1993) Southern California abalones: can stocks be rebuilt using marine refugia? Can J Fish Aquat Sci 50:2010–2018

Tissot BN, Yoklavich MM, Love MS, et al (2006) Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral. Fish Bull 104:167–181

Tunesi L, Diviacco G (1997) Observations by submersible on the bottoms off shore Portofino Promontory (Ligurian Sea). In: Atti XII Congresso A.I.O.L. (Isola di Vulcano, 18–21 Settembre 1996), 1:61–74

Tunesi L, Diviacco G, Mo G (2001) Observations by submersible on the biocenosis of the deep-sea corals off Portofino Promontory (Northwestern Mediterranean Sea). In: Willison JH, Hall J, Gass SE, et al (eds) Deep-sea corals. Ecology Action Centre, pp 76–87

Tupper M, Boutilier RG (1995) Effects of habitat on settlement, growth, and post-settlement survival of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 52:1834–1841

Tupper M, Boutilier RG (1997) Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Mar Ecol Progr Ser 151:225–236

Tursi A, Mastrototaro F, Matarrese A, et al (2004) Biodiversity of the white coral reefs in the Ionian Sea (Central Mediterranean). Chem Ecol 20:107–116

Uiblein F, Lorance P, Latrouite D (2003) Behaviour and habitat utilization of seven demersal fish species on the Bay of Biscay continental slope, NE Atlantic. Mar Ecol Progr Ser 257:223–232

Vafidis D, Mytilineou CH, Mastrototaro F, et al (2006) First records of *Leiopathes glaberrima* (Esper, 1792) and *Isidella elongata* (Esper, 1788) (Cnidaria: Anthozoa) in the Ionian Sea. Proceedings of 10th ICZEGAR, Patra, Greece, p 220

Van Oevelen D, Duineveld G, Lavaleye MSS, et al (2009) The cold-water coral community as hotspot of carbon cycling on continental margins: a food web analysis from Rockall Bank (northeast Atlantic). Limnol Oceanogr 54:1829–1844

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Mound Province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396

Watling L, Norse EA (1998) Disturbance of the seabed by mobile fishing gear: a comparison with forest clear-cutting. Conserv Biol 12:1189–1197

Wheeler AJ, Beck T, Thiede J, et al (2005a) Deep-water coral mounds on the Porcupine Bank, Irish Margin: preliminary results from the Polarstern ARK-XIX/3a ROV cruise. In: Freiwald A, Roberts MJ (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 393–402

Wheeler AJ, Bett BJ, Billett DS, et al (2005b) The impact of demersal trawling on northeast Atlantic coral habitats: the case of the Darwin Mounds, United Kingdom. Am Fish Soc Symp 41:807–817

Wirsing AJ, Ripple WJ (2010) A comparison of shark and wolf research reveals similar behavioral responses by prey. Front Ecol Environ 9:335–341

Cross References

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

31

Past, Present and Future Connectivity of Mediterranean Cold-Water Corals: Patterns, Drivers and Fate in a Technically and Environmentally Changing World

Joana Boavida, Ronan Becheler, Anna Maria Addamo, Florent Sylvestre, and Sophie Arnaud-Haond

Abstract

Given the vastness of the oceans and the small size of larvae and other marine propagules, tracking marine organisms' dispersal particles is unrealistic. When propagules successfully recruit, a genetic profile can be tracked that integrates the movements of multiple generations. Molecular analyses thus provide an indirect means of estimating connectivity among subdivided populations, at any given spatial and/or temporal scale of interest. In general, it remains challenging to disentangle the relative influence of the various processes that cause the observed patterns of genetic differentiation among subpopulations, notably in far-off deep-sea environments. In the past decade only a handful of studies have reported on the genetic patterns in Mediterranean cold-water corals. This represents a substantial limitation for any researcher attempting to understand the dynamics of Mediterranean cold-water coral populations. It affects as well conservation decisions involving these vulnerable species and habitats. Until recently, hypotheses for gene flow of some deep-sea corals in the Atlantic have included moderate to high connectivity at broad and regional scales, through sporadic larval transport mediated by ocean currents, and simultaneous strong discontinuities between ocean basins caused by vicariance or local adaptation. However, progress has been made that is allowing researchers to retrace past major modifications in the patterns of cold-water coral migrations at evolutionary time-scales, in and out of the Mediterranean Sea. Growing evidence of the influence of clonality and its effect on estimates of genetic diversity now stimulate researchers to engage in optimised sampling strategies. Improved estimates are possible to attain, provided a rigorous sampling strategy. Studies of the cosmopolitan corals *Lophelia pertusa* and *Madrepora oculata* have made evident that Atlantic populations are clearly differentiated from Mediterranean ones, suggesting that contemporary gene flow between the two genetic backgrounds is very limited, if at all present. Results support several non-mutually exclusive hypotheses: that subpopulations in the North East Atlantic were recolonised from Mediterranean refugia following the last glacial maximum; that Mediterranean *L. pertusa* reefs appear to have been relevant glacial refugia during the Pleistocene glaciations and the main source for North East Atlantic recolonisation; and that *M. oculata* in the NE Atlantic may have had multiple sources of post-Last Glacial Maximum colonisation, which remain elusive. The solitary *Desmophyllum dianthus* has been shown to share the same genetic identity between very distant populations (Mediterranean and NE Atlantic). Yet, it remains unclear if this is solely due to high contemporary gene flow or if the genetic resemblance is a remnant left by an Atlantic post-glacial recolonisation from a unique Mediterranean source with high population size. Future genome-wide studies with next generation sequencing techniques will undoubtedly help clarifying the interpretations of molecular data in terms of past and present cold-water corals migration pathways. This is strongly needed, as the development of effective conservation strategies relies on well-informed, knowledge-based, policies. These must include thorough species invento-

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ries, relatedness, connectivity metrics and clear identification of genetic units, all of which depending on the use of robust techniques. Indeed, information on the genetic connectivity of Mediterranean cold-water coral populations has proven to be key to the establishment of a protected site under the European Union's Natura 2000 Network of protected areas. We conclude with perspectives on how Next Generation Sequencing will strengthen inferences on connectivity of the majestic cold-water coral habitats in the coming years.

Keywords

Population genetics · Clonality · Connectivity · Next generation sequencing

31.1 Introduction

Connectivity designates many different aspects of movement in ecology. Landscape connectivity is defined as 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor et al. 1993). More relevant to population genetics, connectivity is designated by Moilanen and Hanski (2001) as "typically related to the migration rate and gene flow among populations and colonisation of empty habitat". Before engaging into this synthesis it is essential to clarify that the choice of sampling, molecular and analytical methods impose important differences in the inferred level of population connectivity (past or present) and interdependence (demographic or evolutionary) revealed by molecular estimates (Waples and Gaggiotti 2006; Lowe and Allendorf 2010). In this chapter, the wording "past, present and future connectivity" embeds on one hand the evolutionary history, present day migration and future modification owing to environmental changes, and on the other the constant improvement of molecular tools used to infer those patterns, and the way this progress can modify our perception and inferences.

Numerous reports of fossils of several species of cold-water corals (CWCs) within and surrounding the Mediterranean Sea (Malinverno et al. 2010; Perrin and Bosellini 2012) have guided sampling for use as archives to retrace past climates. Yet, only scarce remotely operated vehicle (ROV) exploration has been performed thus far in canyons and seamounts (e.g. Danovaro et al. 2010; Fabri et al. 2017; Aymà et al., this volume; Lastras et al., this volume), features susceptible of hosting living corals. Living-records, however, spread across the entire Mediterranean. These are dominated by *Madrepora oculata* (Orejas et al. 2009; Gori et al. 2013; Lastras et al. 2016; Fabri et al. 2017), which seems to better resist environmental changes (Wienberg et al. 2010), and *Desmophyllum dianthus* (Freiwald et al. 2009; Orejas et al. 2009; Mytilineou et al. 2014). A diversity of species have been used to reconstruct the past history of the Mediterranean Sea (Montagna et al. 2006; Frank et al. 2011). Nevertheless, mainly three species (*Lophelia pertusa*, *M. oculata* and *D. dianthus*) could be collected with sufficient numbers of specimens to allow the indirect genetic reconstruction of past and present connectivity of Mediterranean CWCs and their present and past exchanges with Atlantic coral specimens.

One of the particularities of most corals is their ability to reproduce sexually and asexually. Partial asexuality ("clonality") complicates both the dynamics and evolution of populations and the strategies needed to sample and to analyse molecular data to allow interpretations in a population genetics framework. It is thus important to explicitly take asexual reproduction into account in sampling designs, data analyses and interpretations (Halkett et al. 2005; Arnaud-Haond et al. 2007).

This chapter will first tackle clonality and its implication for adequate sampling, before engaging into a synthesis of previous work on the population genetics of CWCs (with a focus on scleractinians) in the Mediterranean Sea, and their connection to Atlantic populations. The scarce number of studies published thus far on Mediterranean CWCs and a number of important pitfalls associated with life history traits of corals led us to offer a synthesis of the limited available data. However, here we give a roadmap for future studies: We point the reader to optimised sampling schemes and identify new research avenues opened by the new generation of molecular data -offered by next generation sequencing (NGS)- and computational analyses.

31.2 Considerations for Sampling and Clonality

Partial asexuality (clonality) characterises most coral species: they can reproduce sexually through the production of gametes and recombination, or clonally through the production of colonies sharing the same genome (except for somatic mutations) by fragmentation or parthenogenesis. Clonality is an essential aspect to consider when engaging into a population genetics study on corals. It does not only affect the path for gene transmission, the dynamics of populations at different stages of colonisation or demographic equilibrium, but also their resistance and resilience, and their evolution. More pragmatically for the researcher, it also affects the way sampling should be planned and molecular data interpreted in a population genetics framework. Actually, the population genetics framework was designed and developed for pure sexual organisms and requires dealing with individual genotypes, thus recognising individuals at the demographic and genetic scale (reviewed in Arnaud-Haond et al. 2007).

31.2.1 Clonality and Sampling Strategy

In terms of sampling strategy, working on partially asexual organisms imposes strong constraints on the sampling design (Arnaud-Haond et al. 2007). When researchers are interested in appraising the imprint of clonality on the dynamics of populations, they should go for an explicit, standardised sampling scale (i.e. standardising the sampled area among reefs), and randomised spatial sampling at an accurate spatial scale, in order to be able to compare results obtained in different reefs or coral gardens. The sampling scale should be nested based on previous knowledge of the size of *genets* (i.e. the extent of a genetic individual issued from a single zygote that spreads spatially and temporally through clonality by producing modules, called *ramets*), or the dispersal of clonal propagules. When such knowledge is not available it is highly recommended to perform pilot studies with nested sampling scales in order to appraise the spatial extent of the influence of clonality for the species considered. When researchers are not necessarily interested in appraising the extent of clonality but are just focused on basic genetic analysis to estimate genetic diversity and structure, they may favor a coarse sampling of ramets with a haphazard strategy, and exclude replicates of the same genotypes (i.e. belonging to the same genet) if still occurring in the final dataset. Making the *a priori* choice of ignoring clonality can be imposed by technical limitations when sampling, which are particularly acute in deep-sea research. It is however not necessarily recommended, as clonality can have strong implications in the spatial distribution of polymorphism and in its temporal evolution. At least in such cases, the unique geographical coordinates of each colony should be kept in order to attempt assessing the scale of clonal spread/dispersal on the basis of the best possible sampling in hand. A notable practical example of this strategy was given for *Lophelia pertusa* reefs along the Bay of Biscay (Becheler et al. 2017). Despite a general low incidence of clonality, sampling colonies separated by at least 150 m showed identical genotypes suggesting a rather long dispersal distance.

The choice of sampling gear is also essential to allow isolating georeferenced colonies sampled on the sea floor, discriminating them on the deck and analysing them individually in the laboratory. Trawls, dredge or even ledges are thus to be avoided for various reasons. Leaving aside the interesting and fundamental debates on the ethic of trawling reefs for scientific purposes, fragments of colonies sampled through trawling or dredging cannot be easily teased apart on the deck, preventing the appraisal of clonality in the collected sample. In other words, sampling a coral reef or a coral garden with such gear can be compared to the sampling of tropical forests with a bulldozer, followed by the blind genotyping of broken branches.

Estimates of clonal versus sexual reproduction as well as genetic diversity would obviously suffer serious biases, with some of the individuals being overrepresented due to their large size or position in the middle of the gear trajectory. Submersible or ROV based sampling, with well annotated videos and/or organised sampling material (like drawers with individual and/or labelled cases; see Becheler et al. 2017; Orejas et al. 2017), allow a good traceability which is required. Additionally, accidental bycatch with longlines can provide interesting samples. These may be associated to approximate GPS coordinates and thus valuable, once the extent of clonality has been appraised during pilot or previous studies.

31.2.2 Clonality and Population Genetics: Beware of Bush Mosaicism and the Strategy with Genetic Replicates

A peculiarity of corals is their ability to form coral bushes (also termed "patches" and "thickets"). This capacity was confirmed for CWCs in the North Atlantic (Wilson 1979, Reed et al. 2007) and, more recently, through the description of mosaic colonies of *M. oculata* and *L. pertusa* growing on each other (Arnaud-Haond et al. 2017). In the same way, conspecific colonies of different colors have been observed on the field, for which mosaicism was confirmed by genotyping of *L. pertusa* (Hennige et al. 2014). The occurrence of such coral bushes implies that additional caution is necessary when sampling: to examine the shape of colonies and possible anastomosed branching is fundamental, in order to avoid mixing genets in the lab, which would mix genotypes, making it impossible to reconstruct individuals *a posteriori*.

Estimating gene flow requires the access to a random and representative sampling of the populations studied, with demographic units represented only once. Now, the delineation of what is a "demographic unit" depends on the path of sexual reproduction and on the independent or entangled fates of ramets. Once the colonies are discriminated and the level of clonality is assessed, one will engage in a population genetics analysis in a different way depending on the path of asexual reproduction. For most clonal plants including seagrasses, where modules –ramets- of the same genetic individual –genet- remain connected and potentially metabolically interdependent for some time (Salzman and Parker 1985; Alpert 1996; Arnaud-Haond et al. 2012), the choice of keeping or discarding replicates in the dataset before estimating population genetic structure can be debated. Each of these choices implies underlying assumptions: the lack of a relationship between the reproductive success and the size (in terms of number of ramets) of genets, none of which are usually tested for the species and populations at stake. For corals, the question at hand is a little different: distinct colonies in the same area can be considered as independent metabolic and reproductive units, whether or not they share the same genotype, and thus be included for connectivity estimates. It is thus reasonable in most cases, provided sampled colonies were well discriminated in the field (see above), to engage into connectivity estimates based on the full dataset.

31.3 Case Studies

31.3.1 Context

Despite the fast technological progress that has allowed improved access to the deep-sea, these ecosystems remain hard to explore and information about connectivity is still scarce. For example, direct tracking of free living marine larvae is highly challenging in coastal species (but see Thorrold et al. 2007), and virtually impossible for species such as CWCs (but see recent progress in Orejas et al., this volume). The use of genetic markers is necessary to obtain an indirect mean of levels of connectivity. In this context, population genetics offers the theoretical framework to indirectly assess connectivity through the analysis of the distribution of genetic variation (“polymorphism”), in order to infer the degree of inter-dependence of discretely distributed CWC reefs.

Contemporary genetic processes, such as migration and population size, contribute to explaining the present-day distribution of neutral genetic diversity (i.e. not subject to selection) within species ranges. Yet, past events, such as fluctuations of geographic ranges, demographic bottlenecks and/or expansions, can leave strong and persistent genetic signatures, still detectable today and thus impinging the present day study of the distribution of genetic polymorphism (Hewitt 2000, 2004). Understanding a pattern of genetic structure and appraising the present day level of genetic connectivity among populations, thus requires considering and discriminating both present and past events affecting the demography of species and the present day distribution of their genetic diversity as well as the evolutionary forces driving it (Bierne et al. 2011; Gagnaire et al. 2015).

Geological records and isotopic dating of sediment and coral remains have delivered most of the knowledge about the paleogeography of CWC. The Mediterranean Basin is an historical area for CWC presence (Freiwald et al. 2004; Di Geronimo et al. 2005; Taviani et al. 2005; Montagna and Taviani, this volume; Rebesco and Taviani, this volume; Taviani et al., this volume; Vertino et al., this volume) where the occurrence of deep reefs has been recognised to be continuous for over 480,000 years (McCulloch et al. 2010). The last 50,000 years may correspond to an active growth period for reefs in the western basin of the Mediterranean Sea, as well as in the Gulf of Cádiz (GoC) and Moroccan margin (Schroder-Ritzrau et al. 2005), even if a relative decline is reported since the end of the Last Glacial Maximum (LGM) (Taviani et al. 2011), 10,000–12,000 years ago. An opposite situation was suspected in Northeast (NE) Atlantic, where climatic fluctuations were suggested to be the main driver of geographic distribution and development of reefs. In this region, Ice Ages hampered the growth of CWC reefs (Frank et al. 2011).

Studies of demography, population structure, and reproduction of CWCs are rather scarce (but see Brooke and Young 2003; Waller 2005; Larsson et al. 2014; Pires et al. 2014; Bramanti et al., this volume; Lartaud et al., this volume; Reynaud and Ferrier-Pagès, this volume), as generally applies with other deep-water organisms. However, it is well known that understanding the connectivity of marine populations is vital for conservation and fisheries management, particularly for the strategic design of marine reserves (Hedgecock et al. 2007) or for the sustainable use of marine resources (e.g. implementation of sea-based wind farms and their environmental impact on benthic communities, see for example the European project CoCoNET http://www.coconet-fp7.eu/).

31.3.2 *Madrepora oculata* and *Lophelia pertusa*: Out and Into the Mediterranean

The two reef-building CWCs, *L. pertusa* and *M. oculata,* are suspected to have recolonised the NE-Atlantic from the Mediterranean at the end of the last glacial episode (De Mol et al. 2005; Henry et al. 2014), after a long period of scarcity or extirpation during the late Pleistocene (see Taviani et al., this volume; Vertino et al., this volume; other chapters from the past section in this same volume).

In the work we summarise here, we aimed at addressing those hypotheses about past connectivity by unraveling the genetic differentiation, or the lack of, of CWC populations in the Mediterranean and in the Atlantic Ocean.

31.3.2.1 Sampling Locations and Strategy

As explained above, clonal organisms require an adequate sampling strategy, which is particularly hard to apply in the deep-sea. This is probably one of the main barriers to gathering robust information about the clonal architecture and population genetics of CWC populations. In 2011, during the cruise BobEco (European Project CoralFish, Research Vessel RV *Pourquoi-Pas?*), the scientific team experimented a challenging sampling strategy, allowing a standardised and randomised collection of 25–30 colonies per site of both *L. pertusa* and *M. oculata* (Becheler et al. 2017). Five canyons from the Bay of Biscay (European continental margin) and one location within the Logachev Mounds (Rockall bank) were sampled in this way. In 2012, the same strategy was used in two locations in South Iceland (European project Hermione, RV *Thalassa*). The sampling strategy consisted of a sampling quadrat of 200 * 100 m^2. Then, 30 X-Y coordinates were randomly generated within each quadrat (with $0 < X < 200$ m and $0 < Y < 100$ m). They corresponded to the geographical coordinates of each sampling unit. Such standard strategy, based on known and random spatial coordinates, allowed acquiring high-resolution quantitative information about the association among coral species, notably its spatial extent (Arnaud-Haond et al. 2007), for three regions of the NE-Atlantic. All theoretical and practical details about this strategy can be found in Becheler et al. (2017).

Yet, such sampling is technically complex and time consuming, requiring cruises partly devoted to genetic purposes. Most samples, notably those from the Mediterranean integrated in this study (Santa Maria di Leuca -Ionian Sea, and Canyon of Lacaze-Duthiers –Gulf of Lions, northwestern Mediterranean) were indeed collected in an "opportunistic" way, either during exploratory transects, or within sediment collected with cores or grabs. We could thus retrace population genetics and connectivity of Mediterranean and Atlantic reefs, but could not compare the clonal architecture in the Mediterranean and the Atlantic due to the limitation imposed by the opportunistic sampling strategy.

31.3.2.2 Present-Day Genetic Differentiation Between Mediterranean and North-East Atlantic

The genetic structure of both *L. pertusa* and *M. oculata* was assessed through the use of two types of nuclear markers, i.e. a set of respectively seven and six microsatellites, and internal transcribed spacer (ITS) sequences (Becheler 2013). For both species, Atlantic populations appeared divergent from Mediterranean ones (Fig. 31.1). For example for *L. pertusa* the fixation index (F_{ST}, estimated with microsatellites) between a Mediterranean and an Atlantic population is around ten times higher than a F_{ST} between two Atlantic populations, and two to three times higher for *M. oculata*.

Yet, in the open NE-Atlantic, patterns of genetic structure are strikingly different between these two species. Atlantic populations of *L. pertusa* appeared as a large and single panmictic unit, i.e. one where all individuals are randomly mating, with no clear genetic differences among reefs of the Bay of Biscay, Logachev Mounds and Iceland. In this context, it is worthy to mention that experiments in aquaria have recently reported that larval duration can reach 5 weeks and that larvae were active swimmers (Larsson et al. 2014). Results observed here support the hypothesis that high dispersal potential is realised in the wild. Contrastingly, a regional, pattern of genetic structure was observed among *M. oculata* reefs, with several differentiated units detected in the Atlantic.

The ability to disperse may be lower for *M. oculata* than for *L. pertusa*. In this case, the gene flow among regions would be too low to homogenise the genetically diverging units. Unfortunately, despite its apparently rather widespread distribution (Arnaud-Haond et al. 2017), *M. oculata* has thus far retained less attention than *L. pertusa* and knowledge is lacking about its larval biology. Another, non-mutually exclusive hypothesis can also be formulated: the influence of past events, such as the Last Glacial Maximum, which may have differently affected these two species, depending on their physiological tolerance (see Reynaud and Ferrier-Pagès, this volume) and consequent location of the refuges that would be at the origin of present day Atlantic populations.

31.3.2.3 Past Glacial Events and Their Influence on Shared and Unique Polymorphism Between the Mediterranean and the Atlantic

The ITS sequences delivered complementary information to that obtained based on microsatellites. Their rate of evolution being lower than for microsatellites (Hillis and Dixon 1991; Balloux and Lugon-Moulin 2002), they may be informative for larger temporal and spatial scales. For *L. pertusa*, the haplotype network (Fig. 31.1) revealed two main haplotypes, essentially found in the Mediterranean, Bay of Biscay and in Iceland. Closely related haplotypes separated by few mutations were found in low frequency around the main haplotypes and they originated from the Bay of Biscay, Ireland, and Iceland. This *L. pertusa* haplotype network is organised as a typical "star-like cluster" often recognised as a signature of 'recent' demographic expansion (Teixeira et al. 2011). Additionally, the main haplotypes are shared between the putative source(s) of recolonisation and recolonised areas. Satellite haplotypes are generated within populations having demographically expanded, which together with the significant results obtained using the Fu and Li tests (Fu and Li 1993), support the hypothesis of a recent demographic expansion in NE Atlantic populations.

The network built with *M. oculata*'s ITS haplotypes shows a very different pattern, with a chaotic distribution of frequent and rare haplotypes, and private (endemic) haplotypes found in all regions. The more frequent haplotypes are numerous and can alternatively appear as shared between two, three, four or five regions. Notably, several Mediterranean haplotypes are shared by specimens collected in the Azores (central NE Atlantic), the Bay of Biscay, Ireland and in South Iceland, suggesting a possible common history and/or an ancient genetic connection, whereas they are not shared with the Mediterranean.

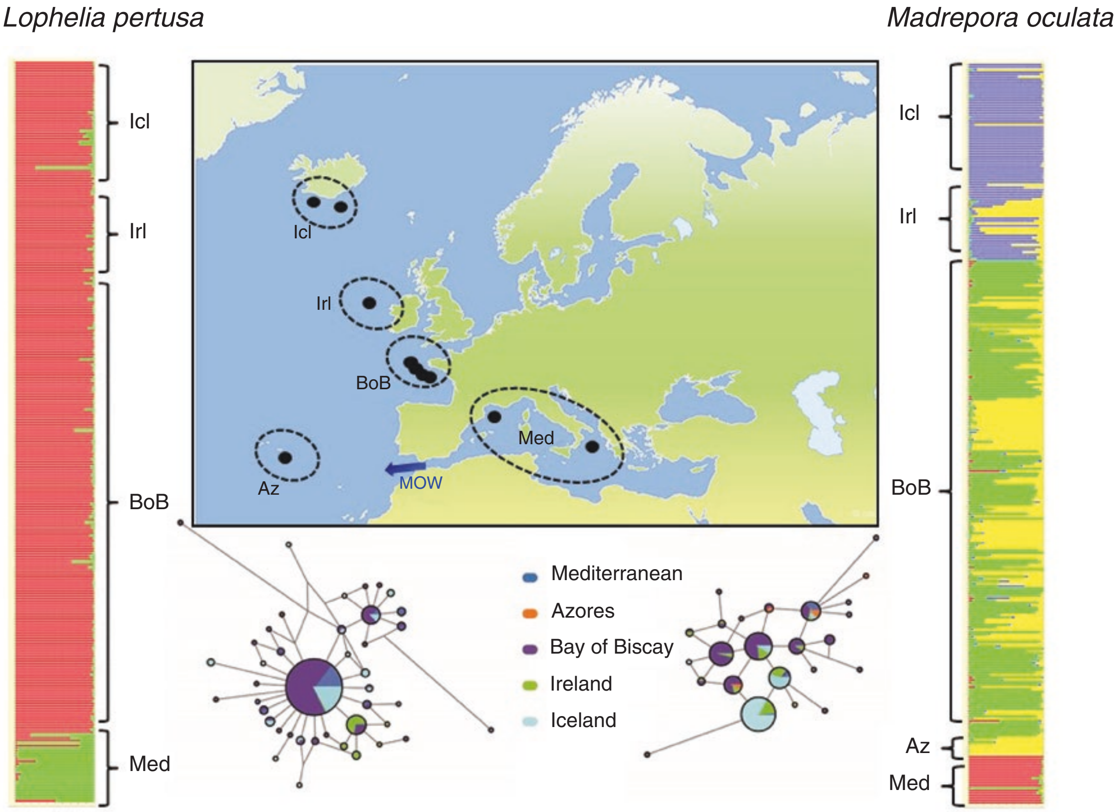

Fig. 31.1 Summarised insight of the known phylogeography of two relevant reef forming cold-water corals (CWCs), *Lophelia pertusa* (on the left) and *Madrepora oculata* (on the right). Black points are located on sampling sites included in this chapter. Bar plots on the left and the right correspond to the clustering analyses (performed with the free software TESS). Each multi-colored unitary bar corresponds to the probability that a genotype belonged to the corresponding cluster, following the idea that one color is for one given cluster. These analyses were based on multi-locus microsatellite genotypes. Below, the internal transcribed spacer (ITS) haplotype-networks are provided. Each circle corresponds to one haplotype, while its size is proportional to the frequency of this haplotype within the full dataset. These circles are divided in colored portions corresponding to the different biogeographic regions. *Icl* Iceland, *Irl* Ireland, *BoB* Bay of Biscay, *Az* Azores Islands, *Med* Mediterranean Sea

If signs of demographic expansions were also detected within *M. oculata*'s dataset, this would support a recent population expansion/recolonisation in some reefs. The contrasting present-day genetic structure between *L. pertusa* and *M. oculata* and the polymorphism differentially shared among regions pleads for two different biogeographic scenarios: a clear support of a Mediterranean origin only for the first species, and a pattern calling for a more complex history for the other.

31.3.2.4 Biogeographic Scenarios: Two Reef-Building Species, Two Distinct Stories?

The genetic data obtained for *L. pertusa* thus supported the hypothesis of De Mol et al. (2005) of a post-glacial (i.e. <20,000 years ago) recolonisation of Atlantic reefs from a Mediterranean refuge. In line with the star-like network observed with ITS haplotypes (Fig. 31.1 bottom left), data suggests a (re) colonisation by the main Mediterranean haplotype, followed by the accumulation of rare mutations during the post-glacial expansion of Atlantic reefs (the satellite haplotypes observed only in the Atlantic). The homogeneous genetic background found in the NE-Atlantic with microsatellites was also found, although in rare instances, in the Mediterranean (see bar plots on Fig. 31.1 left). This also suggests a Mediterranean source of recolonisation for the NE-Atlantic. The possibly large dispersal ability of *L. pertusa* larvae may have maintained genetic homogeneity in the recolonised area of the NE-Atlantic reefs analysed in this study during the last millennia (Boavida et al., under revision).

Madrepora oculata clearly exhibits a more complex pattern likely resulting from marked different historical and present day connectivity. The decline of its populations during the LGM is very plausible. Nonetheless, the coexistence of several genetic backgrounds –and the high number of main haplotypes- suggests an alternative scenario of post-LGM recolonisation: despite the fact that the Mediterranean has likely been a glacial refuge for this species, additional sources of recolonisation in the Atlantic, which remain to be unraveled, may explain this pattern.

31.3.3 Large Scale Connectivity in *Desmophyllum dianthus*

Despite the Mediterranean-wide distribution of *D. dianthus*, from the Alborán Sea in the west to the Marmara Sea in the east, its low frequency of occurrence (but see recent data in Fourt et al., this volume; Aymá et al., this volume) limits and challenges its study. Nevertheless, several studies have been conducted in biology, physiology and ecology revealing that *D. dianthus* is an exceptional proxy for pH and temperature of water masses in marine ecosystems; It has moderate tolerance to elevated seawater temperature and to ocean acidification, but there is a clear synergistic impact when elevated temperature and pCO_2 are combined, resulting in severe reduction of coral metabolism (e.g. Freiwald and Roberts 2005 and references therein; Naumann et al. 2013; Gori et al. 2016).

The presence of the solitary gregarious coral *D. dianthus* (Vertino et al. 2014), or *D. cristagalli* (synonym, Milne Edwards and Haime 1848), has been documented in the Mediterranean since the Early- Middle Miocene. It dwells on hard substrates occurring from the continental shelf to the upper bathyal zone, commonly associated to scleractinian reef framework-forming CWCs in what was described as a "white coral" triad of *Lophelia-Madrepora-Desmophyllum* (Pérès and Picard 1964; Zibrowius 1980; Roberts et al. 2009; Chimienti et al., this volume). Macrohabitats of the coral framework consist of continuous aggregations of branched scleractinian coral colonies (primarily *M. oculata* and secondarily *L. pertusa*), whose skeletons are in mutual contact with the exception of some small sediment pockets (Savini et al. 2014). The solitary *D. dianthus* is thought to have been influenced by the Mediterranean Sea's geologic history in a similar way as the reef-building corals mentioned here above, and their co-occurrence is documented in several places in the Mediterranean and the Atlantic. Hence, we also addressed the hypotheses about past (and present) connectivity of *D. dianthus* populations in the Mediterranean and NE Atlantic through the analysis of genetic polymorphism.

31.3.3.1 Sampling Locations and Strategy

Although solitary corals are not colony forming and do not require a complex sampling strategy compared to their colonial counterparts, particular attention is needed in case of "aggregations" of individuals, where the presence of asexual (clonal) individual is likely and may interfere with the interpretation of molecular results. Since all the Mediterranean samples of *D. dianthus* in this study were collected in an "opportunistic" way, as explained above, it is essential to apply adequate labels to each 'ramet'. Samples have been numbered consecutively, except for those forming an "aggregation", where the same number was applied, followed by a letter further included in the label in order to identify potential clones during the genetic analyses.

31.3.3.2 Past and Present-Day Genetic Polymorphism Between the Mediterranean and Northeastern Atlantic Ocean

Nuclear and mitochondrial genes have been used as molecular markers to determine genetic differentiation, phylogeographic patterns and gene flow within and among populations of *D. dianthus* in the Mediterranean Sea and the northeastern Atlantic Ocean. Nevertheless, the internal transcribed spacer (ITS), the mitochondrial ribosomal small subunit (16S) and the cytochrome c oxidase subunit I (COI) were not informative in terms of distinguishing between geographically and bathymetrically isolated populations from global to regional spatial scales (see Fig. 3 in Addamo et al. 2012; Fig. 31.2). The occurrence of shared haplotypes between specimens could indicate historical patterns of shared genetic diversity (current or recent gene flow, incomplete lineage sorting or retention of ancestral polymorphism), methodological bias (using genes or regions with a substitution rate inadequate to show divergence) or both (differences in the coalescence of these genes combined with population's divergence; Addamo et al. 2012). To assess the population genetic structure and the ability of this species to disperse into different regions and habitats, contributing to the local gene pool (i.e. migration), nuclear microsatellite sequences have provided adequate resolution. Markers with higher evolutionary rates – such as microsatellites – have been developed for *D. dianthus* (Addamo et al. 2015). They allowed the assessment of connectivity among populations dwelling at different depths and to infer biological (e.g. reproduction strategy or larval dispersal) and oceanographic (e.g. bathymetry or water circulation) factors driving isolation. No statistically significant levels of genetic differentiation have been found among geographic populations from the Mediterranean Sea and NE Atlantic Ocean (Fig. 31.3), suggesting high connectivity among deep-sea locations, with some exceptions for northern individuals from the Cantabrian Sea and Ireland.

31.3.3.3 Biogeographic Scenarios for *D. dianthus* Populations in the Mediterranean Sea and the Atlantic Ocean

An interpretation of the shared genetic polymorphism between these two marine regions is the hypothesis of a historical recolonisation homogenising the gene pools in both marine areas. During the Holocene, a colonisation could have taken place from the Mediterranean Sea to the Atlantic Ocean with a sufficiently large number of individuals not to have resulted in a genetic differentiation through a founder effect (i.e. the dramatic change –and loss- of genetic variation that occurs when a population is established in a new area by a very small number of migrants not genetically representative of the larger original population).

On the other hand, a physical connectivity along thousands of miles between the Mediterranean and NE-Atlantic

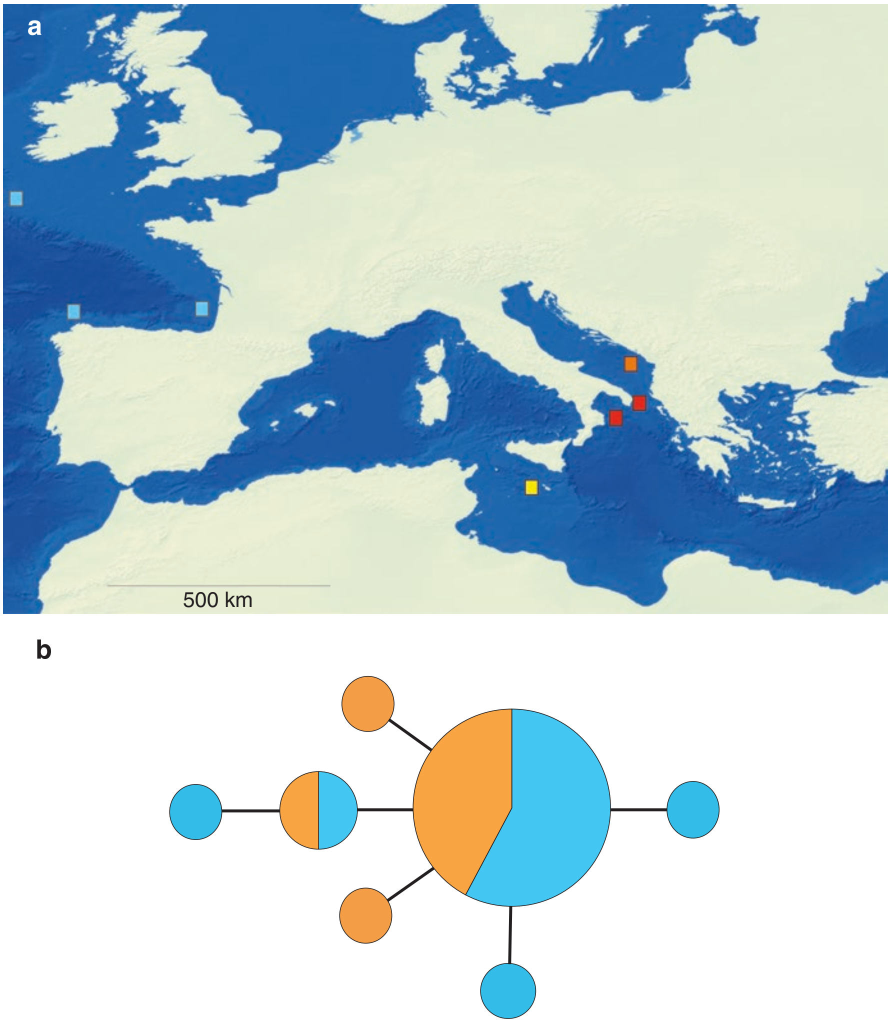

Fig. 31.2 (**a**) Study areas: Mediterranean Sea (orange=Adriatic Sea; red=Ionian Sea; yellow=strait of Sicily) and NE-Atlantic Ocean (light blue=Galicia, Cantabria and Ireland). Squares indicate the sampling locations. (**b**) Haplotype network of internal transcribed spacer (ITS) ribosomal DNA sequence haplotypes of *Desmophyllum dianthus* belonging to Mediterranean Sea populations (orange) and NE-Atlantic Ocean populations (light blue). Sizes of the circles are proportional to the number of samples presenting the same haplotype. (Adapted from Addamo et al. 2012)

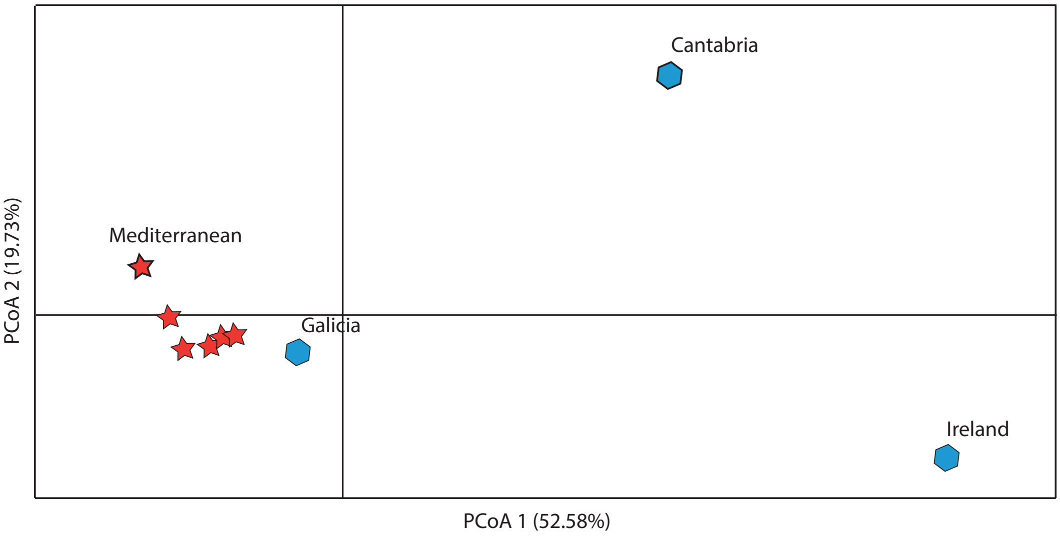

Fig. 31.3 Principal coordinate analysis (PcoA) projecting the relative genetic distances among *Desmophyllum dianthus* populations from the Mediterranean Sea (red stars) and the Atlantic Ocean (blue hexagons)

Ocean sites may be attributed to the principal currents in intermediate and deep waters (see Fig. 19.18 in Chimienti et al., this volume). The intermediate and deep water currents mainly characterising the Mediterranean Sea and the NE-Atlantic Ocean are the Levantine Intermediate Water (LIW), Adriatic Deep Water (AdDW), Aegean Deep Water currents (AeDW), and Atlantic Water (AW) (Millot and Taupier-Letage 2005). The LIW circulates at approximately 200–600 m along the northeastern slope of the Ionian Sea, penetrating into the southern Adriatic Sea, and then continues along the slope to the Strait of Sicily, where most of it outflows into the western Basin (at 400 m depth). The other two currents (AdDW, AeDW) first accumulate in the troughs (1000–1500 m) over which they are formed (in the southern Adriatic and southern Aegean Seas, respectively) before outflowing into the western Basin through various openings. These water masses are depth-stratified and may represent two distinct bathymetric levels that could create depth structuring in species diversity and community composition. Nevertheless, the intermediate and deep water masses circulate and can be identified at greater or lesser distances from their zone of origin. They continuously mix and, finally, outflow at the Strait of Gibraltar as a rather homogeneous water (the so called Mediterranean Outflow Water, MOW), which is saltier and denser than Atlantic water (AW) in that location (Millot et al. 2006). Therefore, the Mediterranean Sea is a "machine" that transforms AW present at the surface just west of the Strait of Gibraltar into denser water that is recognised at 1000–1200 m in most of the northern Atlantic Ocean (Millot and Taupier-Letage 2005). The MOW is a saline water mass occupying the intermediate depths of the NE-Atlantic. It reaches a neutrally buoyant depth between 800 and 1300 m (Price et al. 1993) and spreads into the North Atlantic: westward to the central Atlantic and northward following the coasts of Portugal and Spain (Bozec et al. 2011; and references therein).

Deep-sea and offshore marine protected areas (MPAs) have been recently recognised by international and national organisations as efficient tools for protection of deep habitats (Cordes et al. 2016; Davies et al. 2017; OSPAR https://www.ospar.org/news/ospar-ministers-protect-the-north-east-atlantic-deep-seas-treasures; Colombia Deep-water Coral National Natural Park designated in May 2013 by the Ministry of Environment http://www.parquesnacionales.gov.co/portal/es/parques-nacionales/parque-nacional-natural-corales-de-profundidad). Specifically, results from studies on genetic connectivity of *D. dianthus* populations in the Mediterranean Sea contributed to the classification of a Natura 2000 Site of Community Interest (SCI), the centerpiece of the European Union's conservation policy, in the southern Tyrrhenian Sea. This SCI will be used to characterise and define the novel concept of cells of ecosystem functioning (Boero 2015) as conservation and management units, a key concept for the definition of networks of MPAs and for the identification of suitable areas for off-shore wind farms (Costantini et al. 2017; see also www.coconet-fp7.eu, CoCoNet EU project).

31.4 A Complex Biogeographic History Prevents Teasing Apart Remnants of Past Connectivity from Present Day Migration

The reason for the results observed here (high homogeneity of *Desmophyllum dianthus* between the Atlantic and the Mediterranean compared to a strikingly strong differentiation for *Lophelia pertusa* and *Madrepora oculata*) remains to be elucidated. Subject to similar distributions and currents, these species may respond differently due to specific life history traits. Although largely unknown, these may include a different pelagic larval duration for *D. dianthus* and *M. oculata* relatively to *L. pertusa*, and/or the solitary versus reef forming nature of these three taxa. Yet, it is also likely that differences in their past biogeographical history have led to the present genetic structure patterns. In order to tease apart the evolutionary scenarios explaining individual species patterns, and the cause of their strikingly different levels of differentiation at the scale of European waters, molecular data are needed that would deliver a higher statistical power to feed data analyses and modelling methods.

CWCs in the Mediterranean Sea have a long-term history for which the origin is still mostly unknown (but see chapters of the Past section in this volume). Most Mediterranean deep-water fauna was likely extinct during the Miocene due to the Messinian Salinity Crisis (5.9 Myr ago, Garcia-Castellanos and Villasenor 2011; Freiwald, this volume) after which the re-opening of the Gibraltar Strait is thought to have led to a recolonisation with Atlantic fauna (Bouchet and Taviani 1992; Hsü et al. 1977). The long-term persistence of some coral species in the Mediterranean Sea is however indicated by fossil data (Fink et al. 2012, 2015; Perrin and Bosellini 2012). Most explorations of CWCs in the Mediterranean Sea have occurred during the past 15 years. The results from these studies reflect a dominance of fossil-derived data. Important events of colonisation are likely to have started in the late Pleistocene (Malinverno et al. 2010; Taviani et al., this volume; Vertino et al., this volume). At the end of the Last Glacial Maximum (LGM) coral abundance appears to have declined in the Mediterranean Sea and adjacent Gulf of Cadiz (Taviani et al. 2011), but episodes of local proliferation and contraction varied across basins and species (Fink et al. 2015). In the case of *M. oculata*, notable coral proliferation occurred in the Mediterranean Sea during a cold event after the onset of the deglaciation (a period known as the Younger Dryas 12.9–11.7 kyr ago; Fink et al. 2015). This trend is opposite to the one reconstructed for *L. pertusa* in the North East Atlantic (Frank et al. 2011). There, corals disappeared from higher latitudes (approx. >50°N) during periods of major cooling (e.g. LGM), their presence being largely coincident with warmer conditions. The reappearance of *L. pertusa* in higher latitudes is suspected to have originated from a hypothesised refuge located in the Mediterranean (De Mol et al. 2005; Henry et al. 2014) and/or GoC, including the Moroccan margin (Wienberg et al. 2010). Surprisingly, as summarised here above, results on *M. oculata* data point toward other putative refugia, such as mid-Atlantic seamounts, whereas *D. dianthus* only gives signs of present day or recent exchanges across major basins. The phylogenetic reconstruction of the long-term past history of connectivity and recolonisation between the Atlantic and the Mediterranean is thus likely to be blurred by multiple events with opposite direction. However, Bayesian reconstructions of high-density genome scans[1] using NGS may help reconstruct complex past scenarios.

Numerous cases of connectivity estimates have been blurred by errors in taxonomic identification or description, including artificial exclusion of species described as different on the basis of non-discriminant taxonomic characters, or in contrast, the inclusion of distinct taxa (Pante et al. 2015a; Altuna and Poliseno, this volume) or even by including semi species having developed a certain level of reproductive incompatibility (Bierne et al. 2011; Gagnaire et al. 2015). It is now clear that markers used in population genetic studies should allow ascertaining the taxonomic status of the taxa at stake. Teasing apart the signatures of past events such as the last glacial cycles from the ones of present day connectivity is not a trivial task, especially when relying on a handful of markers, as were the cases presented above.

31.5 Perspectives Arising From Access to Genome Scan Data

Traditional phylogenetic and population genetic studies have relied on few molecular sequence markers. These include mitochondrial and nuclear genes, which can be amplified at low cost with nearly universal primers. However, they present some limitations, such as poor genome representation (Angeloni et al. 2012). The use of mitochondrial sequence markers is further limited in corals due to the remarkable low rate of mitochondrial genome evolution (Hellberg 2006; Huang et al. 2008; Shearer and Coffroth 2008). The introduction of microsatellites in population genetic studies promised great power to assess similarity between individuals and closely related taxa in a cost-effective way, mainly due to their high polymorphism and high mutation rate (Hodel et al. 2016; Jarne and Lagoda 1996; Putman and Carbone 2014). Microsatellites have proven extremely useful when the questions at hand require a very large number of individuals to be analysed, but their power strongly depends on the strength of the genetic signal and of the density and resolution of the set of markers used (Selkoe and Toonen 2006). They do not allow the same level of automatism, cross platform compatibility, and reliability as genome scans when the hypothesis or scenario to be tested requires a high density of markers. The advent of NGS offers a novel opportunity to gather genome-scale sequence information, which may allow a more powerful estimate of genetic variation within and among populations and a much higher resolution in the reconstruction of past and present scenarios susceptible to explain the present day distribution of genetic polymorphism. The NGS includes several techniques, most of which have in common the random sequencing of DNA, RNA or cDNA (Heather and Chain 2016). Hundreds to thousands of polymorphic genetic markers, behaving as independent loci, can be retrieved across the entire genome, in a relatively simple and affordable manner (price per sequenced Gigabase in Goodwin et al. 2016) even for species without a reference genome. Collectively, these techniques are called reduced-representation (RR) methods (e.g. Andrews et al. 2016) because they target a random subset of the genome (or transcriptome), rather than sequencing the entire genome (termed "whole-genome sequencing"), a more costly approach. Even with the typical small sample sizes as those often limiting deep-sea studies, by using thousands of independent markers across the genome, the recent (<10 years) application of NGS approaches to deep-water organisms has improved the power of estimates of demographic parameters in deep-sea octocorals and population histories (Everett et al. 2016). They also allowed detection of genomic areas that are under selection in deep-sea scallops (Van Wyngaarden et al. 2017), and have resolved deep-sea species radiations and phylogenies (Reitzel et al. 2013; Pante et al. 2015a; Herrera and Shank 2016).

One of the challenges of population genetic -and now genomic studies applied to the deep-sea remains the difficulty in obtaining a representative number of samples to make inferences about the evolutionary history of metapopulations. Whereas NGS may require fewer samples than classical genetic analyses to obtain robust statistical inferences, a similar amount of sampling units and a rigorous sampling design will remain a requirement with NGS in order to deal with clonal diversity, and the consequent best sampling strategy to obtain a representative sample of a population.

Also, while RR techniques provide greater depth of coverage (i.e. number of sequences or "reads"), when working on non-model organisms with small genomes (i.e. <0.5 Giga base pairs), such as those characterising many CWC species, assembling draft whole-genomes for reference may become another valuable approach. Low-coverage, cost-effective methods to produce draft *de novo* assemblies are already available (Malmstrom et al. 2017), opening a wider range of

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[1] Genome scan is used here in its primary semantic meaning, thus fitting the definition given by Richard and Hawley (2010, "Human genome"; p 561): "*A survey of genetic markers spread across the whole genome. A genome scan will usually involve hundreds of markers*", rather than the one previously proposed in the Encyclopedic Reference of Genomics and Proteomics in Molecular Medicine (2006), that narrows its scope to the screening for phenotype related markers ("*Genome scan refers to a genetic research method in which the entire DNA of an organism is searched systematically for locations on the chromosomes that are inherited in the same pattern as a specific trait*").

possible studies encompassing selection and adaptation (Ekblom and Wolf 2014), as well as the influence of secondary contacts (Gagnaire et al. 2015). Finally, having a reference genome in combination with a characterised transcriptome (RNA-Seq; Wang et al. 2009) will allow annotating the genome for particular genes, permitting the distinction between selected from neutral variation. Such an approach to pinpoint expressed genes may also assist the fine-tuned identification of appropriate conservation units. The combination of these novel techniques with statistical approaches that test environment-mediated selection and ecological niche modelling is likely to trigger a wave of seascape genomics studies (notably reviewed in Riginos and Liggins (2013); Riginos et al. (2016)), highly relevant for CWC conservation and management. Regardless of the particular vanguard method chosen, for the days that lay ahead, NGS encompasses a range of enticing techniques that promise to set the scene for deciphering the elusive population contours of clonal lineages, CWC species and associated fauna.

The scenarios that could be put forward to explain the present-day geographic distribution of polymorphism among populations that we reviewed here for these three relevant species of CWC scleractinians, are still limited by the level of resolution of markers used attempting to indirectly reconstruct and rank complex biogeographical histories. A higher amount of information (i.e. loci) is necessary to increase the statistical power and unravel previously ignored patterns of moderate differentiation, if it exists. As summarised above, moderate levels of differentiation may exist for *Lophelia pertusa* in the Atlantic or *Desmophyllum dianthus* across the studied range. Besides, denser sampling of the genome is necessary to reliably reconstruct and rank evolutionary scenarios using up to date Bayesian methods, ideally with approximate dating. These methods may help to explain the present day patterns of differentiation and to improve understanding regarding present day patterns of connectivity. For example, the recent work on the coral-associated polychaete *Eunice norvegica* already shows the increased power gained through genome scans (Box 31.1). Similarly,

Box 31.1: Taxonomic Uncertainties Reflect Past and Present Day Connectivity in the Polychaete *Eunice norvegica* Inhabiting Cold-Water Corals (CWC) Along European Margins

The recent (approx. 10 years) development of Next Generation Sequencing (NGS) methods now allows the use of an array of genetic markers to analyse the connectivity of populations. Analysis of nearly 4000 single nucleotide polymorphisms (SNP) on the CWC-associated polychaete *Eunice norvegica* (Fig. 31.B1) using Restriction Site Associated sequencing (RADseq, a kind of RR) has confirmed limited to non-existent gene flow between Atlantic and central Mediterranean samples (Fig. 31.B2). It completes a previous analysis based on maternally inherited mitochondrial markers (Fig. 31.B3), thus excluding the possibility of male-exclusive migration. RADseq loci (sequenced sites along the genome) avoid issues of developing specific markers (such as microsatellites) not necessarily transferrable between two distant genetic backgrounds, and have increased resolution to reliably reflect the variability of patterns across the genome. The application of this sequencing technique also bolstered evidence of a common evolutionary history dating from before the Last Glacial Maximum (LGM) between individuals as distant as the high latitudes on the North East Atlantic and the central Mediterranean Sea. This new exciting data may represent a harbinger of distinct high latitudes and Mediterranean refugia for CWC habitats and associated species during past climatic fluctuations.

Fig. 31.B1 Polychaete worms *Eunice norvegica*. (© Ifremer, Olivier Dugornay, Videocor cruise)

(continued)

Box 31.1 (continued)

Fig. 31.B2 Result from admixture ancestry analysis considering two genetic groups

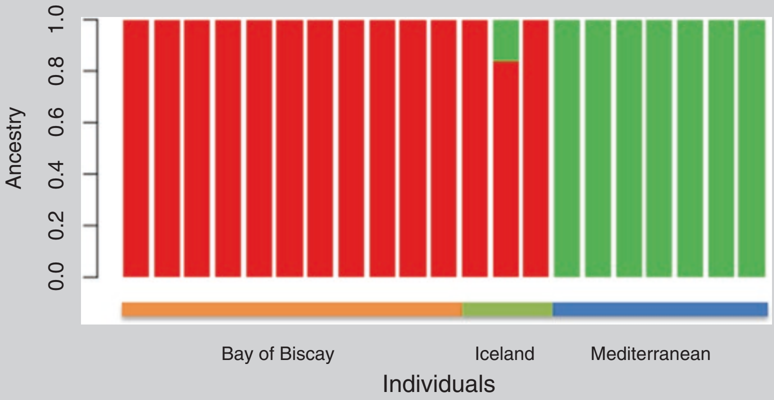
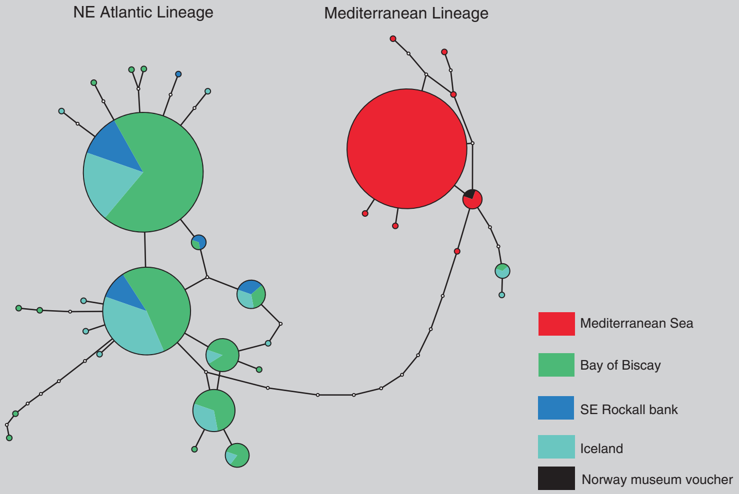


Fig. 31.B3 COI haplotype networks of 45 haplotypes. Each node corresponds to a haplotype, and is divided according to its count in each sampled population



ongoing genomic studies on some of the CWC flagship species *L. pertusa, M. oculata* and *D. dianthus* promise to hasten our understanding of highly contrasting pathways for CWC post-glacial colonisation at the European scale as reported here, to further disentangle existing putative cryptic CWC species diversity and to clarify species hypothesis (Addamo, this volume). Recent results indeed suggest that *L. pertusa* may be a junior synonym of the recently reassigned scientific name of *Desmophyllum pertusum* (Addamo et al. 2016). Here also, genome scans are expected to deliver more robust information to dig deeper into this intriguing similarity.

Discriminating the imprint of past *versus* present day mechanisms acting on the current distribution of genetic diversity is a prerequisite to understand present day drivers and patterns of connectivity across their geographic range. This information is central to development of informed conservation strategies. Teasing apart past and present drivers is needed to differentiate between the ones we can no longer act on from the ones that are relevant to take into account in the definition of sampling strategies, as well as to "*promote evolutionary potential and evolutionary processes to better protect extant biodiversity and biodiversification*" (Olivieri et al. 2016). Despite the historical local and temporary extinctions in the Mediterranean and NE-Atlantic, linked to variations in productivity and oxygen levels (Fink et al. 2012, 2015), it is remarkable that CWC have so swiftly responded to drastic environmental changes (latitudinal shifts in the order of thousands of kilometers-wide for *L. pertusa* and *M. oculata*, as supported in the works cited and synthesised here). Coral reappearance has tracked these environmental fluctuations in just a few hundreds of years (Wienberg et al. 2010). Yet, with the cumulative and synergistic effects of environmental oscillations, habitat loss, overexploitation and pollution of the deep-sea, this ability to promptly track changes and re-establish/re-adjust their geographical and/or bathymetric distributions may be hampered, leading to an increased risk of extinctions (Harnik et al. 2012). Conservation of CWC benefits from well-informed, knowledge-based decisions, for example when it comes to decide how to size and distribute MPAs. Knowledge must include thorough species inventories, which allow for an understanding of their relatedness (Addamo, this volume; Altuna and Poliseno, this volume), their genetic variation and distribution, as well as pinpointing the genetic units and connectivity of CWC populations (Gagnaire et al. 2015; Lagabrielle et al. 2014; Pante et al. 2015b; Costantini et al. 2016).

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References

Addamo AM, Reimer JD, Taviani M, et al (2012) *Desmophyllum dianthus* (Esper, 1794) in the scleractinian phylogeny and its intraspecific diversity. PLoS One 7. https://doi.org/10.1371/journal.pone.0050215

Addamo AM, Garcia-Jimenez R, Taviani M, et al (2015) Development of microsatellite markers in the deep-sea cup coral *Desmophyllum dianthus* by 454 sequencing and cross-species amplifications in scleractinia order. J Hered 106:322–330. https://doi.org/10.1093/jhered/esv010

Addamo AM, Vertino A, Stolarski J, et al (2016) Merging scleractinian genera: the overwhelming genetic similarity between solitary *Desmophyllum* and colonial *Lophelia*. BMC Evol Biol 16:1–17. https://doi.org/10.1186/s12862-016-0654-8

Alpert P (1996) Nutrient sharing in natural clonal fragments of *Fragaria Chiloensis*. J Ecol 84:395–406

Andrews KR, Good JM, Miller MR, et al (2016) Harnessing the power of RADseq for ecological and evolutionary genomics. Nat Rev Genet 17:81–92. https://doi.org/10.1038/nrg.2015.28

Angeloni F, Wagemaker N, Vergeer P, et al (2012) Genomic toolboxes for conservation biologists. Evol Appl 5:130–143. https://doi.org/10.1111/j.1752-4571.2011.00217.x

Arnaud-Haond S, Duarte CM, Alberto F, et al (2007) Standardizing methods to address clonality in population studies. Mol Ecol 16:5115–5139. https://doi.org/10.1111/j.1365-294X.2007.03535.x

Arnaud-Haond S, Duarte CM, Diaz-Almela E, et al (2012) Implications of extreme life span in clonal organisms: millenary clones in meadows of the threatened seagrass *Posidonia oceanica*. PLoS One 7:e30454. https://doi.org/10.1371/journal.pone.0030454

Arnaud-Haond S, van den Beld IMJ, Becheler R, et al (2017) Two "pillars" of cold-water coral reefs along Atlantic European margins: prevalent association of *Madrepora oculata* with *Lophelia pertusa*, from reef to colony scale. Deep-Sea Res Part 2 Top Stud Oceanogr 145:110–119

Balloux F, Lugon-Moulin N (2002) The estimation of population differentiation with microsatellite markers. Mol Ecol 11:155–165

Becheler R (2013) Feedbacks between genetic diversity and demographic stability in clonal organisms. Master II, IUEM. Institut Universitaire Européen de la Mer

Becheler R, Cassone AL, Noël P, et al (2017) Low incidence of clonality in cold water corals revealed through the novel use of a standardized protocol adapted to deep sea sampling. Deep-Sea Res Part 2 Top Stud Oceanogr 145:120–130. https://doi.org/10.1016/j.dsr2.2015.11.013

Bierne N, Welch J, Loire E, et al (2011) The coupling hypothesis: why genome scans may fail to map local adaptation genes. Mol Ecol 20:2044–2072. https://doi.org/10.1111/j.1365-294X.2011.05080.x

Boavida J, Becheler R, Choquet M, et al. Out of the Mediterranean? Post-glacial colonisation pathways varied among cold-water coral species (Under revision)

Boero F (2015) The future of the Mediterranean Sea Ecosystem: towards a different tomorrow. Rend Lincei 26:3–12. https://doi.org/10.1007/s12210-014-0340-y

Bouchet P, Taviani M (1992) The Mediterranean deep-sea fauna: pseudopopulations of Atlantic species? Deep-Sea Res Part 1 Oceanogr Res Pap 39:169–184. https://doi.org/10.1016/0198-0149(92)90103-Z

Bozec A, Lozier MS, Chassignet EP, et al (2011) On the variability of the Mediterranean Outflow Water in the North Atlantic from 1948 to 2006. J Geophys Res: Oceans:116. https://doi.org/10.1029/2011JC007191

Brooke S, Young CM (2003) Reproductive ecology of a deep-water scleractinian coral, *Oculina varicosa*, from the southeast Florida shelf. Cont Shelf Res 23:847–858. https://doi.org/10.1016/S0278-4343(03)00080-3

Cordes EE, Jones DO, Schlacher T, et al (2016) Environmental impacts of the deep-water oil and gas industry: a review to guide management strategies. Front Environ Sci 4:1–54. https://doi.org/10.3389/fenvs.2016.00058

Costantini F, Gori A, Lopez-González P, et al (2016) Limited genetic connectivity between gorgonian morphotypes along a depth gradient. PLoS One 11:e0160678. https://doi.org/10.1371/journal.pone.0160678

Costantini F, Addamo AM, Machordom A, et al (2017) Genetic connectivity and conservation of temperate habitat forming corals. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1061–1082. https://doi.org/10.1007/978-3-319-17001-5_32-1

Danovaro R, Company JB, Corinaldesi C, et al (2010) Deep-sea biodiversity in the Mediterranean sea: the known, the unknown, and the unknowable. PLoS One 5:e11832. https://doi.org/10.1371/journal.pone.0011832

Davies JS, Guillaumont B, Tempera F, et al (2017) A new classification scheme of European cold-water coral habitats: implications for ecosystem-based management of the deep sea. Deep-Sea Res Part 2 Top Stud Oceanogr:1–8. https://doi.org/10.1016/j.dsr2.2017.04.014

De Mol B, Henriet JP, Canals M (2005) Development of coral banks in Porcupine Seabight: do they have mediterannean ancestors. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 513–533

Di Geronimo I, Messina C, Rosso A, et al (2005) Enhanced biodiversity in the deep: early Pleistocene coral communities from southern

Italy. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 61–86

Ekblom R, Wolf JB (2014) A field guide to whole-genome sequencing, assembly and annotation. Evol Appl 7:1026–1042. https://doi.org/10.1111/eva.12178

Everett MV, Park LK, Berntson EA, et al (2016) Large-scale genotyping-by-sequencing indicates high levels of gene flow in the deep-sea octocoral *Swiftia simplex* (Nutting 1909) on the west coast of the United States. PLoS One 11:e0165279. https://doi.org/10.1371/journal.pone.0165279

Fabri MC, Bargain A, Pairaud I, et al (2017) Cold-water coral ecosystems in Cassidaigne Canyon: an assessment of their environmental living conditions. Deep-Sea Res Part 2 Top Stud Oceanogr 137:436–453. https://doi.org/10.1016/j.dsr2.2016.06.006

Fink HG, Wienberg C, Hebbeln D, et al (2012) Oxygen control on Holocene cold-water coral development in the eastern Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96. https://doi.org/10.1016/j.dsr.2011.12.013

Fink HG, Wienberg C, De Pol-Holz R, et al (2015) Spatio-temporal distribution patterns of mediterranean cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) during the past 14,000 years. Deep-Sea Res Part 1 Oceanogr Res Pap 103:37–48. https://doi.org/10.1016/j.dsr.2015.05.006

Frank N, Freiwald A, López-Correa M, et al (2011) Northeastern Atlantic cold-water coral reefs and climate. Geology 39:743–746. https://doi.org/10.1130/g31825.1

Freiwald A, Roberts JM (2005) Cold-water corals and ecosystems – preface cold-water corals and ecosystems. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp Vii–Xii

Freiwald A, Fossa JH, Grehan A, et al (2004) Cold-water coral reefs. UNEP-WCMC, Cambridge, UK, 86 pp

Freiwald A, Beuck L, Rueggeberg A, et al (2009) The white coral community in the Central Mediterranean sea revealed by ROV surveys. Oceanography 22:58–74

Fu YX, Li WH (1993) Statistical tests of neutrality of mutations. Genetics 133:693–709

Gagnaire PA, Broquet T, Aurelle D, et al (2015) Using neutral, selected, and hitchhiker loci to assess connectivity of marine populations in the genomic era. Evol Appl 8:769–786. https://doi.org/10.1111/eva.12288

Garcia-Castellanos D, Villasenor A (2011) Messinian salinity crisis regulated by competing tectonics and erosion at the Gibraltar arc. Nature 480:359–363. https://doi.org/10.1038/nature10651

Goodwin S, McPherson JD, McCombie WR (2016) Coming of age: ten years of next-generation sequencing technologies. Nat Rev Genet 17:333–351. https://doi.org/10.1038/nrg.2016.49

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060. https://doi.org/10.5194/bg-10-2049-2013

Gori A, Ferrier-Pages C, Hennige SJ, et al (2016) Physiological response of the cold-water coral *Desmophyllum dianthus* to thermal stress and ocean acidification. PeerJ 4:e1606. https://doi.org/10.7717/peerj.1606

Halkett F, Simon JC, Balloux F (2005) Tackling the population genetics of clonal and partially clonal organisms. Trends Ecol Evol 20:194–201

Harnik PG, Lotze HK, Anderson SC, et al (2012) Extinctions in ancient and modern seas. Trends Ecol Evol 27:608–617. https://doi.org/10.1016/j.tree.2012.07.010

Heather JM, Chain B (2016) The sequence of sequencers: the history of sequencing DNA. Genomics 107:1–8. https://doi.org/10.1016/j.ygeno.2015.11.003

Hedgecock D, Barber PH, Edmands S (2007) Genetic approaches to measuring connectivity. Oceanography 20:70–79

Hellberg M (2006) No variation and low synonymous substitution rates in coral mtDNA despite high nuclear variation. BMC Evol Biol 6:24

Hennige SJ, Morrison CL, Form AU, et al (2014) Self-recognition in corals facilitates deep-sea habitat engineering. Sci Rep 4. https://doi.org/10.1038/srep06782

Henry LA, Frank N, Hebbeln D, et al (2014) Global ocean conveyor lowers extinction risk in the deep sea. Deep-Sea Res Part 1 Oceanogr Res Pap 88:8–16. https://doi.org/10.1016/j.dsr.2014.03.004

Herrera S, Shank TM (2016) RAD sequencing enables unprecedented phylogenetic resolution and objective species delimitation in recalcitrant divergent taxa. Mol Phylogenet Evol 100:70–79. https://doi.org/10.1016/j.ympev.2016.03.010

Hewitt G (2000) The genetic legacy of the Quaternary ice ages. Nature 405:907–913. https://doi.org/10.1038/35016000

Hewitt GM (2004) Genetic consequences of climatic oscillations in the Quaternary. Philos Trans R Soc B 359:183–195. https://doi.org/10.1098/rstb.2003.1388

Hillis DM, Dixon MT (1991) Ribosomal DNA: molecular evolution and phylogenetic inference. Q Rev Biol 66:411–453. https://doi.org/10.1086/417338

Hodel RGJ, Segovia-Salcedo MC, Landis JB, et al (2016) The report of my death was an exaggeration: a review for researchers using microsatellites in the 21st century. Appl Plant Sci 4:1600025. https://doi.org/10.3732/apps.1600025

Hsü KJ, Montadert L, Bernoulli D, et al (1977) History of the Mediterranean salinity crisis. Nature 267:399–403

Huang D, Meier R, Todd PA, et al (2008) Slow mitochondrial COI sequence evolution at the base of the Metazoan tree and its implications for DNA barcoding. J Mol Evol 66:167–174. https://doi.org/10.1007/s00239-008-9069-5

Jarne P, Lagoda PJL (1996) Microsatellites, from molecules to populations and back. Trends Ecol Evol 11:424–429

Lagabrielle E, Crochelet E, Andrello M, et al (2014) Connecting MPAs – eight challenges for science and management. Aquat Conserv 24:94–110. https://doi.org/10.1002/Aqc.2500

Larsson AI, Jarnegren J, Stromberg SM, et al (2014) Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*. PLoS One 9. https://doi.org/10.1371/journal.pone.0102222

Lastras G, Canals M, Ballesteros E, et al (2016) Cold-water corals and anthropogenic impacts in La Fonera submarine Canyon Head, Northwestern Mediterranean Sea. PLoS One 11. https://doi.org/10.1371/journal.pone.0155729

Lowe WH, Allendorf FW (2010) What can genetics tell us about population connectivity? Mol Ecol 19:5320–5320. https://doi.org/10.1111/j.1365-294X.2010.04878.x

Malinverno E, Taviani M, Rosso A, et al (2010) Stratigraphic framework of the Apulian deep-water coral province, Ionian Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:345–359. https://doi.org/10.1016/j.dsr2.2009.08.025

Malmstrom M, Matschiner M, Torresen OK, et al (2017) Whole genome sequencing data and de novo draft assemblies for 66 teleost species. Sci Data 4:160132. https://doi.org/10.1038/sdata.2016.132

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the younger dryas. Earth Planet Sci Lett 298:143–152. https://doi.org/10.1016/j.epsl.2010.07.036

Millot C, Taupier-Letage I (2005) Circulation in the Mediterranean Sea. Handb Environ Chem 5:29–66

Millot C, Candela J, Fuda JL, et al (2006) Large warming and salinification of the Mediterranean outflow due to changes in its composition. Deep-Sea Res Part 1 Oceanogr Res Pap 53:656–666. https://doi.org/10.1016/j.dsr.2005.12.017

Moilanen A, Hanski I (2001) On the use of connectivity measures in spatial ecology. Oikos 95:147–151

Montagna P, McCulloch M, Taviani M, et al (2006) Phosphorus in cold-water corals as a proxy for seawater nutrient chemistry. Science 312:1788–1791. https://doi.org/10.1126/science.1125781

Mytilineou C, Smith CJ, Anastasopoulou A, et al (2014) New cold-water coral occurrences in the Eastern Ionian Sea: results from experimental long line fishing. Deep-Sea Res Part 2 Top Stud Oceanogr 99:146–157. https://doi.org/10.1016/j.dsr2.2013.07.007

Naumann MS, Orejas C, Ferrier-Pagès C (2013) High thermal tolerance of two Mediterranean cold-water coral species maintained in aquaria. Coral Reefs 32:749–754. https://doi.org/10.1007/s00338-013-1011-7

Olivieri I, Tonnabel J, Ronce O, et al (2016) Why evolution matters for species conservation: perspectives from three case studies of plant metapopulations. Evol Appl 9:196–211. https://doi.org/10.1111/eva.12336

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51. https://doi.org/10.3354/mep08314

Orejas C, Addamo A, Alvarez M, et al (2017) Cruise summary report – MEDWAVES survey. (MEDiterranean out flow water and vulnerable ecosystems), 21st September 26th October 2016. 210 pp and appendices. https://doi.org/10.5281/zenodo.556516

Pante E, Abdelkrim J, Viricel A, et al (2015a) Use of RAD sequencing for delimiting species. Heredity 114:450–459. https://doi.org/10.1038/hdy.2014.105

Pante E, Puillandre N, Viricel A, et al (2015b) Species are hypotheses: avoid connectivity assessments based on pillars of sand. Mol Ecol 24:525–544. https://doi.org/10.1111/Mec.13048

Pérès JM, Piccard J (1964) Nouveau manuel de bionomie benthique de la Mer Mediterranee. Station Marine d'Endoume, Marseille 47:1–137

Perrin C, Bosellini FR (2012) Paleobiogeography of scleractinian reef corals: changing patterns during the Oligocene-Miocene climatic transition in the Mediterranean. Earth Sci Rev 111:1–24. https://doi.org/10.1016/j.earscirev.2011.12.007

Pires DO, Silva JC, Bastos ND (2014) Reproduction of deep-sea reef-building corals from the southwestern Atlantic. Deep-Sea Res Part 2 Top Stud Oceanogr 99:51–63. https://doi.org/10.1016/j.dsr2.2013.07.008

Price JF, Baringer MO, Lueck RG, et al (1993) Mediterranean outflow mixing and dynamics. Science 259:1277–1282. https://doi.org/10.1126/science.259.5099.1277

Putman AI, Carbone I (2014) Challenges in analysis and interpretation of microsatellite data for population genetic studies. Ecol Evol 4:4399–4428. https://doi.org/10.1002/ece3.1305

Reed JK, Koenig CC, Shepard AN (2007) Impacts of bottom trawling on a deep-water Oculina coral ecosystem off Florida. Bull Mar Sci 81:481–496

Reitzel AM, Herrera S, Layden MJ, et al (2013) Going where traditional markers have not gone before: utility of and promise for RAD sequencing in marine invertebrate phylogeography and population genomics. Mol Ecol 22:2953–2970. https://doi.org/10.1111/mec.12228

Riginos C, Liggins L (2013) Seascape genetics: populations, individuals, and genes marooned and adrift. Geogr Compass 7:197–216. https://doi.org/10.1111/gec3.12032

Riginos C, Crandall ED, Liggins L, et al (2016) Navigating the currents of seascape genomics: how spatial analyses can augment population genomic studies. Curr Zool 62:581–601. https://doi.org/10.1093/cz/zow067

Roberts JM, Wheeler A, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334. https://doi.org/10.1017/CBO9780511581588

Salzman AG, Parker MA (1985) Neighbors ameliorate local salinity stress for a rhizomatous plant in a heterogeneous environment. Oecologia 65:273–277. https://doi.org/10.1007/BF00379229

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the Northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108. https://doi.org/10.1371/journal.pone.0091447

Schroder-Ritzrau A, Freiwald A, Mangini A (2005) U/Th-dating of deep-water corals from the eastern North Atlantic and the western Mediterranean Sea. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 157–172. https://doi.org/10.1007/3-540-27673-4_8

Selkoe KA, Toonen RJ (2006) Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. Ecol Lett 9:615–629. https://doi.org/10.1111/j.1461-0248.2006.00889.x

Shearer TL, Coffroth MA (2008) DNA BARCODING: barcoding corals: limited by interspecific divergence, not intraspecific variation. Mol Ecol Resour 8:247–255. https://doi.org/10.1111/j.1471-8286.2007.01996.x

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156. https://doi.org/10.1007/3-540-27673-4_7

Taviani M, Vertino A, López- Correa M, et al (2011) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603. https://doi.org/10.1007/s10347-010-0247-8

Taylor PD, Fahrig L, Henein K, et al (1993) Connectivity is a vital element of landscape structure. Oikos 68:571–573. https://doi.org/10.2307/3544927

Teixeira S, Cambon-Bonavita M-A, Serrão EA, et al (2011) Recent population expansion and connectivity in the hydrothermal shrimp *Rimicaris exoculata* along the Mid-Atlantic Ridge. J Biogeogr 38:564–574. https://doi.org/10.1111/j.1365-2699.2010.02408.x

Thorrold SR, Zacherl DC, Levin LA (2007) Population connectivity and larval dispersal using geochemical signatures in calcified structures. Oceanography 20:80–89

Van Wyngaarden M, Snelgrove PVR, DiBacco C, et al (2017) Identifying patterns of dispersal, connectivity and selection in the sea scallop, *Placopecten magellanicus*, using RADseq-derived SNPs. Evol Appl 10:102–117. https://doi.org/10.1111/eva.12432

Vertino A, Stolarski J, Bosellini FR, et al (2014) Mediterranean corals through time: from Miocene to present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, New York, pp 257–274

Waller RG (2005) Deep-water Scleractinia (Cnidaria: Anthozoa): current knowledge of reproductive processes. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 691–700

Wang Z, Gerstein M, Snyder M (2009) RNA-Seq: a revolutionary tool for transcriptomics. Nat Rev Genet 10:57–63

Waples RS, Gaggiotti O (2006) What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Mol Ecol 15:1419–1439. https://doi.org/10.1111/j.1365-294X.2006.02890.x

Wienberg C, Frank N, Mertens NK, et al (2010) Glacial cold-water coral growth in the Gulf of Cadiz: implications of increased palaeo-productivity. Earth Planet Sci Lett 298:405–416. https://doi.org/10.1016/j.epsl.2010.08.017

Wilson JB (1979) Patch development of the deep-water coral *Lophelia pertusa* (L) on Rockall bank. J Mar Biol Assoc UK 59:165

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Institut Oceanographique Fondation Albert 1er, Prince de Monaco, Paris

Cross References

Addamo AM (this volume) *Desmophyllum dianthus* genetics and more

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Aymà A, Aguzzi J, Canals M, et al (this volume) Occurrence of living cold-water corals at large depths within submarine canyons of the northwestern Mediterranean Sea

Bramanti L, Santangelo G, Benedetti MC, et al (this volume) Demography and conservation of deep corals: the study of population structure and dynamics

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Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Drop Chapter *Desmophyllum dianthus* Genetics and More

32

Anna Maria Addamo

Abstract

The scientific understanding on phylogeny, ecology and evolution of scleractinian corals has been expanded thanks to the numerous applications of molecular markers. Nevertheless, shallow-water tropical corals were the main subject of these studies so far. Just recently scientists have focused their attention on deep and cold-water corals. In the last decade, the solitary coral *Desmophyllum dianthus* (Esper, 1794) has been the subject of several studies focused on phylogeny, ecology, and physiology. This drop chapter seeks to summarise the novel obtained results, and consequently the arguments arise, in molecular ecology, systematics and evolution of the species. Key roles of this species in the evolutionary studies of scleractinian corals are also discussed.

Keywords

Desmophyllum · *Lophelia* · Molecular markers · Integrative taxonomy · Molecular ecology

The application of molecular markers in the natural sciences has enriched and broadened the scientific insight of the natural history and evolution of organisms (see Boavida et al., this volume).

In this context, the scientific knowledge on phylogeny, phylogeography and genetic population of scleractinian corals has been based on - and limited to – principle studies carried out mainly on shallow water and tropical species (see e.g. Fukami et al. 2008; Huang et al. 2014). A minority of works has involved deep-sea and azooxanthellate corals (e.g. Stolarski et al. 2011 and reference therein) that compose half of the total number of corals species identified so far.

Within the azooxanthellate Scleractinia, the family Caryophyliidae Dana, 1846 is the most diverse family, including 51 extant species and 38 fossil species (Roberts 2009, see online appendix, see Altuna and Poliseno, this volume). Representatives of this family include the solitary deep-sea coral *Desmophyllum dianthus* (Esper, 1794).

Since *D. dianthus* is one of the few corals widely distributed, several individuals from different areas of both northern and southern hemispheres have been analysed with new developed 30 species-specific microsatellites (Addamo et al. 2015a). The population structures, detected either in northern or southern hemispheres, presented a clear isolation by distance model of gene flow (IBD). Nevertheless, ocean currents at different depths are also strongly suspected to play a key role on larval dispersal: (I) as a physical barrier: e.g. *D. dianthus* populations, either from New Zealand and Chile, presented their own genetic characteristics; or (II) as a connectivity vector: e.g. gene flow has been detected between individuals from Australia and Argentina, despite their large geographic distance (Addamo et al., submitted).

Furthermore, in spite of it being well known for its high morphological plasticity (Fig. 32.1), analyses performed-based on morphological and morphometric characters of skeleton and cnidom-have detected no obvious relationship between the extreme variable morphology and either ecological or environmental parameters characterised simultaneously (Addamo et al. 2015b).

Phylogenetically speaking, scleractinian corals belong to two main molecularly defined clades (Romano and Palumbi 1996), 'Robusta' and 'Complexa'. Molecular data have confirmed *D. dianthus* belongs to the major clade 'Robusta' and in one of the polyphyletic clades of family Caryophylliidae (Addamo et al. 2012).

However, an in-depth comparative morphological and molecular analyses – including skeletal ontogeny, micromorphological (septal ad wall granulations) and microstructural (arrangement of rapid accretion deposits, thickening deposits) characters, and several nuclear and

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Fig. 32.1 Morphological variability of calice and corallum in *Desmophyllum dianthus*. Origin of specimens: Chile (**a**–**c**, **e**, **j**); New Zealand (**d**, **g**); Ecuador (**i**); Japan (**f**, **k**); New Caledonia (**h**). (See Addamo et al. 2015b for further details, © Elsevier)

mitochondrial molecular markers, characterised by different mutation rates and polymorphism level – contributed to clarify the phylogenetic relationship between *D. dianthus* and its closely related species (Addamo et al. 2016). Indeed, this study revealed a surprising genetic similarity between *D. dianthus* and the largest colonial azooxanthellate species of coral in the deep-sea waters, *Lophelia pertusa*, which has been recently suggested as junior synonym of *Desmophyllum pertusum* (Linnaeus, 1758) nov. comb. (see Addamo et al. 2016 for further details).

The genus adscription shift and the consequences of such unanticipated synonymy should fosters even more to the scientific community to provide a deep revision of taxonomic identification key of Scleractinia. For example, arguments for a dual morphology-molecular approach, the colonialism versus solitary way development in corals are cases in point.

A variety of studies has been performed using *D. dianthus* as a model organism to study the synergistic effect of global change stressors as ocean acidification and sea temperature rise (e.g. Gori et al. 2016; Reynaud and Ferrier-Pagès, this volume). Moreover, this species has been considered as a palaeoclimate and palaeonvironment archive to trace element (B/Ca, Mg/Ca, Sr/Ca, and U/Ca) (e.g. Montagna et al. 2008, Montagna and Taviani, this volume) and as well as to reconstruct seawater pH over the past thousands year (e.g. Stewart et al. 2016).

Despite the difficulties encountered in ecological features (e.g. gathering significant collections from the deep-sea) or laboratory settings (e.g. keep or breed them in aquaria), *D dianthus* has been proved being an interesting species for genomics as well as ecological and experimental analysis, giving insight into the general principles of a broad range of various disciplines, such as genetics, development and evolution.

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References

Addamo AM, Reimer JD, Taviani M, et al (2012) *Desmophyllum dianthus* (Esper, 1794) in the scleractinian phylogeny and its intraspecific diversity. PLoS One 7:e50215. https://doi.org/10.1371/journal.pone.0050215

Addamo AM, García Jiménez R, Taviani M, et al (2015a) Development of microsatellite markers in the deep-sea cup coral *Desmophyllum dianthus* and cross-species amplifications in the Scleractinia Order. J Hered 106:322–330. https://doi.org/10.1093/jhered/esv010

Addamo AM, Martínez-Baraldés I, Vertino A, et al (2015b) Morphological polymorphism of *Desmophyllum dianthus* over a wide ecological and biogeographic range: stability in deep habitats? Zool Anz 259:113–137. https://doi.org/10.1016/j.jcz.2015.10.004

Addamo AM, Vertino A, Stolarski J, et al (2016) Merging scleractinian coral genera: the overwhelming genetic similarity between solitary *Desmophyllum* and colonial *Lophelia*. BMC Evol Biol 16. https://doi.org/10.1186/s12862-016-0654-8

Addamo AM, Miller K, Haüssermann V et al Global-scale genetic structure of cosmopolitan cold-water coral species (under review)

Fukami H, Chen CA, Budd AF, et al (2008) Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). PLoS One 3:e3222. https://doi.org/10.1371/journal.pone.0003222

Gori A, Ferrier-Pagès C, Henninge SJ, et al (2016) Physiological response of the cold-water coral *Desmophyllum dianthus* to thermal stress and ocean acidification. PeerJ 4:e1606. https://doi.org/10.7717/peerj.1606

Huang D, Benzoni F, Fukami F, et al (2014) Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia). Zool J Linn Soc-Lond 171:277–355. https://doi.org/10.1111/zoj.12140

Montagna P, McCulloch M, Mazzoli C, et al (2008) High-resolution geochemical records from Mediterranean cold-water corals: proxies for paleoclimate and paleoenvironmental reconstructions and the role of coral physiology. CIESM Work Monogr 36:55–60

Roberts JM, Wheeler AJ, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334. https://doi.org/10.1017/CBO9780511581588

Romano SL, Palumbi RS (1996) Evolution of Scleractinian corals inferred from molecular systematics. Science 271:640–642. https://doi.org/10.1126/science.271.5249.640

Stewart JA, Anagnostou E, Foster GL, et al (2016) An improved boron isotope pH proxy calibration for the deep-sea coral *Desmophyllum dianthus* through sub-sampling of fibrous aragonite. Chem Geol 447:148–160. https://doi.org/10.1016/j.chemgeo.2016.10.029

Stolarski J, Kitahara MV, Miller DJ, et al (2011) The ancient evolutionary origins of Scleractinia revealed by azooxanthellate corals. BMC Evol Biol 11:316. https://doi.org/10.1186/1471-2148-11-316

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Boavida J, Becheler R, Addamo AM, et al (this volume) Past, present and future connectivity of Mediterranean cold-water corals: patterns, drivers and fate in a technically and environmentally changing world

Montagna P, Taviani M (this volume) Mediterranean cold-water corals as paleoclimate archives

Reynaud S, Ferrier-Pagès C (this volume) Biology and ecophysiology of Mediterranean cold-water corals

33

Diversity of Bacteria Associated with the Cold Water Corals *Lophelia pertusa* and *Madrepora oculata*

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Abstract

Recent research suggests that corals including cold-water corals harbor a diverse community of bacteria that are not only pathogens but also potential mutualists. Here we review data on bacterial community composition and diversity on the main cold-water corals framework builder species: *Lophelia pertusa* and *Madrepora oculata*. Sampling strategies such as box core, video grabs and remotely operated vehicle did not reveal strong differences between bacterial community composition as long as samples were used that looked 'not contaminated'. However, there were strong differences of bacterial diversity between the two coral species. An analysis of bacterial community composition by pyrosequencing of *L. pertusa* and *M. oculata* revealed for the Mediterranean Sea the presence of the potential mutualists already found in the Atlantic indicating a species-specific core microbiome. The data also suggest some biogeographical differences between the Mediterranean Sea and the North Atlantic for both coral species, however, this depends on the phylogenetic levels applied. In addition, there was also indication for a shared microbiome between the Mediterranean Sea and the Atlantic. Therefore species-specific bacterial associations seem to exist, whereas the biogeographical variability can be seen as adaptation to specific environmental conditions.

Keywords

Fingerprints · Pyrosequencing · Biogeography · Microenvironments · Core microbiome

33.1 Introduction

Tropical corals have been intensively investigated e.g. with respect to their associations with algae, their ecology and the ecosystem they populate. However, it is not until comparatively recent (around two decades ago) that the attention has also focused on corals inhabiting the dark cold-water ecosystems (e.g. Roberts et al. 2006, 2009). *Lophelia pertusa* Milne Edwards and Haime 1849 (family *Caryophylliidae*) and *Madrepora oculata* Linnaeus 1758 (family *Oculinidae*) are important species as main frame-builders of such ecosystems, which sustain a large biodiversity and biomass of associated fauna (e.g. Rogers 1999; Henry and Roberts 2007, 2017; D'Onghia, this volume; Rueda et al., this volume). A potential threat to cold-water corals (CWCs) is the decrease in pH due to increased atmospheric pCO_2, since a drop in pH might impair calcification (Maier et al., this volume; Movilla, this volume; Otero and Marin, this volume). Deep water coral ecosystems are abundant above the aragonite saturation level, i.e. the depth where aragonite dissolves (Turley et al. 2007). As predictions indicate that the saturation level will become shallower due to ocean acidification (OA) (Orr et al.

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2005; see for a review Maier et al., this volume), the CWC ecosystems could be negatively affected within the next decades. Also, there are other threats to CWCs such as by pollution, fisheries, oil and gas prospecting and global warming (Roberts et al. 2006; Otero and Marin, this volume).

Lophelia pertusa is a cosmopolitan scleractinian coral with a depth range of ca. 50 to >1500 m. Its geographical and depth distribution overlaps with that of *M. oculata*, although there are also *L. pertusa* reefs such as in the Mingulay Reef without *M. oculata* colonies and *vice versa* (e.g. Rogers 1999; Arnaud-Haond et al. 2015). *Madrepora oculata* has a weaker and more fragile skeleton compared to *L. pertusa* and is generally smaller. Isotope analysis suggests that zooplankton and phytodetritus are the main food sources of these coral species (e.g. Duineveld et al. 2004; Kiriakoulakis et al. 2005; Carlier et al. 2009; Roberts et al. 2009; Reynaud and Ferrier-Pagès, this volume). There is also evidence that the seasonal spawning could be triggered by phytodetrital food fall (Waller and Tyler 2005; Brooke and Jarnegren 2013; Larsson et al. 2014). Others have shown that dissolved free amino acids can be a significant source of carbon and nitrogen (Gori et al. 2014) and that *L. pertusa* has likely an opportunistic feeding strategy (Mueller et al. 2014). In addition, both coral species release significant amounts of mucus into the environment thus potentially fueling bacterial production (Reitner 2005; Wild et al. 2008, 2010; Maier et al. 2011). Attempts have been made to assess viral and microbial abundance in the mucus and coelenteron of CWCs (e.g. Weinbauer et al. 2012).

Although it is long known that the coral mucus can harbour large numbers of bacteria (e.g. Ducklow and Mitchell 1979), it is relatively recent that bacteria have been investigated in more detail. For example, a large diversity of *Bacteria* and *Archaea* in the surface mucus layer of tropical corals has been demonstrated (Rohwer et al. 2002; Kellogg 2004; Ritchie and Smith 2004; Bourne and Munn 2005; Weinbauer et al., this volume). Bacterial communities within the surface layers of hard corals have been shown to play an important nutritional role for corals (and other invertebrates) (e.g. Neave et al. 2017; Silveira et al. 2017); they may play an equally important role in maintaining the health and preventing disease in corals (Ritchie and Smith 2004). There is evidence that bacteria associated to coral mucus produce antibiotics as defense mechanisms against free-living bacteria including potential pathogens (Harder et al. 2003; Ritchie 2006). It has also been suggested recently that associated bacteria (including those in the tissue) function as an equivalent to an immune system (coral probiotic hypothesis) (Reshef et al. 2006). In addition, it has been argued that the prokaryotic community could be a way for the holobiont to counteract environmental disturbances such as those caused by climate change (Rosenberg et al. 2007). Previous work indicated that the coral microbiome can be conceptually divided into three components: (i) a small ubiquitous core microbial (mutualists and symbionts), (ii) a dynamic site and/or species-specific community of intermediate size and (iii) a highly variable and huge community reflecting biotic and abiotic fluctuations (Hernandez-Agreda et al. 2016, 2017). This has also been suggested for CWCs (Kellogg et al. 2017).

Bacteria have been investigated in *L. pertusa* ecosystems (Jensen et al. 2008a, b) and studies on the diversity of bacterial associated with are now available (Neulinger et al. 2008, 2009; Kellogg et al. 2009, 2017; Schöttner et al. 2009, 2012; van Bleijsweijk et al. 2015; Meistertzheim et al. 2016). Bacterial community composition (BCC) has been assessed for *M. oculata* suggesting that *Spongiobacter* (now *Endozoicomonas*) (Neave et al. 2017) could be mutualistic bacteria (Yakimov et al. 2005; Hansson et al. 2009; Meistertzheim et al. 2016). Studies on bacterial diversity on CWCs are also available for the Mediterranean Sea (Meistertzheim et al. 2016). Data from Meistertzheim et al. (2016) also suggest differences of bacterial diversity between with *L. pertusa* and *M. oculata*. Also, both species have relatively few associated archaea or at least rather specific groups of associated archaea compared to other invertebrates for sediment and water column samples of the same environment (Weinbauer et al., this volume). Biogeographical comparisons of bacteria associated with *L. pertusa* have been made indicating that a core microbiome exists for this species. This core microbiome of *L. pertusa* is likely important for carbon and nutrient recycling in the mucus of CWCs (Kellogg et al. 2017).

Here we review data on BCC and diversity of bacteria associated with *L. pertusa* and *M. oculata*. The term microenvironment will be used in the following for sediment, dead corals, skeleton mucus and tissue. In addition, some new data will be presented.

33.2 Effect of Sampling Strategies for Assessing Bacterial Community Composition and Diversity

It has been argued that the technology used to collect CWCs such trawls, nets, dredges, box cores and remotely operated vehicles (ROVs) could influence the outcome of studies on microbial diversity. Potential cross-contamination could occur between coral specimens kept in the same container. Probably more important, the contact with sediment, invertebrates, mobile fauna, or water masses between the collection point and the retrieval at the surface could contaminate the coral samples (e.g. Kellogg et al. 2009).

Sampling strategies were tested with *Lophelia pertusa* from the Mingulay Reef (Großkurth 2007).[1] While dead corals, mucus and tissue clustered well apart using cluster analysis, as long as 'clean', i.e. not contaminated looking colonies were used (see also next section: Community

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[1] Masters thesis available as pdf at wein@obs-vlfr.fr

Composition and Diversity of Bacteria Associated with Coral Mucus and Tissue), no consistent effect on BCC were found for the sampling devices box core and videograb. An exception was dredged samples which clustered together with dead corals. This suggests that sampling strategies do not have a strong influence as long as colonies with visible contamination are not used.

33.3 Community Composition and Diversity of Bacteria Associated with Coral Mucus and Tissue

It has been reported for the North Atlantic that BCC differs between *Lophelia pertusa* microenvironments such as skeleton and mucus (Schöttner et al. 2009, 2012; van Bleisweijk et al. 2015). For example, the number of Automated Ribosomal Intergenic Spacer Analysis (ARISA) Operational Taxonomic Unit (OTUs) was lower for the skeleton (7) than for mucus (14) (Schöttner et al. 2009). Using Denaturing Gradient Gel electrophoresis (DGGE, Großkurth (2007) found for *L. pertusa* that dead corals, mucus and tissue typically showed distinct clusters as long as mucus and tissue was collected from not contaminated looking corals. This author also showed that (1) rinsing of contaminated looking corals resulted in a re-clustering of samples into the 'typical' microenvironment and (2) rinsing of not contaminated looking corals resulted in only minor changes of BCC.

The detailed reasons for the difference between microenvironments remain unknown, however, it has been demonstrated before that specific bacterial groups can invade different tissues of tropical corals (Ainsworth et al. 2006). Other bacteria could have a life strategy to become embedded in the organic matrix of the mucus as shown for marine organic aggregates (Heissenberger et al. 1996). For tropical corals it has been suggested that it is the tissue that harbors the core microbiome (Hernandez-Agreda et al. 2017). Overall, mucus, tissue and skeleton are quite different and specific microenvironments hence, likely providing ecological niches for specific bacteria.

33.4 Community Composition and Diversity of Bacteria Associated with *Lophelia pertusa*

33.4.1 Number of OTUs

A literature survey shows that 14–36 OTUs were found using various fingerprinting techniques, 12–79 using clone libraries and 2–1761 using in-depth sequencing (Table 33.1).

Specific coral-color dependent bacterial consortia were discovered as differences in relative abundance (band intensity or peak height) rather than as differences in bacterial OTUs (Terminal Restriction Fragment Length Polymorphism, T-RFLP analysis) between pink and white colonies (Neulinger et al. 2008). Using ARISA, Schöttner et al. (2012) found no significant differences between color morphs, as observed for pyrosequencing in Meistertzheim et al. (2016). It is possible that the small differences between color morphs found by Neulinger et al. (2009) were due to intracolony and local between colony differences (e.g. Hansson et al. 2009; Meistertzheim et al. 2016).

33.4.2 Sequence Analysis at the OTU Level

Most of the sequences obtained in the literature were close to bacterial sequences found to be associated to (tropical) corals and sponges (Neulinger et al. 2008, 2009; Kellogg et al. 2009, 2017; van Bleijsweijk et al. 2015; Meistertzheim et al. 2016). Potentially these bacteria are the result of the diversification of specific groups of bacteria that are adapted to corals and sponges.

A "symbiontlike thiotrophs cluster" (including uncultured bacterium clone G02_CR02) was found in the Gulf of Mexico and North West Atlantic (Kellogg et al. 2009), the Trondheimsfjord (Neulinger et al. 2008), Rockall Bank, Mingulay Reef and the Apulian Platform (this study, Table 33.2). This indicates a biogeographical constancy of this phylotype between Gulf of Mexico, North Atlantic and Mediterranean Sea. These sequences are of particular interest because they are part of what represents one of the potential *Lophelia*-specific bacterial groups (Kellogg et al. 2009).

Two phylotypes within the *Gammaproteobacteria* (including uncultured bacterium clone G02_CR02) were most closely related to endosymbionts of deep-sea mussels colonising hydrothermal vents (Neulinger et al. 2008). They might utilise reduced sulphur compounds produced by decomposition of Dimethylsulfonioproprionate (DMSP). Hence, it has been speculated that metabolising sulphur compounds is important in CWCs (Neulinger et al. 2008). Raina et al. (2009) suggested that DMSP, DMS, and acrylic acid potentially act as nutrient sources for coral-associated bacteria (*Montipora aequituberculata* and *Acropora millepora*). Such sequences were also found at Rockall Bank, Mingulay Reef and the Apulian Platform (this study, Table 33.2).

Sequences related to *Mycoplasma* spp. and the TMF7 (including uncultured bacterium clone D11_CW02) were found in the North East and North West Atlantic (Neulinger et al. 2008, 2009; Kellogg et al. 2009) and are now also reported for other Atlantic environments (Rockall and Mingulay Reef) and for the Mediterranean Sea by a DGGE approach (this study, Table 33.2) but not by pyrosequencing

Table 33.1 Data compilation from the literature of bacterial diversity associated with the mucus of *Lophelia pertusa*. Only phylogenetic groups with a representation of more than 10% were considered

Environment	Depth (m)	T (°C)	No. of OTUs	Major phylogenetic groups		Method	References
				%	Group		
Mediterranean Sea							
Apulian plateau	784		12	55	*Acidobacteria*	rDNA clone library	
				25	*Nitrospira*		
				19	*Proteobacteria*		
				12	*Alphaproteobacteria*		
	561–625	13.8	2.6	100	*Gammaproteobacteria*	DGGE	Weinbauer et al. (this volume)
			158	52	*Betaproteobacteria*	Pyrosequencing	
				37	*Gammaproteobacteria*		
Lacaze-Duthier canyon	520	13	2–18	79–92	*Alphaproteobacteria*	Pyrosequencing	
				6–78	*Gammaproteobacteria*		
				26–42	*Fusobacteria*		
				31–37	*Bacteroidetes*		
NE Atlantic							
Trondheimsfjord	54	9.6	27–54	28–61	*Alphaproteobacteria*	DNA clone library	Neulinger et al. (2009)
				3–20	*Gammaproteobacteria*		
				19	*Actinobacteria*		
Langenuen fjord	167		14			ARISA	Schöttner et al. (2009)
Norwegian fjords	300–400		36			ARISA	Schöttner et al. (2012)
Rockall Bank	528–745	5.4–10.0	1761	49	*Gammaproteobacteria*	Amplicon sequencing	
	558–781	8.5	7.4	49–60	*Alphaproteobacteria*	DGGE	Weinbauer et al. (this volume)
				13–20	*Bacteroidetes*		
				0–25	*Actinobacteria*		
				0–20	*Gammaproteobacteria*		
				0–13	*Deltaproteobacteria*		
			70	78	*Gammaproteobacteria*	Pyrosequencing	
				17	*Betaproteobacteria*		
Mingulay reef	129–179	9.9	8.1	58	*Alphaproteobacteria*	DGGE	Weinbauer et al. (this volume)
				14	*Gammaproteobacteria*		
				14	*Firmicutes*		
			921	59	*Gammaproteobacteria*	Pyrosequencing	
				22	*Alphaproteobacteria*		
NW Atlantic							
Gulf of Mexico	315–500	7–13	79	52	*Tenericutes*	DNA clone library	Kellogg et al. (2009)
	397–543	8.2-10.0		33	*Gammaproteobacteria*		
Atlantic	743–751	8	94–712	>80	*Proteobacteria*	Pyrosequencing	Kellogg et al. (2017)

For the Weinbauer et al. (this volume) samples, DNA extraction, DGGE and sequencing of bands was done as in Großkurth (2007) and Hansson et al. (2009) and pyrosesquencing for pooled samples (same DNA amount per specimen) as in Ray et al. (2012) and An et al. (2013). For Weinbauer et al. (this volume): n = 3 for the Apulian Plateau, n = 9 for Rockall Bank and n = 10 for Mingulay Reef

(Meistertzheim et al. 2016). Pyrosequencing did also not result in *Mycoplasma* related sequences at Rockall Bank (van Bleisweijk et al. 2015). Kellogg et al. (2017) who found such *Tenericutes* OTUs by pyrosequencing suggest that this could be due to the higher sequencing depth of their study. Also, it is possible that pyrosequencing selects against *Mycoplasma* and/or that DGGE selects for *Mycoplasma*. Using a single cell detection approach and microscopy (fluorescence *in situ* hybridisation, FISH), *Mycoplasma* was detected in the tissue of *L. pertusa* (Neulinger et al. 2009). Thus, it is also possible that *Mycoplasma* is not detected when only mucus is sampled (Kellogg et al. 2017). However, Meistertzheim et al. (2016) did not detect *Mycoplasma* when sampling tissue within

Table 33.2 Data compilation from the literature of bacterial diversity associated with the mucus of *Madrepora oculata*

Environment	Depth (m)	T (°C)	No. of OTUs	Major phylogenetic groups		Method	References
				%	Group		
Mediterranean Sea							
Lacaze-Duthier canyon	520	13	4–28	74–99	*Gammaproteobacteria*	Pyrosequening	Meistertzheim et al. (2016)
				12–16	*Alphaproteobacteria*		
				9–16	*Bacteroidetes*		
Apulian platform	561–625	13.8	10.3	33	*Bacteroidetes*	DGGE	Weinbauer et al. (this volume)
				33	*Deltaproteobacteria*		
				17	*Gammaproteobacteria*		
				17	*Alphaproteobacteria*		
			138	74	*Gammaproteobacteria*	Pyrosequencing	
NE Atlantic							
Rockall Bank	558–781	8.5	6–10	81	*Gammaproteobacteria*	DGGE	Hansson et al. (2009)
				13	*Actinobacteria*		
			5.6	80–87	*Gammaproteobacteria*	DGGE	Weinbauer et al. (this volume)
				10–13	*Bacteroidetes*		
				10	*Alphaproteobacteria*		
			109	83	*Gammaproteobacteria*	Pyrosequencing	
Norwegian fjords	300–400		35			ARISA	Schöttner et al. (2012)

Only phylogenetic groups with a representation of more than 10% were considered. For the Weinbauer et al. (this volume) samples, DNA extraction, DGGE and sequencing of bands was done as in Hansson et al. (2009) and pyrosequencing for pooled samples (same DNA amount per specimen) as in Ray et al. (2012) and An et al. (2013). For Weinbauer et al. (this volume): n = 3 for the Apulian Plateau and n = 18 for Rockall Bank polyps. Hence, the presence of *Mycoplasma* in *L. pertusa* remains enigmatic.

Using next-generation data sets, *Proprionibacterium* was detected on *L. pertusa* in the Gulf of Mexico, the NW Atlantic (Kellogg et al. 2017), the NE Atlantic (van Bleijsweijk et al. 2015) and the Mediterranean Sea (Meistertzheim et al. 2016). This suggests that some bacterial phylotypes are conserved regardless of geographic provenance (Kellogg et al. (2017).

33.4.3 Sequence Analysis at Higher Taxonomic Levels

A high relative contribution of *Gammaproteobacteria* (75%) was found by Yakimov et al. (2005) associated to dead Mediterranean *L. pertusa*, while in living *L. pertusa* from the Apulian Plateau, the most abundant phylotypes were *Holophaga acidobacteria* and *Nitrospirae.* Sequencing of DGGE bands revealed only *Gammaproteobacteria* sequences at the Apulian Plateau; this study and all previous ones suggest that *Gammproteobacteria* are abundant in *L. pertusa* from all sites studied so far (Table 33.1). One of the reasons for the differences for *Gammaproteobacteria* compared to the study of Yakimov et al. (2005) could be that an RNA based clone library was used as an indicator for active bacterial members. If this finding holds, this means that *Gammaproteobacteria* are less active than other bacteria in *L. pertusa*.

33.5 Community Composition and Diversity of Bacteria Associated with *Madrepora oculata*

33.5.1 Number of OTUs

A literature survey shows that between 6 and 35 OTUs were found by fingerprinting techniques and between 4 and 138 OTUs by pyrosequencing (Table 33.3).

33.5.2 Sequence Analysis at the OTU Level

Similar to *Lophelia pertusa*, most sequences of *Madrepora oculata* were related to bacteria associated with (tropical) corals and sponges (Hansson et al. 2009; Schöttner et al. 2012; Meistertzheim et al. 2016).

Several sequenced DGGE bands from Mingulay Reef had a close similarity to *Endozoicomonas*; also a high sequence variability within the genus was detected (Hansson et al. 2009). Such DGGE sequences were also found for Rockall Bank and the Apulian platform (this study, Table 33.2). *Endozoicomonas*-related sequences were also detected in the Mediterranean Sea (Meistertzheim et al. 2016). This further suggests specific associations of *Endozoicomonas* with *M. oculata*. Genomic analyses indicate that *Endozoicomonas* is a symbiotic bacterium with high genetic and metabolic plasticity (Neave et al. 2017).

Endozoicomonas sequences have been observed previously as dominating a culture-independent assessment of *Acropora millepora* at Magnetic Island (Bourne et al. 2008). Bourne et al. (2008) showed that *Endozoicomonas*-related sequences dominated bacterial profiles before and after a bleaching event, but were not dominant during the stress period. The high diversity of 16S rRNA gene sequences of *Endozoicomonas* suggests adaptive radiation in *M. oculata* (Hansson et al. 2009). Littman et al. (2009) demonstrated that *Endozoicomonas*-related sequences accounted for 17–35% of acroporid corals of the Great Barrier Australian Reef. Being such a dominant member of the coral-associated microbial communities could indicate that *Endozoicomonas* plays also a key role in the *M. oculata* holobiont system.

33.5.3 Sequence Analysis at Higher Taxonomic Levels

A literature survey suggests that *Gammaproteobacteria* are a significant and often dominating group of bacteria for *M. oculata* (Table 33.3).

Table 33.3 Phylogenetic affiliation of sequences from DGGE bands with closest uncultured matches for *Lophelia pertusa* and *Madrepora oculata* from this study

Bacterial group	Closest relative (data base accession no)	Similarity (%)	Affiliation
L. pertusa			
Symbiontlike thiotrophs cluster	Uncultured bacterium clone G02_CR02 (AM911391)	100	*Gammaproteobacteria*
	Uncult.bact.envir.samp. (AB254034)	100	*Gammaproteobacteria*
Mycoplasma spp.	Uncultured bacterium clone D11_CW02 (AM911412)	100	*Firmicutes*
M. oculata			
Endozoicomonas	uncultured *Spongiobacter* sp. (DQ917863)	97	*Gammaproteobacteria*
	uncultured *Spongiobacter* sp. (DQ889928)	95	*Gammaproteobacteria*
	Spongiobacter nickelotolerans (AB205011)	97	*Gammaproteobacteria*
	uncultured *Spongiobacter* sp. (DQ917863)	97	*Gammaproteobacteria*
	uncultured *Spongiobacter* sp. (DQ889928)	97	*Gammaproteobacteria*

The number of bases used to calculate sequence similarity ranged from 446 to 502. Identical DGGE bands for these sequences were obtained from the Apulian Plateau, Rockall Bank and Mingulay Reef

33.6 Comparison of Bacterial Diversity Associated with *Lophelia pertusa* and *Madrepora oculata*

Schöttner et al. (2012) using a high resolution method (ARISA) did not find any significant difference between the two species (Table 33.1). On the contrary, differences between the two species were also found in previous studies comparing specimen from the same environment (Hansson et al. 2009; Schöttner et al. 2012; Meistertzheim et al. 2016). As discussed above, several potential mutualists for *Lophelia pertusa* (e.g. Neulinger et al. 2008, 2009; Kellogg et al. 2009, 2017) and one potential mutualist for *Madrepora oculata* (Hansson et al. 2009) were detected in the Atlantic and the Mediterranean Sea. This reinforces the idea that these bacterial phylotypes are indeed constantly associated with specific corals. The finding that *Endozoicomonas* is associated to many tropical corals and sponges in general as well as to *M. oculata* but rarely to *L. pertusa* suggests that even corals living in the same environment can develop quite variable evolutionary solutions.

In a study in the Mediterranean Sea, where both corals species occurred in the same environment, *M. oculata* was dominated by *Gammaproteobacteria* and *L. pertusa* by *Alphaproteobacteria* (Meistertzheim et al. 2016). At Rockall Bank and at the Apulian Plateau samples were collected from both species. Differences between the two species at the class level (assessed from sequenced DGGE bands) were detected in both environments. At Rockall Bank *L. pertusa* was dominated by *Gammaproteobacteria* and *M. oculata* by *Alphaproteobacteria*. At the Apulian Plateau *L. pertusa* was dominated by *Bacteroidetes* and *Deltaproteobacteria* and for *M. oculata* only *Gammaproteobacteria* were found (this study) (Tables 33.1 and 33.2).

From studies in the field of microbial ecology of warm water corals, it is long known that coral-associated microbes appear to be coral species-specific (e.g. Kuhl et al. 1995; Santavy 1995; Rohwer et al. 2001, 2002; Knowlton and Rohwer 2003) as now seen in the sense of a core microbiome (Fernandez-Agreda et al. 2016, 2017).

Lophelia pertusa seems to be a more opportunistic species than *M. oculata*, both in feeding strategies (Mueller et al. 2014) and associated bacteria (Meistertzheim et al. 2016). Also, there are potential differences in the uptake of dissolved free amino acids by mucus bacteria (Gori et al. 2014) and in the composition of mucus (Wild et al. 2010). The two coral species might have a different temperature tolerance (e.g. Naumann et al. 2014; Maier et al., this volume; Movilla, this volume; Reynaud and Ferrier-Pagès, this volume) and this could influence the microbiome. In addition, genetic differences between coral populations in the same environment could influence bacterial diversity. For example, it was shown that the genetic structure of *L. pertusa* differed between continental margins, offshore banks and fjords in the NE Atlantic (Le Goff-Vitry et al. 2004; Boavida et al., this volume). These factors could contribute to the finding of different bacterial communities associated with *L. pertusa* and *M. oculata*.

33.7 Spatial Variability

Comparative analysis of *Lophelia pertusa* derived 16S rRNA gene sequences from different areas showed that with the exception of potential mutualists, Mediterranean *L. pertusa* hosted bacterial phylotypes (Yakimov et al. 2005) that were almost completely different from those in Norwegian specimens (Neulinger et al. 2008). As discussed above, one of the reasons for that could be that *L. pertusa* has been described as a rather opportunistic species with respect to associated bacteria, whereas for *Madrepora oculata* the host influence could be stronger (Meistertzheim et al. 2016). The spatial differences of bacterial communities could also be due to different biotic or/and abiotic environmental factors between the two areas. For example, in the North Atlantic *L. pertusa* occurs preferentially at a salinity of 32–38.8 and a temperature from 4 to 13 °C (Roberts et al. 2006; Dodds et al. 2007). At Rockall Bank temperature is 6.6–10 °C and salinity ca. 35.5 (van Bleijsweijk 2015), whereas temperature was 9.4–10.4 °C and salinity 35.5 at the Mingulay Reef (this study). Samples of *L. pertusa* from Norwegian CWC reefs were sampled at 8.8 °C and 30.8 (Neulinger et al. 2008). Differences could be due to variations in physicochemical factors between the two areas. Yakimov et al. (2005) found that most deep-water scleractinians collected from the Mediterranean were dead and covered by Fe–Mn oxides. It has been suggested that the relatively limited occurrence of living corals in the Mediterranean Sea compared to the Atlantic is a consequence of the high temperature and salinity in deep waters (12.7–14.5 °C, salinity 38.4–39.0) (Taviani et al. 2005; this study). This temperature seems to be at the upper limit of the thermal tolerance of this species (e.g. Maier et al., this volume).

Environmental factors could also explain the band variability (band number and pattern) and sequence variability at a local scale as reported before for *L. pertusa* (Großkurt 2007; Meistertzheim et al. 2016) and *M. oculata* (Hansson et al. 2009; Meistertzheim et al. 2016). Localised circulation patterns due to the 3D structure of the reef, presence of slopes resulting in differences of the support of nutrition, daily variations of temperature and salinity could affect the physiology of corals, hence the coral associated bacteria (van Bleijsweijk et al. 2015). At Rockall Bank, temperature showed a prominent and relatively large daily variation of ca.

2 °C reflecting the alternation of deep cold water flowing upslope and warmer water flowing downslope (see also van Bleijsweijk et al. 2015). At Mingulay Reef temperature variations of 0.75 °C were observed within 3 h and the hydrographic environment such as downwelling and bottom currents shape the food supply (Davies et al. 2009; Roberts et al. 2009; Findlay et al. 2013). This could result in a variation of the food sources for the corals and thus, influence their metabolism. It is possible that different environmental parameters of the sampled area could affect the diversity of the bacteria consortia associated to the corals.

Biogeographical constancy of certain bacterial groups was reported using DGGE fingerprinting of three different acroporid corals species of two different areas in the Great Barrier Reef (Magnetic island and Orpheus island) separated by 40 km (Littman et al. 2009). The biogeographical constancy of certain bacterial groups was cross-validated by T-RFLP and clone libraries analyses. Nonetheless the numbers of non-shared bacterial groups were conspicuous, indicating geographic separation of coral associated bacteria separated only even by 40 km (Littman et al. 2009). Previous studies have reported that similar bacterial populations have been found on the same coral species that are geographically separated (Rohwer et al. 2001, 2002), suggesting that corals associate with certain bacteria despite geographic separation.

One prerequisite to call an observed coral-microbe association truly “specific” is biogeographical constancy (Neulinger et al. 2008). Schöttner et al. (2012) found that habitat was the main structuring factor for bacterial diversity associated with CWCs. Coral mucus could trap particles and microbes that pass by in the water column (Wild et al. 2004), thus, many microbes trapped in coral mucus are less likely to be true ‘residents’, but rather ‘visitors’ consisting of transient commensal microorganisms (that do no good or harm), or organisms that can potentially become opportunistic under appropriate conditions (Ritchie and Smith 1995). A large bacterial local variability within Mingulay *L. pertusa* was observed by Großkurth (2007). Band variability within areas could be due to fluctuations of local flora and fauna (Ritchie and Smith 1995). Another reason could be related to the different age of the polyps sampled. Different calcification rates between different polyps of different age were observed before for *L. pertusa* and *M. oculata* (Maier et al. 2009; Lartaud et al. 2013, 2014, 2017, this volume; Orejas et al. 2011; Movilla et al. 2014; Reynaud and Ferrier-Pagès this volume), hence different physiological parameters could affect the quality of exuded mucus leading to different microbial associations (Hansson et al. 2009).

The diversity of bacteria associated with CWCs depends on the level of taxonomic resolution applied and differences of levels and methods are likely responsible for some of the differences found between studies (Kellogg et al. 2017). The diversity of bacteria associated with CWCs also varies at variable spatial scales ranging from the within-coral to the across ocean level, and this could also partly explain differences between studies. Concepts such as the three components model of the coral microbiome (Hernandez-Agreda et al. 2017) represent a framework for better understanding CWCs. However, there are also other potentially useful (ecological) concepts such as the metacommunity theory. This concept is an important way to think about linkages between different spatial scales in ecology. A metacommunity can be defined as a set of local communities that are linked by dispersal of multiple potentially interacting species (Leibold et al. 2004). Applied to specific bacterial types associated with CWCs, one could argue within the framework of this concept that the dispersal of bacteria released from or with mucus from corals and the colonisation of other coral specimen contributes to and sustains the bacterial diversity of CWCs at least the site-specific and/or species-specific community and the highly variable community influenced by abiotic and biotic factors in the sense of Hernandez-Agueda et al. (2016).

Overall, these findings indicate that in-depth studies of the role of specific bacteria for the functioning of the coral holobiont constitute a reasonable quest in CWC research. *M. oculata* has received less attention than *L. pertusa* and other scleractinians or gorgonians remain even less studied. Such research is also warranted considering that CWCs are host spots for marine diversity and breeding ground or habitat for fishes and crabs and that they are threatened by fisheries, oil and gas prospecting, global warming and OA.

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References

Ainsworth TD, Fine M, Blackall LL, et al (2006) Fluorescence in situ hybridization and spectral imaging of coral-associated bacterial communities. Appl Environ Microbiol 72:3016–3020

An S, Couteau C, Luo F, et al (2013) Bacterial diversity of surface sand samples from the Gobi and Taklamaken deserts. Microb Ecol 66:850–860

Arnaud-Haond S, Van den Beld IMJ, Becheler R, et al (2015) Two “pillars” of cold-water coral reefs along Atlantic European margins: prevalent association of *Madrepora oculata* with *Lophelia pertusa*, from reef to colony scale. Deep-Sea Res Part 2 Top Stud Oceanogr 145:110–119

Bourne DG, Munn CB (2005) Diversity of bacteria associated with the coral *Pocillopora damicornis* from the Great Barrier Reef. Environ Microbiol 7:1162–1174

Bourne DG, Iida Y, Uthicke S, et al (2008) Changes in coral-associated microbial communities during a bleaching event. ISME J 2:350–363

Brooke S, Jarnegren J (2013) Reproductive periodicity of the scleractinian coral *Lophelia pertusa* from the Trondheim Fjord. Nor Mar Biol 160:139–153

Carlier A, Le Guilloux E, Olu K, et al (2009) Trophic relationships in a deep Mediterranean cold-water coral bank (Santa Maria di Leuca, Ionian Sea). Mar Ecol Progr Ser 397:125–137

Davies AJ, Duineveld GCA, Lavaleye MSS, et al (2009) Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef complex. Limnol Oceanogr 54:620–629

Dodds LA, Roberts JM, Taylor AC, et al (2007) Metabolic tolerance of the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature and dissolved oxygen change. J Exp Mar Biol Ecol 349:205–214

Ducklow HW, Mitchell R (1979) Bacterial populations and adaptations in the mucus layers on living corals. Limnol Oceanogr 24:715–725

Duineveld GCA, Lavaleye MSS, Berghuis EM (2004) Particle flux and food supply to a seamount coldwater coral community (Galicia Bank, NW Spain). Mar Ecol Progr Ser 277:12–23

Findlay HS, Artioli Y, Navas JM, et al (2013) Tidal downwelling and implications for the carbon biogeochemistry of cold-water corals in relation to future ocean acidification and warming. Glob Chang Biol 19:2708–2719

Gori A, Grover R, Orejas C, et al (2014) Uptake of dissolved free amino acids by four cold-water coral species from the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr:42–50

Großkurth A (2007) Analysis of bacterial community composition on the cold-water coral *Lophelia pertusa* and antibacterial effects of coral extracts. Diploma thesis, Carl von Ossietzky Universität, Oldenburg, Germany, 93 pp

Hansson L, Agis M, Maier C, et al (2009) Community composition of bacteria associated with cold-water coral *Madrepora oculata*: within and between colony variability. Mar Ecol Progr Ser 397:89–102

Harder T, Lau SCK, Dobretsov S, et al (2003) A distinctive epibiotic bacterial community on the soft coral *Dendronephthya* sp. and antibacterial activity of coral tissue extracts suggest a chemical mechanism against bacterial epibiosis. FEMS Microbiol Ecol 43:337–347

Heissenberger A, Leppard GG, Herndl GJ (1996) Relationship between the intracellular integrity and the morphology of the capsular envelope in attached and free-living marine bacteria. Appl Environ Microbiol 62:4521–4528

Henry LA, Roberts JM (2007) Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. Deep-Sea Res Part 1 Oceanogr Res Pap 54:654–672

Henry LA, Roberts JM (2017) Global biodiversity in cold-water coral reef ecosystems. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 235–256

Hernandez-Agreda A, Leggat W, Bongaerts P, et al (2016) The microbial signature provides insight into the mechanistic basis of coral success across reef habitats. MBio 7:1–10

Hernandez-Agreda A, Gates RD, Ainsworth TC (2017) Defining the core microbiome in corals' soup. Trends Microbiol 25:125–140

Jensen S, Neufeld JD, Birkeland NK, et al (2008a) Insight into the microbial community structure of a Norwegian deep-water coral reef environment. Deep-Sea Res Part 1 Oceanogr Res Pap 55:1554–1563

Jensen S, Neufeld JD, Birkeland NK, et al (2008b) Methane assimilation and trophic interactions with marine Methylomicrobium in deep-water coral reef sediment off the coast of Norway. FEMS Microbiol Ecol 66:320–330

Kellogg CA (2004) Tropical archaea: diversity associated with the surface microlayer of corals. Mar Ecol Progr Ser 273:81–88

Kellogg CA, Lisle JT, Galkiewicz JP (2009) Culture- independent characterization of bacterial communities associated with the cold-water coral *Lophelia pertusa* in the northeastern Gulf of Mexico. Appl Environ Microbiol 73:5642–5647

Kellogg C, Goldsmith D, Gray M (2017) Biogeographic comparison of *Lophelia*-associated bacterial communities in the western Atlantic reveals conserved core microbiome. Front Microbiol 8:1–15

Kiriakoulakis K, Fisher E, Wolff GA, et al (2005) Lipids and nitrogen isotopes of two deep-water corals from the North-East Atlantic: initial results and implications for their nutrition. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 715–729

Knowlton N, Rohwer F (2003) Multispecies microbial mutualisms on coral reefs: the host as a habitat. Am Nat 162:S51–S62

Kuhl M, Cohen Y, Dalsgaard T, et al (1995) Microenvironment and photosynthesis of zooxanthellae in scleractinian corals studied with microsensors for O2, pH and light. Mar Ecol Progr Ser 117:159–172

Larsson AI, Jarnegren J, Stromberg SM, et al (2014) Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*. PLoS One 9:e102222

Lartaud F, Pareige S, de Rafelis M, et al (2013) A new approach for assessing cold-water coral growth using fluorescent calcein staining. Aquat Living Resour 26:187–196

Lartaud F, Pareige S, de Rafelis M, et al (2014) Temporal changes in the growth of two Mediterranean cold-water coral species, in situ and in aquaria. Deep-Sea Res Part 2 Top Stud Oceanogr 99:64–70

Lartaud F, Meistertzheim AL, Peru E, et al (2017) In situ growth experiments of reef-building cold-water corals: the good, the bad and the ugly. Deep-Sea Res Part 1 Oceanogr Res Pap 121:70–78

Le Goff-Vitry MC, Pybus OG, Rogers D (2004) Genetic structure of the deep-sea coral *Lophelia pertusa* in the northeast Atlantic revealed by microsatellites and internal transcribed spacer sequences. Mol Ecol 13:537–549

Leibold MA, Holyoak M, Mouquet N, et al (2004) The metacommunity concept: a framework for multi-scale communitgy ecology. Ecol Lett 7:601–613

Littman RA, Willis BL, Pfeffer C, et al (2009) Diversity of coral-associated bacteria differs with location but not species for three acroporids on the Great Barrier Reef. FEMS Microbiol Ecol 68:152–163

Maier C, Hegeman J, Weinbauer MG, et al (2009) Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. Biogeosciences 6:1671–1680

Maier C, De Kluijver A, Agis M, et al (2011) Dynamics of nutrients, total organic carbon, prokaryotes and viruses in onboard incubations of cold-water corals. Biogeosciences 8:1–34

Meistertzheim AL, Lartaud F, Arnaud-Haond S, et al (2016) Patterns of bacteria-host associations suggest different ecological strategies between two reef building cold-water coral species. Deep-Sea Res Part 1 Oceanogr Res Pap 114:12–22

Mueller CE, Larsson AL, Veuger B, et al (2014) Opportunistic feeding on various organic food sources by the cold-water coral *Lophelia pertusa*. Biogeosciences 11:123–133

Naumann MS, Orejas C, Ferrier-Pagès C (2014) Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. Deep-Sea Res Part 2 Top Stud Oceanogr 99:36–41

Neave M, Mitchell C, Apprill A, et al (2017) *Endozoicomonas* genomes reveal functional adaptation and plasticity in bacterial strains symbiotically associated with diverse marine hosts. Sci Rep 7:40579

Neulinger SC, Jarnegren J, Ludvigsen M, et al (2008) Phenotype specific bacterial communities in the cold-water coral *Lophelia pertusa*

(Scleractinia) and their implications for the coral's nutrition, health, and distribution. Appl Environ Microbiol 74:7272–7285

Neulinger SC, Gärtner A, Järnegren J, et al (2009) Tissue-associated "Candidatus Mycoplasma corallicola" and filamentous bacteria on the cold-water coral *Lophelia pertusa* (Scleractinia). Appl Environ Microbiol 75:1437–1444

Orejas C, Ferrier-Pagès C, Reynaud S, et al (2011) Long-term growth rates of four Mediterranean cold-water coral species maintained in aquaria. Mar Ecol Progr Ser 429:57–65

Orr JC, Fabry VJ, Aumont O, et al (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Raina JB, Tapiolas D, Willis BL, et al (2009) Coral-associated bacteria and their role in the biogeochemical cycling of sulfur. Appl Environ Microbiol 11:3492–3501

Ray JL, Töpper B, An S, et al (2012) Effect of increased $p\mathrm{CO}_2$ on bacterial assemblage shifts in response to glucose addition in Fram Strait seawater mesocosms. FEMS Microbiol Ecol 82:713–723

Reitner J (2005) Calcifying extracellular mucus substances (EMS) of *Madrepora oculata* – a first geobiological approach. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 731–744

Reshef L, Koren O, Loya Y, et al (2006) The coral probiotic hypothesis. Environ Microbiol 8:2068–2073

Ritchie KB (2006) Regulation of microbial populations by coral surface mucus and mucus-associated bacteria. Mar Ecol Progr Ser 322:1–14

Ritchie KB, Smith GW (1995) Preferential carbon utilization by surface bacterial communities from water mass, normal and white-band diseased *Acropora cervicornis*. Mol Mar Biol Biotechnol 4:345–335

Ritchie KB, Smith GW (2004) Microbial communities of coral surface mucopolysaccharide layers. In: Rosenberg E, Loya Y (eds) Coral health and disease. Springer, Berlin, pp 259–263

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Roberts JM, Davies AJ, Henry LA, et al (2009) Mingulay reef complex: an interdisciplinary study of cold-water coral habitat, hydrography and biodiversity. Mar Ecol Progr Ser 397:139–151

Rogers D (1999) The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef- forming corals and impacts from human activities. Int Rev Hydrobiol 84:315–406

Rohwer F, Breitbart M, Jara J, et al (2001) Diversity of bacteria associated with the Caribbean coral *Montastraea franksi*. Coral Reefs 20:85–95

Rohwer F, Seguritan V, Farooq A, et al (2002) Diversity and distribution of coral- associated bacteria. Mar Ecol Progr Ser 243:1–10

Rosenberg E, Koren O, Reshef L, et al (2007) The role of microorganisms in coral health, disease and evolution. Nat Rev Microbiol 5:355–362

Santavy DL (1995) The diversity of microorganisms associated with marine invertebrates and their roles in the maintenance of ecosystems. In: Allsopp D, Colwell RR, Hawksworth DL (eds) Microbial diversity and ecosystem function. CAB International, Wallingford, pp 211–229

Schöttner S, Hoffmann F, Wild C, et al (2009) Inter- and intra-habitat bacterial diversity associated with cold-water corals. ISME J 3:756–769

Schöttner S, Wild C, Hoffmann F, et al (2012) Spatial scales of bacterial diversity in cold-water coral reef ecosystems. PLoS One 7:e3209324

Silveira CB, Cavalcanti GS, Walter JM, et al (2017) Microbial processes driving coral reef organic carbon flow. FEMS Microbiol Rev 41:575–595

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Turley CM, Roberts JM, Guinotte JM (2007) Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? Coral Reefs 26:445–448

van Bleijsweijk JDL, Whalen C, Duineveld GCA, et al (2015) Microbial assemblages on a cold-water coral mound at the SE Rockall Bank (NE Atlantic): interactions with hydrography and topography. Biogeochemistry 12:4483–4496

Waller RG, Tyler PA (2005) The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic Ocean. Coral Reefs 24:514–522

Weinbauer MG, Ogier J, Maier C (2012) Microbial abundance in the coelenteron and mucus of the cold-water coral *Lophelia pertusa* and in bottom water of the reef environment. Aquat Biol 16:209–216

Wild C, Huettel M, Klueter A (2004) Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. Nature 428:66–70 59

Wild C, Mayr C, Wehrmann L, et al (2008) Organic matter release by cold water corals and its implication for fauna-microbe interactions. Mar Ecol Progr Ser 372:67–75

Wild C, Naumann M, Niggl W, et al (2010) Carbohydrate composition of mucus released by scleractinian warm- and cold-water reef corals. Aquat Biol 10:41–45

Yakimov MM, Cappello S, Crisafi E (2005) Phylogenetic survey of metabolically active microbial communities associated with the deep-sea coral *Lophelia pertusa* from the Apulian plateau, Central Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 53:62–75

Cross References

Boavida J, Becheler R, Addamo A, et al (this volume) Past, present and future connectivity of Mediterranean cold-water corals: patterns, drivers and fate in a technically and environmentally changing world

D'Onghia G (this volume) Cold-water coral as shelter, feeding and life-history critical habitats for fish species: ecological interactions and fishing impact

Lartaud F, Mouchi V, Chapron L, et al (this volume) Growth patterns of Mediterranean calcifying cold-water corals

Maier C, Weinbauer MG, Gattuso J-P (this volume) Fate of Mediterranean scleractinian Cold-Water Corals as a Result of Global Climate Change. A Synthesis

Movilla J (this volume) A case study: variability in the calcification response of Mediterranean cold-water corals to ocean acidification

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Reynaud S, Ferrier-Pagès C (this volume) Biology and ecophysiology of Mediterranean cold-water corals

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Weinbauer MG, Oregoni D, Maier C (this volume) *Lophelia pertusa* and *Madrepora oculata*: an Archaea riddle?

Drop Chapter
Lophelia pertusa and *Madrepora oculata*: An Archaea Riddle?

34

Markus G. Weinbauer, Davide Oregioni,
and Cornelia Maier

Abstract

Lophelia pertusa and *Madrepora oculata* are the two main species building cold-water coral reefs. Habitats within cold-water coral reefs ecosystems such as the water column, sediments, coral rubble, sponges and other corals host a diverse archaeal community. However, *L. pertusa* and *M. oculata* host, if at all, a different archaeal community. The question arises why (some) *Archaea* are excluded from the holobiont and whether this is potentially contributing to the success of *L. pertusa* and *M. oculata* as cold-water coral reef builders.

Keywords

Bacteria · Archaea · Corals · Diversity · Holobiont

In the water column of the oceans, the relative amount of *Archaea* increases with water depth and reaches roughly equivalent numbers compared to *Bacteria* in the mesopelagic zone of the ocean, i.e. the twilight zone between about 200 and 1000 m where the light intensity is too low for sustaining photosynthesis. This increase of archaeal abundance is due to the phylum *Crenarchaeota* (now termed *Thaumarcheota*), whereas the relative abundance of the phylum *Euryarchaeota* remains roughly constant (e.g., Fuhrman et al. 1992; Massana et al. 1997; Fuhrman and Ouverney 1998; Delong and Pace 2001; Delong et al. 1994; Vetriani et al. 1999; Karner et al. 2001). The mesopelagic zone is also the habitat of many cold-water coral reefs (CWCRs). The water column and the sediments surrounding CWCRs are inhabited by *Archaea* (Yakimov et al. 2006; Beman et al. 2007; Hansson et al. 2009); also in CWCRs sponges up to 30% of the prokaryotes could be affiliated to *Archaea* (van Duyl et al. 2008). Studies of prokaryotes on tropical corals have revealed that *Archaea* can be a diverse group of microorganisms associated with the coral holobiont, i.e. the coral itself plus associated microorganisms (Kellogg 2004; Wegley et al. 2004). However, there is comparatively little evidence of *Archaea* associated with the CWCs *Lophelia pertusa* and *Madrepora oculata* as discussed below (see also Table 34.1).

In the present study, samples of *L. pertusa* and *M. oculata* from the NE Atlantic (Rockall Bank and Mingulay reef complex) and the Mediterranean Sea (Apulian plateau) were investigated to assess the presence of *Archaea* in the mucus and whole coral microhabitats. The DNA extraction and PCR approach was the same as used in Hansson et al. (2009) and Weinbauer et al. (this volume). The archaeal primers 344F-GC/915R targeting a 16S rRNA gene fragment, were used with the intention to perform denaturing gradient gel electrophoresis (DGGE) fingerprints. However, no amplification products were obtained from any of the investigated samples (control samples from mesopelagic water revealed PCR products). The DNA was extracted from these samples with a simplified extraction method based on heat and salt treatment (HEATSALT method), thus, this extraction could be biased against *Archaea*. However, an extraction method involving repeated freeze-thawing cycles, proteinase K-lysozyme digestion and phenol-chloroform extraction and the same primers also did not result in a positive PCR product for *Archaea* (Hansson et al. 2009). Further, PCR products were obtained for *Bacteria* in these samples and the amount of PCR product and the number of DGGE products was not systematically different between extraction methods. In addition, there was no difference in the amount of PCR products and the number of DGGE bands between the two DNA

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Table 34.1 Compilation of studies attempting to detect *Archaea* in the cold water corals *Lophelia pertusa* and *Madrepora oculata*

Species	Environment/habitat	Methods	Presence/absence	Type	Reference
L. pertusa	Med Sea, Apulia plateau	cr clone library	–	NA	Yakimov et al. (2006)
L. pertusa + *M. oculata*	NE Atlantic, Rock Bank	16S rRNA PCR	–	NA	Hansson et al. (2009)
L. pertusa + *M. oculata*	NE Atlantic, Med Sea	16S rRNA PCR	–	NA	This study
L. pertusa + *M. oculata*	NE Atlantic, Rockall Bank	CARD-FISH	+	0.9% vs 3%	Unpublished
L. pertusa	Nord-Leska, Norway	454 sequencing	+	*Nitrosopumilus*, *Nitrosoarchaeum*, *Cenarchaeum*	Emblem et al. (2012)
L. pertusa	NE Atlantic, Rockall Bank	454 sequencing	+	11% *Thaumarchaeota* marine class I and 0.5% *Euryarchaeota*	van Bleijsweijk et al. (2015)

For details of methods see Weinbauer et al. this volume (full chapter) and Hansson et al. (2009)
NA: not applicable

extraction methods for mesopelagic water samples from the Mediterranean Sea (Hansson et al. 2009). Also, no archaeal DNA PCR product was obtained when DNA was extracted from corals using a soil extraction kit (Weinbauer et al. unpublished data). It is worthwhile mentioning that the used primers are more specific for *Euryarchaeota* than for *Crenarchaeota* (Winter et al. 2009). However, using the above mentioned primers, archaeal PCR products were obtained for some sponges (the hexactinellidan sponge *Rossella nodastrella* and the demosponges *Hexadella dedritifera, Higginsia thielei* and *Tentorium semisuberites*), the solitary stony coral *Desmophyllum* sp., the gorgonian coral genus *Paramuricea* and an unidentified antipatharian coral from the Rockall Bank CWCR study area (Weinbauer et al. unpublished data).

Using another method, i.e. a DNA library targeting 16S rRNA transcripts, no archaeal PCR products could be detected from metabolically active microbial communities (as assessed by targeting rRNA) associated with the deep water coral *L. pertusa* from the Apulian plateau (Mediterranean Sea; Yakimov et al. 2006). Primers targeting the marker gene accC encoding the biotin carboxylase gene subunit (biotin carboxylase) from Atlantic and Mediterranean coral samples revealed PCR products and sequencing of bands from genetic fingerprints (DGGE) was used to potentially detect *Archaea* and *Bacteria*. The sequences were only related to *Bacteria* and bacterial sequences were similar to the phylotypes obtained from 16S rRNA-based sequences; no *Archaea* were detected. Using Catalysed Reporter Deposition–Fluorescence *In situ* Hybridisation (CARD-FISH), i.e. a single cell based analysis, ≤3% of prokaryotic abundance was due to *Archaea* on. *L. pertusa* (0.9%) and *M. oculata* (3%) in samples from Rockall Bank, whereas, for the same CWCR environment, 9% of the prokaryotes were *Archaea* on *Paramuricea* sp., 8% on *Desmophyllum* sp. and between 5% and 11% on various sponge species (same species as mentioned above). However, data on autofluorescence which could interfere with the CARD-FISH approach do not allow for a definitive proof of the presence of *Archaea* for *L. pertusa* and *M. oculata*, whereas the archaeal counts for other corals and for sponges from the CWCR were higher than the detectable autofluorescence (Weinbauer et al. in preparation). Using 454 sequencing, archaeal sequences (11% *Thaumarchaeota* marine class I and 0.5% *Euryarchaeota*) were detected in the mucus of *L. pertusa* (van Bleijsweijk et al. 2015). In addition, a sequence covering 60% of the whole genome of an archaeon was detected in *L. pertusa* (Emblem et al. 2012). The possibility of contamination from ambient water or sediments during sampling cannot be fully excluded. However, as more than 10% of the sequences were affiliated with *Archaea*, this seems unlikely.

The in-depth sequencing suggests that *Archaea* are present in *L. pertusa*, however, the lack of positive sequences using other primers or probes and the cr clone library indicate that these *Archaea* represent poorly studied (e.g. not detected by all primers) or metabolically not active phylotypes. This compilation of data supports the idea that *L. pertusa* and *M. oculata* specifically exclude (at least some) *Archaea* compared to the water column, sediment, sponges and some other corals in CWCRs. Also, the idea can be put forward that this feature could be linked to the reef forming capacity of *L. pertusa* and *M. oculata.* As *Archaea* are plentiful in tropical hermatypic corals (Kellogg 2004; Wegley et al. 2004), this suggests that *Archaea*-coral associations (or the lack of them) in CWCR are ecosystem-specific. Indeed, archaeal diversity was only habitat-specific in the mucus of Caribbean corals, whereas bacterial diversity was influenced by habitat, coral species and spatial distance (Frade et al. 2016). The reasons could be linked to differences in temperature or lack of photosynthesis, however, this remain unknown. As habitat-specificity seems unlikely –in contrast to tropical corals (Glasl et al. 2017) –species-specific associations seem possible. Considering the high abundance of

Archaea in the abiotic and biotic environment of CWCRs, this represents the riddle why (and how) do *L. pertusa* and *M. oculata* exclude (at least some) *Archaea* from their holobiont.

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References

Beman JM, Roberts KJW, Rohwer F, et al (2007) Distribution and diversity of archaeal ammonia monooxygenase genes associated with corals. Appl Environ Microbiol 73:5642–5647

Delong EF, Pace NR (2001) Environmental diversity of *Bacteria* and *Archaea*. Syst Biol 50:470–478

Delong EF, Wu KY, Prézeli BB, et al (1994) High abundance of *Archaea* in Antarctic marine phytoplankton. Nature 371:695–697

Emblem A, Karlsen BO, Evertsen J, et al (2012) Mitogenome polymorphism in a single branch sample revealed by solid deep sequencing of the *Lophelia pertusa* coral genome. Gene 506:344–349

Frade PR, Roll K, Bergauer K, et al (2016) Archaeal and bacterial communities associated with the surface mucus of Caribbean corals differ in their degree of host specificity and community turnover. PLoS One. https://doi.org/10.1371/journal.pone.0144702

Fuhrman J, Ouverney C (1998) Marine microbial diversity studied via 16S rRNA sequences: cloning results from coastal waters and counting of native archaea with fluorescent single cell probes. Aquat Ecol 32:3–15

Fuhrman JA, McCallum K, Davies AA (1992) Novel major archaebacterial group from marine plankton. Nature 356:148–149

Glasl B, Pongaerts P, Elizabeth NH, et al (2017) Microbiome variation in corals with distinct depth distribution ranges across a shallow–mesophotic gradient (15–85 m). Coral Reefs 36:447–452

Hansson L, Agis M, Maier C, et al (2009) Community composition of bacteria associated with cold-water coral *Madrepora oculata*: within and between colony variability. Mar Ecol Progr Ser 397:89–102

Karner MB, Delong EF, Karl DM (2001) Archaeal dominance in the mesopelagic zone of the Pacific Ocean. Nature 409:507–510

Kellogg C (2004) Tropical *Archaea*: diversity associated with the surface microlayer of corals. Mar Ecol Progr Ser 272:81–88

Massana R, Murray AE, Preston CM, et al (1997) Vertical distribution and phylogenetic characterization of marine planktonic archaea in the Santa Barbara channel. Appl Environ Microbiol 63:50–56

van Bleijsweijk JDL, Whalen C, Duineveld GCA, et al (2015) Microbial assemblages on a cold-water coral mound at the SE Rockall Bank (NE Atlantic): interactions with hydrography and topography. Biogeosciences 12:4483–4496

van Duyl FC, Hegeman J, Hoogstraten A, et al (2008) Dissolved carbon fixation by sponge-microbe consortia of deep water coral mounds in the NE Atlantic Ocean. Mar Ecol Progr Ser 358:137–150

Vetriani C, Jannasch HW, Macgregor BJ, et al (1999) Population structure and phylogenetic characterization of marine benthic *Archaea* in deep-sea sediments. Appl Environ Microbiol 65:4375–4384

Wegley L, Yu Y, Breitbart M, et al (2004) Coral-associated *Archaea*. Mar Ecol Progr Ser 273:89–96

Winter C, Kerros ME, Weinbauer MG (2009) Seasonal changes of bacterial and archaeal communities in the dark ocean: evidence from the Mediterranean sea. Limnol Oceanogr 54:160–170

Yakimov MM, Cappello S, Crisafi E, et al (2006) Phylogenetic survey of metabolically active microbial communities associated with the deep-sea coral *Lophelia pertusa* from the Apulian plateau, central Mediterranean sea. Deep-Sea Res Part 1 Oceanogr Res Pap 53:62–75

Cross Reference

Weinbauer MG, Oregoni D, Grosskurth A, et al (this volume) Diversity of bacteria associated with the cold-water corals *Lophelia pertusa* and *Madrepora oculata*

Biology and Ecophysiology of Mediterranean Cold–Water Corals

35

Stéphanie Reynaud and Christine Ferrier-Pagès

Abstract

Cold-water coral ecosystems represent an important and diverse benthic community in the Mediterranean Sea. Although the distribution of cold-water corals, as well as their diversity, has started to be well studied, little is known about the effects of environmental changes on the physiology of these corals. This chapter presents the state of knowledge on the rates of calcification, respiration, feeding, mucus production and reproduction of the different Mediterranean species under their normal living conditions, and discusses the effects of climate change on the corals' physiology. Our review indicates the need for further investigations, especially on the calcification processes, as well as the natural food sources available in the deep for these corals.

Keywords

Cold water corals · Mediterranean Sea · Respiration · Calcification · Reproduction · Organic matter · Global change

35.1 Introduction

The first observations on the distribution of coral reefs performed at the beginning of the twentieth century suggested that they were mostly thriving in the warm and shallow waters of tropical and subtropical regions; however, more recent investigations, which used advanced technologies, have discovered large coral reefs in the dark, cold, and nutrient-rich deep waters of all world's oceans. While most expeditions have been carried out on cold-water reefs of high latitudes (Freiwald et al. 2004), thriving from 40 to 4000 m depth, large reefs have also been observed in the Mediterranean Sea, where they prosper between 150 and 1200 m (e.g. Zibrowius 1980; Tursi et al. 2004; Taviani et al. 2005; Freiwald et al. 2009; Orejas et al. 2009; Mastrototaro et al. 2010; Addamo et al. 2012; Gori et al. 2013; Savini et al. 2014; Altuna and Poliseno, this volume; Chimienti et al., this volume).

Scleractinian deep-sea corals, often referred as cold-water corals (CWC), are the main reef builders in the deep ocean (Freiwald et al. 2004; Baillon et al. 2012; Roberts and Cairns 2014). Thus, studies on their physiological traits, such as calcification, respiration, reproduction and nutrition are of main importance, because the growth and development of reefs will depend on the health of their main builders. The principal human threats to the deep sea are the disposal of wastes (structures, radioactive wastes, munitions and carbon dioxide), fishing, oil, gas and marine mineral extraction, as well as climate change (Roberts et al. 2009). CWC health is largely impacted by global change threats (Guinotte et al. 2006; Roberts et al. 2006), which could affect more rapidly the Mediterranean Sea than the other oceans, due to its small size and the expected rapid response to global change (Bethoux et al. 1990; Coll et al. 2010; Calvo et al. 2011; Marbà et al. 2015; Maier et al., this volume; Otero and Marin, this volume). Large-scale warming of the Mediterranean Sea has already been observed (Walther et al. 2002; Coma et al. 2009; Vargas-Yáñez et al. 2010), with a 0.5 °C increase in the mean temperature between 1985 and 2000 (Rixen et al. 2005). This mini-ocean is also threatened by seawater acidification (Orr et al. 2005), which has decreased seawater pH by 0.05–0.14 pH units since pre-industrial times (Touratier and Goyet 2011), especially in deep waters where the pH change is estimated to be between −0.005 and −0.086 pH units (Orr et al. 2005; Guinotte et al. 2006; Palmieri et al. 2015). Human-induced global changes have been recognised as main threats to corals in general, whose calcification, among others, is affected both by increased temperature and acidification (Gattuso et al. 1998; Langdon et al. 2000;

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Kleypas et al. 2006; Gazeau et al. 2007; Kuffner et al. 2007); CWC are particularly sensitive to both threats (Guinotte et al. 2006; Roberts et al. 2006; Maier et al. 2013a, b; Movilla et al. 2014a, b). A reduction in CWC distribution has thus been observed between today and the Last Glacial period, during which they were more abundant in continental margins and seamounts (Delibrias and Taviani 1985; Di Geronimo et al. 2005; Wienberg et al. 2010; Vertino et al. 2014, this volume; Taviani et al., this volume; other chapters from the «Past» section of this volume). There is thus an urgent need to investigate which are the best conditions for CWC growth and how they respond to changes in their environment. CWC physiology has been much less studied than tropical species, owing to the difficulty in accessing their habitats and maintaining them for laboratory studies. The physico-chemical conditions which favor CWC growth are thus not well-known; however, several factors, such as the hydrographic conditions and the reef geomorphology, combined to other key environmental parameters such as temperature (Frederiksen et al. 1992; Freiwald et al. 2009; Davies et al. 2009; Roberts et al. 2009; Orejas et al. 2011a; Naumann et al. 2013, 2014; Gori et al. 2014a) and nutrient supply (Mortensen et al. 2001; Roberts et al. 2009; Gori et al. 2015; Orejas et al. 2016) are of major importance for CWC growth. We propose here to review the existing knowledge on calcification, respiration, organic matter (OM) release, feeding rate and reproduction, and how the climate changes influences scleractinian CWC physiology.

35.2 Environmental Effects on Feeding Rates

Food availability is an important factor controlling coral health, because corals need food to survive, as well as to increase their tissue and skeletal mass. *In situ* investigations and isotopes and lipid signature analyses (Duineveld et al. 2004, 2007, 2012; Kiriakoulakis et al. 2005; Carlier et al. 2009; Dodds et al. 2009), as well as experiments performed under laboratory conditions (Mortensen 2001; Roberts and Anderson 2002; Purser et al. 2010; Tsounis et al. 2010; Gori et al. 2015; Orejas et al. 2016; Orejas et al., this volume) have shown that CWC can feed on a wide range of food sources, including detritus, phytoplankton and different size spectrum of zooplankton. Food particles are captured and stuffed into the mouth by the tentacles, or are trapped in mucus and then sucked into the mouth (Yonge and Nicholls 1931; Lewis and Price 1975; Shimeta and Koehl 1997; Riisgard and Larsen 2010). The most conspicuous Mediterranean CWC (*Lophelia pertusa*, *Madrepora oculata*, *Desmophyllum dianthus*, and *Dendrophyllia cornigera*) can also actively take up dissolved OM, such as free amino acids (DFAA) (Gori et al. 2014b). The fact that some animals have the faculty to take up dissolved compounds indicates that this food source can be important when particulate food is scarce (Ambariyanto and Hoegh-Guldberg 1999; Naumann et al. 2011; Gori et al. 2014a). Nevertheless, most studies having investigated the natural feeding behavior of CWC, either using the nitrogen and carbon isotopic signature (Carlier et al. 2009), the fatty acid-lipid composition of prey and coral tissue (Dodds et al. 2009; Naumann et al. 2015), or the prey capture rate (Purser et al. 2010; Tsounis et al. 2010; Orejas et al. 2016), have shown that zooplankton was the preferred food of Mediterranean and Atlantic CWC. However, a study performed on *L. pertusa* using ^{15}N and ^{13}C-labeled prey demonstrated that this CWC species can have an opportunistic feeding strategy according to the external food source (Mueller et al. 2014).

The CWC thus often concentrate on ridges where strong currents enhance food accessibility (Thiem et al. 2006; Davies et al. 2009; Roberts et al. 2009). As such, capture rates depend on water flow (Purser et al. 2010, 2014; Gori et al. 2015; Orejas et al. 2016), which is a primary factor affecting feeding success of passive suspension feeders (LaBarbera 1984; Shimeta and Jumars 1991; Shimeta and Koehl 1997; Wildish and Kristmanson 1997; Wijgerde et al. 2012). High flow speeds (10–16 cm s^{-1}) increase prey encounter and thus prey capture rates (Fabricius et al. 1995; Sebens et al. 1998; Gori et al. 2015), although they can also distort coral polyps, reducing their exposed surface area (Purser et al. 2010; Wijgerde et al. 2012; Gori et al. 2015; Orejas et al. 2016) and the efficiency of nematocysts at holding preys (Sebens et al. 1998). Therefore, an optimal flow speed is specific for each coral species. For example, zooplankton capture efficiency of *L. pertusa* decreases from low (1 and 2.5 cm s^{-1}) to high (10 cm s^{-1}) flow speed (Purser et al. 2010; Tsounis et al. 2010; Orejas et al. 2016), due to the fact that *L. pertusa*, which builds complex three-dimensional reef structures, lives in areas exposed to high flow speed (up to 20 cm s^{-1}), however periods with very reduced flow velocities (<2 cm s^{-1}) are often associated with tides (Davies et al. 2009). On the other hand, capture rates of mesozooplankton by *D. cornigera* are constant over a wide range of flow speeds (up to 10 cm s^{-1}; Gori et al. 2015), because this species does not form, as far as it is currently know, any truly reef structure and has polyps directly exposed to flow (Le Danois 1948; Brito and Ocaña 2004; Sánchez et al. 2009). In addition, the large size of *D. cornigera* polyps allows them to have sufficient tentacle surface exposed to water flow even if they are partially deformed by high flow speed. Food concentration can however mitigate the effect of flow, as capture rates will be positively and significantly correlated with prey abundance (Purser et al. 2010; Osinga et al. 2011). Finally, seawater temperature was shown to be a second major factor affecting feeding success in tropical coral species (Mayor 1916; Edmondson 1928). To protect themselves from a hot or cold shock, CWC are able to slow down polyp contraction or nematocyst function, two factors that reduce feeding rates (Johannes and Tepley 1974; Palardy et al. 2005).

Recent studies have shown that zooplankton starvation induces a general decrease in CWC metabolic functions, leading to reduced calcification and respiration rates as well as mucus excretion (Naumann et al. 2011; Larsson et al. 2013; Baussant et al. 2017). This observation, which needs to be further investigated with different coral species sampled from different environments, suggest that zooplankton abundance plays a major role in the distribution pattern of CWC species. At the moment, there is little information on the natural feeding rates of CWC; although we know they form reefs in food-rich areas (Findlay et al. 2013), information on the nutritional needs of CWC and on the availability of plankton and detrital particles in deep reef environments are still lacking (van Oevelen et al. 2016). As food availability is likely to vary according to locations and seasons, measurements of plankton and other particle concentrations in deep waters, on geographical and temporal scales, are also needed. Analyses of fatty acid and lipid composition of coral tissue and potential food sources can also bring further insights into the nutritional ecology of CWC (Dodds et al. 2009; Gori et al. 2014b; Mueller et al. 2014). Recently, the discovery of chemoautotrophy, the nitrogen fixation and efficient recycling of nitrogen by bacterial community, may play a role in CWC energy intake and may be advantages CWC in a dark and resources-limited conditions (Middelburg et al. 2015; see Orejas et al., this volume).

35.3 Growth Rates and Environmental Response

Several factors determine the expansion of CWC reefs, such as recruitment success, larval distribution, and tolerance to environmental changes. Coral growth rate is also an important parameter, as it concerns the deposition of the carbonate structure of the reef. It can be expressed as linear extension rate or as calcification rate. Linear extension rate corresponds to a skeletal change in one dimension (length), while calcification rate is a change in volume and is equal to the linear extension multiplied by the skeletal density (see Lartaud et al., this volume).

35.3.1 Linear Extension Rates

The first estimations for *Lophelia pertusa* from colonies that had settled on telegraph cables (Duncan 1877), or growing over oil platforms (Bell and Smith 1999; Gass and Roberts 2003) were unusually variable, ranging from 6 to 35 mm year^{-1}. Other measurements performed using skeletal stable isotopes of carbon and oxygen (Mikkelsen et al. 1982; Mortensen and Rapp 1998) have also resulted in variable growth rates, ranging from 6 to 25 mm year^{-1}. These rates were much higher than that recently measured using staining, which ranged from 3.77 to 7.5 mm year^{-1} for branches of *L. pertusa* deployed *in situ* during several months (in the Gulf of Mexico: Brooke and Young 2009; in the northwestern Mediterranean: Lartaud et al. 2013). Food was however suggested to exert a more important control than temperature (Mortensen 2001; Roberts and Anderson 2002). In the Mediterranean Sea, only two studies have investigated the linear extension rates of two CWC species: they ranged from 8 to 17 mm year^{-1}, with an addition of four polyps year^{-1} for *L. pertusa*, and from 3 to 18 mm year^{-1} and five new polyps year^{-1} for *Madrepora oculata* (Orejas et al. 2008, 2011a).

35.3.2 Calcification Rates

The highest calcification rates are measured for tropical corals (between 0.4% and 2.3% increase day^{-1}, Erez 1978; Ferrier-Pagès et al. 2000; Reynaud et al. 2003) since calcification is enhanced by photosynthates provided by the zooxanthellae, the so-called light enhanced calcification process (Goreau 1959; Allemand et al. 1998). Azooxanthellate Mediterranean CWCs have generally lower growth rates compared to shallow-water zooxanthellate species (see Orejas et al. 2011b).

Calcification rates of the species *Dendrophyllia cornigera* from the Mediterranean are consistent among studies and vary between 0.04% day^{-1} and 0.06% day^{-1} (±0.005%) (Orejas et al. 2011a; Naumann et al. 2013; Gori et al. 2014a; Reynaud, *pers. obs.*) (Fig. 35.1). *M. oculata* has however twofold higher growth rates (*ca*. 0.11–0.12% day^{-1} (±0.03%) (Orejas et al. 2011a; Naumann et al. 2014), maybe due to its different shape and tissue thickness compared to *D. cornigera* (Fig. 35.1). It has indeed been hypothesised that the branching form, the high polyp density and polyp budding rate of *M. oculata*, may favor the prey capture efficiency, the energy acquisition and thus, allocation to skeletal growth (Orejas et al. 2011a). Conversely, *D. cornigera*, which has large polyps with a thick soft tissue above the skeleton, may allocate the acquired energy to tissue growth as observed in tropical coral species by Anthony et al. (2002). This "morphology hypothesis" is however not consistent with further measurements performed with solitary corals (*Desmophyllum dianthus*) and branching species *L. pertusa*, which presented similar growth rates: from 0.06 ± 0.03% day^{-1} to 0.23 ± 0.08% day^{-1} for *D. dianthus* (Orejas et al. 2011a; Naumann et al. 2013, 2014), and from 0.02 ± 0.01% day^{-1} to 0.22 ± 0.06% day^{-1} for *L. pertusa* (Orejas et al. 2011a; Naumann et al. 2013). Another hypothesis given as

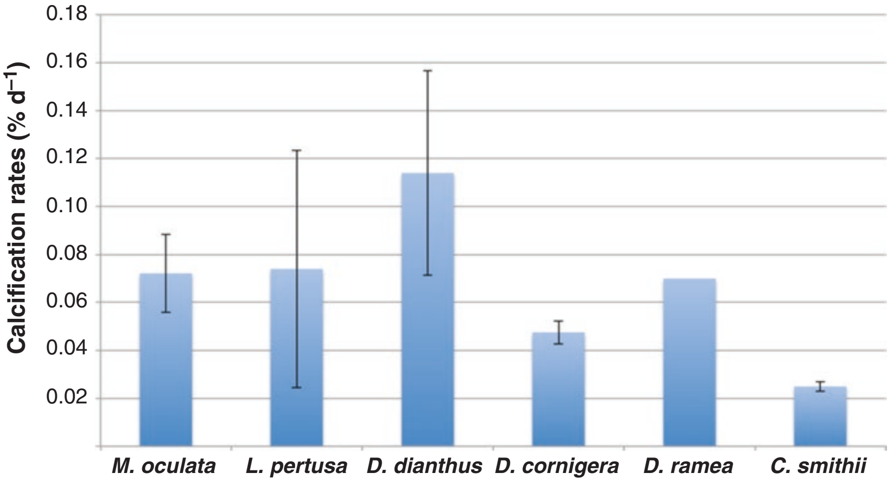

Fig. 35.1 Calcification rates (% day^{-1}) of different Mediterranean CWC species (mean ± SE). The high values for standard errors are due to different techniques used to measured calcification rates (buoyant weight or total alkalinity anomaly), to different feeding regimes, and to different culture temperatures. (Data from Orejas et al. 2011a; Naumann et al. 2011, 2013, 2014; Maier et al. 2012, 2013a, 2016; Gori et al. 2014a; Rodolfo-Metalpa et al. 2015; Reynaud unpublished data). *M. oculata: Madrepora oculata, L. pertusa: Lophelia pertusa, D. dianthus: Desmophyllum dianthus, D. cornigera: Dendrophyllia cornigera, D. ramea: Dendrophyllia ramea, C. smithii: Caryophyllia smithii*

an explanation of the large variation in observed calcification rates is that these rates may rather vary with the age of the colony. In *L. pertusa*, calcification is indeed four orders of magnitude lower in old than in young polyps (Maier et al. 2009; Lartaud et al. 2013; Movilla et al. 2014a), suggesting that bulk calcification is an intermediate value of fast and slow growth rates of young and old corallites, and significantly depends on the ratio of each type of polyps in a branch. In addition, Mortensen (2001) also observed that calcification is not a continuous process in corals, but rather alternates rapid growth periods (max.: 1.2 mm day^{-1}) followed by long pauses (>4 weeks) with almost no growth, being this periodic growth responsible for the density band in coral skeletons. Finally, the budding of new polyps could also contribute to rapid *vs*. long pauses in the growth rate (Gateno and Rinkevich 2003; Maier et al. 2009).

In the Mediterranean Sea, the distribution and growth of CWCs seems to be more limited by temperature than depth, since corals are most commonly distributed between 12.5 and 14 °C, whereas they can thrive between 150 and 1100 m depth (Zibrowius 1980; Taviani et al. 2005; Freiwald et al. 2009; Orejas et al. 2009; Mastrototaro et al. 2010; Gori et al. 2013; Savini et al. 2014; Altuna and Poliseno, this volume; Chimienti et al., this volume). This is in agreement with the common observation that calcification of ectotherm organisms (i.e. organisms whose body temperature varies with the surrounding temperature) is tightly controlled by the ambient seawater temperature (Clausen and Roth 1975; Coles and Jokiel 1977; Howe and Marshall 2002; Dodds et al. 2007; Naumann et al. 2013; Gori et al. 2014a). Above or below an optimal thermal range, many corals indeed lower their calcification and their polyp activity (Howe and Marshall 2001; Previati et al. 2010; Ferrier-Pagès et al. 2012; Gori et al. 2014a), before showing lethal signs (Jokiel and Coles 1977; Coles and Fadlallah 1991; Rodolfo-Metalpa et al. 2006). Physiological experiments performed under laboratory conditions have however demonstrated that some Mediterranean CWC species can grow at maximal rates for temperatures well above their current natural thermal range (12–14 °C). For example, *D. cornigera* colonies maintained during weeks to months at their *in situ* temperature of 12 °C grew twice to three times slower (0.061 ± 0.020% day^{-1}) than those maintained at 16 °C (0.116 ± 0.040% day^{-1}, Gori et al. 2014a), or 17 °C (0.14 ± 0.07% day^{-1}, Naumann et al. 2013). The same observation was made for *Dendrophyllia ramea*, which increased its growth rates between 12 °C (0.021 ± 0.007% day^{-1}) and 24 °C (0.211 ± 0.026% day^{-1}) in a 18-months experiment (Reynaud et al. unpublished data). In addition to presenting increased growth, both *Dendrophyllia* species also formed new polyps, suggesting efficient thermal acclimatisation. Higher thermal threshold was also tested on *D. dianthus*, which showed 87 days constant growth rate at 12 °C (*in situ* temperature) and 17 °C (0.23 ± 0.08% day^{-1} *vs*. 0.19 ± 0.06% day^{-1}) (Naumann et al. 2013). However, when exposed to a longer period at elevated temperature (8 months at 15 °C, Gori et al. 2016), calcification rates significantly decreased. Contrary to a thermal increase, a decrease in temperature from 12 to 8 °C, or 6 °C (temperature occurring in the reefs of the North Sea and Atlantic) induced a drop in the calcification rates of Mediterranean colonies of *L. pertusa* (58%, Naumann et al. 2014), *M. oculata* (69%, Naumann et al. 2014), and *D. cornigera* (69%, Gori et al. 2014a). However, no mortality was observed between 6–8 °C and 17 °C, suggesting that

CWC of the Mediterranean Sea have thermal thresholds higher than previously assumed (Naumann et al. 2013).

Calcification rates of CWC may also be impacted by ocean acidification (OA), however, as two chapters of this volume (Maier et al., this volume; Movilla, this volume) deal with this topic, no much detail will be offer on this aspect in the present chapter. Briefly, among the studies that have experimentally assessed CWC calcification rates under different pH/$p\mathrm{CO}_2$ levels, seven were conducted with Mediterranean species. Maier et al. (2012) showed that colonies of *M. oculata,* incubated under high $p\mathrm{CO}_2$ (from 404 to 867 µatm) for 24 h directly after sampling, didn't show any change in calcification rates (0.06 ± 0.06% day^{-1}). These rates however doubled (0.12 ± 0.06% day^{-1}) when colonies were incubated at the pre-industrial $p\mathrm{CO}_2$ level (285 µatm), compared to the current higher level. It is possible that *M. oculata* exhibits a nonlinear response to $p\mathrm{CO}_2$ increase as it has been observed with the temperate shallow and symbiotic coral *Oculina arbuscula*, whose calcification rate only decreased at a $p\mathrm{CO}_2$ above 2800 µatm (Ries et al. 2010). Concerning *L. pertusa,* its calcification declined by 26–29% during a short-term exposure (1 week) to a 0.1 unit decrease in pH, but was slightly enhanced when the corals were exposed to low pH for more than 6 months (Form and Riebesell 2012). A lack of calcification decline at high $p\mathrm{CO}_2$ was also observed for *L. pertusa* and *M. oculata* reared between 6 and 9 months at pH values expected by the end of the century (Maier et al. 2013a; Movilla et al. 2014a), and for *D. cornigera* after 11 months of culture (Movilla et al. 2014b). These studies therefore suggest that short-term experiments may underestimate the acclimation capacities of CWC to OA and their capacity to maintain maximal calcification rates under carbonate chemistry changes.

Food availability can also influence CWC response to pH decline. Until now, OA studies were performed with starved corals (Maier et al. 2012), or corals fed with artificial food (Hennige et al. 2013; Carreiro-Silva et al. 2014; Movilla et al. 2014a,b; Rodolfo-Metalpa et al. 2015). Sometimes artificial diet was used several years before the beginning of the experiment (e.g. Movilla et al. 2014a, b), inducing a coral metabolism probably completely different than the one they display under natural conditions. Only one study (Rodolfo-Metalpa et al. 2015) carried out a transplantation experiment in the $p\mathrm{CO}_2$ vent of Ischia (Italy), with the aim to investigate both natural OA and feeding conditions. Under both high and low $p\mathrm{CO}_2$ conditions, calcification rates were 44% lower than those measured in aquaria with artificially fed corals (at similar temperature and pH). This experiment suggests that artificial feeding significantly changes the calcification rates and response of CWC to stress; however, CWC in Ischia were transplanted in very shallow waters which are not the normal living area of CWC, which might have significantly differed in nutritional quality compared to the deep environment. Nonetheless, *in situ* and experimental studies all show that CWC are able to calcify at maximal rates even at predicted levels of increased $p\mathrm{CO}_2$ and normal growth temperatures. The only study combining rising temperatures and $p\mathrm{CO}_2$ on *D. dianthus* calcification (Gori et al. 2016) showed that temperature had a greater impact than pH. Furthermore, a clear synergistic effect of the two stressors was observed, resulting in a higher reduction in coral metabolism compared to thermal stress alone.

Since temperature and $p\mathrm{CO}_2$ are likely to increase in parallel in the future, more studies combining both stressors are needed to fully understand the impact of climate change on CWC physiology. In addition to these physical stressors, in the future acidified ocean there might also be a decrease of particulate organic matter (POM) supply to the deep-sea, due to the reduction of surface primary production (Mora et al. 2013; Jones et al. 2014). Hence, further studies should also include scenarios with reduce POM load to better understand the importance of the nutritional status on the CWC response to stress.

35.4 Respiration Rates

In aerobic organisms, such as CWC, the oxygen consumption rate or respiration is directly proportional to the basic metabolic rate, which corresponds to the rate of energy used by an organism to support basic body functions essential for its maintenance (mainly the metabolic costs of protein turnover and ion homeostasis). Cellular respiration is thus a set of metabolic reactions that convert biochemical energy from stored nutrients (sugars, fatty acids and amino acids) into adenosine triphosphate (ATP) required for metabolism.

Respiration rates of many Mediterranean CWC species measured at their *in situ* temperatures are in the same order of magnitude, suggesting that these corals have the same metabolic needs: *Dendrophyllia cornigera* (2.0 ± 0.3 µmol C cm^{-2} day^{-1}, Gori et al. 2014a), *Lophelia. pertusa*, *Madrepora oculata* (3.8 ± 1.0 and 3.2 ± 0.6 µmol C cm^{-2} day^{-1}; Naumann et al. 2014), and *Desmophyllum dianthus* (3.0 ± 0.8 µmol C cm^{-2} day^{-1} in Naumann et al. 2011; 1.34 µmol C cm^{-2} and 3.6 µmol C cm^{-2} in Gori et al. 2014b, 2016, respectively). Mediterranean CWC respiration rates are however lower than those measured in tropical corals (e.g. *Stylophora pistillata* maintained in the dark: 4.0–7.4 µmol C cm^{-2} day^{-1}; Houlbrèque et al. 2003), indicating a reduced metabolic activity in CWC compared to their warm water congeners. On the contrary, Atlantic *L. pertusa* respiration rates are lower than those measured from Mediterranean: 30% lower for specimens of Scottish waters (Dodds et al. 2007) and even lower for *L. pertusa* in the Norwegian fjords 75% (Larsson et al. 2013). Coral metabolic activity is indeed generally positively correlated to temperature (e.g. Edmunds

2005; Dodds et al. 2007; Naumann et al. 2014), independently of the corals' symbiotic state (Jacques and Pilson 1980).

Several other environmental factors affect CWC respiration rates, such as zooplankton consumption. As zooplankton is a main source of nutrients rapidly convertible into energy, respiration rates were positively correlated with grazing rates (Jacques and Pilson 1980; Naumann et al. 2011; Gori et al. 2014b). In turn, zooplankton exclusion (i.e. starvation) reduced respiration rates of *D. dianthus* from the Mediterranean by 20% after 1 week of maintenance in such conditions, by 49% and 62% after 2 and 3 weeks respectively (Naumann et al. 2011), and 39% after 28 weeks in *L. pertusa* from Northeast Atlantic waters (Larsson et al. 2013). Respiration rates were also observed to increase in parallel to seawater temperature, in *L. pertusa* sampled in Scotland (from 9 to 11 °C, Dodds et al. 2007), *D. cornigera* from Spain (from 12 to 16 °C, Gori et al. 2014a; Reynaud unpublished data), in *D. dianthus* from Italy (Gori et al. 2016) and in *Dendrophyllia ramea* from Cyprus (from 20 to 24 °C Reynaud et al. unpublished data), suggesting that corals can tightly control their metabolic activity within their natural thermal range. Outside this thermal range, stress induced an abnormal elevation in CWC respiration rates (Khripounoff et al. 2014). Similarly, a 3–4 °C decrease in seawater temperature induced a parallel decline in respiration rates of *M. oculata* (from 12 to 9 °C, Naumann et al. 2014) and *D. cornigera* (from 12 to 8 °C, Gori et al. 2014a). This pattern was however not observed for all temperatures and coral species: respiration rates were thus unaffected in *L. pertusa* between 12 and 6 °C, nor in *M. oculata* between 9 and 6 °C (Naumann et al. 2014), suggesting a wide thermal tolerance window (perhaps due to regional differences and biogeographic variability) and/or strong physiological capacity for thermal adjustment for these species to low temperatures. Laboratory experiments also showed that respiration rates were unaffected by acidification in many CWC species (Maier et al. 2013b, 2016; Rodolfo-Metalpa et al. 2015). It would have been expected that the up-regulation of the internal pH under acidification stress would have required more energy, and thus higher respiration rates. This discrepancy might be due to the corals feeding in laboratory experiments, masking the real effect of acidification on the respiration rates (Carreiro-Silva et al. 2014; Rodolfo-Metalpa et al. 2015; Gori et al. 2016; Maier et al. 2016). Future research should therefore aim to further investigate the effect of short- and long-term starvation on the respiration rates of CWC and combine both, starvation and environmental stresses, to assess the resistance and resilience of CWC. Another explanation for this discrepancy might be partially due to natural variation among the studied populations (Georgian et al. 2016). These authors have tested the physiological response of *L. pertusa* populations to three pH treatments in the Gulf of Mexico (GoM, USA) and the Tisler Reef (Norway). The authors found that GoM populations exhibited decrease in respiration rates, conversely the populations from the Tisler Reef displayed higher respiration rates. These differences are likely the result of environmental disparities between the two regions, invoking the potential for local adaptation or acclimatisation to global change. The lack of understanding of how biogeographically disconnected populations will answer to OA hampers our prediction capability.

35.5 Organic Matter Fluxes

It is well known from the first studies performed on tropical corals that all coral species, including CWC, release organic matter (OM) into the surrounding seawater, in dissolved (DOM) or particulate (POM) forms (Ferrier-Pagès et al. 1998; Wild et al. 2008; Naumann et al. 2010), including spawning products and mucus (e.g. Harrison et al. 1984; Crossland 1987; Brown and Bythell 2005; Bythell and Wild 2011). Mucus is used to capture small food particles (Lewis and Price 1975; Shimeta and Koehl 1997; Riisgard and Larsen 2010) and it is also considered as a protection against sedimentation (Schuhmacher 1977) and microbe infection (Ritchie 2006; Bythell and Wild 2011). OM release makes an essential contribution to the ecological functioning of coral reefs, because it is degraded by prokaryotes through their extracellular enzyme activity and is used for bacterial growth (Cunha et al. 2010), or it enters into the recycling pathways of carbon and nitrogen (Wild et al. 2004). OM therefore supports pelagic and benthic production and plays a major role in the nutrient cycles and trophic structure of reef ecosystems (Bythell and Wild 2011). Recently, the importance of coral mucus to fuel the entire ecosystem *via* a sponge loop has also been demonstrated in tropical reefs (Rix et al. 2016). Both healthy and stressed corals can take up particulate (Anthony 1999, 2000; Ferrier-Pagès et al. 2011) and dissolved OM (Tremblay et al. 2012; Levas et al. 2015) for their own energetic needs. This is particularly important in deep-sea environments, which are considered to be energy-limited ecosystems (McClain et al. 2012) and where CWCs have an opportunistic feeding (Duineveld et al. 2007; van Oevelen et al. 2009; Mueller et al. 2014). OM fluxes are therefore in two directions: from the corals to seawater and inversely. In general, POC release by the CWC tended to be lower, and DOC release rates tended to be higher than rates reported for warm water corals. In CWC reefs, where more planktonic food is usually available for the corals (Freiwald et al. 2004), it may be energetically more favorable to release DOC into the surrounding water.

Studies on OM fluxes have mainly been performed in laboratory experiments, by measuring, over few hours, the quality and quantity of OM released or taken up by a coral

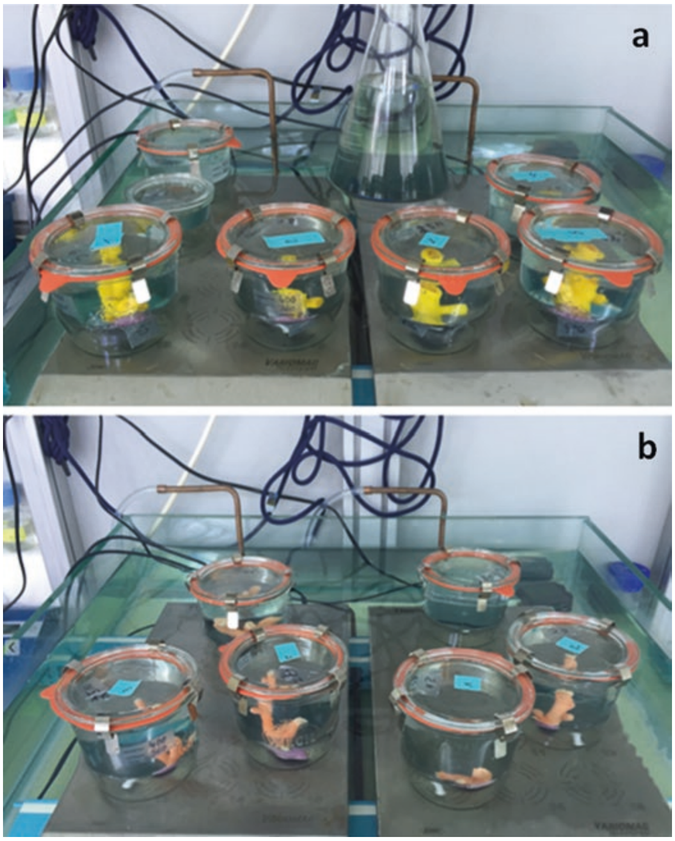

Fig. 35.2 Incubation of *Dendrophyllia cornigera* (**a**) and *Dendrophyllia ramea* (**b**) in closed chambers containing a small magnet in order to keep the water in movement thanks to the magnetic plate where the chambers are placed. During the incubations, rates of calcification, respiration and Total Organic Carbon (TOC) excretion were measured. Incubations last for 6 h. (Photographs: © S. Reynaud)

colony reared in incubation chambers (Fig. 35.2). Several studies reported high amounts of total organic carbon (TOC), or DOC, excreted by CWCs under their normal growth conditions and without a stimulus (Wild et al. 2008, 2010; Maier et al. 2011, 2016; Naumann et al. 2011, 2014; Gori et al. 2014a). Higher OM release rates were observed in response to food supply, mechanical and electrical disturbances (Shelton 1980; Mortensen et al. 2001; Zetsche et al. 2016), microorganisms' infection and exposure to high concentrations of suspended sediment (Brooke et al. 2009; Larsson et al. 2013). Depending on the type of stimuli, the quality of the released mucus can however be different (more or less "watery"), and will thus require more or less energetic investment (Zetsche et al. 2016). The use of digital holographic microscopy (DHM) also showed that mucus production starts from the thecal regions and moves from the calyx to the base of the coral polyp (Zetsche et al. 2016). The highest release rates for CWCs under natural conditions were observed for *Lophelia pertusa* from NE Atlantic (~9.6 μmol C cm^{-2} day^{-1}, Wild et al. 2008, and 4.6 μmol C cm^{-2} day^{-1}, Maier et al. 2011) and *Madrepora oculata* (4.2 μmol C cm^{-2} day^{-1}, Maier et al. 2011). Lower release rates were measured in Mediterranean corals, for *Dendrophyllia cornigera* (0.88 ± 0.34 μmol C cm^{-2} day^{-1}; Gori et al. 2014a) and *Desmophyllum dianthus* (0.4 μmol C cm^{-2} day^{-1}, Naumann et al. 2011). This large difference in OM production can be species specific, as found for tropical zooxanthellate corals (Naumann et al. 2010), or linked to the coral morphology (Lewis and Price 1975; Shimeta and Koehl 1997), since species with large polyps (*D. cornigera* and *D. dianthus*), that can capture big preys, do not usually need to release large amounts of mucus for small prey capture. The huge discrepancy in OM production can also be due to the differences in food quantity, quality and richness, the seasonality in OM production, or related to the dynamic physical environment in which CWC reefs occur (Duineveld et al. 2007; Davies et al. 2009; Purser et al. 2010; Findlay et al. 2013).

Several environmental factors can affect OM fluxes in CWCs, as already described above. However, temperature and feeding are the two main parameters tested on mucus release. A short-term (5 weeks) increase in temperature reduced TOC release rates in *D. ramea*, or *D. cornigera* (unpublished data), while a long-term temperature increase (5 months) had no effect on the OM production by *D. cornigera* (Gori et al. 2014a). On the contrary, a temperature decrease induced a shift from TOC release to uptake in *D. cornigera* (Gori et al. 2014a). This finding is in agreement with the significant reduction observed in coral metabolism at this low temperature, since OM release depends on the corals' metabolic activity (Wild et al. 2008; Naumann et al. 2011). Such a reduction was previously observed in tropical corals when seawater temperature fell below their natural thermal range (Coles and Fadlallah 1991; Kemp et al. 2011). OM fluxes are also affected by the corals' feeding status, but due to the high variability from one species to another one, or even from one colony to another (e.g. in Maier et al. 2016, from −4.16 to 55.46 μmol TOC g^{-1} skeleton h^{-1}), it's difficult to understand the effect of feeding and/or starvation on TOC release rates. Well-fed colonies of *D. dianthus* were shown to release, mainly in the form of DOC, 7% of the daily organic carbon uptake through zooplankton feeding (Wild et al. 2008). Subsequent studies performed on *Madrepora* tended to show however that TOC release rates were generally higher for slightly fed or starved corals than for well-fed corals (Maier et al. 2016; Baussant et al. 2017) (respectively 1.89 and −0.12 μmol g^{-1} skeleton h^{-1} for starved and fed corals, Maier et al. 2016).

The above studies clearly show that more investigations are needed to fully understand which factors induce OM release and/or uptake in CWC. Climate change can directly or indirectly alter the quality and quantity of the released OM and change the associated bacterial diversity, as observed in tropical corals (Ainsworth and Hoegh-Guldberg 2009) and in CWC (see Weinbauer et al., this volume), likely affecting OM degradation rates. Understanding how the different stresses alter OM fluxes, microbial degradation rates and microbial growth will improve our understanding on future changes of the deep reef biogeochemical cycling, remineralisation pathway and trophic structure.

35.6 Reproduction

Knowledge about reproductive seasonality, gamete quality, fecundity and larval supply is essential for understanding ecosystem resilience and biogeographic dispersion. In addition, the distribution pattern of larvae gives insights into population connectivity and colonisation of different oceanic areas. Reproduction is highly stress dependent (a coral will stop reproducing when stressed) so the reproductive status of coral populations can be used as a health proxy. For example, Waller and Tyler (2005) observed that under trawling stress no *Lophelia* were sexually mature, while they were all in a reproductive state in a preserved area. To survive to their environment, corals have developed several asexual reproductive strategies: fragmentation (Highsmith 1982), polyp bail-out (Rosen and Taylor 1969; Sammarco 1982), parthenogenesis (Stoddart 1983; Ayre and Resing 1986; Yeoh and Dai 2010), or production of genetically identical larvae due to cleavage (Heyward and Negri 2012). To date, fragmentation is the only known mode of asexual reproduction in *L. pertusa* (Dahl et al. 2012). Fragmentation occurs naturally when coral pieces are broken off a colony as a result of waves and storms for shallow corals (Lirman 2000), or induced by animal/human activities. Under favorable conditions, these fragments can attach to a substrate and develop into new colonies. Sexual reproduction (fusion of sperm and eggs) is however essential to maintain genetic diversity of a species.

Little is known of the basic reproductive biology of CWC and most observations were performed on few coral species, such as *Lophelia pertusa* (e.g. Waller and Tyler 2005; Brooke and Järnegren 2013; Pires et al. 2014), *Madrepora oculata* (Waller and Tyler 2005; Pires et al. 2014), *Oculina varicosa* (Brooke and Young 2003), *Enallopsammia rostrata*, *Solenosmilia variabilis* (Burgess and Babcock 2005; Waller 2005; Pires et al. 2014), *Goniocorella dumosa* (Waller 2005) and *Fungiacyathus marenzelleri* (Waller and Feehan 2013). In contrast to structure-forming colonial species, which appear to be uniformly gonochoristic broadcast spawners (Brooke and Young 2003; Burgess and Babcock 2005; Waller 2005; Waller and Tyler 2005; Pires et al. 2014), cold-water solitary scleractinians, such as *Flabellum* sp. (Waller et al. 2008; Mercier et al. 2011; Waller and Tyler 2011), *Caryophyllia* sp. (Waller et al. 2005), and *Fungiacyathus* sp. (Waller et al. 2002; Flint et al. 2007; Waller and Feehan 2013), have various reproductive features and strategies, including hermaphroditism, gonochorism, brooding, and broadcast spawning. It is impossible to distinguish the sex of individual polyps from external morphology. Gametes can only be observed after fixation and decalcification (Brooke 2002; Waller 2003). Microscopic observations showed that sperm develop in cysts held together by a mesogleal envelope (spermacysts or spermatic cysts), while oocytes are often found in groups or 'pockets', but without connection between them. All gonads develop in the lamellae of the mesenteries, eventually migrating into the mesoglea (Brooke 2002; Waller et al. 2002; Waller 2005; Waller and Feehan 2013). Gametogenesis can be quasi-continuous in *Caryophyllia* species (Waller et al. 2002), in *E. rostrata* (Burgess and Babcock 2005), or in *F. marenzelleri* (Waller et al. 2002, 2005; Waller and Feehan 2013) or clearly continuous in *M. oculata* (Pires et al. 2014). Gametogenesis can also be periodic, or seasonally-controlled in *L. pertusa* (Waller and Tyler 2005; Brooke and Järnegren 2013; Pires et al. 2014). The seasonal control is not through temperature or light (moon light) as in shallow species (Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990), because CWC live in the dark and below the thermocline; therefore, seasonal fluctuations in phytodetritus input from surface waters (Billett et al. 1983; Tyler et al. 1992, 1993; Rice and Lambshead 1994) may rather control reproduction (Waller and Tyler 2005; Mercier et al. 2011; Brooke and Järnegren 2013). However, this is not the case for *L. pertusa*, as well as *O. varicosa*, since they produce a single cohort per year (Brooke and Young 2003; Waller and Tyler 2005; Brooke and Järnegren 2013) of small oocytes (an average of 3300 oocytes per cm^2, 140 μm diameter maximum) and do not seem to be affected by food supply (Larsson et al. 2014).

Most CWC species, such as the reef builders *L. pertusa* and *M. oculata* are gonochoric, i.e. males and females exist as separate individuals (Brooke and Young 2003; Burgess and Babcock 2005; Waller 2005; Kerr et al. 2010; Pires et al. 2014), while their tropical congeners are rather hermaphroditic, i.e. the same polyp displays both active male and female gonads (Fadlallah 1983; Richmond and Hunter 1990; Harrison 2011). Only the genus *Caryophyllia* (Waller et al. 2005), and *Flabellum* (Mercier et al. 2011; Waller and Tyler 2011) are hermaphroditic CWC. Gonochorism is a more primitive adaptation than hermaphroditism (Goffredo et al. 2002) and may be more important for maintaining genetic diversity (Szmant 1986). In addition, all CWC investigated to date are broadcast spawners, releasing sperm or eggs near-continually in the water column and preventing self-fertilisation (Waller 2005; Waller and Feehan 2013; Pires et al. 2014), while some tropical, and Antarctic sea anemona species (Rodriguez et al. 2013) can also be brooders (internal fertilisation and embryogenesis before releasing larvae).

The larval stage has been poorly studied in CWC, due to the difficulty in observing larvae at several hundreds or thousands of meters depth. Like many species of shallow-water reef corals, deep-sea species need hard substrates for larval settlement. Deep-water coral species therefore settle on dead scleractinian skeletons, rock fragments, shells or Polychaeta tubes (Rogers 1999). The larval lifespan has only been studied under laboratory conditions. A larval lifespan of 14–21 days has been observed for the coral *O. varicosa*, before settlement on a hard substratum (Brooke 2002; Brooke and Young 2003), while a lifespan of 8 weeks was recorded for the larvae of *L. pertusa* (Larsson et al. 2014). In addition, Rinkevich and Loya (1979) first stipulated that all CWC larvae are lecithotrophic, i.e. they feed only after settlement and metamorphosis. This is in agreement with the observations of large mature oocytes in *M. oculata*, *S. variabilis* and *E. rostrata*. However, Larsson et al. (2014) observed that *L. pertusa* larvae were rather planktotrophic as previously suggested by Waller and Tyler (2005). Before settlement, larvae have thus a planktonic life, and their swimming behavior is similar to that of other scleractinian larvae. Most larvae swim in a rotary clockwise or counter-clockwise mode around the oral-aboral axis, and many of them are characterised by positive phototactic and/or negative geotactic responses (Fadlallah 1983). Therefore, in *O. varicosa*, early stage larvae swim towards the surface responding to geotactic signals, whereas later stage larvae display negative phototactic behaviour (Brooke and Young 2005). In *L. pertusa*, larvae show strongly negatively geotactic signal during the 1st week following fertilisation (Larsson et al. 2014), and reach the bottom 3 weeks after fertilisation. Such behavior avoids the risk of being eaten by benthic predators (Brooke and Young 2003), and/or is a way to reach the photic layer with a higher quality and quantity of food.

It is obvious from the few observations above that more work is needed on CWC reproduction and especially on the larval stages, which are particularly understudied. For instance, future experiments assessing the impact of low pH on the reproductive investment would be crucial for understanding the response of CWC to OA.

35.7 Conclusions

Although CWCs function as ecosystem engineers in many deep environments, they have received significantly less attention than shallow tropical and temperate corals, whose physiology and holobiont composition have been extensively studied. CWC are, however, severely affected by anthropogenic changes or pollution, and therefore deserve further research, particularly at the physiological level, for processes such as calcification, growth, reproduction or feeding. Such knowledge is required to understand which environmental factors determine the abundance and development of CWC in the Mediterranean Sea, as well as their response to climate-change induced perturbations. More basic research on the CWC trophic ecology is needed to assess which type of food is available in deep waters and understand how resource supply and demand by CWC determine their relative abundance in the deep oceans. Overall, understanding deep food webs will help to more accurately assess the function of these complex reef systems and predict how they will be affected by climate change. In addition, targeting knowledge gaps in CWC life history (such as growth rates, age, size of reproductive maturity, larval dispersal, etc.…) will be essential for conservation and management of CWC species worldwide.

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References

Addamo AM, Reimer JD, Taviani M, et al (2012) *Desmophyllum dianthus* (Esper, 1794) in the Scleractinian phylogeny and its intraspecific diversity. PLoS One 7:1–9

Ainsworth TD, Hoegh-Guldberg O (2009) Bacterial communities closely associated with coral tissues vary under experimental and natural reef conditions and thermal stress. Aquat Biol 4:289–296

Allemand D, Furla P, Bénazet-Tambutté S (1998) Mechanisms of carbon acquisition for endosymbiont photosynthesis in Anthozoa. Can J Bot Rev Can Bot 76:925–941

Ambariyanto, Hoegh-Guldberg O (1999) Net uptake of dissolved free amino acids by the giant clam, *Tridacna maxima*: alternative sources of energy and nitrogen? Coral Reefs 18:91–96

Anthony KRN (1999) Coral suspension feeding on fine particulate matter. J Exp Mar Biol Ecol 232:85–106

Anthony KRN (2000) Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). Coral Reefs 19:59–67

Anthony KRN, Connolly SR, Willis BR (2002) Comparative analysis of energy allocation to tissue and skeletal growth in corals. Limnol Oceanogr 47:1417–1429

Ayre DJ, Resing JM (1986) Sexual and asexual production of planulae in reef corals. Mar Biol 90:187–190

Baillon S, Hamel JF, Wareham VE, et al (2012) Deep cold-water corals as nurseries for fish larvae. Front Ecol Environ 10:351–356

Baussant T, Nilsen M, Ravagnan E, et al (2017) Physiological responses and lipid storage of the coral *Lophelia pertusa* at varying food density. J Toxicol Environ Health A 80:266–284

Bell N, Smith J (1999) Coral growing on North Sea oil rigs. Nature 402:601

Bethoux JP, Gentili B, Raunet J, et al (1990) Warming trend in the western Mediterranean deep water. Nature 347:660–662

Billett DSM, Lampitt RS, Rice AL, et al (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature 302:520–522

Brito A, Ocaña O (2004) Corales de las islas Canarias. Antozoos con esqueleto de los fondos litorales y profundos. Francisco Lemus Editor, La Laguna, 475 pp

Brooke SD (2002) Reproductive ecology of a deep-water scleractinian coral, *Oculina varicosa* from the South East Florida Shelf. PhD thesis, School of Ocean and Earth Science, Southampton Oceanography Centre, Southampton, p 160

Brooke S, Järnegren J (2013) Reproductive periodicity of the deep-water scleractinian coral, *Lophelia pertusa* from the Trondheim Fjord, Norway. Mar Biol 160:139–153

Brooke S, Young CM (2003) Reproductive ecology of a deep-water scleractinian coral, *Oculina varicosa*, from the southeast Florida shelf. Cont Shelf Res 23:847–858

Brooke S, Young CM (2005) Embryogenesis and larval biology of the ahermatypic scleractinian *Oculina varicosa*. Mar Biol 146:665–675

Brooke S, Young CM (2009) Direct measurements of *in situ* survival and growth of *Lophelia pertusa* in the northern Gulf of Mexico. Mar Ecol Progr Ser 397:153–161

Brooke S, Holmes M, Young CM (2009) Effects of sediment on two morphotypes of *Lophelia pertusa* from the Gulf of Mexico. Mar Ecol Progr Ser 390:137–144

Brown BE, Bythell JC (2005) Perspectives on mucus secretion in reef corals. Mar Ecol Progr Ser 296:291–309

Burgess S, Babcock RC (2005) Reproductive ecology of three reef-forming, deep-sea corals in the New Zealand region. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 701–713

Bythell JC, Wild C (2011) Biology and ecology of coral mucus release. J Exp Mar Biol Ecol 408:88–93

Calvo E, Simo R, Coma R, et al (2011) Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. Clim Res 50:1–29

Carlier A, Le Guilloux E, Olu K, et al (2009) Trophic relationships in a deep Mediterranean cold-water coral bank (Santa Maria di Leuca, Ionian Sea). Mar Ecol Progr Ser 397:125–137

Carreiro-Silva M, Cerqueira T, Godinho A, et al (2014) Molecular mechanisms underlying the physiological responses of the cold-water coral *Desmophyllum dianthus* to ocean acidification. Coral Reefs 33:465–476

Clausen CD, Roth AA (1975) Estimation of coral growth-rates from laboratory ^{45}Ca-incorporation rates. Mar Biol 33:85–91

Coles SL, Fadlallah YH (1991) Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. Coral Reefs 9:231–237

Coles SL, Jokiel PL (1977) Effects of temperature on photosynthesis and respiration in hermatypic corals. Mar Bio 143:209–216

Coll M, Piroddi C, Steenbeek J, et al (2010) The biodiversity of the Mediterranean Sea: estimates, patterns and threats. PLoS One 5:e11842. https://doi.org/10.1371/journal.pone.0011842

Coma R, Ribes M, Serrano E, et al (2009) Global warming-enhanced stratification and mass mortality events in the Mediterranean. Proc Natl Acad Sci U S A 106:6176–6181

Crossland CJ (1987) *In situ* release of mucus and DOC-lipid from the corals *Acropora variabilis* and *Stylophora pistillata* in different light regimes. Coral Reefs 6:35–42

Cunha A, Almeida A, Coelho F, et al (2010) Bacterial extracellular enzymatic activity in globally changing aquatic ecosystems. Appl Microbiol Biotechnol 13:978–984

Dahl MP, Pereyra RT, Lundälv T, et al (2012) Fine-scale spatial genetic structure and clonal distribution of the cold-water coral *Lophelia pertusa*. Coral Reefs 31:1135–1148

Davies AJ, Duineveld GCA, Lavaleye MSS, et al (2009) Down-welling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef complex. Limnol Oceanogr 54:620–629

Delibrias G, Taviani M (1985) Dating the death of Mediterranean deep-sea scleractinian corals. Mar Geol 62:175–180

Di Geronimo I, Messina C, Rosso A, et al (2005) Enhanced biodiversity in the deep: early Pleistocene coral communities from Southern Italy. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 61–86

Dodds LA, Roberts JM, Taylor AC, et al (2007) Metabolic tolerance of the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature and dissolved oxygen change. J Exp Mar Biol Ecol 349:205–214

Dodds LA, Black KD, Orr H, et al (2009) Lipid biomarkers reveal geographical differences in food supply to the cold-water coral *Lophelia pertusa* (Scleractinia). Mar Ecol Progr Ser 397:113–124

Duineveld GCA, Lavaleye MSS, Berghuis EM (2004) Particle flux and food supply to a seamount cold-water coral community (Galicia Bank, NW Spain). Mar Ecol Progr Ser 277:13–23

Duineveld GCA, Lavaleye MSS, Bergman EM, et al (2007) Trophic structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in relation to the near-bottom particle supply and current regime. Bull Mar Sci 81:449–467

Duineveld GCA, Jeffreys RM, Lavaleye MSS, et al (2012) Spatial and tidal variation in food supply to shallow cold-water coral reefs of the Mingulay Reef complex (Outer Hebrides, Scotland). Mar Ecol Progr Ser 444:97–115

Duncan PM (1877) On the rapidity of growth and variability of some Madreporaria on an Atlantic cable, with remarks upon the rate of accumulation of foraminiferal deposits. Ann Mag Nat Hist 20:361–365

Edmondson CH (1928) The ecology of an Hawaiian coral reef. Bull Bernice P Bishop Mus 45:1–64

Edmunds PJ (2005) The effect of sub-lethal increases in temperature on the growth and population trajectories of three scleractinian corals on the southern Great Barrier Reef. Oecologia 146:350–364

Erez J (1978) Vital effect on stable-isotope composition seen in Foraminifera and coral skeletons. Nature 273:199–202

Fabricius KE, Genin A, Benayahu Y (1995) Flow-dependent herbivory and growth in zooxanthellae-free soft corals. Limnol Oceanogr 40:1290–1301

Fadlallah YH (1983) Sexual reproduction, development and larval biology in scleractinian corals: a review. Coral Reefs 2:129–150

Ferrier-Pagès C, Reynaud S, Allemand D (2012) Shallow water scleractinian corals of the Mediterranean Sea. In: Stambler N (ed) Life in the Mediterranean Sea: a look at habitat changes. Nova Science Publishers, New York, pp 355–389

Ferrier-Pagès C, Gattuso JP, Cawet G, et al (1998) Release of dissolved organic carbon and nitrogen by the zooxanthellate coral *Galaxea fascicularis*. Mar Ecol Progr Ser 172:265–274

Ferrier-Pagès C, Gattuso JP, Dallot S, et al (2000) Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. Coral Reefs 19:103–113

Ferrier-Pagès C, Peirano A, Abbate M, et al (2011) Summer autotrophy and winter heterotrophy in the temperate symbiotic coral *Cladocora caespitosa*. Limnol Oceanogr 56:1429–1438. https://doi.org/10.4319/lo.2011.56.4.1429

Findlay HS, Artioli Y, Moreno N, et al (2013) Tidal downwelling and implications for the carbon biogeochemistry of cold-water corals in relation to future ocean acidification and warming. Glob Chang Biol 19:2708–2719. https://doi.org/10.1111/gcb.12256

Flint H, Waller R, Tyler P (2007) Reproductive ecology of *Fungiacyathus marenzelleri* from 4100 m depth in the Northeast Pacific Ocean. Mar Biol 151:843–849

Form AU, Riebesell U (2012) Acclimation to ocean acidification during long-term CO_2 exposure in the cold-water coral *Lophelia pertusa*. Glob Chang Biol 18:843–853

Frederiksen R, Jensen A, Westerberg H (1992) The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing. Sarsia 77:157–171

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs. UNEP-WCMC, Cambridge, UK, 86 pp

Freiwald A, Beuck L, Ruggeberg A, et al (2009) The white coral community in the central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Gass SE, Roberts JM (2003) The environmental sensitivity of cold-water corals. Erlanger Geol Abh (Special Issue 4):109

Gateno D, Rinkevich B (2003) Coral polyp budding is probably promoted by a canalized ratio of two morphometric fields. Mar Biol 142:971–973

Gattuso JP, Frankignoulle M, Bourge I, et al (1998) Effect of calcium carbonate saturation of seawater on coral calcification. Glob Planet Chang 18:37–46

Gazeau F, Quiblier C, Jansen JM, et al (2007) Impact of elevated CO_2 on shellfish calcification. Geophys Res Lett 34:L07603. https://doi.org/10.1029/2006GL028554

Georgian SE, Dupont S, Kurman M, et al (2016) Biogeographic variability in the physiological response of the cold-water coral *Lophelia pertusa* to ocean acidification. Mar Ecol 37:1345–1359. https://doi.org/10.1111/maec.12373

Goffredo S, Arnone S, Zaccanti F (2002) Sexual reproduction in the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). Mar Ecol Progr Ser 229:83–94

Goreau TF (1959) The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. Biol Bull Mar Biol Lab Woods Hole 116:59–75

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze- Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Gori A, Reynaud S, Orejas C, et al (2014a) Physiological performance of the cold-water coral *Dendrophyllia cornigera* reveals its preference for temperate environments. Coral Reefs 33:665–674. https://doi.org/10.1007/s00338-014-1167-9

Gori A, Grover R, Orejas C, et al (2014b) Uptake of dissolved free amino acids by four cold-water coral species from the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 99:42–50. https://doi.org/10.1016/j.dsr2.2013.06.007

Gori A, Reynaud S, Orejas C, et al (2015) The influence of flow velocity and temperature on zooplankton capture rates by the cold-water coral *Dendrophyllia cornigera*. J Exp Mar Biol Ecol 466:92–97

Gori A, Ferrier-Pagès C, Hennige SJ, et al (2016) Physiological response of the cold-water coral *Desmophyllum dianthus* to thermal stress and ocean acidification. PeerJ 26855864. https://doi.org/10.7717/peerj.1606

Guinotte JM, Orr JC, Cairns SS, et al (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? Front Ecol Environ 4:141–146

Harrison PL (2011) Sexual reproduction of scleractinian corals. In: Dubinsky Z, Stambler N (eds) Coral reefs: an ecosystem in transition. Springer, Berlin, pp 59–85

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Ecosystems of the world: coral reefs. Elsevier, New York, pp 133–207

Harrison PL, Babcock RC, Bull GD, et al (1984) Mass spawning in tropical reef corals. Science 223:1186–1189

Hennige SJ, Wicks LC, Kamenos NA, et al (2013) Short term metabolic and growth responses of the cold-water coral *Lophelia pertusa* to ocean acidification. Deep-Sea Res Part 2 Top Stud Oceanogr. https://doi.org/10.1016/j.dsr2.2013.07.005

Heyward AJ, Negri AP (2012) Turbulence, cleavage, and the naked embryo: a case for coral clones. Science 335:1064

Highsmith RC (1982) Reproduction by fragmentation in corals. Mar Ecol Progr Ser 7:207–226

Houlbrèque F, Tambutté E, Ferrier-Pagès C (2003) Effect of zooplankton availability on the rates of photosynthesis, and tissue and skeletal growth in the scleractinian coral *Stylophora pistillata*. J Exp Mar Biol Ecol 296:145–166

Howe SA, Marshall AT (2001) Thermal compensation of metabolism in the temperate coral *Plesiastrea versipora* (Lamark 1816). J Exp Mar Biol Ecol 259:231–248

Howe SA, Marshall AT (2002) Temperature effects on calcification rate and skeletal deposition in the temperate coral *Plesiastrea versipora* (Lamarck). Exp Mar Biol Ecol 275:63–81

Jacques TG, Pilson MEQ (1980) Experimental ecology of the temperate scleractinian coral *Astrangia danae*. 1. Partition of respiration, photosynthesis and calcification between host and symbionts. Mar Biol 60:167–178

Johannes RE, Tepley L (1974) Examination of feeding of the reef coral *Porites lobata* in situ using time lapse photography. Proc 2nd Int Coral Reef Symp 1:127–131

Jokiel PL, Coles SL (1977) Effects of temperature on the mortality and growth of Hawaiian reef corals. Mar Biol 143:201–208

Jones DOB, Yool A, Wei C-L, et al (2014) Global reductions in seafloor biomass in response to climate change. Glob Chang Biol 20:1861–1872. https://doi.org/10.1111/gcb.12480

Kemp DW, Oakley CA, Thornhill DJ, et al (2011) Catastrophic mortality on inshore coral reefs of the Florida Keys due to severe low-temperature stress. Glob Chang Biol 17:3468–3477

Kerr AM, Baird AH, Hughes TP (2010) Correlated evolution of sex and reproductive mode in corals (Anthozoa: Scleractinia). Proc R Soc B 278:75–81

Khripounoff A, Caprais JC, Le Bruchec J, et al (2014) Deep cold water coral ecosystems in the Brittany submarine canyons (Northeast Atlantic): hydrodynamics, particle supply, respiration, and carbon cycling. Limnol Oceanogr 59:87–98

Kiriakoulakis K, Fischer E, Wolff GA, et al (2005) Lipids and nitrogen isotopes of two deep-water corals from the North-East Atlantic: initial results and implications for their nutrition. In: Freiwald A, Roberts JM (eds) Cold water corals and ecosystems. Springer, Berlin, Heidelberg, pp 715–729

Kleypas JA, Feely RA, Fabry VJ, et al (2006) Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research. Report of a workshop held 18–20 April 2005, St. Petersburg, FL, 88pp

Kuffner IB, Andersson AJ, Jokiel PL, et al (2007) Decreased abundance of crustose coralline algae due to ocean acidification. Nat Geosci 1:114–117. https://doi.org/10.1038/ngeo100

LaBarbera M (1984) Feeding currents and particle capture mechanisms in suspension feeding animals. Am Zool 24:71–84

Langdon C, Takahashi T, Sweeney C, et al (2000) Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. Glob Biogeochem Cycles 14:639–654

Larsson AI, van Oevelen D, Purser A, et al (2013) Tolerance to long-term exposure of suspended benthic sediments and drill cuttings in the cold-water coral *Lophelia pertusa*. Mar Pollut Bull 70:176–188

Larsson AI, Järnegren J, Strömberg SM, et al (2014) Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*. PLoS One 9:e102222. https://doi.org/10.1371/journal.pone.0102222

Lartaud F, Pareige S, de Rafeli M, et al (2013) A new approach for assessing cold-water coral growth *in situ* using fluorescent calcein staining. Aquat Living Resour 26:187–196

Le Danois E (1948) Les profondeurs de la mer. Payot, Paris, p 303

Levas S, Grottoli AG, Schoepf V, et al (2015) Can heterotrophic uptake of dissolved organic carbon and zooplankton mitigate carbon budget deficits in annually bleached corals? Coral Reefs 35:495–506. https://doi.org/10.1007/s00338-015-1390-z

Lewis JB, Price WS (1975) Feeding mechanisms and feeding strategies of Atlantic reef corals. J Zool Long 176:527–544

Lirman (2000) Fragmentation in the branching coral *Acropora palmata* (Lamarck): growth, survivorship, and reproduction of colonies and fragments. J Exp Mar Biol Ecol 255:41–57

Maier C, Hegeman J, Weinbauer MG, et al (2009) Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. Biogeosciences 6:1671–1680

Maier C, De Kluijver A, Agis M, et al (2011) Dynamics of nutrients, total organic carbon, prokaryotes and viruses in onboard incubations of cold-water corals. Biogeosciences 8:2609–2620

Maier C, Watremez P, Taviani M, et al (2012) Calcification rates and the effect of ocean acidification on Mediterranean cold-water corals. Proc R Soc B 279:1716–1723

Maier C, Schubert A, Berzunza Sànchez MM, et al (2013a) End of the century pCO_2 levels do not impact calcification in Mediterranean cold-water corals. PLoS One 8:e62655. https://doi.org/10.1371/journal.pone.0062655

Maier C, Bils F, Weinbauer MG, et al (2013b) Respiration of Mediterranean cold-water corals is not affected by ocean acidification as projected for the end of the century. Biogeosciences 10:5671–5680

Maier C, Popp P, Sollfrank N, et al (2016) Effects of elevated pCO_2 and feeding on net calcification and energy budget of the Mediterranean cold-water coral *Madrepora oculata*. J Exp Biol 219:3208–3217. https://doi.org/10.1242/jeb.127159

Marbà N, Jordà G, Agusti S, et al (2015) Footprints of climate change on Mediterranean Sea biota. Front Mar Sci 2:56. https://doi.org/10.3389/fmars.2015.00056

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

Mayor AG (1916) The lower temperatures at which reef-corals lose their ability to capture food. Carnegie Inst Wash Yearb 14:212

McClain CR, Allen AP, Tittensor DP, et al (2012) Energetics of life on the deep seafloor. Proc Natl Acad Sci U S A 109:15366–15371

Mercier A, Sun Z, Hamel JF (2011) Reproductive periodicity, spawning and development of the deep-sea scleractinian coral *Flabellum angulare*. Mar Biol 158:371–380

Middelburg JJ, Mueller CE, Veuger B, et al (2015) Discovery of symbiotic nitrogen fixation and chemoautotrophy in cold-water corals. Sci Rep 5:17962. https://doi.org/10.1038/srep17962

Mikkelsen N, Erlenkeuser H, Killingley JS, et al (1982) Norwegian corals: radiocarbon and stable isotopes in *Lophelia pertusa*. Boreas 11:163–171

Mora C, Wei CL, Rollo A, et al (2013) Biotic and human vulnerability to projected changes in ocean biogeochemistry over the 21st century. PLoS Biol 11:e1001682. https://doi.org/10.1371/journal.pbio.1001682

Mortensen PB (2001) Aquarium observations on the deepwater coral *Lophelia pertusa* (L., 1758) (Scleractinia) and selected associated invertebrates. Ophelia 54:83–104

Mortensen PB, Rapp HT (1998) Oxygen and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia pertusa* (L.) (Anthozoa, Scleractinia): implications for determination of linear extension rates. Sarsia 83:433–446

Mortensen PB, Hovland MT, Fossa JH, et al (2001) Distribution, abundance and size of *Lophelia pertusa* coral reefs in mid-Norway in relation to seabed characteristics. J Mar Biol Assoc UK 81:581–597

Movilla J, Gori A, Calvo E, et al (2014a) Resistance of two Mediterranean cold-water coral species to low pH conditions. Water 6:59–67. https://doi.org/10.3390/w6010059

Movilla J, Orejas C, Calvo E, et al (2014b) Differential response of two Mediterranean cold-water coral species to ocean acidification. Coral Reefs 33:675–686. https://doi.org/10.1007/s00338-014-1159–9

Mueller CE, Larsson AI, Veuger B, et al (2014) Opportunistic feeding on various organic food sources by the cold- water coral *Lophelia pertusa*. Biogeosciences 11:123–133

Naumann MS, Haas A, Struck U, et al (2010) Organic matter release by dominant hermatypic corals of the Northern Red Sea. Coral Reefs 29:649–659

Naumann MS, Orejas C, Wild C, et al (2011) First evidence for zooplankton feeding sustaining key physiological processes in a scleractinian cold-water coral. J Exp Biol 214:3570–3576

Naumann MS, Orejas C, Ferrier-Pagès C (2013) High thermal tolerance of two Mediterranean cold-water coral species maintained in aquaria. Coral Reefs 32:749–754. https://doi.org/10.1007/s00338-013-1011-7

Naumann MS, Orejas C, Ferrier-Pagès C (2014) Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. Deep-Sea Res Part 2 Top Stud Oceanogr 99:36–41. https://doi.org/10.1016/j.dsr2.2013.05.025

Naumann M, Tolosa I, Taviani M, et al (2015) Trophic ecology of two cold-water coral species from the Mediterranean Sea revealed by lipid biomarkers and compound-specific isotope analyses. Coral Reefs 34:1165–1175

van Oevelen D, Duineveld GCA, Lavaleye MSS, et al (2009) The cold-water coral community as hotspot of carbon cycling on continental margins: a food web analysis from Rockall Bank (northeast Atlantic). Limnol Oceanogr 54:1829–1844

van Oevelen D, Mueller CE, Lundälv T, et al (2016) Food selectivity and processing by the cold-water coral *Lophelia pertusa*. Biogeosciences 13:5789–5798

Orejas C, Gori A, Gili JM (2008) Growth rates of live *Lophelia pertusa* and *Madrepora oculata* from the Mediterranean Sea maintained in aquaria. Coral Reefs 27:255

Orejas C, Gori A, Lo Iacono C, et al (2009) Coldwater corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37

Orejas C, Ferrier-Pagès C, Reynaud S, et al (2011a) Long-term growth rates of four Mediterranean cold-water coral species maintained in aquaria. Mar Ecol Progr Ser 429:57–65

Orejas C, Ferrier-Pagès C, Reynaud S, et al (2011b) Experimental comparison of skeletal growth rates in the cold-water coral *Madrepora oculata* Linnaeus, 1758 and three tropical scleractinian corals. J Exp Mar Biol Ecol 405:1–5

Orejas C, Gori A, Rad-Menéndez C, et al (2016) The effect of flow speed and food size on the capture efficiency and feeding behaviour of the cold-water coral *Lophelia pertusa*. J Exp Mar Biol Ecol 481:34–40

Orr JC, Fabry VJ, Aumont O, et al (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686. https://doi.org/10.1038/nature04095

Osinga R, Van Delft S, Wahyudin Lewaru M, et al (2011) Determination of prey capture rates in the stony coral *Galaxea fascicularis*: a critical reconsideration of the clearance rate concept. J Mar Biol Assoc UK 1–7

Palardy JE, Grottoli AG, Matthews KA (2005) Effects of upwelling, depth, morphology and polyp size on feeding in three species of Panamanian corals. Mar Ecol Progr Ser 300:79–89

Palmiéri J, Orr JC, Dutay JC, et al (2015) Simulated anthropogenic CO_2 storage and acidification of the Mediterranean Sea. Biogeosciences 12:781–802

Pires DO, Silva JC, Bastos ND (2014) Reproduction of deep-sea reef-building corals from the southwestern Atlantic. Deep-Sea Res Part 2 Top Stud Oceanogr 99:51–63

Previati M, Scinto A, Cerrano C, et al (2010) Oxygen consumption in Mediterranean octocorals under different temperatures. J Exp Mar Biol Ecol 390:39–48

Purser A, Larsson AI, Thomsen L, et al (2010) The influence of flow velocity and food concentration on *Lophelia pertusa* (Scleractinia) zooplankton capture rates. J Exp Mar Biol Ecol 395:55–62

Purser A, Orejas C, Moje A, et al (2014) The influence of flow velocity and suspended particulate concentration on net prey capture rates by the scleractinian coral *Balanophyllia europaea* (Scleractinia: Dendrophylliidae). J Mar Biol Assoc UK 94:687–696

Reynaud S, Leclercq N, Romaine-Lioud S, et al (2003) Interacting effects of CO_2 partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. Glob Chang Biol 9:1660–1668

Rice AL, Lambshead PJD (1994) Patch dynamics in the deep-sea benthos: the role of heterogenous supply of organic matter. In: Giller PS, Hildrew AG, Rafaelli DG (eds) Aquatic ecology: scale, pattern and processes. Blackwell, Oxford, pp 469–497

Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific and the Red Sea. Mar Ecol Progr Ser 60:185–203

Ries JB, Cohen AL, McCorkle DC (2010) A nonlinear calcification response to CO_2- induced ocean acidification by the temperate coral *Oculina arbuscula*. Coral Reefs 29:661–674

Riisgård HU, Larsen PS (2010) Particle capture mechanisms in suspension-feeding invertebrates. Mar Ecol Progr Ser 418:255–293

Rinkevich B, Loya Y (1979) The reproduction of the Red Sea coral *Stylophora pistillata*. I. Gonads and planulae. Mar Ecol Progr Ser 1:133–144

Ritchie KB (2006) Regulation of microbial populations by coral surface mucus and mucus-associated bacteria. Mar Ecol Progr Ser 322:1–14

Rix L, de Goeij JM, Mueller CE, et al (2016) Coral mucus fuels the sponge loop in warm- and cold-water coral reef ecosystems. Sci Rep 6:18715. https://doi.org/10.1038/srep18715

Rixen M, Beckers JM, Levitus S, et al (2005) The Western Mediterranean deep water: a proxy for climate change. Geophys Res Lett 32:12608

Roberts JM, Anderson RM (2002) A new laboratory method for monitoring deep-water coral polyp behaviour. Hydrobiologia 471:143–148

Roberts JM, Cairns SD (2014) Cold-water corals in a changing ocean. Curr Opin Environ Sustain 7:118–126

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Roberts JM, Wheeler AJ, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, Cambridge, p 334

Rodolfo-Metalpa R, Richard C, Allemand D, et al (2006) Growth and photosynthesis of two Mediterranean corals *Cladocora caespitosa* and *Oculina patagonica* under normal and elevated temperatures. J Exp Biol 209:4546–4556

Rodolfo-Metalpa R, Montagna P, Aliani S, et al (2015) Calcification is not the Achilles' heel of cold-water corals in an acidifying ocean. Glob Chang Biol 21:2238–2248

Rodríguez E, Orejas C, López-González PJ, et al (2013) Reproduction in the externally brooding sea anemone *Epiactis georgiana* in the Antarctic Peninsula and the Weddell Sea. Mar Biol 160:67–80

Rogers AD (1999) The biology of *Lophelia pertusa* (Linnaeus, 1758) and other deep-water reef-forming corals and impacts from human activities. Int Rev Hydrobiol 84:315–406

Rosen BR, Taylor JD (1969) Reef coral from Aldabra – new mode of reproduction. Science 166:119–121

Sammarco PW (1982) Polyp bail-out: an escape response to environmental stress and a new means of reproduction in corals. Mar Ecol Progr Ser 10:57–65

Sánchez F, Serrano A, Ballesteros MG (2009) Photogrammetric quantitative study of habitat and benthic communities of deep Cantabrian Sea hard grounds. Cont Shelf Res 29:1174–1188

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the Northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108. https://doi.org/10.1371/journal.pone.0087108

Schuhmacher H (1977) Ability of fungiid corals to overcome sedimentation. Proc 3rd Int Coral Reef Symp 1:503–509

Sebens KP, Grace SP, Helmuth B, et al (1998) Water flow and prey capture by three scleractinian corals, *Madracis mirabilis, Montastrea cavernosa* and *Porites porites*, in a field enclosure. Mar Biol 131:347–360

Shelton G (1980) *Lophelia pertusa* (L.): electrical conduction and behavior in a deep-water coral. J Mar Biol Assoc UK 60:517–528

Shimeta J, Jumars PA (1991) Physical mechanisms and rates of particle capture by suspension feeders. Oceanogr Mar Biol A Rev 29:191–257

Shimeta J, Koehl MAR (1997) Mechanisms of particle selection by tentaculate suspension feeders during encounter, retention, and handling. J Exp Mar Biol Ecol 209:47–73

Stoddart JA (1983) Asexual production of planulae in the coral *Pocillopora damicornis*. Mar Biol 76:279–284

Szmant AM (1986) Reproductive ecology of Caribbean reef corals. Coral Reefs 5:43–54

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, pp 137–156

Thiem Ø, Ravagnan E, Fossa JH, et al (2006) Food supply mechanisms for cold-water corals along a continental shelf edge. J Mar Syst 26:1481–1495

Touratier F, Goyet C (2011) Impact of the Eastern Mediterranean Transient on the distribution of anthropogenic CO_2 and first estimate of acidification for the Mediterranean Sea. Deep-Sea Res I Oceanogr Res Pap 58:1–15. https://doi.org/10.1016/j.dsr.2010.10.002

Tremblay P, Naumann MS, Sikorski S, et al (2012) Experimental assessment of organic carbon fluxes in the scleractinian coral *Stylophora pistillata* during a thermal stress event. Mar Ecol Progr Ser 453:63–77

Tsounis G, Orejas C, Reynaud S, et al (2010) Prey-capture rates in four Mediterranean cold water corals. Mar Ecol Progr Ser 398:149–155

Tursi A, Mastrototaro F, Matarrese A, et al (2004) Biodiversity of the white coral reefs in the Ionian Sea (Central Mediterranean). Chem Ecol 20:107–116

Tyler PA, Harvey R, Giles LA, et al (1992) Reproductive strategies and diet in deep-sea nuculanid protobranchs (Bivalvia: Nuculoidea) from the Rockall Trough. Mar Biol 114:571–580

Tyler PA, Gage JD, Paterson GJL, et al (1993) Dietary constraints on reproductive periodicity in two sympatric deep-sea astropectinid seastars. Mar Biol 115:267–277

Vargas-Yáñez M, Moya F, Garcia-Martinez MC, et al (2010) Climate change in the Western Mediterranean Sea 1900−2008. J Mar Syst 82:171–176

Vertino A, Stolarski J, Bosellini FR, et al (2014) Mediterranean corals through time: from miocene to present. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea: its history and present challenges. Springer, Dordrecht, pp 257–274. https://doi.org/10.1007/978-94-007-6704-1_14

Waller RG (2003) The reproductive ecology of deep-water scleractinians. PhD thesis, School of Ocean and Earth Science, Southampton Oceanogr Cent

Waller RG (2005) Deep water scleractinians: current knowledge of reproductive processes. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 691–700

Waller RG, Feehan KA (2013) Reproductive ecology of a polar deep-sea scleractinian, *Fungiacyathus marenzelleri* (Vaughan, 1906). Deep-Sea Res Part 2 Top Stud Oceanogr 92:201–2016

Waller RG, Tyler PA (2005) The reproductive biology of two deepwater, reef-building scleractinians from the NE Atlantic Ocean. Coral Reefs 24:514–522

Waller RG, Tyler PA (2011) Reproductive patterns in two deep-water solitary corals from the north-east Atlantic – *Flabellum alabastrum* and *F. angulare* (Cnidaria: Anthozoa: Scleractinia). J Mar Biol Assoc UK 91:669–675

Waller RG, Tyler PA, Gage JD (2002) Reproductive ecology of the deep-water scleractinian coral *Fungiacyathus marenzelleri* (Vaughan, 1906) in the northeast Atlantic Ocean. Coral Reefs 21:325–331

Waller RG, Tyler PA, Gage JD (2005) Sexual reproduction in three hermaphroditic deep-sea *Caryophyllia* species (Anthozoa: Scleractinia) from the NE Atlantic Ocean. Coral Reefs 24:594. https://doi.org/10.1007/s00338-005-0031-3

Waller RG, Tyler PA, Smith CR (2008) Fecundity and embryo development of three Antarctic deep-water scleractinians*: Flabellum thouarsii, F. curvatum* and *F. impensum*. Deep-Sea Res Part 2 Top Stud Oceanogr 55:2527–2534

Walther G-R, Post E, Convey P, Menzel A, et al (2002) Ecological responses to recent climate change. Nature 416:389–395

Wienberg C, Frank N, Mertens KN, et al (2010) Glacial cold-water coral growth in the Gulf of Cádiz: implications of increased palaeo-productivity. Earth Planet Sci Lett 298:405–416

Wijgerde T, Spijkers P, Karruppannan E, et al (2012) Water flow affects zooplankton feeding by the scleractinian coral *Galaxea fascicularis* on a polyp and colony level. J Mar Biol (ID 854849), 7 pp. https://doi.org/10.1155/2012/854849

Wild C, Rasheed M, Werner U, et al (2004) Degradation and mineralization of coral mucus in reef environments. Mar Ecol Progr Ser 267:159–171

Wild C, Mayer C, Wehrmann L, et al (2008) Organic matter release by cold water corals and its implication for fauna–microbe interaction. Mar Ecol Progr Ser 372:67–75

Wild C, Naumann M, Niggl W, et al (2010) Carbohydrate composition of mucus released by scleractinian warm- and cold-water reef corals. Aquat Biol 10:41–45

Wildish D, Kristmanson D (1997) Benthic suspension feeders and flow. Cambridge University Press, Cambridge, p 409

Yeoh SR, Dai CF (2010) The production of sexual and asexual larvae within single broods of the scleractinian coral, *Pocillopora damicornis*. Mar Biol 157:351–359

Yonge CM, Nicholls AG (1931) Studies on the physiology of corals. V. On the relationship between corals and zooxanthellae. Scient Rep Gt Barrier Reef Exped 1:177–211

Zetsche E-M, Baussant T, Meysman FJR, et al (2016) Direct visualization of mucus production by the cold-water coral *Lophelia pertusa* with digital holographic microscopy. PLoS One 11:e0146766. https://doi.org/10.1371/journal.pone.0146766

Zibrowius H (1980) Les Scleractiniaires de la Méditerranée et de l'Atlantique Nord-Oriental, vol 11. Mémoires de l'Institut Océanographique, Monaco, p 284

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Lartaud F, Mouchi V, Chapron L, et al (this volume) Growth patterns of Mediterranean calcifying cold-water corals

Maier C, Weinbauer MG, Gattuso JP (this volume) Fate of Mediterranean scleractinian cold-water corals as a result of global climate change. A synthesis

Movilla J (this volume) A case study: variability in the calcification response of Mediterranean cold-water corals to ocean acidification

Orejas C, Taviani M, Carreiro-Silva M, et al (this volume) Cold-water coral in aquaria: advances and challenges. A focus in the Mediterranean

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of mediterranean cold-water corals

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Weinbauer MG, Oregiani D, Grosskurth A, et al (this volume) Diversity and biogeography of bacteria associated with the cold-water corals *Lophelia pertusa* and *Madrepora oculata*: Mediterranean Sea vs NE Atlantic

36 Growth Patterns of Mediterranean Calcifying Cold-Water Corals

Franck Lartaud, Vincent Mouchi, Leïla Chapron,
Anne-Leïla Meistertzheim, and Nadine Le Bris

Abstract

Skeletal growth is a key physiological function, which in the case of calcifying organisms, provides support for the general colony structure together, whilst simultaneously providing protection for internal soft tissues. Given this fundamental importance, growth patterns can therefore reflect the health status of organisms. Additionally, engineer species forming 3D structures, such as scleractinian cold-water corals, enhance local biodiversity through the provision of new structural and hydrodynamic habitats. Furthermore, cold-water corals may be used as paleoclimate indicators, and act as sources for novel pharmaceutical compounds as well as represent significant sinks for CO_2 sequestration. At time of writing, cold-water coral reefs are facing several serious threats, particularly in the Mediterranean Sea, where the combined effects of climate change and other anthropogenic environmental disturbances are interacting in regions of coral colonisation. The characterisation of the Mediterranean cold-water coral growth patterns is thus a crucial step for accurate forecasting of reef resilience under environmental change and for the establishment of adequate conservation strategies. From the organisation of soft tissues to the resulting mineralogical structures formed from the polyp to the reef scale, this chapter gives an overview of the state of the art of the current understanding of scleractinian cold-water coral growth patterns. The main environmental parameters that control calcification and their influence on cold-water corals in the context of ongoing global environmental change are illustrated with examples from studies conducted with different calcifying species from the Mediterranean Sea, utilising both aquaria and *in situ* experimental studies.

Keywords

Scleractinia · Skeleton · Calcification · Environmental factors · Forecast of reef growth · Cold-water corals · Mediterranean

36.1 Introduction

The appearance of hard structure calcifying fauna during the Cambrian was a major step in the evolution of the animal kingdom tightly linked with the global CO_3^{2-} and CO_2 budgets. The skeleton secreted by these fauna both supports the general shape of the organism as well as protects soft tissues against biotic (e.g., predation) or abiotic threats. Though a range of substances may be secreted to form hard structure skeletons, calcium carbonate based skeletal structure are the most abundant and diversified in terms of mineralogy and structure. Shells and skeletons may be made from a range of calcium carbonate compounds (e.g. aragonite, low or high-magnesium calcite, amorphous calcium carbonate), and dozens of microstructures have been identified among which the most widespread are prismatic, fibro-prismatic, nacreous and crossed-lamellar (Carter 1980).

Calcifying species build their skeletons by the periodic addition of carbonate. Both environmental conditions and metabolic activity control the rhythm and growth rates of the biomineralising fauna and deposition rate of the carbon-

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ate material. Together with respiration, reproduction and energy storage, calcification is one of the key physiological indicators of organism fitness in calcifying fauna. Biomineralisation studies offer the capacity to address research questions on both short-term (i.e., hourly to daily) and long-term (i.e., annual or multi-annual) scales, with a dual perspective: (1) to address the rapid response of organisms to biotic and/or abiotic changes in the ecosystem, and (2) to assess the resilience of calcifying species to ongoing and persistant environmental change. Additionally, calcifying organisms may be used as oceanographic and paleoceanographic environmental archives, by the analysis of geochemical proxies locked within their carbonate skeletons at the time of deposition. In particular, changes in deep-water mass dynamics can be inferred from trace metal and isotope analyses of cold-water coral (CWC) skeletons (Montero-Serrano et al. 2013).

As it is the case for their shallow water counterparts, CWCs act as ecosystem engineers, forming reefs in cold and deep waters. Indeed, scleractinian corals form three-dimensional structures, potentially accumulating over millennia following death, that provide various ecological niches for associated fauna, including feeding, spawning and nursery habitats for a variety of species (Rueda et al., this volume; D'Onghia, this volume). As a result, corals are key species that partially support the biodiversity of marine ecosystems. Hence, reef-building scleractinian corals are species of great ecological value. In the Mediterranean Sea there are several locations where well developed CWC ecosystems have been described, such as the Santa Maria di Leuca coral province in the Ionian Sea (Vertino et al. 2010; D'Onghia et al. 2011; Chimienti et al., this volume) and the submarine canyons of the Gulf of Lion (Orejas et al. 2009; Fiala-Medioni et al. 2012; Gori et al. 2013; Fourt et al., this volume; Puig and Gili, this volume) and Catalan Margin (Lastras et al. 2016, this volume; Aymà et al., this volume).

The biology of CWCs is much less understood than that of tropical corals, but during the last few decades significant research efforts have been dedicated to the characterisation of CWC physiology and ecology (Roberts et al. 2009). The analysis of CWC growth patterns to date has been based on both aquaria and *in situ* studies. Many studies have been conducted in the North-East Atlantic and in the Gulf of Mexico, though in recent years a substantial number of works focusing on CWCs within the world ocean have been published, including the Mediterranean. Many CWC studies conducted in the Mediterranean have been focused in the influence of temperature and acidification in these communities, being thus particularly relevant to the forecasting of CWC reef resilience to global change (see Maier et al., this volume; Movilla, this volume).

36.2 Living Tissues and Calcified Material

36.2.1 Anatomy of Corals

Corals are characterised by stinging cells (cnidocytes) that are used for prey capture and as a defence mechanism against predators. Each polyp is made of two cell layers: ectodermal and endodermal layers, separated by the mesoglea which is a collagen network (Allemand et al. 2004). The polyps are linked together by the coenosarc made by an oral (facing seawater) and aboral (facing skeleton) epithelium. Polyps and coenosarc thus cover the skeleton much like a glove (Fig. 36.1), leading to an endogenous biomineralisation.

Biomineralisation occurs in a submicrometric interface between the cells and the skeleton known as the extracellular calcifying medium, from an organic matrix composed of a mixture of proteins, glycoproteins, and polysaccharides that precisely self-assemble and control the $CaCO_3$ crystal formation (Allemand et al. 2011). Different functions have been attributed to this organic matrix, including control of the concentration of precursor ions, constitution of a tridimensional framework, template for crystal nucleation, for determination of the calcium carbonate polymorph, control of crystal elongation, inhibition of crystal growth, determination of spatial arrangement of crystal units, and involvement with enzymatic functions and cell signalling (Marin et al. 2008).

During the calcification process, carbonic anhydrase is involved in hydration/dehydration reactions by supplying dissolved inorganic carbon to the calcification site and removing carbonic acid from the calcification site. This process is performed by the metabolic conversion of CO_2 into HCO_3^- and HCO_3^- into CO_3^{2-} (Bertucci et al. 2013). Finally, the nucleation – the pathfinder for crystal formation in the extracellular calcifying medium – allows the formation of an initial thermodynamically unstable mineral form, the amorphous calcium carbonate, prior to its transformation into aragonite. As an example, for the shallow-water coral *Stylophora pistillata* from the Gulf of Aqaba, this transient skeletal compartment has a short half-life (12.9 min) compared to the bulk of the skeleton (167 h) (Tambutté et al. 1996). The resulting structure is thus composed of self-assembled aragonite minerals with an inter- and intracrystalline organic matrix.

36.2.2 Anatomical Particularities of Scleractinian Cold-Water Corals and Their Implications for Skeletal Growth

Although reef-building CWCs exhibit many similar growth traits to other calcifying cnidarians, they also form some distinct patterns in morphology which have to be taken into

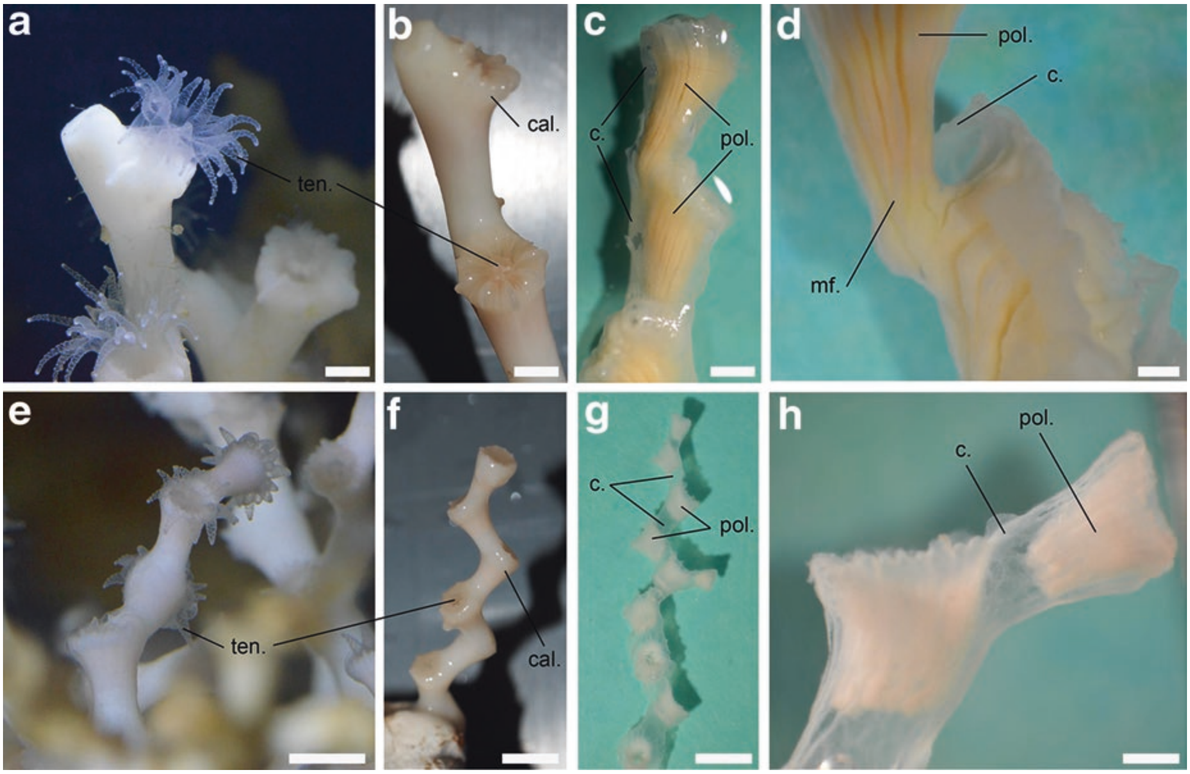

Fig. 36.1 Anatomy of two cold-water coral species from the Gulf of Lion, northwestern Mediterranean Sea. (**a**) *Lophelia pertusa* fragment showing polyp distribution along the skeleton with open polyps displaying the tentacles, (**b**) *Lophelia* polyps retracted inside the calices, (**c**, **d**) Coral tissues after decalcification showing polyp junction by both mesenterial filaments and the ceonosarc cover, (**e–h**) Same sequence of images as from (**a**) to (**d**) but corresponding in this case to a *Madrepora oculata* nubbin; note that in *M oculata* the coenosarc only connects the polyps. *Ten* tentacles, *cal* calix, *c* coenosarc, *pol* polyp, *mf* mesenterial filaments. Scale is 5 mm in (**a–c**) and (**e–g**) and 1 mm in (**d**) and (**h**). (Photographs © A.L. Meistertzheim (CNRS) and F. Lartaud (Sorbonne University))

account in growth studies (Lartaud et al. 2017a). This is particularly true for colonial species that form tree-like structures, such as *Lophelia pertusa* (recently synonymised to *Desmophyllum pertusum*) (Addamo et al. 2016), *Madrepora oculata, Solenosmilia variabilis* and *Dendrophyllia cornigera*.

Even though CWC colonies display the same general anatomy as many shallow-tropical corals, with polyps linked externally together by the coenosarc tissues, CWCs tend to exhibit larger polyps that extend linearly (Gass and Roberts 2011; Lartaud et al. 2017a). A branch of colonial CWC is formed by the successive addition of large calices, growing directly on tip of previous generations of polyps, which can lead to a considerable separation between polyps (Fig. 36.1a, b, e, f), in contrast to the closely packed, tiny polyps often forming the colonial structure of most tropical corals (Lartaud et al. 2017a).

The distance between polyps could also have consequences for energy distribution within a colony. Decalcification of coral skeletons shows that different species do not display the same patterns in soft tissue connection (Fig. 36.1c, d, g, h). *Lophelia pertusa* polyps are connected by both the coenosarc and mesenterial filaments, located within the calix. This provides different pathways for molecule transfer within the tissues. On the opposite, *M. oculata* grows with a clear separation between polyps, only connected by the thin coenosarc. This leads to a single route (i.e. the coenosarc) for molecule transfer inside the colony.

Coral calcification also occurs extracellularly. This is particularly prevalent for azooxanthellate colonial corals such as *L. pertusa*, which produce large amounts of extracellular mucus (EMS), which can contribute to the calcification of the parchment-like tube of the symbiotic worm *Eunice norvegica* (Roberts 2005) (Fig. 36.2). This mucus has various functions, such as acting as an antifouling agent, protecting the coral skeleton from attacks from endolithic and boring organisms, and also as an aid in removing sediment particles. The occurrence of identical protein patterns within EMS and the newly formed aragonite suggests that EMS plays a central role in the calcification process of the skeletal parts (Reitner 2005). Mucus could also be involved in facilitating coral attachment to the substrate (e.g., rock, dead or still living corals), as it is frequently observed *in situ*, as well as in association with corals maintained in aquaria (Fig. 36.3).

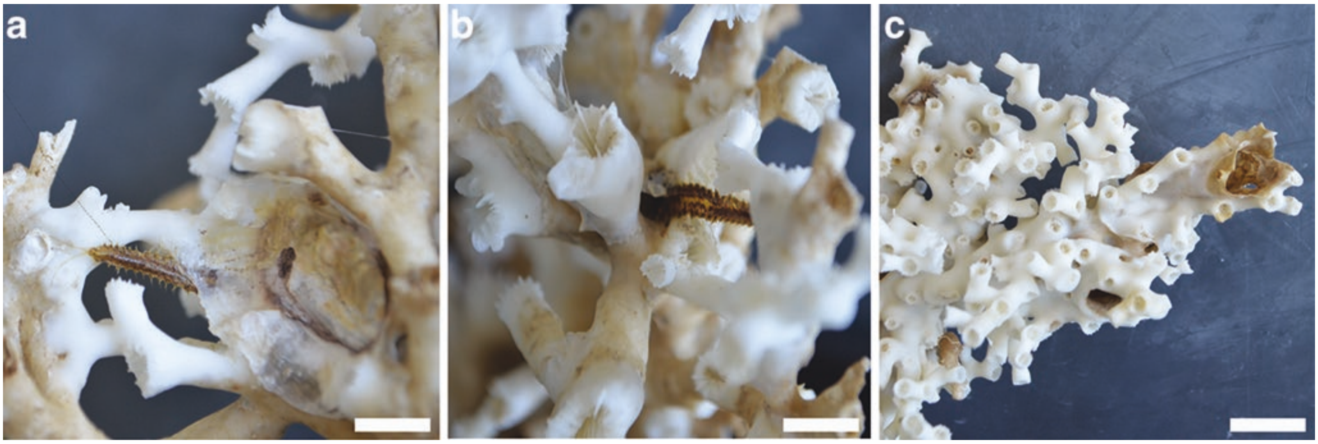

Fig. 36.2 Coral fragments where the calcification over the tube produced by the symbiotic worm *Eunice norvegica* can be seen. (**a**) *E. norvegica* coming out from its tube (behind the oyster shell). (**b**) Opposite view of the same worm showing the tube covered by *Lophelia pertusa* polyps. (**c**) Calcified tube of *E. norvegica* by *Madrepora oculata*. Those specimens were collected in the Lacaze-Duthiers canyon, northwestern Mediterranean Sea. Scale bar is 1 cm. (Photographs © F. Lartaud (Sorbonne University))

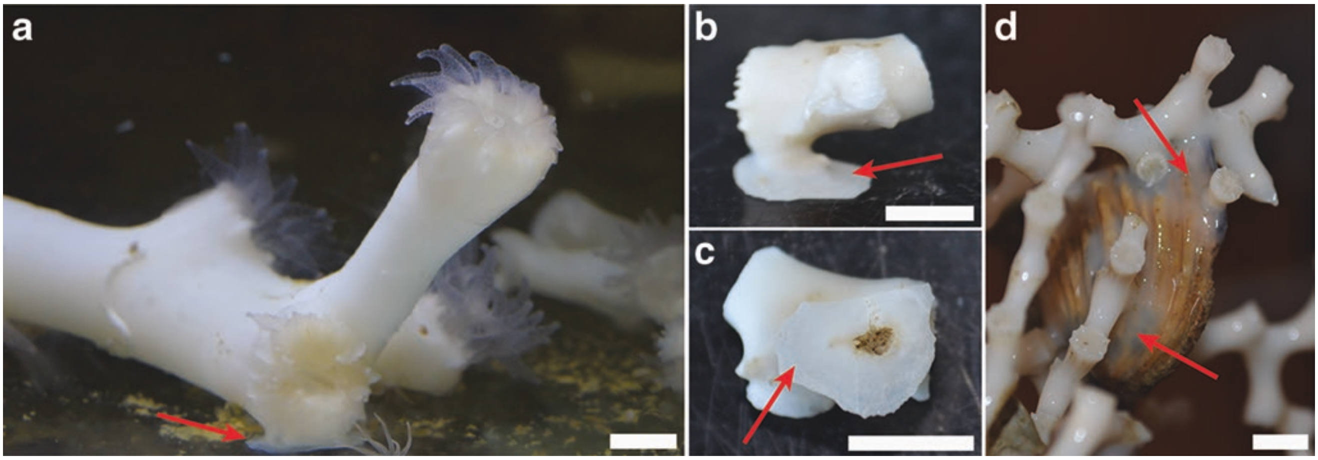

Fig. 36.3 (**a**) Coral extra-skeleton calcification at the base of *Lophelia pertusa* polyp when deployed lengthened in aquaria (highlighted by a red arrow). The specimen was collected in the Lacaze-Duthiers canyon, northwestern Mediterranean Sea (**b**) lateral view of the polyp showing the extra-polyp cementation, (**c**) view from the polyp basis of extra-skeleton calcification, (**d**) *Madrepora oculata* colony from the Lacaze-Duthiers canyon covering a bivalve shell with extra-skeleton mineralisation (© UPMC-Fondation TOTAL). Scale bars are 5 mm. (Photographs © F. Lartaud (Sorbonne University))

36.3 Skeleton Microstructure and Crystallography

36.3.1 Initiation of Calcification and Growth Models

The observation of scleractinian CWC skeletal features reveals two types of microstructures. Aragonite fibres are the main skeletal components, representing the vast majority of the calcified volume. Spatially-restricted areas of micrometric scale are also present, traditionally called centers of calcification (COC) and also referred to as early mineralisation zones (EMZ) or rapid accretion deposits (RAD). These zones are characterised by granular crystals arranged in clusters (Constantz 1989). The distribution of these structures differs according to the species, with arrangements varying from discrete clusters to continuous chains (Cohen and McConnaughey 2003). In *Lophelia pertusa*, they are organised in a continuous line from the base of the corallite up to the calix, near the inner edge of the wall, as shown in the scanning electron microscope (SEM) image after treating the samples with an acid etching solution (Fig. 36.4a). These regions are located close to the starting point of diverting fibres and are considered to be nucleation sites for calcification (Bryan and Hill 1941). Indeed, contrary to the meaning of the traditional name (centers of calcification), these structures are not formed by a unique crystal (Fig. 36.4b), nor are they located at the physical middle of the coral wall. The

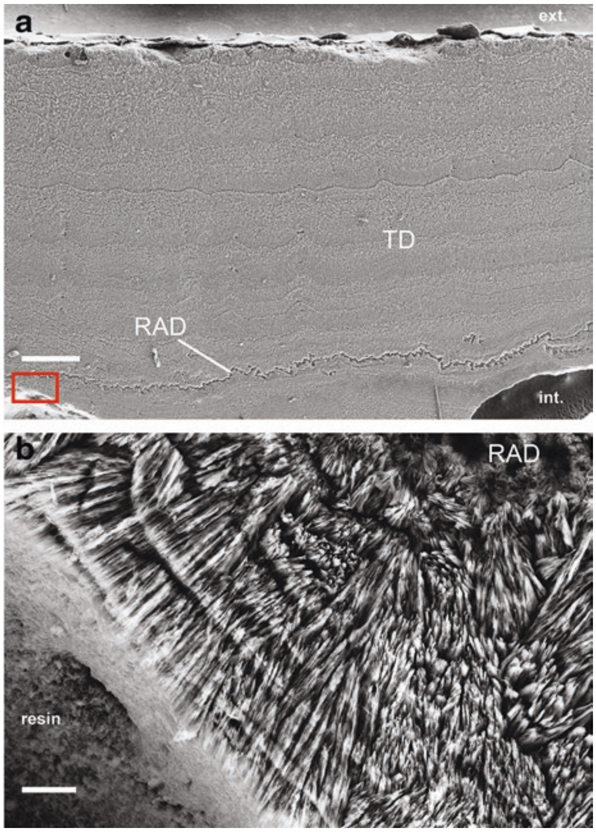

Fig. 36.4 (**a**) Microstructures in the wall of *Lophelia pertusa* skeleton from the Whittard canyon (NE Atlantic) under SEM, showing the Rapid Accretion Deposit (RAD) arranged in a continuous line and the Thickening Deposits (TD) layers made of aragonite fibres. Longitudinal growth direction is from left to right. Scale bar: 200 μm. *ext.* external part of the skeleton, *int.* internal part, located in the calix, (**b**) Detail of the bottom left part of (**a**) included in the red rectangle. SEM view of layers in aragonite fibres near the RAD on the internal edge of the skeleton. Scale bar: 10 μm

COCs (or RADs) are the first biomineralised structures to appear in the wall formation (Rollion-Bard and Blamart 2014), and this term is generally used in regards to their initial support role in further crystallisation events.

Since the granular crystals have a sub-micron size, it is likely that part of the calcification process is intracellular (Constantz 1989). Vesicles have been observed in the apical membrane of the epithelium which are probably responsible for providing some material to the calcifying space (Johnston 1980), as they can be a pathway for seawater. Though no mineralised structures have been observed in these vesicles, they may act as stabilisation sites for amorphous calcium carbonate (Cohen and McConnaughey 2003; Rollion-Bard et al. 2010).

It is widely agreed that the calicoblastic layer plays a role in calcification (Tambutté et al. 2011); however different models grant it a more or less important function in this process: a direct control of the calicoblastic layer (Barnes 1970; Johnston 1980), a two-steps model (Cuif and Dauphin 1998; Cuif et al. 2011), and a layered model (Stolarski 2003). In the later, COCs are called Centres of Rapid Accretion (CRA) and they are arranged into a Rapid Accretion Front (RAF). CRA and RAF form deposits composing of a mineral phase as well as an organic phase (dCRA and dRAF, respectively), themselves recovered by successive layers of mainly mineral Thickening Deposits (TD).

In the calcifying space, the supersaturation state allows spontaneous formation of nucleation clusters comprised of hydrated ions (Cölfen and Antonietti 2005). As these clusters grow, they eventually become critical crystal nuclei, putatively composed of amorphous calcium carbonate (ACC), which is thought to act as a precursor of mineralised calcium carbonate (Addadi et al. 2003). ACC is known to be present in numerous biominerals (Weiner et al. 2003), but its presence in coral skeletons is debated (Cuif and Dauphin 1998; Falini et al. 2013). Proteins and polysaccharides present in the matrix fix themselves around these nanoparticles and induce a stabilisation of the particles that can orientate themselves for association with other similar nuclei. By forming clusters and welding, they are able to form single crystals (Cartwright et al. 2012).

After putative ACC turned into nanometric crystals, aragonite fibres (located in the TD region) grow from these RADs to form sclerodermites, shaped in fans towards the external side of the skeleton and polyp to increase skeleton thickness.

36.3.2 Growth Structures in the Thickening Deposits Region

The skeleton resulting from sclerodermite formation is not homogenous. Density layers, such as the annual bands formed in tropical corals have not been observed in CWCs, but growth structures defined by opaque and translucent bands in the coral wall have been seen under transmitted light of *L. pertusa* from Sweden (Wainwright 1964) and *Desmophyllum dianthus* collected from the NW Atlantic (Lazier et al. 1999). These optically visible bands were originally interpreted as annual patterns (Risk et al. 2005). The bands were thought to have been formed by successive nucleation phases during the life of the polyp, associated with advances and retreats of the outer tissue layer that covers the corallite (Lazier et al. 1999). It has been demonstrated that the opaque and translucent bands are indeed thickening phases of the wall but their temporal meaning is probably not uniform. Indeed, Gass and Roberts (2011) found the same amount of annual banding in living polyps of different ages from the same *L. pertusa* colony growing on North Sea oil platforms. As a result of this analysis, it seems that these bands are not useful to establish temporal calibrations of polyp age.

Recently, new microlayers (20–100 μm width) were observed under SEM after light etching of skeletal sections

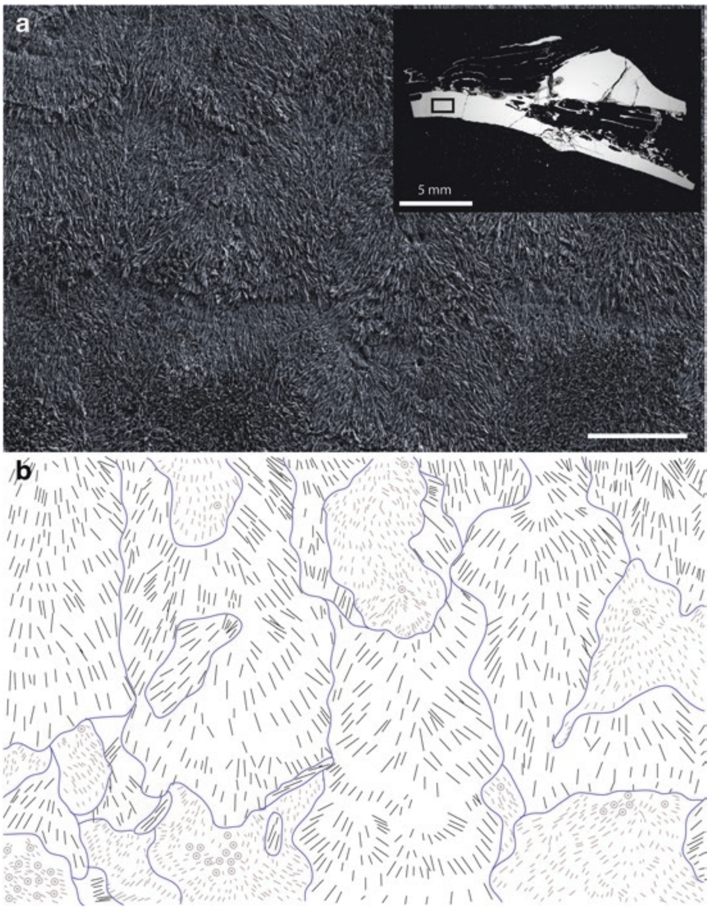

Fig. 36.5 (**a**) SEM view of Thickening Deposits (TD) in the middle of the wall of a *Lophelia pertusa* specimen from the Porcupine Seabight (NE Atlantic), showing different packets of aragonite fibre orientations. Scale bar 100 μm, (**b**) interpretation of the SEM image from (**a**): Black lines represent subhorizontal fibres, grey lines represent oblique fibers and circles represent subvertical fibers compared to the section. Longitudinal growth is from left to right and radial growth from top to bottom

from *L. pertusa* of the NE Atlantic and the Mediterranean Sea (Mouchi et al. 2014). General growth rates and strontium fluctuations across an orthogonal transect to these increments tend to indicate that each microlayer corresponds to a period of one lunar month of growth. Though temporal calibration of the skeleton from these microlayers is promising, it is often hampered by the apparent lateral discontinuity of these structures, particularly when occurring in opaque bands. From SEM observations of *L. pertusa* specimens, taken from a variety of locations in the NE Atlantic and the Mediterranean Sea, coral skeletons seem to exhibit successive growth phases in all three dimensions (Fig. 36.5) that prevents continuity of microlayers (Mouchi et al. 2014).

It is also worthwhile mentioning that no bands or layers have been observed in *L. pertusa* by Mouchi et al. (2014) which may indicate growth patterns along the longitudinal axis (i.e., in the maximum growth direction of the corallite). Still, longitudinal growth do occur as indicated by proof of crystal growth competition on solely one side of sclerodermites (i.e., the side facing the basis of the corallite with pre-existing sclerodermites), while the other side (opposite to the basis) is well ordered without disturbance (Mouchi et al. 2017). Mortensen and Rapp (1998) described white and dark lines in both the transverse and the longitudinal sections of the theca and the septa of *L. pertusa* from Norway, but without clear temporal pattern. Thin microlayers (<10 μm) have been observed in the septa of the cup coral *D. dianthus* (Lazier et al. 1999) and the authors suggested a possible relationship between these microlayers and biological clocks, such as (real or inherited) feeding cycles. Still, further chronological calibration is required to improve the understanding of skeletal growth in time and space, and facilitate the interpretations of analysed transects of geochemical proxies in terms of climatic conditions, as was the case for tropical corals and the identification of annual banding.

36.4 Synthesis of the Different Methods Used for CWC Growth Measurements

Contrary to solitary polyps such as *Desmophyllum dianthus* collected from the NW Atlantic, which form their skeleton along a unidirectional growth axis, the structural complexity inferred by the three-dimensional morphology of colonial species (both stony and soft corals) makes it more difficult to measure colony growth. Additionally, compared to their shallow-water counterparts, direct measurements of growth are constrained by the limited accessibility to deep-waters where CWCs live. As a result, *in situ* growth studies are still scarce for CWCs compared to other biogenic carbonates.

Methods to gauge the skeletal growth patterns of colonial CWCs are mainly derived from those developed for the investigation of shallow-water scleractinians. They include both non-destructive methods and those which require the sacrifice of live coral fragments. Some methods can only be used in aquaria experiments, whereas others can be implemented under *in situ* conditions. All of these methods provide useful complementary information but with several restrictions. The selection of the method is determined by the scientific objectives of the studies and the time available to conduct the study. *In situ* direct observations are suitable for the study at colony level, but the specific role of various parameters influencing growth can be difficult to interpret. Regarding aquaria experiments, the complexity of the natural habitat is difficult to mimic, but the advantage of this kind of experiments is that the environmental conditions can be manipulated, with results of experimental studies therefore providing insight into the understanding of the potential drivers and environmental controls on CWC growth (see Orejas et al., this volume). Whenever possible, *in situ* experiments are recommended, in order to investigate the influence of environmental variability and the combination of abiotic factors in their natural habitats on coral growth processes (e.g., Brooke and Young 2009 for *Lophelia pertusa* in the Gulf of Mexico and Lartaud et al. 2014 for Mediterranean *L. pertusa* and *Madrepora oculata*).

The main methods for the study of CWC growth can be summarised into different sets of techniques, each providing different types of information.

The first group relates to techniques that measure calcification rates (generally expressed as g $CaCO_3$ g^{-1} skeleton day^{-1} or % day^{-1}). These techniques are mainly used in aquaria experiments to test the causal relationship between physicochemical changes in water chemistry and the biomineralisation response of the CWCs (e.g., Orejas et al. 2011a, b; Naumann et al. 2014; Gori et al. 2014; Rodolfo Metalpa et al. 2015 for *L. pertusa*, *M. oculata*, *Dendrophyllia cornigera* and *D. dianthus* from the Mediterranean Sea). The techniques most frequently used to measure calcification rates are: the alkalinity anomaly, the buoyant weight or the radioisotope techniques (Maier et al. 2009; Form and Riebesell 2012).

The second group of techniques quantify linear or surface growth rates (expressed in mm $year^{-1}$ or cm^2 $year^{-1}$). These methods can be used in aquaria and *in situ* (see Orejas et al. 2011a; Lartaud et al. 2017b for *L. pertusa*, *M. oculata*, *D. cornigera* and *D. dianthus*, in both cases with specimens from the Mediterranean Sea). The surface and linear growth extension of coral fragments can be measured at the colony level, or more accurately at polyp level using sclerochronological or sclerochemical tools. Radiometric dating is also used to determine the rates of extension.

The third group of methods investigates the renewal rate of the colony, by determining the budding rate (i.e. new polyp addition over a period of time) (see Mortensen 2001; Lartaud et al. 2014). Due to logistical constraints and the long life cycle of many CWC species, the modelling approach (Galli et al. 2016) is a further promising technique for the study of CWC growth patterns.

36.4.1 Alkalinity Anomaly

Alkalinity anomaly is a commonly used technique to estimate skeletal growth. Measures take place in closed chambers where coral fragments are incubated; water samples are collected from the chambers at the beginning and at the end of the experimental period. The water volume of the chambers needs to be small enough to allow an accurate measure of potential changes in the total alkalinity (A_T). Calcification rates use the 2:1 stoichiometric relationship between the decrease of A_T and $CaCO_3$ precipitation (Chisholm and Gattuso 1991). A correction must be applied for the changes of A_T due to the significant release of inorganic nutrients during incubation, as has been documented for *L. pertusa* and *M. oculata* collected from the Lacaze-Duthiers canyon in the Gulf of Lion (Maier et al. 2013). The alkalinity anomaly technique is however not always applicable for long-term experiments due to several side-effects on the water chemistry (e.g. microbial activity of biofilters, water exchanges, feeding) which are indistinguishable from the corals' calcification activity (Form and Riebesell 2012 in *L. pertusa* from the Norwegian coast).

36.4.2 Buoyant Weight

The buoyant weight technique is a common method used for CWC growth experiments in aquaria. Calcification is inferred from changes in weight of the living organism in seawater of known density. The method is based on the Archimedes' Principle and a correction factor is applied as it has been observed that tissue weight accounts for 3–4% of the skeletal buoyant weight for *M. oculata* from Cap de Creus canyon in the NW Mediterranean and *L. pertusa* from the Island of Malta (Orejas et al. 2011a) and 14 ± 4% for *D. cornigera* corals from Cap de Creus canyon and *D. dianthus* from the Island of Malta (Movilla et al. 2014b). The net buoyant weight values of corals is converted into dry weight (DW) using the density of the pure aragonite (2.94 $g.cm^{-3}$) (Rodolfo Metalpa et al. 2015 on *D. dianthus* from Malta and *D. cornigera* from the Ionian Sea). Although a negative influence of handling cannot be excluded, this method is suitable for measuring calcification over monthly intervals or longer and it can be recommended for long-term rather than short-term experiments. Results however need to be taken with caution as potential artefacts of coral response can be associated to long-term aquaria studies.

36.4.3 Radioisotopes

The radioisotope method involves the incubation of a fresh coral fragment in a seawater volume containing radioactive elements (^{45}Ca or ^{14}C). After an incubation period of several minutes to hours, the coral pieces are rinsed in filtered seawater, the tissue removed, the skeleton dried and dissolved with a strong acid and the incorporated radioactivity measured using a scintillation counter (e.g. Hennige et al. 2014b for *L. pertusa* from the Mingulay Reef Complex, NE Atlantic). The radioisotope method is highly accurate for measurements at short timescales (periods can be minutes), but this method requires sacrificing the organism for analyses and is restricted to small volumes (e.g., 50 mL Falcon tubes).

36.4.4 Surface and Linear Growth Extension

This is a useful technique, both for *in situ* and aquaria measurements. The growth measures are performed by means of image analysis of photographs taken at different periods. The surface extension provides information on the colony size changes (in cm^2) (see Larcom et al. 2014 on *L. pertusa* from the Gulf of Mexico), and the linear growth extension highlights the growth rate (in mm year^{-1}) of coral branches along the main growth axis (Orejas et al. 2008 for *L. pertusa* and *M. oculata* from Cap de Creus canyon, northwestern Mediterranean Sea; Orejas et al. 2011a for *M. oculata* and *L. pertusa* from the Cap de Creus canyon and *L. pertusa* and *D. dianthus* from the Island of Malta; Lartaud et al. 2017b for *L. pertusa* and *M. oculata* from the Lacaze-Duthiers canyon, NW Mediterranean Sea). Key benefits of this method are the “low cost” of the approach and that the technique is non-destructive and particularly suitable for aquaria studies.

36.4.5 Sclerochronology and Sclerochemistry

The analysis of growth increments (sclerochronology) or fluctuations of geochemical signals throughout the growth (sclerochemistry) requires sacrificing the organisms under study. These analyses however provide an accurate measure of growth rates in coral stem and branches and/or time allowing a better characterisation of the temporal dynamics in CWC growth.

Sclerochronology is the “biomineral” equivalent to dendrochronology used on trees. The concept is based on the assumption that each growth increment has been formed by the organism in successive equivalent time intervals whatever their thickness (Knutson et al. 1972). The production of carbonate structures by calcifying species periodically decelerates and eventually ceases, although environmental conditions still remain favourable for skeletal growth. Growth increments (also called growth bands or growth rings) are formed according to different periodicities, from infra-daily to annual rates. The observations are made on skeletal sections (radial or longitudinal, depending on the species) under optical microscopy, scanning electron microscopy or X-ray fluorescence. The method is currently used for deep-water octocorals and antipatharians (e.g., Sherwood et al. 2005 on *Primnoa resedaeformis* collected offshore Nova Scotia, Canada) and for shallow-water stony corals (Le Tissier et al. 1994 on *Porites lutea* from Indo-Pacific and *Porites porites* from Caribbean Sea), but it is still rarely applied to scleractinian CWCs due to limited knowledge on the growth periodicity increments formation (Lartaud et al. 2017a and references in Sect. 36.3.2 of this chapter).

The use of chemical markers is very useful, as they allow a “time 0” point to be marked within the coral (i.e. the date of dye use), and the growth of the coral after this point can then be measured. The incorporation of fluorochromes into the skeleton produces an internal fluorescent mark and subsequently the growth increment can be readily estimated. Calcein (Hassenrück et al. 2013 for *D. dianthus* from Patagonia; Lartaud et al. 2013 for *L. pertusa* and *M. oculata* from the Gulf of Lion) and alizarin red (Brooke and Young 2009 for *L. pertusa* from the Gulf of Mexico; Form and Riebesell 2012 for *L. pertusa* from Norwegian coast) are classically used in mark and recapture experiments with CWCs. However, recent comparison between calcein and alizarin red stainings have shown that calcein appears more suitable than alizarin red, as the last has been shown to strongly limit growth of NW Mediterranean *L. pertusa* and *M. oculata* by delaying coral recovery following the treatment (Lartaud et al. 2017b).

Geochemical proxies (e.g., stable isotopes, minor and trace metals) can also be analysed along the growth profile to determine growth patterns. Sclerochemistry methods were developed for shallow-water species, particularly for scleractinian corals (Pätzold 1984). However, the use of the sclerochemistry is limited with CWCs due to important metabolically-induced skeleton geochemical changes (so called “vital effects”), leading to an uptake of isotopes and elements during the ion transfer between seawater and skeleton (Adkins et al. (2003) for *L. pertusa* and *D. dianthus* from the NW Atlantic; López-Correa et al. (2010) for *L. pertusa* from the Santa Maria di Leuca coral province in the Ionian Sea; Marali et al. (2013) for *D. dianthus* from the

Azores; Raddatz et al. (2013) for *L. pertusa* from various locations from the European continental margin).

36.4.6 Radiometric Dating

Radiometric or radioactive dating compares the abundance of a naturally occurring radioactive isotope within the skeleton to the abundance of its decay products, which form at a constant rate. Different techniques are used for CWC species, including ^{14}C (Roark et al. 2006 for *Corallium secundum*, *Gerardia* sp. and *Leiopathes glaberrima* off Hawaii), ^{230}Th-U (Cheng et al. 2000 for *D. dianthus* from the Pacific, Atlantic and Southern Oceans) and ^{210}Pb-^{226}Ra (Sabatier et al. 2012 for *L. pertusa* and *M. oculata* from Røst Reef, off Norway). Initially applied for ageing fossil-reef structures, radiogenic isotopes are also useful to determine the life span of long-lived species when ring counting is not possible.

36.4.7 Budding Rate

Colonial CWCs (such as *L. pertusa* and *M. oculata*) produce large polyps compared to octocorals and most tropical scleractinians. Colony growth is primarily driven by the addition of new polyps (Gass and Roberts 2011). Quantifying the new polyp additions over a period of time (budding rate) is a useful and non-destructive technique to measure colony-growth. Comparison between studies is however difficult as different works start with different polyp number. A standardised method was proposed by Lartaud et al. (2014) for *L. pertusa* and *M. oculata* from the Lacaze-Duthiers canyon, NW Mediterranean Sea, using the rate of new polyp addition per polyp initially present per year (expressed in %).

36.4.8 Growth Modelling

A complementary approach to the direct measurement of growth is CWC modelling. Numerical simulation techniques for marine fauna have been developed across different scales, ranging from small-scale physiological processes to whole ecosystem dynamics. Organism and population growth models are based on the "bioenergetics approach", calibrated with experimental observations. A bioenergetic growth model describes growth as the evolution of a quantity (energy, biomass or mass of a specific compound) over time through the balance of input and output fluxes, through the system boundary and between compartments within the system. The simplest formula considers one single compartment for biomass (or energy), one input and one output flux that depend on the system biomass/energy usage according to allometric laws (Glazier 2005). The resulting estimations typically allow forecasting of the number of polyps and colony masses over time (see more details in Lartaud et al. 2017a). Those models appear particularly relevant for the study of ecological properties and their impacts on coral growth under changing environmental conditions, such as illustrated by Galli et al. (2016) on *Corallium rubrum,* an endemic species to the Mediterranean Sea.

36.5 Growth: From the Colony to the Reef

36.5.1 Extension of the Colony

For scleractinian corals, colony-growth rate measurements refer mainly to the linear extension (increase in length), whereas growth rate estimates for soft corals (gorgonian, zoanthid and antipatharian species) mostly derive from radial thickening analysis. As they form the largest reef structures across many regions of the North and South Atlantic, as well as the Mediterranean, growth studies were principally dedicated to *Lophelia pertusa*. In contrast, little effort has thus far been dedicated at determining growth rates of other Mediterranean scleractinians such as *Madrepora oculata*, *Dendrophyllia cornigera* or *Dianthus dianthus*.

Lophelia pertusa exhibits the highest growth rates from all CWC known species thus far investigated, ranging from 0.01 to 38.1 mm year^{-1} (see Table 36.1 and Roberts et al. 2009). The reason for this large inter-individual variability is unknown. At present, no clear influence of bathymetry has been detected in CWC growth rates. However different environmental conditions can contribute to partially explain the high variability recorded in *L. pertusa* growth rates. Environmental variability can be considered at different scales (e.g. between oceans or at the habitat scale) and local topography or current flow exposition may explain the large growth fluctuations observed within the same geographic area. An example of these local variations are the growth rates recorded for corals from two different locations in the western Mediterranean: (1) 2.2–17 mm year^{-1}, for specimens collected at ~200 m in the Cap de Creus canyon (Orejas et al. 2008, 2011a) and (2) 0.01–38.1 mm year^{-1} for specimens growing at ~500 m in the Lacaze-Duthiers canyon (Lartaud et al. 2014, 2017b). This example also shows that Mediterranean CWC specimens of *L. pertusa* can reach similar maximum growth rates to those observed to date in the North Sea and in the Gulf of Mexico (maximum observed of 34 mm year^{-1} in the North Sea (Gass and Roberts 2006) and 32.3 mm year^{-1} in the Gulf of Mexico (Larcom et al. 2014)). Finally, *in situ* tag and recapture techniques have shown a decrease in colony growth rate over time (Fig. 36.6). This may reflect faster growth in younger colonies (Larcom et al. 2014) and suggest that the age of a colony could also play an important role, partially explaining differences between growth rate measurements (Table 36.1).

Table 36.1 Linear extension (in mm year^{-1}) measured for scleractinian cold-water corals from different locations

Species	Localisation	Depth (m)	Growth rates (mm.year^{-1})	Method	References
Lophelia pertusa	Central Mediterranean Sea	300	15–17	Aquaria	Orejas et al. (2008)
Lophelia pertusa	Central Mediterranean Sea	300	8.8 ± 6.6	Aquaria	Orejas et al. (2011a)
Lophelia pertusa	Western Mediterranean Sea	520	1.3 ± 1.5 (old) – 7.5 ± 1.2 (young polyps)	*In situ* mark and recapture	Lartaud et al. (2013)
Lophelia pertusa	Western Mediterranean Sea	520	0.01–12.1	*In situ* deployment and recapture	Lartaud et al. (2014)
Lophelia pertusa	Western Mediterranean Sea	480–520	2.2–38.1	*In situ* mark and recapture	Lartaud et al. (2017b)
Lophelia pertusa	Northeast Atlantic	955–1005	7.0	Observations of colonies from man-made structure	Duncan (1877)
Lophelia pertusa	Northeast Atlantic	800	6.0	Observations of colonies from man-made structure	Wilson (1979)
Lophelia pertusa	Northeast Atlantic	220	2.2–5.0	U-Th dating	Pons-Branchu et al. (2005)
Lophelia pertusa	North Sea	60–110	26.0	Observations of colonies from man-made structure	Bell and Smith (1999)
Lophelia pertusa	North Sea	100	5.0	Observations of colonies from man-made structure	Roberts (2002)
Lophelia pertusa	North Sea	90–115	19.0–34.0	Observations of colonies from man-made structure	Gass and Roberts (2006)
Lophelia pertusa	Norway	300	25.0	Sclerochemistry	Mikkelsen et al. (1982)
Lophelia pertusa	Norway	250	19.0	Sclerochemistry	Freiwald et al. (1997)
Lophelia pertusa	Norway	200–350	6.0	Sclerochemistry	Mortensen and Rapp (1998)
Lophelia pertusa	Norway	80–315	9.4	Aquaria	Mortensen (2001)
Lophelia pertusa	Norway	340	8.0	Pb-Ra dating	Sabatier et al. (2012)
Lophelia pertusa	Gulf of Mexico	460–510	2.4–3.8	*In situ* mark and recapture	Brooke and Young (2009)
Lophelia pertusa	Gulf of Mexico	200–800	3.2–32.3	Observations of colonies from man-made structure	Larcom et al. (2014)
Madrepora oculata	Western Mediterranean Sea	250	3.0–18.0	Aquaria	Orejas et al. (2008)
Madrepora oculata	Western Mediterranean Sea	250	5.1 ± 2.6	Aquaria	Orejas et al. (2011a)
Madrepora oculata	Western Mediterranean Sea	520	1.2 ± 1.2 (old) – 3.5 ± 2.1 (young polyps)	*In situ* mark and recapture	Lartaud et al. (2013)
Madrepora oculata	Western Mediterranean Sea	520	0.5–8.4	*In situ* deployment and recapture	Lartaud et al. (2014)
Madrepora oculata	Western Mediterranean Sea	480–520	0.01–18.0	*In situ* mark and recapture	Lartaud et al. (2017b)
Madrepora oculata	Norway	340	14.4 ± 1.1	Pb-Ra dating	Sabatier et al. (2012)
Oculina varicosa	Florida	80	16		Reed (2002)
Enallopsammia rostrata	North Atlantic	1410	5.0	Pb-Ra dating	Adkins et al. (2004)
Solenosmilia variabilis	Tasmania	890–1455	0.84–1.25	^{14}C dating	Fallon et al. (2014)
Desmophyllum dianthus	Atlantic, Pacific, Southern Oceans	420–2200	0.1–3.0	U-Th dating	Cheng et al. (2000)
Desmophyllum dianthus			0.5–1.0	U-Th and ^{14}C dating	Risk et al. (2002)
Desmophyllum dianthus	South Pacific		0.5–2.0	Pb-Ra dating	Adkins et al. (2004)

(continued)

Table 36.1 (continued)

Species	Localisation	Depth (m)	Growth rates (mm.year^{-1})	Method	References
Desmophyllum dianthus	Patagonia	25	2	Observations of colonies from man-made structure	Försterra and Häussermann (2003)
Desmophyllum dianthus	Patagonia	15–20	0.4–1.0	*In situ* mark and recapture	Hassenrück et al. (2013)

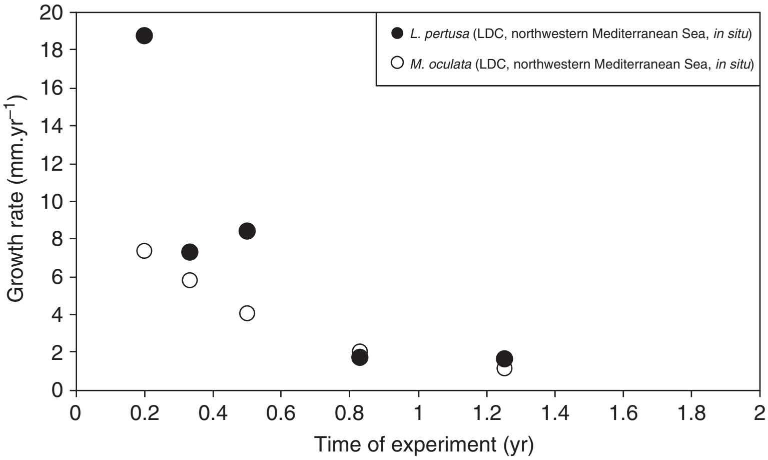

Fig. 36.6 Estimated growth rates of coral nubbins throughout the experimental time (in years: yr). *LDC* Lacaze-Duthiers Canyon. (Adapted from Lartaud et al. 2014, 2017b)

Madrepora oculata from the NW Mediterranean Sea shows mean growth rates ranging from 0.01 to 18 mm year^{-1} (Orejas et al. 2008, 2011a; Lartaud et al. 2013, 2014, 2017b). These values are within the same range as those measured in the Norwegian Sea for this species and elsewhere for other colonial species, except for *Solenosmilia variabilis* which has been observed to have very slow growth rates (~1 mm year^{-1}; Table 35.1). As for *L. pertusa*, a decrease in colony growth rate over time for *M. oculata* is observed (Fig. 36.6).

Currently, no data exist for the rates of extension of *D. cornigera* in its habitat. However, several studies have been conducted with this species in aquaria, using the buoyant weight technique. *D. cornigera* displays growth rates of 7–30% per year (Orejas et al. 2011a; Gori et al. 2014), which are similar to the calcification rates of the long-life span *D. dianthus* (>200 years, Risk et al. 2002), with calcification rates of 11–33% (Orejas et al. 2011a; Rodolfo Metalpa et al. 2015). This last species exhibits growth rates lower than 3 mm year^{-1} (Table 36.1).

36.5.2 Growth Dynamics

In addition to long-term changes, seasonal differences in growth rates have been identified. In the Lacaze-Duthiers canyon differences have been observed over the year for *M. oculata* growth patterns (budding and polyp growth rates) (Lartaud et al. 2014); these differences may be owed to the seasonal change in hydrodynamic conditions that occurs in the canyon heads of the Gulf of Lion (NW Mediterranean). For instance, the observed increase in budding rate during the winter/spring period may be promoted by organic particle supply induced by episodes of dense water shelf cascades and associated resuspension events (Canals et al. 2006; Heussner et al. 2006; Palanques et al. 2006). The response to environmental changes seems however species-specific as *L. pertusa* specimens living in the same habitat display the same growth rates throughout the year (Lartaud et al. 2014). This behaviour suggests more plasticity in the energetic requirement of this species, likely associated with different feeding strategies (Kiriakoulakis et al. 2005) and bacterial-host associations (Meistertzheim et al. 2016). This growth pattern contrasts with the seasonal reproductive cycle described for *L. pertusa* but not for *M. oculata* (Waller and Tyler 2005).

Differences in growth patterns also occur at a long term scale. *L. pertusa* from the NE Atlantic produces micro-layers according to monthly lunar cycle (28 days) and the Sr/Ca composition inside the micro-layers revealed an additional cycle related to semi-lunar oscillations (14 days) (Mouchi et al. 2014). Drivers of those growth rate changes seem to be related to the hydrological context, as in the studied region of the N Atlantic, rapid downwelling of surface waters are caused by hydraulic control of tidal flow, associated with advection onto deep bottom water reefs during peak tides, which periodically increase the availability of organic particles for coral colonies (Davies et al. 2009). As deep as 900 m water depth, tidal influence induces substantial temperature changes (1.5–2 °C) and input of organic matter in canyon ecosystems (van Haren et al. 2014). The thickness of carbonate micro-layers varies according to growth rate changes, showing two slow phases during each year: one in winter months likely caused by a decrease in food availability, with the second possibly correlated with the gametogenesis period (Mouchi et al. 2014).

Similar micro-layers have been detected but poorly revealed in Mediterranean *L. pertusa* (Mouchi et al. 2014). To date, no chronological calibration has been done and more investigations of these structures in an ecosystem free of strong tidal control would be of great interest to better determine the role of environmental or endogenous rhythms on the biomineralisation of scleractinians.

36.5.3 Main Environmental Parameters Governing CWC Growth

A large number of environmental factors (e.g. temperature, salinity, nutrient concentration, currents) and/or biotic factors (symbiosis, predation, competition) can affect coral calcification (Miller 1995). The direct impact and relative importance of these various parameters on CWC growth remains to be defined, and most probably they will be different for the different species. Laboratory studies suggest that an increase in food supply (considering quality and quantity), rather than temperature, may be more important in determining growth rates of scleractinian CWCs (as seen for *L. pertusa* from Norway by Mortensen 2001 and *M. oculata* from Cap de Creus canyon, NW Mediterranean by Orejas et al. 2011b). Growth rates observed in aquaria for NW Mediterranean *M. oculata* are higher when corals are fed five times a week with a mixed diet of *Mysidacea*, frozen Cyclops and *Artemia salina* nauplii (Orejas et al. 2011a) compared to growth rates of corals fed three times a week with *A. salina* nauplii only (Lartaud et al. 2013). Temperature and pH are also important parameters that can affect growth rates, with distinct responses depending on the species or local habitat conditions (cf. details from Sect. 36.6 of this chapter, as well as chapters by Reynaud and Ferrier-Pagès, this volume; Maier et al., this volume; and Movilla, this volume).

Sediment accumulation stress slows coral growth, as seen for *L. pertusa* from south Norway (Larsson et al. 2013). The authors suggest that lower growth is likely due to the additional energy for polyps to clean themselves which decrease the energy available for feeding, or to a lower polyp extension to reduce abrasion risk by sediment particles, limiting ion exchanges from the environment to extracellular medium (i.e., the area where mineralisation occurs). Anthropogenic pollutants such as drill cuttings can create a similar stressor to sedimentation (Larsson et al. 2013 on *L. pertusa* from south Norway).

36.5.4 Reef Formation

After settlement of a coral larva, asexual formation of new polyps drives extension of the colony in three dimensions. Self-recognition of adjacent coral colonies, as well as skeletal fusion in areas with low levels of aragonite crystal organisation and strong molecular bonding, facilitate ecosystem engineering, as described for *L. pertusa* from Norway (Hennige et al. 2014a). Morevover, coral skeleton cementation can also occur between different species, such as for *L. pertusa* and *M. oculata* from the NW Mediterranean (Fig. 36.7), inducing spatial complexity of the living area. Polyp death rates at the base of colonies increase with the colony lifespan, and hence the proportion of dead coral framework increases, leading to zonation of the habitat (Buhl-Mortensen et al. 2010). Other organisms actively promote reef aggregation as well, such as the symbiotic worm *Eunice norvegica*, which stimulates excessive calcification of Norwegian *L. pertusa* (Roberts 2005; Mueller et al. 2013). Coral calcification over the tube produced by worms living within the coral branches strengthens the framework by thickening and connecting coral branches (Fig. 36.2).

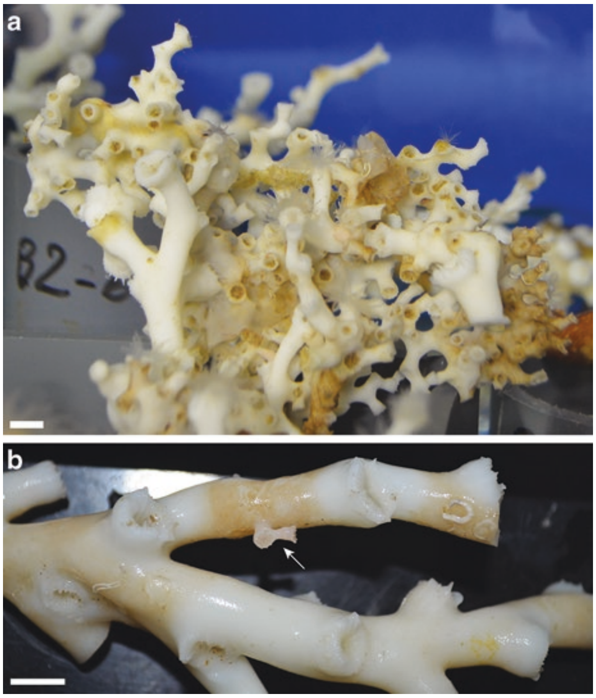

Fig. 36.7 (**a**) Skeleton cementation between *Lophelia pertusa* and *Madrepora oculata* corals from the Gulf of Lion (Lacaze-Duthiers canyon). (**b**) *M. oculata* (white arrow) growing on the wall of two living *L. pertusa* polyps. Scale bar:1 cm. (Photographs © F. Lartaud (Sorbonne University))

Sponges and fungi that attack dead coral parts at the base of the reef tend to form coral rubble by bioerosion. Rubble also contributes in reef formation by providing a substratum for new larvae settlement (Roberts et al. 2009).

Colony extension occurs over the whole lifespan of the coral, and it is supported by the long lifespan of some reef-building species. Radioisotope measurements reveal that the age of a 40 cm high *L. pertusa* colony from the NE Atlantic can be up to 250 years (Pons-Branchu et al. 2005). This means that a 2–3 m high colony needed several centuries to reach this size. However, lifespan differs depending on the species and/or the environment as a 45 cm high *M. oculata* colony from Norway has been estimated to be ~40 years old (Sabatier et al. 2012). Nevertheless if sedimentation takes place at a slower rate than coral growth, colony growth and colonisation by additional coral larvae in the dead or living part of the reef contributes to maintain reef formation over very long periods. The oldest *L. pertusa* reef found to date is estimated in 8600 years old and it is located in Norwegian waters (Hovland and Mortensen 1999).

Reef growth is divided into five stages, corresponding to: (1) reef initiation, (2) framework expansion, (3) framework collapse, (4) partial burial of the coral rubble by superficial sediments, and (5) finally possible larval recruitment on the coral rubble depending on the environmental conditions, allowing the formation of a geological structure induced by cyclic alternation of these different phases (Douarin et al. 2014). The cyclic stages are facilitated by climatic evolution (e.g., glacial/interglacial cycles) allowing formation of coral carbonate mounds over thousands of years (Roberts et al. 2006). The present-day CWC reefs in the Mediterranean Sea were initiated at the Late Pliocene/Early Pleistocene (Taviani et al. 2005, this volume). Depending on the area, reef formation may have been interrupted for long periods inducing temporary extinction of CWCs in the eastern Mediterranean Sea during the early to middle Holocene from 11.4 to 5.9 kyr BP linked to low oxygen conditions (Fink et al. 2012).

36.6 Growth in the Future Mediterranean Sea

36.6.1 Potential Influence of Climate Change on the Mediterranean CWCs

It is estimated that >80% of global warming over the last 40 years has been taken up by the oceans and penetrated to depths of at least 700 m (Barnett et al. 2005). Among other anthropogenic stressors, the imprint of climate change on deep and intermediate Mediterranean waters is expected to generate specific threats to CWC habitats, such as in canyons or seamount flanks (see Ramirez-Llodra et al. 2010; Levin and Le Bris 2015). The combination of warming and acidification of mediterranean intermediate waters combined with change in nutrient supply and deoxygenation could affect the capacity of CWCs to maintain growth rates (Cordes et al. 2016). Predictive habitat modelling approaches and global datasets of key environmental parameters (e.g. temperature, salinity, dissolved O_2 and nutrients), are suggesting changes in the distribution of suitable habitats for CWC taxa in future climate scenarios (IPCC 2014), though there are still large uncertainties in these approaches (Davies and Guinotte 2011). The spatial resolution and accuracy of these models are still largely insufficient to anticipate responses due to short-term changes in local conditions (e.g. recovery times after physical disturbance, fluctuations of environmental factors and feeding constraints). According to future predicted climate IPCC-A2 scenario (IPCC 2014), the average temperature for the deep Mediterranean Sea may increase by 1.5 °C by the end of the twenty-first century with an increase of 0.23 for salinity (Somot et al. 2006). Together with the increase of temperature, pH will decrease as a result of anthropogenic CO_2 absorbed by seawater. In the future (year 2100) Mediterranean deep waters, the pH change is estimated to be between −0.005 and −0.06 units (Palmiéri et al. 2015). The local enhancement of acidification (e.g. due to an increase in organic matter remineralisation) and associated cumulative stressors yet constitute potential threats to CWCs.

Consequences of climate change for Mediterranean CWCs and their associated communities have to be evaluated. Details on this topic are given by Maier et al. (this volume) and Movilla (this volume).

36.6.2 Impact of Temperature

Physiological behaviour of scleractinian CWCs have been monitored in aquaria under different thermal conditions. Long-term (12 months) aquaria experiments on *Lophelia pertusa* from the Atlantic Ocean do not show absolute changes in calcification rates under seawater temperatures of 9 °C and 12 °C (Hennige et al. 2015). *Lophelia pertusa* and *M. oculata* from the Mediterranean Sea however revealed species-specific growth rate responses with similar calcification rates at 9 °C and 12 °C for *L. pertusa*, but lower rates at 9 °C for *M. oculata*. At 6 °C, both species show low calcification rates (Naumann et al. 2014). Similarly, calcification of *Dendrophyllia cornigera* from the Menorca Channel decreases from 12 to 8 °C (Gori et al. 2014).

Thermal acclimation of calcification processes is well established for a number of temperate and tropical scleractinian coral species and the optimal temperatures for several species have been determined. However, for scleractinian CWCs the thermal optimum and the potential for adaptation to temperature changes are still unknown. *In situ* and aquaria experiments suggested that the upper lethal temperature for

L. pertusa from the Gulf of Mexico is near 15 °C (Brooke et al. 2013). Freiwald et al. (2004) suggested that scleractinian CWCs, which occur less frequently in the Mediterranean Sea than in Atlantic and Pacific oceans, are at the uppermost of their thermal tolerance range in the Mediterranean (14 °C). Considering this optimal range, it would be expected that growth experiments conducted at temperatures higher than 13 °C, should display a decline in the calcification rate for CWCs. However, not all CWC species follow this rule as the calcification of *D. cornigera* from the shallow part of the Menorca Channel (~200 m) increases when temperature rises from 12 to 16 °C (Gori et al. 2014). *Desmophyllum dianthus* from a deeper location in the Adriatic Sea (430 m) shows significant decreases in calcification rates when exposed for a long period (8 months) to 15 °C waters (Gori et al. 2016); this might be linked to the decline in activity of enzymes involved in calcification (e.g., carbonic anhydrase). Reef formation in the future Mediterranean may be dramatically affected by global warming or, assuming the different thermal tolerances of species (e.g. *D. cornigera* exhibits a metabolism more efficient at higher temperature, Gori et al. 2014), an increase in temperature may contribute to a shift in Mediterranean CWC community composition. Analyses of fossils (Wienberg et al. 2009) and recent corals from the Atlantic (Keller and Os'kina 2008) suggest a higher temperature tolerance of *M. oculata* compared to *L. pertusa*. Additionally, scleractinian deep-water corals (*Dendrophyllia* sp. and *Eguchipsammia fistula*) have been found in the Red Sea at temperatures exceeding 20 °C, leading to a revisiting on the main persistence and resilience concepts for CWCs (Roder et al. 2013). If the future baseline temperature changes in the deep Mediterranean provinces, questions regarding acclimation of Mediterranean corals have to be addressed. *D. cornigera* from Cap de Creus canyon, NW Mediterranean, and *D. dianthus* from south of Malta, tolerate elevated temperatures (17.5 °C) during 3 months in aquaria, showing higher growth rates for *D. cornigera* when temperature increases, which suggests that those species may be more capable of surviving in warmer environments than previously thought (Naumann et al. 2013).

36.6.3 Ocean Acidification

Acidification is known to alter growth rate of calcifying organisms as global ocean composition becomes undersaturated in calcium carbonate. However, for scleractinian CWCs, long-term aquaria studies generally suggest that calcification of *L. pertusa*, *M. oculata* and *D. cornigera* colonies and *D. dianthus* solitary corals from the Mediterranean Sea are not affected by the pCO_2 level projected at the end of the century (Maier et al. 2013; Rodolfo Metalpa et al. 2015; Gori et al. 2016), although some studies report an expected higher sensititvity of *L. pertusa* and *D. cornigera* species (Movilla et al. 2014b). McCulloch et al. (2012) estimated that the energetic cost associated with pH up-regulation was ~10% per 0.1 pH unit decreases in seawater. A recent study suggests that a small fraction (<3%) of the total energy demand is required for *M. oculata* calcification, allowing corals from the Adriatic Sea to maintain growth rates in more acidic waters even under low feeding conditions (Maier et al. 2016).

The synergic effect of temperature and ocean acidification has been recently tested and the first results suggest that crystallographic and molecular-scale bonding organisation rather than calcification rate of *L. pertusa* from NE Atlantic are affected by thermal and pCO_2 changes (Hennige et al. 2015). Nevertheless, additional studies providing information on the main sources of energy metabolised are required, as highlighted by results from Gori et al. (2016) on *D. dianthus* from the Adriatic Sea.

As this volume includes two chapters (already mentioned in this text) dealing with effects of ocean acidification in CWCs, no more details on this topic will be included in this section.

36.6.4 Impact of Oceanographic Conditions on the Growth of CWCs: The Case Study of Dense Water Shelf Cascades in the Mediterranean Sea

In the Mediterranean Sea, different areas (Aegean Sea, Adriatic Sea, Catalan Margin, Creta Island, Gulf of Lion) are influenced by episodic dense water shelf cascades driven by wind-induced conditions (Canals et al. 2006). These dense water plumes that overflow the shelf edge are associated with significant decreases in temperature, significant increases in the current speed and they may transport of large amounts of coarse sediment and organic matter (Palanques et al. 2006; Heussner et al. 2006; Canals et al. 2006). The precise effects of cascading on CWC communities are not well documented (but see Puig and Gili, this volume). As mentioned before, *in situ* experiments showed a seasonal difference in the growth patterns of *M. oculata*, which are suspected to result from differences in the food availability induced by winter cascading events in the Lacaze-Duthiers canyon (Lartaud et al. 2014). The expected scenario for the end of the twenty-first century by the IPCC suggests a stronger stratification of the water column, which would result in a decrease of cascading events of at least 60%, compared to the present climate conditions (Hermann et al. 2008). Considering these preliminary results, the effects of climate change could result in additional strong threats to the resilience of CWC reefs in the Mediterranean Sea.

36.7 Conclusion

The study of growth patterns is a basic approach to determine the age of corals and to better understand the ecological features of CWCs. The evolution of methodologies and techniques to determine growth rates of CWCs provides increasily more precise approaches to measure growth, and also improvements in the standardisation to compare results obtained from CWCs and tropical and temperate corals, as well as among juvenile and adult individuals. Unexpected results have been highlighted by recent research, for instance the observation that some CWC species can reach growth rates similar to those of some tropical species. Still, growth rates differ depending on location, age of colony or the period of the year. Differences between species, including those living in the same habitat, have also been identified, raising the possibility that specific ecological niches may be preferencially occupied by specific species. These observed differences point out that further work is needed to determine the most effective conservation strategies for the CWC fauna which display diverse ecological performance.

Further, more studies are necessary to elucidate the key environmental and physiological drivers of growth, from the integration of inter-disciplinary studies to take into consideration skeletal growth as a part of the response of the whole organism. For example, a detailed understanding of the biology of the main CWC species still lacks, including knowledge of the role of reproductive cycle, the associated microbiome or the energy invested in growth by the calcifying species. Understanding critical aspects of CWC growth will require studies with substantial multi-parameter monitoring – both biotic and abiotic – focusing on several temporal scales. Within this framework, the Mediterranean Sea is a perfect fieldwork environment as numerous CWC species have been identified in the area, and the effects of global environmental changes on these could be particularly remarkable in this semi-enclosed sea. For the survival of the associated biodiversity, the growth and survival of CWC species in this small ocean is critical.

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References

Addadi L, Raz S, Weiner S (2003) Taking advantage of disorder: amorphous calcium carbonate and its roles in biomineralization. Adv Mater 15:959–970

Addamo AA, Vertino A, Stolarski J, et al (2016) Merging scleractinian genera: the overhelming genetic similarity between solitary *Desmophyllum* and colonial *Lophelia*. BMC Evol Biol 16:108. https://doi.org/10.1186/s12862-016-0654-8

Adkins JF, Boyle EA, Curry WB, et al (2003) Stable isotopes in deep-sea corals and a new mechanisms for "vital effects". Geochim Cosmochim Acta 67:1129–1143

Adkins JF, Henderson GM, Wang SL, et al (2004) Growth rates of the deep-sea scleractinia *Desmophyllum cristagalli* and *Enallopsammia rostrata*. Earth Planet Sci Lett 227:481–490

Allemand D, Ferrier-Pagès C, Furla P, et al (2004) Biomineralisation in reef-building corals: from molecular mechanisms to environmental control. CR Palevol 3:453–467

Allemand D, Tambutté É, Zoccola D, et al (2011) Coral calcification, cells to reefs. In: Dubinsky Z, Stambler N (eds) Coral reefs: an ecosystem in transition. Springer, Dordrecht, pp 119–150

Barnes DJ (1970) Coral skeletons: an explanation of their growth and structure. Science 170:1305–1308

Barnett TP, Pierce DW, AchutaRao KM, et al (2005) Penetration of human-induced warming into the world's oceans. Science 309:284–287

Bell N, Smith J (1999) Coral growing on North Sea oil rigs. Nature 402:601

Bertucci A, Moya A, Tambutté S, et al (2013) Carbonic anhydrases in anthozoan corals—a review. Bioorg Med Chem 21:1437–1450

Brooke S, Young CM (2009) In situ measurement of survival and growth of *Lophelia pertusa* in the northern Gulf of Mexico. Mar Ecol Progr Ser 397:153–161

Brooke S, Ross SW, Bane JM, et al (2013) Temperature tolerance of the deep-sea coral *Lophelia pertusa* from the southeastern United States. Deep-Sea Res Part 2 Top Stud Oceanogr 92:240–248

Bryan WB, Hill D (1941) Spherulitic crystallization as a mechanism of skeletal growth in the hexacorals. Proc R Soc Qld 52:78–91

Buhl-Mortensen L, Vanreusel A, Gooday A, et al (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Mar Ecol 31:21–50

Canals M, Puig P, de Durrieu de Madron X, et al (2006) Flushing submarine canyons. Nature 444:354–357

Carter JG (1980) Guide to bivalve shell microstructures. In: Rhoads DC, Lutz RA (eds) Skeletal growth of aquatic organisms. Plenum Press, New York, pp 645–673

Cartwright JH, Checa AG, Gale JD, et al (2012) Calcium carbonate polyamorphism and its role in biomineralization: how many amorphous calcium carbonates are there? Angew Chem Int Ed 51:11960–11970

Cheng H, Adkins JF, Edwards RL, et al (2000) U-Th dating of deep-sea corals. Geochim Cosmochim Acta 64:2401–2416

Chisholm JRM, Gattuso JP (1991) Validation of the alkalinity anomaly technique for investigating calcification of photosynthesis in coral reef communities. Limnol Oceanogr 36:1232–1239

Cohen AL, McConnaughey TA (2003) Geochemical perspectives on coral mineralization. In: Dove PM, De Yoreo JJ, Weiner S (eds) Biomineralization, reviews in mineralogy and geochemistry. Mineralogical Society of America and the Geochemical Society, Washington, DC, 54:151–187

Cölfen H, Antonietti M (2005) Mesocrystals: inorganic superstructures made by highly parallel crystallization and controlled alignment. Angew Chem Int Ed 44:5576–5591

Constantz BR (1989) Skeletal organisation in *Acropora*. In: Crick RE (ed) Origin, evolution and modern aspects of biomineralization in plants and animals. Plenum Press, New York, pp 175–200

Cordes E, Arnaud-Haond S, Bergstad OA, et al (2016) Cold-water corals. In: Inniss L, Simcock A (eds) The first global integrated marine assessment: World Ocean Assessment I. United Nations regular process for global reporting and assessment of the state of the marine environment, including socioeconomic aspects. United Nations, New York, 28 p

Cuif JP, Dauphin Y (1998) Microstructural and physicochemical characterization of centers of calcification in septa of some recent Scleractinian corals. Paläontol Z 72:257–270

Cuif JP, Dauphin Y, Sorauf J (2011) Biominerals and fossils through time. Cambridge University Press, Cambridge, p 490

D'Onghia G, Indennidate A, Giove A, et al (2011) Distribution and behaviour of deep-sea benthopelagic fauna observed using towed cameras in the Santa Maria di Leuca cold-water coral province. Mar Ecol Progr Ser 443:95–110

Davies AJ, Guinotte JM (2011) Global habitat suitability for framework-forming cold-water corals. PLoS One 6:e18483

Davies AJ, Duineveld GCA, Lavaleye MSS, et al (2009) Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef complex. Limnol Oceanogr 54:620–629

Douarin M, Sinclair DJ, Elliot M, et al (2014) Changes in fossil assemblage in sediment cores from Mingulay Reef Complex (NE Atlantic): implications for coral reef buid-up. Deep-Sea Res Part 2 Top Stud Oceanogr 99:286–296

Duncan PM (1877) On the rapidity of growth and variability of some Madreporaria on an Atlantic Cable, with remarks upon the rate of accumulation of foraminiferal deposits. Proc R Soc Lond 26:133–137

Falini G, Reggi M, Fermani S, et al (2013) Control of aragonite deposition in colonial corals by intra-skeletal macromolecules. J Struct Biol 183:226–238

Fallon SJ, Thresher RE, Adkins J (2014) Age and growth of the cold-water scleractinian *Solenosmilia variabilis* and its reef on SW Pacific seamounts. Coral Reefs 33:31–38

Fiala-Medioni A, Madurell T, Romans P, et al (2012) Rov and submersible surveys on faunal assemblages in a deep-sea canyon (rech Lacaze-Duthiers, western Mediterranean Sea). Vie Milieu 62:173–190

Fink HG, Wienberg C, Hebbeln D, et al (2012) Oxygen control on Holocene cold-water coral development in the eastern Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96

Form AU, Riebesell U (2012) Acclimatation to ocean acidification during long-term CO_2 exposure in the cold-water coral *Lophelia pertusa*. Glob Chang Biol 18:843–853

Försterra G, Häussermann V (2003) First report on large scleractinian (Cnidaria: Anthozoa) accumulations in cold-temperate shallow water of south Chilean fjords. Zool Verh Leiden 345:117–128

Freiwald A, Henrich R, Pätzold J (1997) Anatomy of a deep-water coral reef mound from Stjernsund, West Finnmark. North Nor SEPM Spec Publ 56:141–162

Freiwald A, Fossa JH, Grehan A, et al (2004) Cold-water coral reefs: out of sight – no longer out of mind. UNEP-WCMC, Cambridge, 86 p

Galli G, Bramanti L, Priori C, et al (2016) Modelling red coral (*Corallium rubrum*) growth in response to temperature and nutrition. Ecol Model 337:137–148

Gass SE, Roberts JM (2006) The occurrence of the cold-water coral *Lophelia pertusa* (Scleractinia) on oil and gas platforms in the North Sea: colony growth, recruitment and environmental controls on distribution. Mar Pollut Bull 52:549–559

Gass SE, Roberts JM (2011) Growth and branching patterns of *Lophelia pertusa* (Scleractinia) from the North Sea. J Mar Biol Assoc UK 91:831–835

Glazier DS (2005) Beyond the: variation in the intra- and interspecific scaling of metabolic rate in animals. Biol Rev 80:611

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Gori A, Reynaud S, Orejas C, et al (2014) Physiological performance of the cold-water coral *Dendrophyllia cornigera* reveals its preference for temperate environments. Coral Reefs 33:665–674

Gori A, Ferrier-Pagès C, Hennige S, et al (2016) Physiological response of the cold-water coral *Desmophyllum dianthus* to thermal stress and ocean acidification. PeerJ 4:e1606

Hassenrück C, Jantzen C, Försterra G, et al (2013) Rates of apical septal extension of *Desmophyllum dianthus*: effect of association with endolithic photo-autotrophs. Mar Biol 160:2919–2927

Hennige SJ, Morrison CL, Form AU, et al (2014a) Self-recognition in corals facilites deep-sea habitat engineering. Sci Rep 4:6782

Hennige SJ, Wicks LC, Kamenos NA, et al (2014b) Short-term metabolic and growth responses of the cold-water coral *Lophelia pertusa* to ocean acidification. Deep-Sea Res Part 2 Top Stud Oceanogr 99:27–35

Hennige SJ, Wicks LC, Kamenos NA, et al (2015) Hidden impacts of ocean acidification to live and dead coral framework. Proc R Soc B 282:20150990

Hermann M, Estournel C, Déqué M, et al (2008) Dense water formation in the Gulf of Lions shelf: impact of atmospheric interannual variability and climate change. Cont Shelf Res 28:2092–2112

Heussner S, Durrieu de Madron X, Calafat A, et al (2006) Spatial and temporal variability of download particle fluxes on a continental slope: lessons from an 8-yr experiment in the Gulf of Lions (NW Mediterranean). Mar Geol 234:63–92

Hovland M, Mortensen PB (1999) Norske korallrev og prosesser i havbunnen (Norwegian coral reefs and seebed processes). J Grieg, Bergen, p 167

IPCC (2014) In: Pachauri RK, Meyer LA (eds) Climate change 2014: synthesis report. Contribution of working groups I, II and III tot the fifth assessment report of the intergovernmental panel on climate change. IPCC, Geneva, 151 p

Johnston IS (1980) The ultrastructure of skeletogenesis in hermatypic corals. Int Rev Cytol 67:171–214

Keller NB, Os'kina NS (2008) Habitat temperature ranges of azooxantellate scleractinian corals in the world ocean. Oceanology 48:77–84

Kiriakoulakis K, Fisher E, Wolff GA, et al (2005) Lipids and nitrogen isotopes of two deep-water corals from the North-East Atlantic: initial results and implications. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 715–729

Knutson DW, Buddemeier RW, Smith SV (1972) Coral chronometers – seasonal growth bands in corals. Science 177:270–272

Larcom AA, McKean DL, Brooks JM, et al (2014) Growth rates, densities, and distribution of *Lophelia pertusa* on artificial structures in the Gulf of Mexico. Deep-Sea Res Part 1 Oceanogr Res Pap 85:101–109

Larsson AI, van Oevelen D, Purser A, et al (2013) Tolerance to long-term exposure of suspended benthic sediments ad drill cuttings in the cold-water coral *Lophelia pertusa*. Mar Pollut Bull 70:176–188

Lartaud F, Pareige S, de Rafelis M, et al (2013) A new approach for assessing cold-water coral growth in situ using fluorescent calcein staining. Aquat Living Resour 26:187–196

Lartaud F, Pareige S, de Rafelis M, et al (2014) Temporal changes in the growth of two Mediterranean cold-water coral species, in situ and in aquaria. Deep-Sea Res Part 2 Top Stud Oceanogr 99:64–70

Lartaud F, Galli G, Raza A, et al (2017a) Growth patterns in long-lived coral species. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 595–626

Lartaud F, Meistertzheim AL, Peru E, et al (2017b) In situ growth experiments of reef-building cold-water corals: the good, the bad and the ugly. Deep-Sea Res Part 1 Oceanogr Res Pap 121:70–78

Lastras G, Canals M, Ballesteros E, et al (2016) Cold-water corals and anthropogenic impacts in La Fonera submarine canyon head, Northwestern Mediterranean Sea. PLoS One 11:e0155729

Lazier AV, Smith JE, Risk MJ, et al (1999) The skeletal structure of *Desmophyllum cristagalli*: the use of deep-water corals in sclerochronology. Lethaia 32:119–130

Le Tissier MDA, Clayton B, Brown BE, et al (1994) Skeletal correlates of coral density banding and an evaluation of radiography as used in sclerochronology. Mar Ecol Progr Ser 110:29–44

Levin LA, Le Bris N (2015) The deep ocean under climate change. Science 350:766–768

Lopez-Correa M, Montagna P, Vendrell-Simon B, et al (2010) Stable isotopes ($\delta^{18}O$ and $\delta^{13}C$), trace and minor element compositions of Recent scleractinians and Last Glacial bivalves at the Santa Maria di Leuca deep-water coral province, Ionian sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:471–486

Maier C, Hegeman J, Weinbauer MG, et al (2009) Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. Biogeosciences 6:1671–1680

Maier C, Schubert A, Berzunza Sànchez MM, et al (2013) End of the century pCO_2 levels do not impact calcification in Mediterranean cold-water corals. PLoS One 8:e62655

Maier C, Popp P, Sollfrank N, et al (2016) Effects of elevated pCO_2 and feeding on net calcification and energy budget of the Mediterranean cold-water coral *Madrepora oculata*. J Exp Biol 219:3208–3217

Marali S, Wisshak M, Lopez-Correa M, et al (2013) Skeletal microstructure and stable isotope signature of three bathyal solitary cold-water corals from the Azores. Palaeogeogr Palaeoclimatol Palaeoecol 373:25–38

Marin F, Luquet G, Marie B, et al (2008) Molluscan shell proteins: primary structure, origin, and evolution. Curr Top Dev Biol 80:209–276

McCulloch M, Trotter J, Montagna P, et al (2012) Resilience of cold-water scleractinian corals to ocean acidification: boron isotopic systematics of pH and saturation state up-regulation. Geochim Cosmochim Acta 87:21–34

Meistertzheim AL, Lartaud F, Arnaud-Haond S, et al (2016) Patterns of bacteria- host associations suggest different ecological strategies between two reef building cold-water coral species. Deep-Sea Res Part 1 Oceanogr Res Pap 114:12–22

Mikkelsen N, Erlenkeuser H, Killingley JS, et al (1982) Norwegian corals: radiocarbon and stable isotopes in *Lophelia pertusa*. Boreas 11:163–171

Miller MW (1995) Growth of a temperate coral: effects of temperature, light, depth, and heterotrophy. Mar Ecol Progr Ser 122:217–225

Montero-Serrano JC, Frank N, Tisnérat-Laborde N, et al (2013) Decadal changes in the mid-depth water mass dynamic of the Northeastern Atlantic margin (Bay of Biscay). Earth Planet Sci Lett 364:134–144

Mortensen PB (2001) Aquarium observations on the deep-water coral *Lophelia pertusa* (L., 1958) (scleractinia) and selected associated invertebrates. Ophelia 54:83–104

Mortensen PB, Rapp HT (1998) Oxygen and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia pertusa* (L.) (Anthozoa, Scleractinia): implications for determining of linear extension rates. Sarsia 83:433–446

Mouchi V, Crowley QG, Jackson AL, et al (2014) Potential seasonal calibration for palaeoenvironmental reconstruction using skeletal microstructures and strontium measurements from the cold-water coral *Lophelia pertusa*. J Quat Sci 29:803–814

Mouchi V, Vonlanthen P, Verrecchia EP, et al (2017) Multi-scale crystallographic ordering in the cold-water coral *Lophelia pertusa*. Sci Rep 7:8987

Movilla J, Gori A, Calvo E, et al (2014a) Resistance of two Mediterranean cold-water coral species to low-pH conditions. Water 5:59–67

Movilla J, Orejas C, Calvo E, et al (2014b) Differential response of two Mediterranean cold-water coral species to ocean acidification. Coral Reefs 33:675–686

Mueller CE, Lundälv T, Middelburg JJ, et al (2013) The symbiosis between *Lophelia pertusa* and *Eunice norvegica* stimulates coral calcification and worm assimilation. PLoS One 8:e58660

Naumann MS, Orejas C, Ferrier-Pagès C (2013) High thermal tolerance of two Mediterranean cold-water coral species maintained in aquaria. Coral Reefs 32:749–754

Naumann MK, Orejas C, Ferrier-Pagès C (2014) Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. Deep-Sea Res Part 2 Top Stud Oceanogr 99:36–41

Orejas C, Gori A, Gili JM (2008) Growth rates of live *Lophelia pertusa* and *Madrepora oculata* from the Mediterranean Sea maintained in aquaria. Coral Reefs 27:255

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51

Orejas C, Ferrier-Pagès C, Reynaud S, et al (2011a) Long-term growth rates of four Mediterranean cold-water coral species maintained in aquaria. Mar Ecol Progr Ser 429:57–65

Orejas C, Ferrier-Pagès C, Reynaud S, et al (2011b) Experimental comparison of skeletal growth rates in the cold-water coral *Madrepora oculata* Linnaeus, 1758 and three tropical sceractinian corals. J Exp Mar Biol Ecol 405:1–5

Palanques A, Durrieu de Madron X, Puig P, et al (2006) Suspended sediment fluxes and transport processes in the Gulf of Lions submarine canyons. The role of storms and dense water cascading. Mar Geol 234:43–61

Palmiéri J, Orr JC, Dutay JC, et al (2015) Simulated anthropogenic CO_2 storage and acidification of the Mediterranean Sea. Biogeosciences 12:781–802

Pätzold J (1984) Growth rythms recorded in stable isotopes and density bands in the reef coral *Porites lobata* (Cebu, Philippines). Coral Reefs 3:87–90

Pons-Branchu E, Hillaire-Marcel C, Deschamps P, et al (2005) Early diagenesis impact on precise U-series dating of deep-sea corals: example of a 100–200 year old *Lophelia pertusa* sample from the Northeast Atlantic. Geochim Cosmochim Acta 69:4865–4879

Raddatz J, Liebetrau V, Rüggeberg A, et al (2013) Stable Sr-isotope, Sr/Ca, Mg/Ca, Li/Ca and Mg/Li ratios in the scleractinian cold-water coral *Lophelia pertusa*. Chem Geol 352:143–152

Ramirez-Llodra E, Brandt A, Danovaro R, et al (2010) Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences 7:2851–2899

Reed JK (2002) Deep-water Oculina coral reefs of Florida: biology, impacts, and management. Hydrobiologia 471:43–55

Reitner J (2005) Calcifying extracellular mucus substances (EMS) of *Madrepora oculata* – a first geobiological approach. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 731–744

Risk MJ, Heikoop JM, Snow MG, et al (2002) Lifespans and growth patterns of two deep-sea corals: *Primnoa resedaeformis* and *Desmophyllum cristagalli*. Hydrobiologia 471:125–131

Risk MJ, Hall-Spencer J, Williams B (2005) Climate records from the Faroe-Shetland Channel using *Lophelia pertusa* (Linnaeus, 1758). In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 1097–1108

Roark EB, Guilderson TP, Dunbar RB, et al (2006) Radiocarbon-based ages and growth rates of Hawaiian deep-sea corals. Mar Ecol Progr Ser 327:1–14

Roberts JM (2002) The occurrence of the coral *Lophelia pertusa* and other conspicuous epifauna around an oil platform in the North Sea. J Soc Underw Technol 25:83–91

Roberts JM (2005) Reef-aggregating behaviour by symbiotic eunicid polychaetes from cold-water corals: do worms assemble reefs? J Mar Biol Assoc UK 85:813–819

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Roberts JM, Wheeler A, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334. https://doi.org/10.1017/CBO9780511581588

Roder C, Berumen ML, Bouwmeester J, et al (2013) First biological measurements of deep-sea corals from the Red Sea. Sci Rep 3:2802

Rodolfo Metalpa R, Montagna P, Aliani S, et al (2015) Calcification is not the Achilles' heel of cold-water corals in an acidifying ocean. Glob Chang Biol 21:2238–2248

Rollion-Bard C, Blamart D (2014) SIMS method and examples of applications in coral biomineralization. In: DiMasi E, Gower LB (eds) Biomineralization sourcebook: characterization of biominerals and biomimetic materials. Taylor & Francis Group, London, pp 249–258

Rollion-Bard C, Blamart D, Cuif JP, et al (2010) In situ measurements of oxygen isotopic composition in deep-sea coral, *Lophelia pertusa*: re-examination of the current geochemical models of biomineralization. Geochim Cosmochim Acta 74:1338–1349

Sabatier P, Reyss JL, Hall-Spencer J, et al (2012) ^{210}Pb-^{226}Ra chronology reveals rapid growth rate of *Madrepora oculata* and *Lophelia pertusa* on world's largest cold-water coral reef. Biogeosciences 9:1253–1265

Sherwood O, Scott D, Risk M, et al (2005) Radiocarbon evidence for annual growth rings in the deep-sea octocoral *Primnoa resedaeformis*. Mar Ecol Progr Ser 301:129–134

Somot S, Sevault F, Deque M (2006) Transient climate change scenario simulation of the Mediterranean Sea for the 21st century using a high-resolution ocean circulation model. Clim Dyn 27:851–879

Stolarski J (2003) Three-dimensional micro- and nanostructural characteristics of the scleractinian coral skeleton: a biocalcification proxy. Acta Palaeontol Pol 48:497–530

Tambutté E, Allemand D, Mueller E, et al (1996) A compartmental approach to mechanisms of calcification in hermatypic corals. J Exp Biol 199:1029–1041

Tambutté S, Holcomb M, Ferrier-Pagès C, et al (2011) Coral biomineralization: from the gene to the environment. J Exp Mar Biol Ecol 408:58–78

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

van Haren H, Mienis F, Duineveld GCA, et al (2014) High-resolution temperature observations of a trapped nonlinear diurnal tide influencing cold-water corals on the Logachev mounds. Progr Oceanogr 125:16–25

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396

Wainwright SA (1964) Studies of the mineral phase of coral skeleton. Exp Cell Res 34:213–230

Waller RG, Tyler PA (2005) The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic Ocean. Coral Reefs 24:514–522

Weiner S, Levi-Kalisman Y, Raz S, et al (2003) Biologically formed amorphous calcium carbonate. Connect Tissue Res 44:214–218

Wienberg C, Hebbeln D, Fink HG, et al (2009) Scleractinian cold-water corals in the Gulf of Cádiz – first clues about their spatial and temporal distribution. Deep-Sea Res Part 1 Oceanogr Res Pap 56:1873–1893

Wilson JB (1979) Patch' development of the deep-water coral *Lophelia pertusa* (L.) on Rockall Bank. J Mar Biol Assoc UK 59:165–177

Cross-References

Aymà A, Aguzzi J, Canals M, et al (this volume) Occurrence of living cold-water corals at large depths within submarine canyons of the Northwestern Mediterranean Sea

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

D'Onghia G (this volume) Cold-water coral as shelter, feeding and life-history critical habitats for fish species: ecological interactions and fishing impact

Fourt M, Goujard A, Chevaldonné P (this volume) Working with visual methods, comparison among the french deep-sea Canyons

Lastras G, Sanchez-Vidal A, Canals M (this volume) A cold-water coral habitat in La Fonera submarine Canyon, Northwestern Mediterranean Sea

Maier C, Weinbauer MG, Gattuso JP (this volume) Fate of Mediterranean scleractinian cold-water corals as a result of global climate change. A synthesis

Movilla J (this volume) A case study: variability in the calcification response of Mediterranean cold-water corals to ocean acidification

Orejas C, Taviani M, Ambroso S, et al (this volume) Cold-water coral in aquaria: advances and challenges. A focus on the Mediterranean

Puig P, Gili JM (this volume) Submarine Canyons in the Mediterranean: a shelter for cold-water corals

Reynaud S, Ferrier-Pagès C (this volume) Biology and ecophysiology of Mediterranean cold-water corals

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean sea and adjacent areas

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals

37 Demography and Conservation of Deep Corals: The Study of Population Structure and Dynamics

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Abstract

The science of demography was developed for the study of human populations, but the theoretical framework and analytical techniques can be easily applied to animal populations, giving powerful instruments for conservation and management. Demography is then a paradigmatic example of the advantages of interdisciplinary approaches which allow transferring the techniques developed in one field (e.g. human population studies) to different fields (e.g. nature conservation and management). Cold-water corals have been approached relatively recently by scientist due to the technical constrains linked to the deep habitat where they live. However the fast development of underwater observation technologies is allowing to gather data on those deep and not easily accessible ecosystems, showing their paramount role in the ecosystem functioning. Due to the peace at which environmental changes are threatening natural ecosystems, increasing our knowledge on cold-water corals is urgent and time constrained. Due to the slow life cycles of the cold-water coral species, forecasting capacity is needed to understand the dynamics of their populations. Demography can give this forecasting capacity but, up to now, the paucity of data from deep coral populations still not allowed to apply demographic models to those environments. Fortunately, the application of demographic models to other species with similar characteristics can help a fast development of similar instruments to cold-water corals. The present chapter aims at introducing demography from an historical point of view, showing how this science evolved from the study of human populations to the conservation of animal populations. We then review the application of demographic modeling to coral populations and in particular we focus on the case study of the Mediterranean red coral (*Corallium rubrum*). This species is endemic to the Mediterranean Sea and besides it is not considered as a cold-water coral species, it dwells in relatively cold environment and can be found at considerable depths.

Keywords

Demography · Population dynamics · Corals · Cold-water corals · Mediterranean Sea

37.1 Demography: A Human Population Science

Demography is the science that studies populations, focusing on their structure and their changes over time due to births, deaths, migration and aging.

To find the origins of demography we have to go long back in time. This science was born to study human populations, to collect taxes and recruit men for military purposes. The main instrument for the collection of demographic data is the *census*. A census is the procedure of systematically acquiring and recording information about the members of a given population. The first known census dates several thousands years ago: with the appearance of the first states in the Fertile Crescent and in Egypt, in the third millennium before Common Era (BCE), the practice of registering people and goods began, as an essential instrument of power to control taxes and benefits (Frier 2000). Only the relevant data were collected for this purpose and only when and where it was necessary. Censuses throughout antiquity then, were not aimed at collecting global demographic information, but to establish the social position linked to wealth, or to generate

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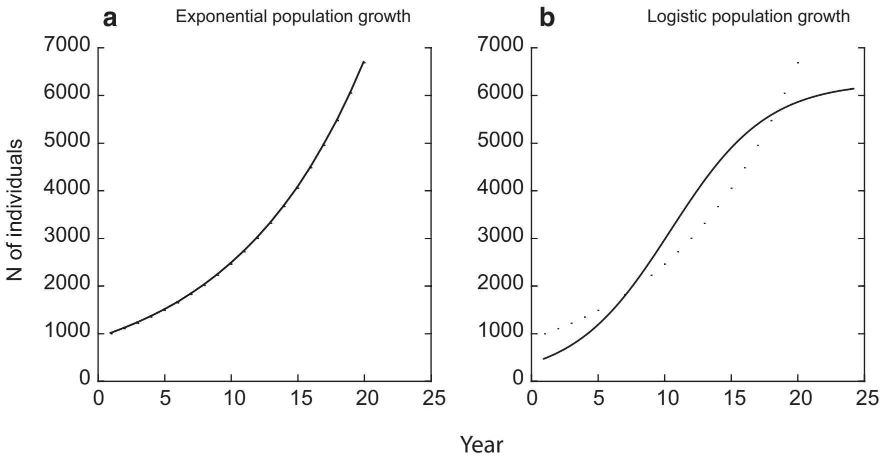

Fig. 37.1 (**a**) Exponential population growth, also known as Malthusian growth. (**b**) Logistic population growth. The growth rate decreases as the population reaches the maximum number of individuals in a population

lists for specific purposes: military cams, tribute collection, corvees, food distributions (Scheidel 2007). Archeological records suggest that Sumerians used to take censuses at 7 year intervals with the purpose of counting the number of people and livestock, as well as quantities of olive oil, butter, honey, milk, wool and vegetables (Kuhrt 1995). During the Roman Republic, censuses were taken regularly as a list, to keep track of all adult males fit for military service, such as for example the census ordered by roman emperor Caesar Augustus, the first census made in Judea when it became a province of the Roman Empire and which record can be found in the New Testament (Luke 2:1–7, ESV).

In ancient times, demography was used only as an instrument to gather information on the number of citizens of a country and was then reduced to a simple enumeration of individuals and eventually of goods. When governments started to need information not only on the number of citizens at the specific time of the census, but also on their future number, demographic studies started to consider populations as dynamic entities.

Population dynamics is a branch of demography that studies populations as dynamic systems. The aim of population dynamic studies is the understanding of mechanisms driving changes in the number of individuals in a population and finally to give tools to forecast the number of individuals in the future.

The need of forecasting capacity is linked to the application of models that consist in a simple mathematical representation of reality. The simplest demographic models take the name from Thomas Robert Malthus, which in 1798 discussed the infinite human population growth (Fig. 37.1a). Despite the concept of infinite population growth is linked to Malthus (malthusian growth), the first mathematical formalisation is due to Euler, which in 1748 (50 years before Malthus) published a essay entitled “Introduction to Analysis of the Infinite” where he dealt about human population dynamics problems linked to the repopulation of earth after big disasters (Bacaer 2010).

The work of Euler and the subsequent consideration of Malthus represent a milestone in the field of population dynamics as they start to mathematically treat the dynamics of the populations, passing from a description of the process to an attempt of forecasting. However, the dynamics described are not realistic as they do not account for the limitation due to the environmental carrying capacity (i.e. the maximum population size that the environment can sustain indefinitely, given resources available in the environment). This limitation was solved by Pierre Francois Verhulst (1838), who developed the *logistic model* describing a non-exponential population growth model characterized by a decreasing rate as the population approaches a threshold saturation level (Fig. 37.1b).

37.2 Animal Demography

Demographic models have been largely applied to simulate the dynamics of animal and plant populations. Derived from the logistic equation, the famous Lotka-Volterra multi-equation model was independently developed by Volterra and Lotka, with the aim to describe the dynamics of non human populations under intra and interspecific competitive interactions (Volterra 1931). In 1957 Beverton and Holt applied the logistic equation to fishery, proposing the *yield per recruit* model, which represents the sustainable yield of a fish population as a function of both individual growth and mortality (Beverton and Holt 1957). Since the Beverton-Holt model, demographic approaches have been frequently applied to the conservation of marine species (e.g. Gerber et al. 2005; Rossi et al. 2017a, b), and population models are now a common instrument for marine ecologists. In the last decades scientists started to apply different families of models other than the ones derived from the logistic equation. In particular *matrix population models* have been frequently applied due to their capacity of dealing with long-lived species.

37.2.1 Matrix Population Models

Population dynamic models based on transition matrices have been applied to a variety of organisms and they revealed to be a powerful instrument in conservation and management of structured populations of long-lived species. Advices for the conservation measures of several marine species derived from the results of this family of models. The Mediterranean red coral (*Corallium rubrum*) is a paradigmatic example of this direct relationship between modeling and conservation: the ban of harvesting with trawling techniques, as well as the ban of harvesting shallower than 50 m depth, were decided by FAO on the basis of demographic studies (Santangelo and Bramanti 2006; Tsounis et al. 2013). Other species, characterized by long life cycles, have been the object of demographic studies based on matrix population models; as examples we can find cetaceans, with models applied to the study of the right whale (e.g. Fujiwara and Caswell 2001), the fin whale (e.g. Arrigoni et al. 2011) and the killer whale (e.g. Brault and Caswell 1993). Sea turtles as well as polar bears have been object of population dynamics modeling studies (e.g. Crouse et al. 1987; Molnár et al. 2014). Not only vertebrates are object of demographic studies. In marine environment, corals are long-lived species whose population dynamics can be modeled with matrix population models. The topic of coral demography will be more extensively treated in the Sect. 37.2.3 (Coral demography).

Matrix population models have been introduced to describe the dynamics of structured populations. In such populations, individuals are classified in categories based on their demographic traits. One of the most important traits is age, which allows a temporal resolution of the model (Bramanti et al. 2015). Age structured models were firstly set out by Lewis (1942) and Leslie (1945, 1948) in their seminal works on population dynamics, but some other characteristics such as size, life cycle stage etc., can be used, depending on the question. A comprehensive description of matrix population models and their properties have been given by Caswell (2001).

Objective of a matrix population model is to project the structure of a given population along time under the conditions imposed by the model. In order to project the structure of a population all the data necessary to describe the present structure of the population as well as the basic data on the life history traits driving its dynamics (e.g. reproductive and survival rates) have to be collected. Population data are organized in *static* "life-tables" which contain the basic information on the population structure in a defined time; in particular, for example, under the assumption of "steady state" mortality can be calculated as the difference between the number of individuals in one age class or vital stage and that in the following (younger) one. A population is considered in steady state if the ratio between two following classes remains constant overtime (i.e. a *proportional mortality occurs;* Caswell 2001). In this case, age classes distribution follows a *monotonic*, decreasing pattern (olds are less numerous than young).

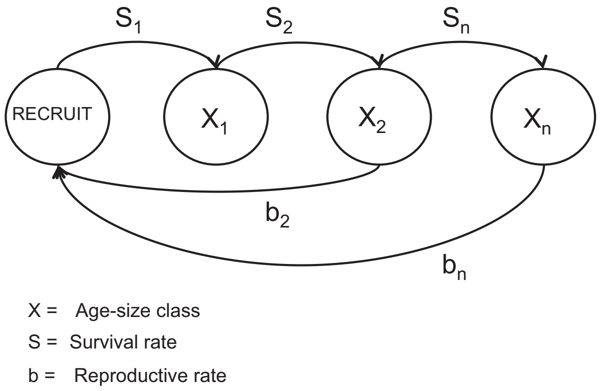

Fig. 37.2 Conceptual model representing the dynamics of a stage structured population. Each stage (circle) is linked to the previous through survival probability (Sx) and the first stage (recruitment) is linked to the fecundity of the reproductive stages bx)

The graphical representation of a conceptual model for the dynamics of an age-structured population is shown in Fig. 37.2. The graph represents the dynamics of the population highlighting the role of the different life history traits. The dynamic relationships between the different classes or vital stages are described by a Markov chain in which survival probability S_i links the number of individuals in one class to that in the subsequent class, while recruitment is linked to population reproductive output b_i (Fujiwara and Caswell 2001). Population dynamics are then described mathematically in the form of a recurrence equation in which the iteration of a transfer matrix allows to project the structure of the population overtime. Population trend will depend on the leading eigenvalue of the transfer matrix, population growth occurring when the latter is larger than 1 (Caswell 2001).

37.2.2 Metapopulation Models

The model of Fig. 37.2 is based on the assumption of "closed populations", where recruitment is linked to local reproduction. In an "open" population, local reproduction and local recruitment are not univocally linked. This means that local population dynamics approach should be replaced by a meta-population approach at the scale where a set of populations form a closed network (Fig. 37.3). The closed

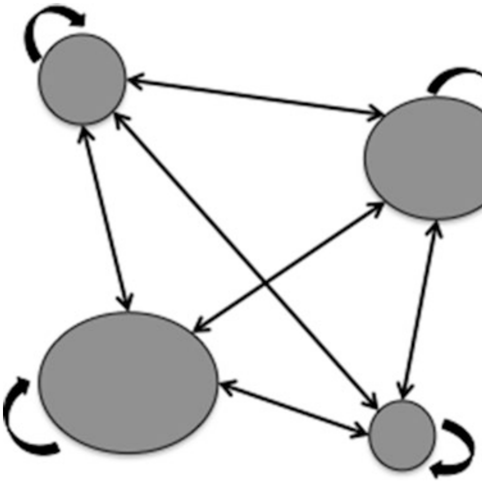

Fig. 37.3 Meta-population conceptual model. Circles represents populations. Each population has its own dynamics (round arrows) and exchange individuals with other populations (straight arrows)

network (i.e. meta-population) is defined by the populations among which exchange of individuals happens (i.e. colonisation).

The early meta-population model of Levins (1969) described the presence / absence of a species in a set of similar patches, assuming the same rate of extinction and the same level of connectivity for every patch. In such a network, species persistence occurred only if colonisation was larger or equal to local extinction. By making explicit the variation of colonisation with geographical distance and surface area of patches, Hanski and Ovaskainen (2000) formulated a spatially structured meta-population model describing the probability of patch occupation according to patches distance and surface for a species with uniform colonisation and extinction probability. However, such approach is useful only for mobile species, which displacement results from a tradeoff between energetic reserve and motion cost, such as terrestrial mammals, on the contrary, it is not useful for species dispersing in a restricted period of the life cycle in form of oocytes or larvae, such as corals. In the ocean, where the flow is anisotropic (variable according to the direction it is measured), eggs and larvae transport is spatially structured and colonisation among a set of populations vary according to the location of source and sink populations. The transfer rates within a marine meta-population are therefore described by spatially explicit connectivity matrices resulting from ocean current transport and specie-specific larvae motility behavior (e.g. Katz et al. 1994; Guizien et al. 2006; Luiz et al. 2013). In a spatially explicit discrete meta-population model, connectivity matrices are combined with data on the fecundity of source populations and data on the recruitment success in sink populations. The objective is to describe the redistribution of the meta-population reproductive output proceeding from each population within the population's network which will balance the local mortality between two reproductive events (Hastings and Botsford 2006).

The mathematical description of this meta-population model is similar to a model for age-structured population by a recurrence relationship based on a transition matrix redistributing offspring in space, and meta-population viability is determined by the leading eigenvalue of the transition matrix being larger or equal to 1. For long-lived species with fecundity proportional to age and dispersing life stage, such as corals, the two transition matrices can be combined in an age-structured meta-population model, as done by Guizien and Bramanti (2014) for the Mediterranean red coral (see Sect. 37.3.1.4: connectivity matrix for more details).

37.2.3 Coral Demography

Corals are among the most long-lived marine species (Roark et al. 2006; Lartaud et al. 2017) and they form structured populations composed by individuals of different ages. Being sessile animals, corals can disperse only during a restricted period of time (each year) in form of pelagic eggs or lecitotrophic larvae (planulae). Despite clonal propagation has been observed in some species (Highsmith 1982; Lasker 1990), dispersal is mainly linked to the larval phase due to the low dispersal capacities of coral fragments.

Population dynamic models have been applied to tropical and temperate coral species to project the evolution of their demography in time. The first studies derive from the seminal work of Hughes (1984) and are focused on tropical species (e.g. Hughes and Jackson 1985; Bak and Meesters 1998; Edmunds and Elahi 2007; Bramanti et al. 2015). Projections can be used either with forecasting purposes (i.e. anticipating the changes in population structure under different scenarios) or with description purposes (i.e. for understanding the functioning of the studied population; Shannon 1975).

In temperate seas, several works on coral population dynamics have been focused on species dwelling in relatively shallow environments (e.g. *C. rubrum*, *Paramuricea clavata*, *Balanophyllia europaea*) assuming closed populations maintaining themselves through self-recruitment (Santangelo et al. 2007; Bramanti et al. 2009; Linares et al. 2010; Caroselli et al. 2012). The preferential application to shallow populations is dictated by the intrinsic characteristics of matrix models which are high data demanding. In order to apply a matrix population model, in fact, data on several life history traits are required, such as population density, colony growth rates, population structure, reproductive output and mortality.

37.3 Mediterranean Corals

The world "coral" immediately recall images of colorful tropical coral reefs in shallow crystal waters. However, it is now widely known that coral *bioformations* are not exclusive of shallow tropical waters (Fig. 37.4). Massive biogenic formations mainly composed by corals (i.e. *deep coral reefs*) have been found in deep, dark, cold, nutrient-rich waters, also at not tropical latitudes. These formations are known as cold-water corals (CWCs) and can occur in fjords, along the edge of the continental shelf and around offshore submarine cliffs and seamounts at almost all the latitudes (Freiwald et al. 2004, 2009, 2017; OSPAR 2015; Freiwald and Roberts 2005; Roberts et al. 2006, 2009; Altuna and Poliseno, this volume). CWC, similarly to tropical corals, form three-dimensional biogenic structures (the so called animal forests; Fig. 37.5 *sensu* Rossi et al. 2017a, b), but unlike tropical reef species, CWC do not host symbiotic algae in their polyps and consequently, for their survival they do not depend on sunlight, but on the capture of seston from the surrounding water (Duineveld et al. 2004; Thiem et al. 2006).

The CWCs are not only restricted to reef forming scleractinian species (e.g. *Lophelia pertusa* and *Madrepora oculata*). The so called deep coral gardens occupy huge areas in which octocorals dominate: species belonging to Alcyonacea, Pennatulacea and Anthipataria, for example, have been found at high densities in the UK waters (Lancaster 2014) and Gulf of Mexico (Quattrini et al. 2014). Also in the Mediterranean Sea several species of deep, not reef forming species are present which can form millennial underwater forests (Fig. 37.6). Coral gardens formed by *Callogorgia verticillata, Antipathella subpinnata* and *Parantipathes larix* as well as dense and pristine forest of the black coral *Leiopathes glaberrima* and the bamboo coral *Isidella elongata* have been found in the Sardinian waters (Bo et al. 2015; Cau et al. 2017a, b; Bo and Bavestrello, this volume; Rueda et al., this volume; Altuna and Poliseno, this volume; Chimienti et al., this volume) as well as in Maltese waters (Deidun et al. 2015; Knittweis et al., this volume). Forests of the gold coral (*Savaglia savaglia*) have been reported from the southern Tyrrhenian Sea (Cerrano et al. 2010).

37.3.1 Matrix Models for Conservation: The Case Study of the Mediterranean Red Coral (*Corallium rubrum*)

Due to the difficulty of data collection on deep dwelling species, none of the deep CWC has been object of demographic modeling, with the exception of the Mediterranean red coral (*Corallium rubrum*) which although is not a "true" CWC, can be found in relatively deep (800 m, Costantini et al. 2010) and cold (<12 °C) environments. Due to its wide bathymetric range (populations of this species can be found as shallow as 10 m depth Rossi et al. 2008) and its economic importance (Tsounis et al. 2010) it has been object of accu-

Fig. 37.4 Tropical coral bioformation. Moorea, French Polynesia. (© Lorenzo Bramanti, LECOB-CNRS)

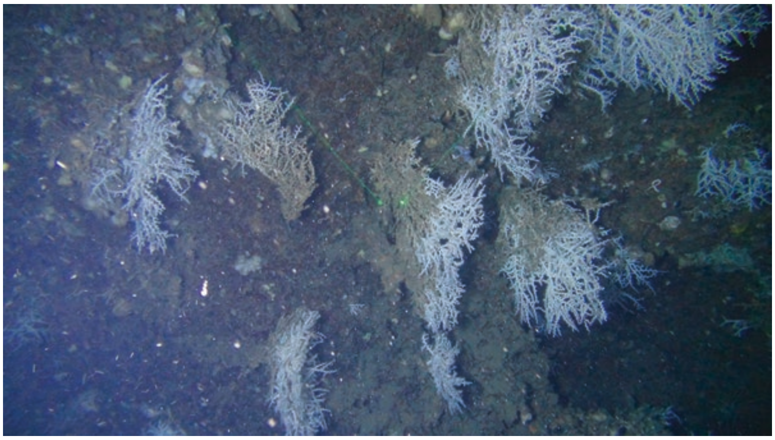

Fig. 37.5 CWC bioformation composed by *Madrepora oculata* at 325 m depth in the Lacaze-Duthiers canyon (North western Mediterranean sea). Distance between the two laser beams is 6 cm. (© UPMC-Fondation TOTAL)

Fig. 37.6 *Leiopathes glaberrima* from Mediterranean sea. (© Alessandro Cau, University of Cagliari)

Fig. 37.7 Mediterranean red coral (*Corallium rubrum*) shallow population (30 m depth) at Cap de Creus (Spain). (© Francisco Romero)

rate demographic studies (Garrabou and Harmelin 2002; Santangelo et al. 2007; Bramanti et al. 2009, 2014, 2017; Priori et al. 2013; Santangelo et al. 2015).

Corallium rubrum is distributed throughout the Mediterranean Sea and neighboring Atlantic rocky shores between 10 and 800 m depth (Costantini et al. 2010). It is an extremely long-lived species which life span can overcome one century (Garrabou and Harmelin 2002; Priori et al. 2013). Harvested and traded since thousands of years due to the use of its red carbonatic skeleton in jewelry industry (Jimenez and Orejas 2017), *C. rubrum* is a paradigmatic example of an overexploited species (Tsounis et al. 2010 and references herein). The General Fishery Commission for the Mediterranean (GFCM) highlighted the necessity to forecast the structure of the most endangered populations of this species under harvesting scenarios in order to plan management and conservation actions (GFCM 2011).

Hundreds of years of harvesting (Tsounis et al. 2010) likely brought to the alteration of the structure and density of the shallow populations of *C. rubrum* (Santangelo and Abbiati 2001; Cau et al. 2016; Garrabou et al. 2017). Despite those changes, data on shallow water populations have been useful to develop matrix population models to project population structure over time under human (harvesting) and environmental (climate change) disturbances (Bramanti et al. 2017). The model helped researchers in understanding the main drivers of deep and shallow population dynamics (Bramanti et al. 2009) and should help in planning conservation measures (Santangelo et al. 2015). Moreover, the results of the projections have been recently validated by direct observations on deep populations (Cau et al. 2016).

Here we present an example of the steps followed in the development of a matrix population model for a closed population of *C. rubrum* dwelling in the shallower portion of the species bathymetric range in the NW Mediterranean Sea (Fig. 37.7; Santangelo et al. 2007). To describe the life history traits of the population, a “life table” has been compiled. The “life–table” summarizes the data on size/age structure (number of colonies in each size/age class), survival and fecundity (number of larvae produced per colony of each class).

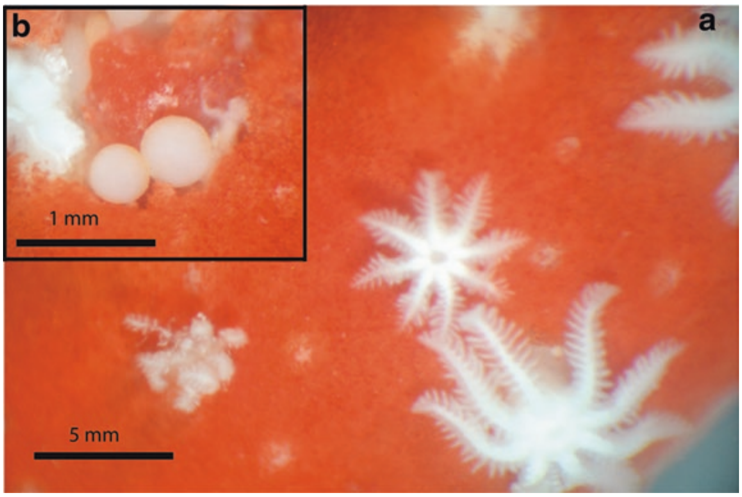

Fig. 37.8 Fecundity estimation. (**a**) Polyps of *Corallium rubrum*. (**b**) Mature oocytes found inside one of the polyps

37.3.1.1 Fecundity

Fecundity (number of larvae produced per individual) is a key trait of a population, as it allows to link the present structure of the population to its reproductive output. In many cases values of fecundity cannot be directly measured and have to be estimated on the basis of other measurable traits such as fertility (% of fertile colonies), number of mature oocytes and / or immature planulae per female polyp, number of polyps per colony and sex ratio (Santangelo et al. 2003; Priori et al. 2013). The main difficulty in this procedure is due to the need of a minimum number of mature colonies that have to be sampled just before larval release. Moreover, the number of larvae released is estimated on a subsample of the polyps of the colony (Fig. 37.8). Alternatively, fecundity can be directly quantified on colonies maintained in aquaria, as it has been done in the case of *Pocillopora damicoris* (Bramanti et al. 2015) and *C. rubrum* (Martínez-Quintana et al. 2015), where female colonies are isolated in different aquaria during the spawning period and the released larvae are counted. The advantage of this method is that the number of larvae released is directly counted and not estimated. The drawback is that the colonies have to be maintained in aquaria and fecundity can be measured only on a limited number of colonies.

37.3.1.2 Colony Growth and Survival

For the application of a matrix model, populations are divided in classes. Classes can be represented by demographic traits such as life stage (e.g. right whale; Fujiwara and Caswell 2001) or size (e.g. *Porites astreoides*, *Diploria strigosa* and *Paramuricea clavata*; Edmunds 2010; Linares et al. 2008 respectively). In the case of *C. rubrum*, the populations have been divided in size/age classes according to the relationship found between colony size (basal diameter) and colony age (Santangelo et al. 2007; Priori et al. 2013; Bramanti et al. 2014). Colony age was estimated on a subsample of colonies of different size, applying the *organic matrix staining method* (OMS), proposed by Marschal et al. (2004) and validated by Gallmetzer et al. (2010) and Benedetti et al. (2016). The relationship between age and size was then used to divide a larger sample of colonies in size/age classes based on the measured diameter.

Although *de facto* the model for the red coral is based on size classes, we use the growth rate to estimate the most probable age of colonies in each size class and the width of the size class that can be transitioned with the growth occurring in a defined time period. This last aspect is a fundamental and necessary information for the demographic model as it allows to determine the time unit of the projection interval.

Due to the extremely long life cycle of the species, which can overcome one century, it is not possible to follow the fate of a single cohort along its life span. For this reason, a static “life table” (*sensu* Ricklefs and Miller 2000) was set out.

The analysis of the frequency distribution of size-age classes performed in different years showed that population size-age structure exhibits a monotonic, regularly decreasing trend (Fig. 37.9; Santangelo et al. 2007; Bramanti et al. 2014), suggesting that the populations were in *steady state* (i.e. proportional life stages, Caswell 2001). To estimate survival/mortality, therefore, the ratio between the number of individual present in an age class and the number of individual present in the following age class was used. For each size-age class, this ratio represents the probability of survival of the colonies in the passage from 1 year to another.

37.3.1.3 Recruitment

To develop the demographic model, larval success has been calculated as the proportion of larvae surviving until settlement. Under the assumption of closed populations (no

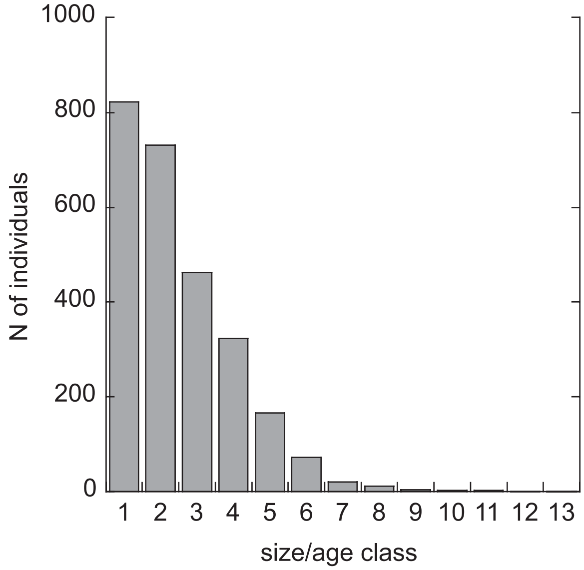

Fig. 37.9 Size/age structure of a *Corallium rubrum* shallow population. (Reprinted from Santangelo et al. (2007), Copyright (2007), with permission from Elsevier)

input from other populations), recruitment success is the ratio between observed recruits and number of larvae produced by the population. A recruit is defined as a new individual added to the population. Recruitment is the first age class of the population and the number of recruits depends yearly on the fecundity and, in case of density dependent recruitment, on the density of adults. For these reasons larval success is not a fixed number but it changes according to adult density (Santangelo et al. 2007; Bramanti et al. 2009, 2015). For the development of *C. rubrum* demographic model, recruitment has been estimated both on natural and artificial substrates (Bramanti et al. 2005, 2014; Santangelo et al. 2012).

In the case of open populations, recruitment success cannot be known from observations and should be estimated from experiments. For example introducing a known number of larvae in controlled conditions and quantify the percentage of settled larvae. The percentage of settled larvae survival will allow estimating the recruitment success, bearing in mind that it will be always overestimated due to the impossibility to quantify predation rate in laboratory conditions.

37.3.1.4 Connectivity Matrices

When populations form a network, offspring produced in each population are redistributed among them by a connectivity matrix that upscales dispersal of individual larvae at the meta-population scale. Connectivity matrices containing transfer rates of individuals between source and sink populations can be established in two ways. On one hand, transfer rates can be estimated from contemporary gene flow, based on the analysis of genetic similarity between individuals in the populations forming the network (Wilson and Rannala 2003). However, this method includes part of the fate of a larva after it reaches its destination, namely recruitment and survival until the age it was sampled for genotyping. Hence, ideally, this method requires sampling recruits only, solving in this way, the problem of the unknown recruitment success, but it has not been implemented yet. On the other hand, transfer rates can be estimated from larval transport, on the basis of biophysical models integrating ocean current and larval traits (Guizien et al. 2006; Cowen and Sponaugle 2009; Butler et al. 2011; Luiz et al. 2013). The interest of this latter method lies in its forecasting potential: if ocean current changes (for instance with climate change) changes in larval transport can be predicted. The limitation of this method lies in the gap of knowledge on larval traits (such as spawning period, spawning duration, pelagic larval duration, and motility behavior) for many deep coral species (but see Brooke and Young 2005; Larsson et al. 2014) In particular, motility behavior is decomposed in a passive part defined by the larval buoyancy (in general negative resulting in a sinking behavior) and an active part defined by larval swimming activity rate and swimming speeds which can compensate or outcompete sinking at the expenses of energy loss. For *C. rubrum*, the larval motility behavior has been quantified and resulted unexpectedly highly active (taking into account that larvae are lecitotrophic) leading to an upward larval motion despite the negative buoyancy of the larvae (Martínez-Quintana et al. 2015). In the Mediterranean Sea, a connectivity matrix approach to metapopulation modeling has been applied to *C. rubrum* by Guizien and Bramanti (2014). Results suggested that connectivity can affect population structure, suggesting that this species is organised in a metapopulation framework, at least at the scale of the Gulf de Lion.

37.4 Conclusive Remarks

Despite the importance of a modeling approach for conservation, demographic models have still not been developed for CWC species, mainly due to the technical difficulties of sampling in deep environment. The Mediterranean red coral (*Corallium rubrum*) represent an exception as it have a wide bathymetric range (10–800 m; Costantini et al. 2010) and shallow populations are easily accessible to SCUBA divers. For this reasons, *C. rubrum* has been object of detailed demographic studies which resulted in the development of population dynamic models based on transition matrices (Santangelo et al. 2007; Bramanti et al. 2009). The model developed for shallow populations has been used to explain some characteristics of deep populations structure and dynamics (Bramanti et al. 2009, Cau et al. 2016), however its capacity to forecast the dynamics of deep populations in a conservation framework is limited, due to the possible difference in basic life traits between deep and shallow populations. Despite the limitations in data acquisition due to the technical constraints, recent technological advances allowed an impulse trough the study of life history parameters of CWC species. For the Mediterranean Sea CWCs there are several studies on the distribution and conservation status (e.g. Álvarez-Pérez et al. 2005; Orejas et al. 2009; Freiwald et al. 2009; Savini et al. 2014) as well as on the effects of climate change and anthropogenic impacts (e.g. Orejas et al. 2009; Maier et al. 2013; Movilla et al. 2014; Danovaro et al. 2017) and on the ecological role and associated biodiversity (e.g. Mastrototaro et al. 2010; Bongiorni et al. 2010; D'Onghia et al. 2011, 2012). The number of studies on Mediterranean CWC life history traits is increasing, with several works on the growth rates (e.g. Taviani et al. 2005; Orejas et al. 2008, 2011; Lartaud et al. 2013) and population size structure (e.g. Gori et al. 2013) while the only studies on reproductive features of CWC have been carried outside the Mediterranean Sea (e.g. Burgess and Babcock 2005; Waller 2005; Waller and Tyler 2005; Brooke and Järnegren 2013; Larsson et al. 2014). On the other side, it is still difficult to find quantitative studies on the connectivity between CWC populations (but see De Mol et al. 2005; Morrison et al. 2015; Fox et al. 2016).

The road towards the development of demographic models for CWC is still long. In the next years, interdisciplinary approaches as well as joint sampling efforts on CWC will be needed, with the aim of developing the theoretical framework and obtain the extensive dataset needed for demographic modeling.

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References

Álvarez-Pérez G, Busquets P, Sandoval N, et al (2005) Deep-water coral occurrences in the Strait of Gibraltar. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 207–221

Arrigoni M, Manfredi P, Panigada S, et al (2011) Life-history tables of the Mediterranean fin whale from stranding data. Mar Ecol 32:1–9

Bacaer N (2010) A Short history of mathematical population dynamics. Springer, London. ISBN: 978-0-85729-114-1. e-ISBN: 978-0-85729-115-8. https://doi.org/10.1007/978-0-85729-115-8

Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony size-frequency distributions. Mar Ecol Progr Ser 162:301–306

Benedetti MC, Priori C, Erra F, et al (2016) Growth patterns in mesophotic octocorals: timing the branching process in the highly-valuable Mediterranean *Corallium rubrum*. Est Coastl Shelf Sci 171:106–110

Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations, fishery investigations series II vol XIX, Ministry of Agriculture, Fisheries and Food, 533 p

Bo M, Bavestrello G, Angiolillo M, et al (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS One 10:e0119393. https://doi.org/10.1371/journal.pone.0119393

Bongiorni L, Mea M, Gambi C, et al (2010) Deep-water scleractinian corals promote higher biodiversity in deep-sea meiofaunal assemblages along continental margins. Biol Conserv 143:1687–1700

Bramanti L, Magagnini G, De Maio L, et al (2005) Recruitment, early survival and growth of the Mediterranean red coral *Corallium rubrum* (L 1758), a 4-year study. J Exp Mar Biol Ecol 314:69–78

Bramanti L, Santangelo G, Iannelli M (2009) Mathematical modelling for conservation and management of gorgonians corals: young and olds, could they coexist? Ecol Model 20:2851–2856

Bramanti L, Vielmini I, Rossi S, et al (2014) Demographic parameters of two populations of red coral (*Corallium rubrum*) in the North Western Mediterranean. Mar Biol 161:1015–1026. https://doi.org/10.1007/s00227-013-2383-5

Bramanti L, Iannelli M, Fan TY, et al (2015) Demographic models forecast the effects of climate change on scleractinian corals: *Pocillopora damicornis* as a case study. Coral Reefs 34: 505–515. https://doi.org/10.1007/s00338-015-1269-z

Bramanti L, Benedetti MC, Cupido R, et al (2017) Demography of animal forests: the example of Mediterranean Gorgonians. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 529–548. https://doi.org/10.1007/978-3-319-17001-5_13-1

Brault S, Caswell H (1993) Pod-specific demography of killer whales (*Orcinus orca*). Ecology 74:1444–1454

Brooke S, Järnegren J (2013) Reproductive periodicity of the scleractinian coral *Lophelia pertusa* from the Trondheim Fjord. Nor Mar Biol 160:139–153

Brooke S, Young CM (2005) Embryogenesis and larval biology of the ahermatypic scleractinian *Oculina varicosa*. Mar Biol 146:665–675

Burgess S, Babcock RC (2005) Reproductive ecology of three reef-forming, deep-sea corals in the New Zealand region. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, pp 701–713

Butler MJ, Paris CB, Goldstein JS, et al (2011) Behavior constrains the dispersal of long-lived spiny lobster larvae. Mar Ecol Progr Ser 422:223–237

Caroselli E, Zaccanti F, Mattioli G, et al (2012) Growth and demography of the solitary scleractinian coral *Leptosammia pruvoti* along a sea surface temperature gradient in the Mediterranean Sea. PLoS One 7:e37848. https://doi.org/10.1371/journal.pone.0037848

Caswell H (2001) Matrix population models, 2nd edn. Sinauer Associates, Sunderland

Cau A, Bramanti L, Cannas R, et al (2016) Habitat constraints and self-thinning shape Mediterranean red coral deep population structure: implications for conservation practice. Sci Rep 6:23322. https://doi.org/10.1038/srep23322

Cau A, Follesa MC, Moccia D, et al (2017a) *Leiopathes glaberrima* millennial forest from SW Sardinia as nursery ground for the small spotted catshark *Scyliorhinus canicula*. Aquat Conserv Mar Freshw Ecosyst 27:731–735. https://doi.org/10.1002/aqc.2717

Cau A, Moccia D, Follesa MC, et al (2017b) Coral forests diversity in the outer shelf of the south Sardinian continental margin. Deep-Sea Res Part 1 Oceanogr Res Pap 122:60–70. https://doi.org/10.1016/j.dsr.2017.01.016

Cerrano C, Danovaro R, Gambi C, et al (2010) Gold coral (*Savalia savaglia*) and gorgonian forests enhance benthic biodiversity and ecosystem functioning in the mesophotic zone. Biodivers Conserv 19:153–167. https://doi.org/10.1007/s10531-009-9712-5

Costantini F, Taviani M, Remia A, et al (2010) Deep-water *Corallium rubrum* L. (1758) from the Mediterranean sea: preliminary genetic characterization. Mar Ecol 31:261–269

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annu Rev Mar Sci 1:443–466

Crouse D, Crowder L, Caswell H (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423. https://doi.org/10.2307/1939225

Danovaro R, Aguzzi J, Fanelli E, et al (2017) An ecosystem-based deep-ocean strategy. Science 355:452 LP-454

Deidun A, Andaloro F, Bavestrello G, et al (2015) First characterisation of a *Leiopathes glaberrima* (Cnidaria: Anthozoa: Antipatharia) forest in Maltese exploited fishing grounds. Ital J Zool 82:271–280. https://doi.org/10.1080/11250003.2014.986544

De Mol B, Henriet JP, Canals M (2005) Development of coral banks in Porcupine Seabight: do they have Mediterranean ancestors? In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, pp 137–156

D'Onghia G, Indennidate A, Giove A, et al (2011) Distribution and behaviour of deep-sea benthopelagic fauna observed using towed cameras in the Santa Maria di Leuca cold-water coral province. Mar Ecol Progr Ser 443:95–110

D'Onghia G, Maiorano P, Carlucci R, et al (2012) Comparing deep-sea fish fauna between coral and non-coral "megahabitats" in the Santa Maria di Leuca cold-water coral province (Mediterranean Sea). PLoS One 7:e44509

Duineveld GCA, Lavaleye MSS, Berghuis EM (2004) Particle flux and food supply to a seamount cold-water community (Galicia Bank, NW Spain). Mar Ecol Progr Ser 277:13–23

Edmunds PJ (2010) Population biology of *Porites astreoides* and *Diploria strigosa* on a shallow Caribbean reef. Mar Ecol Progr Ser 418:87–104. https://doi.org/10.3354/meps08823

Edmunds PJ, Elahi R (2007) The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastrea annularis*. Ecol Monogr 77:3–18

Fox AD, Henry LA, Corne DW, et al (2016) Sensitivity of marine protected area network connectivity to atmospheric variability. R Soc Open Sci 3:160494. https://doi.org/10.1098/rsos.160494

Freiwald A, Roberts MJ (2005) Cold water corals and ecosystems. Springer, Berlin, Heidelberg, 1243 pp

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs: out of sight – no longer out of mind. Biodiversity series 22. UNEP World Conservation Monitoring Centre, Cambridge, 86 pp. https://archive.org/details/coldwatercoralre04frei

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Freiwald A, Rogers A, Hall-Spencer J, et al (2017) Global distribution of cold-water corals (version 3.0). Second update to the dataset in Freiwald et al (2004) by UNEP-WCMC, in collaboration with Andre Freiwald and John Guinotte. Cambridge, UK: UNEP World Conservation Monitoring Centre. http://data.unep-wcmc.org/datasets/3

Frier BW (2000) Demography. In: Bowman AK, Garnsey P, Rath-Bone D (eds) The Cambridge Ancient History, vol 11, 2nd edn. Cambridge University Press, Cambridge, pp 787–816

Fujiwara M, Caswell H (2001) Demography of the endangered North Atlantic right whale. Nature 414:537–541

Gallmetzer I, Haselmair A, Velimirov B (2010) Slow growth and early sexual maturity: bane and boon for the red coral *Corallium rubrum*. Estuar Coast Shelf Sci 90:1–10

Garrabou J, Harmelin JG (2002) A 20-year study on life-history traits of a harvested long-lived temperate coral in the NW Mediterranean: insights into conservation and management needs. J Anim Ecol 71:966–978

Garrabou J, Sala E, Linares C, et al (2017) Re-shifting the ecological baseline for the overexploited Mediterranean red coral. Sci Rep 7:42404. https://doi.org/10.1038/srep42404

Gerber LR, Heppell SS, Ballantyne F, et al (2005) The role of dispersal and demography in determining the efficacy of marine reserves. Can J Fish Aquat Sci 62:863–871

GFCM (General Fisheries Commission for the Mediterranean Scientific Advisory Committee SAC) (2011) Report of the Workshop on the Regional Management Plan on Red Coral in the Mediterranean. Brussels, 21–22 January 2014. http://www.fao.org/3/a-ax793e.pdf

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold water coral populations in the Cap de Creus and Lacaze-Duthiers canons (Northwestern Mediterranean). Biogeosciences 10:2049–2060

Guizien K, Bramanti L (2014) Modelling ecological complexity for marine species conservation: the effect of variable connectivity on species spatial distribution and age structure. Theor Biol Forum 107:47–56

Guizien K, Brochier T, Duchene JC, et al (2006) Dispersal of *Owenia fusiformis* larvae by wind-driven currents: turbulence, swimming behaviour and mortality in a three- dimensional stochastic model. Mar Ecol Progr Ser 311:47–66

Hanski I, Ovaskainen O (2000) The metapopulation capacity of a fragmentedlandscape. Nature 404:755–758

Hastings A, Botsford LW (2006) Persistence of spatial populations depends on returning home. Proc Natl Acad Sci 103:6067–6072

Highsmith RC (1982) Reproduction by fragmentation in corals. Mar Ecol Progr Ser 7:207–226

Hughes TP (1984) Population dynamics based on individual size rather than age: a general model with a reef coral example. Am Nat 123:778–795

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55:141–166

Jimenez C, Orejas C (2017) The Builders of the Oceans – Part II: Corals from the past to the present (The Stone from the Sea). In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 657–697

Katz CH, Cobb JS, Spaulding M (1994) Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*. Mar Ecol Progr Ser 103:265–272

Kuhrt A (1995) The Ancient near east c. 3000–330 B.C.E, vol 2. Routledge, London, p 695

Lancaster J McCallum S, Lowe AC, et al (2014) Development of detailed ecological guidance to support the application of the Scottish MPA selection guidelines in Scotland's seas. Scottish Natural Heritage Commissioned Report No.491. Coral Gardens – supplementary document

Larsson AI, Jarnegren J, Stromberg SM, et al (2014) Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*. PLoS One 9:e102222

Lartaud F, Pareige S, De Rafelis M, et al (2013) A new approach for assessing cold-water coral growth in situ using fluorescent calcein staining. Aquat Living Resour 26:187–196

Lartaud F, Galli G, Raza A, et al (2017) Growth patterns in long-lived coral species. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1–32. https://doi.org/10.1007/978-3-319-17001-5_15-1

Lasker HR (1990) Clonal propagation and population dynamics of a gorgonian coral. Ecology 71:1578–1589

Leslie JPH (1945) On the use of matrices in certain population mathematics. Biometrika 33:183–212

Leslie JPH (1948) Some further notes on the use of matrices in population mathematics. Biometrika 35:213–245

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15:237–240

Lewis EG (1942) On the generation and growth of a population. Sankhya 6:93–96

Linares C, Coma R, Zabala M (2008) Effects of a mass mortality event on gorgonian reproduction. Coral Reefs 27:27–34. https://doi.org/10.1007/s00338-007-0285-z

Linares C, Zabala M, Garrabou J, et al (2010) Assessing the impact of diving in coralligenous communities: the usefulness of demographic studies of red gorgonian populations. Sci Rep Port-Cros Natl Park, Fr 24:161–184

Luiz OJ, Allen AP, Robertson DR, et al (2013) Adult and larval traits as determinants of geographic range size among tropical reef fishes. Proc Natl Acad Sci 110:16498–16502. https://doi.org/10.1073/pnas.1304074110

Maier C, Bils F, Weinbauer MG, et al (2013) Respiration of Mediterranean cold-water corals is not affected by ocean acidification as projected for the end of the century. Biogeosciences 10:7617–7640

Malthus TR (1798) An essay on the principle of population as it affects the future improvement of society, with remarks on the speculations of Mr Goodwin, M Condorcet and Other Writers, 1st edn. J. Johnson in St Paul's Church-yard, London. Retrieved 20 June 2015. via Internet Archive

Marschal C, Garrabou J, Harmelin JG, et al (2004) A new method for measuring growth and age in the precious Mediterranean red coral *Corallium rubrum* (L.). Coral Reefs 23:423–432

Martínez-Quintana A, Bramanti L, Viladrich N, et al (2015) Quantification of *Corallium rubrum* larvae motility behavior: implications for population connectivity. Mar Biol 162:309–318

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral ecosystem off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

Molnár PK, Lewis MA, Derocher AE (2014) Estimating Allee dynamics before they can be observed: polar bears as a case study. PLoS One 9:e85410. https://doi.org/10.1371/journal.pone.0085410

Morrison CL, Baco AR, Nizinski MS, et al (2015) Population connectivity of deep-sea corals. In: Hourigan TF, Etnoyer PJ, Cairns SD (ed) The state of deep-sea coral and sponge ecosystems of the United States: 2015. NOAA Technical Memorandum X. NOAA, Silver Spring, pp 12-1–12-30.

Movilla J, Orejas C, Calvo E, et al (2014) Differential response of two Mediterranean cold-water coral species to ocean acidification. Coral Reefs 33:675–686

Orejas C, Gori A, Gili JM (2008) Growth rates of live *Lophelia pertusa* and *Madrepora oculata* from the Mediterranean Sea maintained in aquaria. Coral Reefs 27:255–264

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 307:37–51

Orejas C, Ferrier-Pagès C, Reynaud S, et al (2011) Long-term growth rates of four Mediterranean cold-water coral species maintained in aquaria. Mar Ecol Progr Ser 429:57–65. https://doi.org/10.3354/meps09104

OSPAR Commission (2015) OSPAR Threatened and/or Declining Habitats 2015. http://www.ospar.org/work-areas/bdc/species-habitats/list-of-threatened-declining-species-habitats. Data http://www.emodnet-seabedhabitats.eu/download

Priori C, Mastascusa V, Erra F, et al (2013) Demography of deep-dwelling red coral populations. Age and reproductive structure assessment. Estuar Coast Shelf Sci 116:1–7

Quattrini AM, Etnoyer PJ, Doughty C, et al (2014) A phylogenetic approach to octocoral community structure in the deep Gulf of Mexico. Deep-Sea Res Part 2 Top Stud Oceanogr 99:92–102

Ricklefs RE, Miller GL (2000) Ecology. WH Freeman and Co, New York City, 849 pp

Roark EB, Guilderson TP, Dunbar RB, et al (2006) Radiocarbon-based ages and growth rates of Hawaiian deep-sea corals. Mar Ecol Progr Ser 327:1–14

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547. https://doi.org/10.1126/science.1119861

Roberts JM, Wheeler AJ, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, Cambridge, New York, p 334

Rossi S, Tsounis G, Orejas C, et al (2008) Survey of deep-dwelling red coral (*Corallium rubrum*) populations at Cap de Creus (NW Mediterranean). Mar Biol 154:533–545

Rossi S, Bramanti L, Gori A, et al (2017a) Animal forests of the wold: an overview. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1–28

Rossi A, Scordamaglia E, Bellingeri M, et al (2017b) Demography of the bottlenose dolphin *Tursiops truncatus* (Mammalia: Delphinidae) in the Eastern Ligurian Sea (NW Mediterranean): quantification of female reproductive parameters. Eur Zool J 84. https://doi.org/10.1080/24750263.2017.1334839

Santangelo G, Abbiati M (2001) Red coral: conservation and management of an overexploited Mediterranean species. Aquat Conserv Mar Freshw Ecosyst 11:253–259

Santangelo G, Bramanti L (2006) Ecology through time, an overview. Riv Biol/Biol Forum 99:395–424

Santangelo G, Bramanti L, Iannelli M (2007) Population dynamics and conservation biology of the over-exploited Mediterranean Red coral. J Theor Biol 244:416–423

Santangelo G, Carletti E, Maggi E, et al (2003) Reproduction and population of the sexual structure of the overexploited Mediterranean red coral *Corallium rubrum*. Mar Ecol Progr Ser 248:99–108

Santangelo G, Bramanti L, Rossi S, et al (2012) Patterns of variation in recruitment and post-recruitment processes of the Mediterranean precious gorgonian coral *Corallium rubrum*. J Exp Mar Biol Ecol 411:7–13

Santangelo G, Cupido R, Cocito S, et al (2015) Effects of increased mortality on gorgonian corals (Cnidaria, Octocorallia): different demographic features may lead affected populations to unexpected recovery and new equilibrium points. Hydrobiologia 759:171–187. https://doi.org/10.1007/s10750-015-2241-1

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the Northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108

Scheidel W (2007) Demography. In: Scheidel W, Morris I, Saller R (eds) The Cambridge economic history of the Greco-Roman world, Cambridge, pp 38–86

Shannon RE (1975) Simulation modelling and methodology. ACM SIGSIM Simulation 8:33–38. ACM, New York. https://doi.org/10.1145/1102766.1102770

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Thiem O, Ravagnan E, Fosså JH, et al (2006) Food supply mechanisms for cold-water corals along a continental shelf edge. J Mar Syst 60:207–219

Tsounis G, Rossi S, Grigg R, et al (2010) The exploitation and conservation of precious corals. Oceanogr Mar Biol Annu Rev 48:161–221

Tsounis G, Rossi S, Bramanti L, et al (2013) Management hurdles for sustainable harvesting of *Corallium rubrum*. Mar Policy 39:361–364

Verhulst PF (1838) Notice sur la loi que la population suit dans son accroissement. Correspondance mathématique et physique 10:113–121

Volterra V (1931) Variations and fluctuations of the number of individuals in animal species living together. In: Chapman RN (ed) Animal Ecology. McGraw-Hill, New York

Waller RG (2005) Deep-water Scleractinia (Cnidaria: Anthozoa): current knowledge of reproductive processes. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 691–700

Waller RG, Tyler PA (2005) The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic Ocean. Coral Reefs 24:514–522

Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163:1177–1191

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Bo M, Bavestrello G (this volume) Mediterranean black coral communities

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

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Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Cold-Water Coral in Aquaria: Advances and Challenges. A Focus on the Mediterranean

38

Covadonga Orejas, Marco Taviani, Stefano Ambroso, Vasilis Andreou, Meri Bilan, Marzia Bo, Sandra Brooke, Paal Buhl-Mortensen, Erik Cordes, Carlos Dominguez-Carrió, Christine Ferrier-Pagès, Antonio Godinho, Andrea Gori, Jordi Grinyó, Cristina Gutiérrez-Zárate, Sebastian Hennige, Carlos Jiménez, Ann I. Larsson, Franck Lartaud, Jay Lunden, Cornelia Maier, Sandra R. Maier, Juancho Movilla, Fiona Murray, Erwan Peru, Autun Purser, Maria Rakka, Stéphanie Reynaud, J. Murray Roberts, Pedro Siles, Susanna M. Strömberg, Laurenz Thomsen, Dick van Oevelen, Alfredo Veiga, and Marina Carreiro-Silva

Abstract

Knowledge on basic biological functions of organisms is essential to understand not only the role they play in the ecosystems but also to manage and protect their populations. The study of biological processes, such as growth, reproduction and physiology, which can be approached *in situ* or by collecting specimens and rearing them in aquaria, is particularly challenging for deep-sea organisms like cold-water corals. Field experimental work and monitoring of deep-sea populations is still a chimera. Only a handful of

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research institutes or companies has been able to install *in situ* marine observatories in the Mediterranean Sea or elsewhere, which facilitate a continuous monitoring of deep-sea ecosystems. Hence, today's best way to obtain basic biological information on these organisms is (1) working with collected samples and analysing them *post-mortem* and / or (2) cultivating corals in aquaria in order to monitor biological processes and investigate coral behaviour and physiological responses under different experimental treatments. The first challenging aspect is the collection process, which implies the use of oceanographic research vessels in most occasions since these organisms inhabit areas between ca. 150 m to more than 1000 m depth, and specific sampling gears. The next challenge is the maintenance of the animals on board (in situations where cruises may take weeks) and their transport to home laboratories. Maintenance in the home laboratories is also extremely challenging since special conditions and set-ups are needed to conduct experimental studies to obtain information on the biological processes of these animals. The complexity of the natural environment from which the corals were collected cannot be exactly replicated within the laboratory setting; a fact which has led some researchers to question the validity of work and conclusions drawn from such undertakings. It is evident that aquaria experiments cannot perfectly reflect the real environmental and trophic conditions where these organisms occur, but: (1) in most cases we do not have the possibility to obtain equivalent *in situ* information and (2) even with limitations, they produce relevant information about the biological limits of the species, which is especially valuable when considering potential future climate change scenarios. This chapter includes many contributions from different authors and is envisioned as both to be a practical "handbook" for conducting cold-water coral aquaria work, whilst at the same time offering an overview on the cold-water coral research conducted in Mediterranean laboratories equipped with aquaria infrastructure. Experiences from Atlantic and Pacific laboratories with extensive experience with cold-water coral work have also contributed to this chapter, as their procedures are valuable to any researcher interested in conducting experimental work with cold-water corals in aquaria. It was impossible to include contributions from all laboratories in the world currently working experimentally with cold-water corals in the laboratory, but at the conclusion of the chapter we attempt, to our best of our knowledge, to supply a list of several laboratories with operational cold-water coral aquaria facilities.

Keywords

Azooxanthellate corals · Husbandry · Aquaria experimental work · Behaviour · Ecophysiology · Mediterranean Sea

38.1 Aquaria Maintenance and Experimental Work with Cold-Water Corals. From the Beginning to the Present

38.1.1 The Challenges of Mimicking the Natural Environment

Conducting experimental work with cold-water corals (CWCs) in aquaria is a fairly recent research field. To our best knowledge, the first attempts to keep CWCs alive were conducted in 1980 when G.A.B. Shelton kept fragments of the reef-building CWC *Lophelia pertusa* in the Department of Zoology at the University of Oxford in order to study the behaviour of this coral (Shelton 1980). He was specifically interested in the electrical conduction mechanisms underlying coral behaviour and coordination. In the laboratory, *L. pertusa* has been successfully reared in the facilities of Tjärno Marine Lab (University of Gothenburg, Sweden) since the late 1990s.

Eighteen after the initial work by Shelton, Mortensen and Rapp (1998) studied the growth patterns of the same coral species, maintaining colonies in aquaria with running seawater for more than 18 months in the Trondhjem Biological Station (Norwegian University of Science and Technology).

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This pioneering work allowed obtaining the first *ex situ* data on this coral, contributing to increase our knowledge of a basic and fundamental aspect of the biology and ecology of a CWC species, spurring the modern era of experimental CWC studies. Starting in 1999, P. Mortensen further developed methods for studying the growth and behaviour of *L. pertusa* in aquaria (Mortensen 2001); this work demonstrated that it is possible to keep corals alive in closed water circulation systems for more than a month, and for more than a year with a continuous supply of seawater. Keeping *L. pertusa* in aquaria for such a long period allows for controlled experiments covering many aspects of its biology (e.g. behaviour, physiology, growth and reproduction).

After these pioneer studies, the field rapidly evolved in the last two decades. Large advances have been achieved in both the technical aspects regarding aquaria infrastructures to maintain CWCs alive (e.g. Olariaga et al. 2009), and the development of specific experimental set-ups to investigate particular aspects of the biology, physiology and ecology of CWCs. The first years of the twenty-first century were particularly fruitful in this respect. Dodds et al. (2007) published the first aquarium-based ecophysiology study on *L. pertusa*. Dodds and her team conducted experiments to study the respiratory physiology of *L. pertusa* under altered temperature and oxygen levels at the Scottish Association of Marine Science (SAMS), using aquaria infrastructures specially designed to maintain CWCs. The first results on growth rates of Mediterranean specimens of *L. pertusa* and *Madrepora oculata* measured in aquaria were published in 2008 (Orejas et al. 2008). That same year, Maier (2008) published the first work on the recovery capacity of *L. pertusa* in aquaria from tissue injuries. After these initial studies, several experimental works on feeding ecology of CWCs were conducted with different CWC species (e.g. Purser et al. 2010; Tsounis et al. 2010; Reynaud and Ferrier-Pagès, this volume; more details given in Sect. 38.5.2).

During the last 15 years, advances in the experimental approaches have increased exponentially. Several studies on growth rates in aquaria of CWCs from the Mediterranean and elsewhere have been published (e.g. Maier et al. 2009, 2012; Orejas et al. 2011; Naumann et al. 2011, 2013; Lartaud et al. 2013, 2014, this volume) as well as studies on the physiological response of CWCs to various experimental conditions (e.g. Gori et al. 2014a, 2015; Roik et al. 2015; Reynaud and Ferrier-Pagès, this volume). These studies included experiments conducted under future IPCC (Intergovernmental Panel on Climate Change) scenarios of global warming and acidification (Maier et al. 2009, 2012, 2013a, b, 2016, this volume; Movilla et al. 2014a, b, this volume; Carreiro-Silva et al. 2014; Hennige et al. 2015; Gori et al. 2016, among others), as well as experiments carried out to better understand the potential consequences of deep-sea drilling activities on CWC habitats (Larsson and Purser 2011), or the effects of oil spills on these species (DeLeo et al. 2016). The advances in rearing *L. pertusa* has also lead to a number of successful spawning seasons in the laboratory when embryo development and larval behaviour could be studied (Larsson et al. 2014; Strömberg and Larsson 2017). The current chapter provides an overview of the advances made on the maintenance and *ex situ* experimenting with CWCs, placing the focus in the Mediterranean region, but also adding integrative relevant experiences from elsewhere.

38.2 Cold-Water Coral Sampling and Maintenance on Board

This section presents an overview of different approaches used for CWC sampling as well as maintenance on board and transport to home laboratories. Some experiences on short-term experiments on board are also included.

38.2.1 Cold-Water Coral Sampling and Transport to Home Laboratories

Over recent years several methods have been employed for the collection of CWCs for maintenance and experimentation, such as dredges, box-cores, grabs, remotely operated vehicles (ROV) and manned submersibles (e.g. Mortensen 2001; Roberts et al. 2006; Brooke et al. 2009; Maier et al. 2009; Orejas et al. 2011; Taviani et al. 2011), as well as through opportunistic sampling of corals accidentally captured (as bycatch) in fishing vessels (e.g. Sampaio et al. 2012). The collection of living CWC could be a relatively "simple" operation, but the subsequent procedure of keeping them alive on-board of the ship and their later safely transfer to a designated scientific aquarium can be a highly demanding task and needs appropriate preparation. It is generally acknowledged that more impacting methods such as dredges can cause significant stress to the organisms (visible as increased mucus production, or polyp retraction for extended periods of time), and can cause severe damage to coral tissue. Indeed, any method to collect living CWC from their habitats unavoidably generates a profound stress on the coral polyps. Entire coral colonies or coral fragments are suddenly and dramatically extracted from their habitat, reposed in canisters or analogue containers on the ROV or submersible, and exposed to changes in pressure and thermal shocks during their journey from the seabed to the surface. The induced stress represents a significant loss of energy, and can affect the survival of corals in captivity. Here we provide basic and practical information on how to best maintain coral viability, largely derived from empirical experience (Box 38.1).

Box 38.1: Best Practice for Ship-Board Maintenance of CWC

Immediately after collection, corals should be transferred with care to temperature-controlled aquaria filled with deep-sea water (collected with Niskin bottles from a CTD-Rosette or with a submersible water pump, for instance). Coral maintenance on board may be pursued through sophisticated or less sophisticated systems, according to the situation. Whenever possible, the best practice is to set-up a laboratory equipped with plastic or glass containers filled with seawater maintained at deep-sea temperature. Ideally, a closed system benefits survival chances. Flow is maintained by recycling filtered seawater between the container and a chilling unit connected to a pump, with an aeration system. Handling should be minimised as much as possible during the following weeks to allow corals to acclimate to aquarium conditions. Gently washing the corals with a small water stream from the tank, could help to keep corals clean. Further this also helps to eliminate the mucus layer they generate after the stress of the capture, increasing remarkably the survival rate. Corals should not be fed during this initial period as they will generally not eat (polyps are frequently retracted during the first days) and food decomposition may negatively affect water quality. From our experience, clean water and high current flow are more relevant for maintaining coral viability than abundant food.

To ensure maximal survival rates and the best physiological condition, corals should be preferentially collected with video-assisted technology (ROV, manned submersible) to minimise damage during collection. After the experience from M. Carreiro-Silva and her team from IMAR (Azores), the use of a thermo-insulated bio-box installed in the ROV with close-fitting lid is particularly recommended for corals collected at greater depths. The bio-box allows the storage of corals with deep-sea water, minimising exposure to temperature fluctuations during ascendance to the surface. To further minimise the risk of mortality, it is fundamental that coral colonies are quickly transferred from the stressing deck conditions to an environment that mimics as much as possible their original ambient situation; in practice this is primarily accomplished by placing the corals in a cold seawater tank in darkness. On the open ocean seabed, CWCs typically occur in environments with temperatures ranging from 4 to 8 °C (although summer temperature can reach 12 °C off Norway or in the Gulf of Mexico), depending on location. In the deep Mediterranean Sea, temperature is about 12 °C with little deviation from this figure (e.g. maximal temperatures of 14 °C have been registered in the Ionian Sea and of 13 °C in the Gulf of Lions). The geographic location of the Mediterranean basin translates into considerably high surface temperatures, especially in summer months, typically the season when many oceanographic surveys are conducted. These issues must be taken into account when planning the ship-board maintenance and later transfer of live CWCs.

Minimising coral air exposure after collection is another important factor, particularly when collecting gorgonians, because some species oxidise (become black) when exposed to air and die rapidly (e.g. *Dentomuricea* aff. *meteor*, *Acanthogorgia* spp.).

Even for less sophisticated systems, some good planning is advisable. The maintenance of corals after collection may also be achieved either by temporarily storing them in on-board refrigerators or cold rooms at temperatures between 10–12.5 °C for Mediterranean CWCs. As mentioned, seawater for on board maintenance should be collected in advance, giving preference to ambient bottom seawater, rather than surface water. This will provide seawater at ambient temperature and avoid potential contamination with microorganisms from shallower depths untypical for CWC sites. Water collected by means of Niskin bottles can also be stored in a dark cool room for some days to replace the water from the tanks if necessary. This is recommended if weather conditions or stays at harbours do not allow collection of seawater on a regular basis.

Under situations where ideal storage devices and equipment are unavailable (tank, seawater flow, aeration system), the collection and maintenance of living corals can be best safeguarded by keeping corals in a bucket filled with cooled seawater, ensuring frequent water substitution to provide oxygenation and storing if possible in darkness until transport and transfer to the selected aquarium can be arranged.

The aquarists from the Aquarium Finisterrae (A Coruña, Spain), who frequently collect deep-sea organisms (including corals) for exhibition and experimental purposes, use a 300 L tank to keep animals alive, if space is available on board the collection vessel. They place coral fragments in plastic grid boxes inside the tank to avoid samples moving out of place and getting hit during transportation. The tank is covered with a lid and kept under constant water inflow (open circuit) until it arrives to land. The specimens from deep areas (800–1200 m depth) are immediately put into an isothermal 400 L tank with a watertight cover and equipped with a chiller unit that maintains water temperature at a level similar to their natural habitat. This tank also has mechanical, biological and chemical filtration as well as a protein fractionator, an ultraviolet (UV) unit and a recirculating pump that generates water currents inside the tank (Fig. 38.1). This system is very convenient for expeditions that take several days, as it allows holding CWC in a closed circuit for 10–15 days.

Fig. 38.1 The isothermal tank used by the Aquarium Finisterrae to keep deep-sea fauna alive at sea. The tank is located on the top of the so called "vital support" system which contains a skimmer and mechanical, chemical and biological filters (all of them placed in the black box). Behind the isothermal tank (not visible in the photograph) are located the ultraviolet unit as well as the chiller. (Photo: © A. Veiga)

The following steps concern sample transportation to the scientific aquaria facilities and coral transfer and acclimation into the aquaria. These operations are also highly critical for the viability of corals. Corals need to be transferred from the ship to a vehicle while keeping them refrigerated. A fully equipped cooled vehicle is the best solution for such purpose. Alternatively, electric or cool boxes, portable refrigerators and/or thermal bags may be adequate. Careful planning of appropriate paperwork may also be required. It is necessary to be aware of the protection status of many CWC species, as for instance all scleractinian and antipatharian corals are included in CITES Appendix II (https://www.cites.org) and many are protected under different regulations (in the case of the Mediterranean Sea, it is necessary to check the Barcelona Convention: http://web.unep.org/unepmap/).

Another important aspect to consider is to ensure that the requirements set forth by port authorities are met in order to get the official clearance to leave the harbour. Living corals may also be transported by other means than land vehicles, such as ships or aeroplanes. It should however be kept in mind that not all air companies allow the transport of living corals.

The final destination for collected corals is often a scientific laboratory or exhibition aquarium. These host aquaria should be aware of the type of material to be received and the time of arrival. It is the responsibility of the host aquaria to adjust the system settings in advance (aerators, filters, proper seawater temperature, and light level) to guarantee the wellness of the corals. A few days of acclimation are optimal to progressively reduce the level of stress. To achieve acclimation it is important to monitor polyp activity and tissue condition several times per day. Stress signs include closed polyps, and tissue sloughing and loss, as well as extensive mucus production. Assessing tissue condition is relatively easy in corals with coloured tissue, as it is the case for the yellow *Dendrophyllia cornigera*, but in the case of the white corals, the degree of polyp opening should be used as a "control" of coral condition instead. Different methodologies can be applied to help in reducing the signs of stress and achieve acclimation, depending on which are the feasible logistics. If ambient seawater is available, a slow mix of this water and the water of the home aquaria is a good strategy to facilitate coral acclimation. Current speed should also be tested and optimised to achieve polyp extension, as this is frequently one of the most important aspects for successfully keeping corals in a good shape. From our experience, feeding should be restricted during the first days following transfer, however after a couple of days, the addition of liquid food close to the polyps can stimulate their extension, probably as a result of stimulus on coral's chemical receptors. Once the polyps are open it is also easier to check which is the current speed they prefer. In the specific case of Mediterranean CWCs collected for tank experiments, various *Lophelia pertusa* and *D. cornigera* collected in 2006 and 2008 are still alive and in healthy conditions in the aquaria facilities of the ICM-CSIC (Barcelona, Spain) and the CSM (Monaco) respectively.

38.2.2 Short Term Experiments on Board

Fully equipped research vessels may provide opportunities to conduct short-term experiments with live CWCs on board (e.g. Maier et al. 2006, 2007; Taviani et al. 2011; Hennige et al. 2014; Orejas et al. 2017). Such practice presents advantages and disadvantages. Advantages include: (1) measuring physiological functions very shortly after sampling using freshly collected specimens that might be more closely mimicking the response of *in situ* conditions than specimens maintained over long periods under more artificial aquarium conditions; (2) the possibility to use seawater from the coral collection point, instead of artificial seawater or water from shallow areas. Indeed, obtaining clean seawater can be expensive and time consuming, and coastal water does not always mimic conditions found near CWC habitats. This is particularly true if corals are maintained in a region different from where they were collected; for example, the chemistry of the Pacific and Atlantic oceans differs greatly. Disadvantages include: (1) short acclimation time even in long cruises; (2) the response of the organisms is only "short term" and need to be considered with caution. Some species are tolerant to sub-optimal conditions, thus experiments conducted under these conditions should be interpreted with caution. This is especially the case if corals have been living in aquaria for extended periods (e.g. years), since its unknown if aquaria conditions can modify basic aspects of the physiology of CWCs, related to changes in feeding regimes and chemical properties of seawater. Therefore both short- and long-term experiments encompass limitations with respect to the interpretation of a CWC response to measured variables for different reasons which should be kept in mind when evaluating *ex situ* experiments in general.

In the following paragraphs some selected examples of short-term experiments conducted on board research vessels are presented.

In 2012, S. Hennige from the University of Edinburgh and his co-workers conducted short-term ocean acidification (OA) experiments under different temperature regimes, on freshly collected *L. pertusa* samples on board of the Bristish RRS *Discovery* (Hennige et al. 2014). Corals were maintained on board in experimental 'coral hotels', which are self-contained 430 L units containing ~350 L of seawater, with built in water circulation pumps, filtration units and chillers (Fig. 38.2).

Water circulation in these closed systems was ~300 L h^{-1}. To alter the carbonate chemistry in the experimental tank, pre-mixed (e.g. with mass flow controllers) or purchased gases with elevated CO_2 were bubbled continuously into the water. To reduce the change in pH following water changes, freshly collected seawater was pre-bubbled prior to addition to the tanks. Subsequently, 30% of the seawater in the tanks was exchanged every 2 days following feeding to ensure build-up of detritus to be minimal. This kind of experimental set-up contributed to get insight on the short-term behaviour and physiological response of CWC to the predicted effects of global climate change (global warming and OA). Results of these experiments are reported in Hennige et al. (2014, 2015).

Another example of short-term experiment on board is a study conducted by A. Gori and C. Orejas (unpublished data) in 2015 during the ANNA cruise on board the German RV *Meteor* off Angola, a location where the CWC *L. pertusa* builds impressive reefs under very low oxygen (O_2) concentrations. They conducted a physiological experiment on board aimed at analysing the physiological response under the natural low O_2 conditions (2 mL L^{-1}) and saturated O_2 conditions by measuring respiration, ammonium excretion and calcification rates of the corals. The experimental set-up on board consisted of incubation chambers (~400 mL volume), which were filled with water collected close to the seafloor using Niskin bottles. Each experimental chamber included a stirrer to keep the water in movement; once filled, chambers were closed with a lid and sealed with parafilm to avoid any gas exchange. During the entire experiment water renewal was manually carried out every 6 h in order to provide the corals with fresh seawater and to avoid an ammonium increase in the chambers. Temperature and O_2 concentration were carefully controlled in every chamber before each water renewal. Figure 38.3 displays the experimental set-up on board of the RV *Meteor*. No differences were observed in the respiration rates between corals maintained under natural low O_2 and increased O_2 conditions, whereas respiration significantly increased during the week of incubation.

From 2005–2008 cruises to the North Atlantic and Skagerrak took place on the Dutch RV *Pelagia* equipped with a cool- and a radioisotope container for on board experimentation with CWCs and deep-sea sponges (van Duyl and Duineveld 2005; Maier et al. 2006, 2007). This allowed the study of nutrient dynamics and the role of prokaryotes on CWC ecosystems using freshly collected specimen of *L. per-*

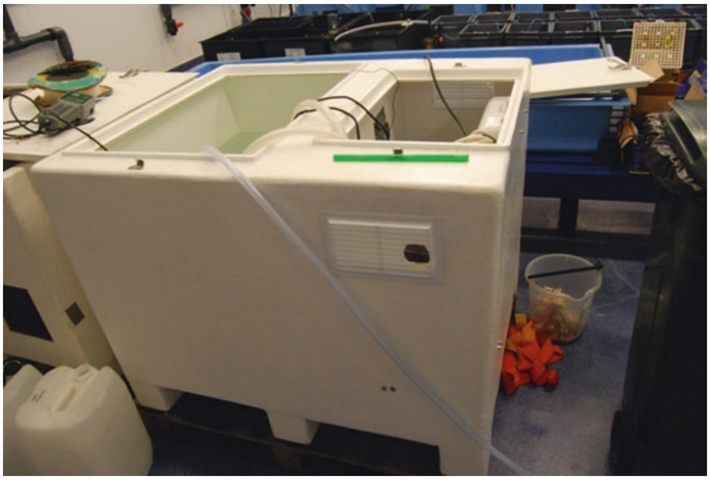

Fig. 38.2 "Coral hotels" used at SAMS to keep the corals alive. The compartment in the right contains the chiller and electronic devices and the compartment in the left is filled with sea water to host the corals. (Photo: © A. Gori)

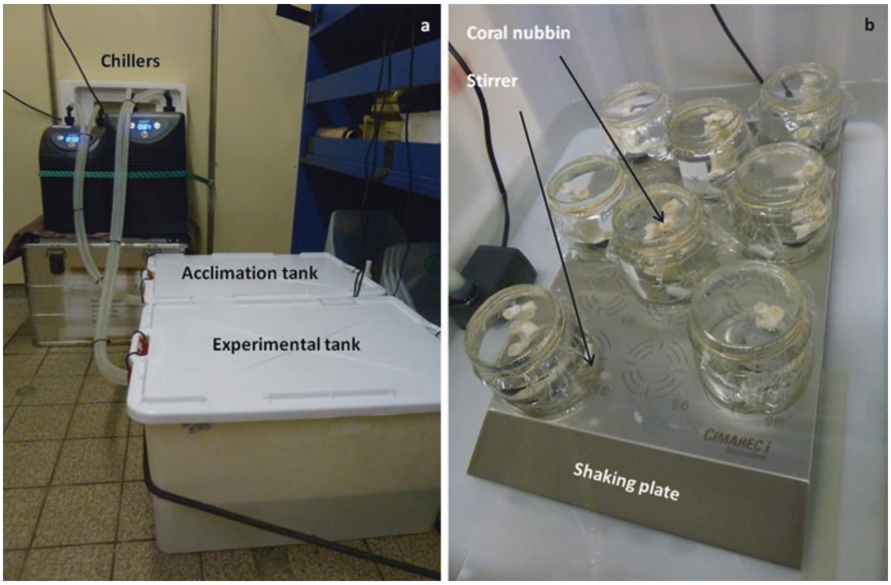

Fig. 38.3 Maintenance and experimental set-up for CWC on board RV *Meteor*. **a**) Two chillers are connected to two tanks (acclimation and experimental) to maintain a constant temperature, **b**) experimental set-up with control and experimental jars (containing *Lophelia pertusa* nubbins) to measure respiration and calcification rates. The water is kept in motion by the shaking plate underneath the jars and the stirrers inside the jars. (Photos: © A. Gori)

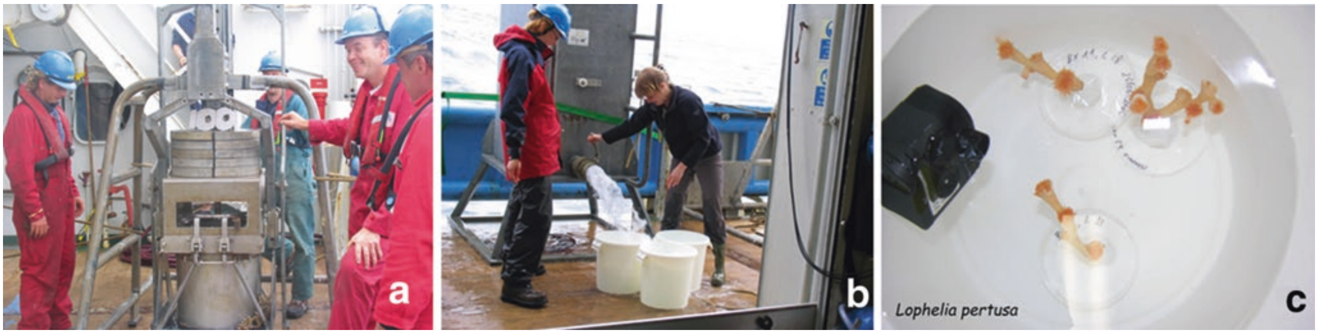

Fig. 38.4 Sampling of CWC during cruises in the North Atlantic and Skagerrak. (**a**) Sampling of CWCs using a box corer with a lid. The box corer was sealed with bottom substrate avoiding contamination of bottom seawater with shallower water when hauling the box core back on board, (**b**) ambient bottom water used for on board experiments was sampled using a 1000 L water box, (**c**) *Lophelia pertusa* nubbins mounted in methacrylat bases to conduct the experiments on board. (Photos: © C. Maier)

tusa and *Madrepora oculata* (Fig. 38.4; Maier et al. 2011, unpublished data; Weinbauer et al. 2012) or sponges (van Duyl et al. 2008). During the cruises in 2007 and 2008, additional radiotracer studies were conducted using 45-calcium to measure skeletal growth of *L. pertusa* from two sites (Mingulay and Skagerrak) and to conduct a first test on the effects of OA on CWCs (Maier et al. 2009). As the calcification rates obtained during these first onboard experiments appeared realistic (unfortunately no comparative *in situ* data were available at that time, but see new recent data in Lartaud et al., this volume and references therein), the approach of on board experimentation was continued during two projects (MECCA and COMP) to study the calcification of Mediterranean CWCs under the lead of the Marine Protected Areas Agency (AAMP) on board the French RV *Minibex* (COMEX), as well as during the MEDCOR cruise 2009 on board the Italian RV *Urania* (Maier et al. 2012). Currently there are published *in situ* growth rates measurements for *L. pertusa* and *M. oculata* from the Mediterranean (Lartaud et al. 2013, 2014, 2017a, b, this volume) as well as for *L. pertusa* from the Gulf of Mexico (Brooke and Young 2009). Results indicate comparable growth rates for *in situ* and *ex situ* measurements for old polyps of both species and faster growth rates for young polyps of *L. pertusa* in the Mediterranean (Lartaud et al. 2013). In contrast, for *L. pertusa* from the Gulf of Mexico, growth rates comparable to those in the lower range obtained in aquaria, have been documented (Brooke and Young 2009).

To minimise stress during CWC collection, a special sampling device was designed by the COMEX engineers. This device is a miniature copy of the “Croix St. André” formerly used to sample the precious red coral *Corallium rubrum* (Fig. 38.5a, b). The device is an extremely efficient and less destructive sampling tool reducing fragmentation of coral

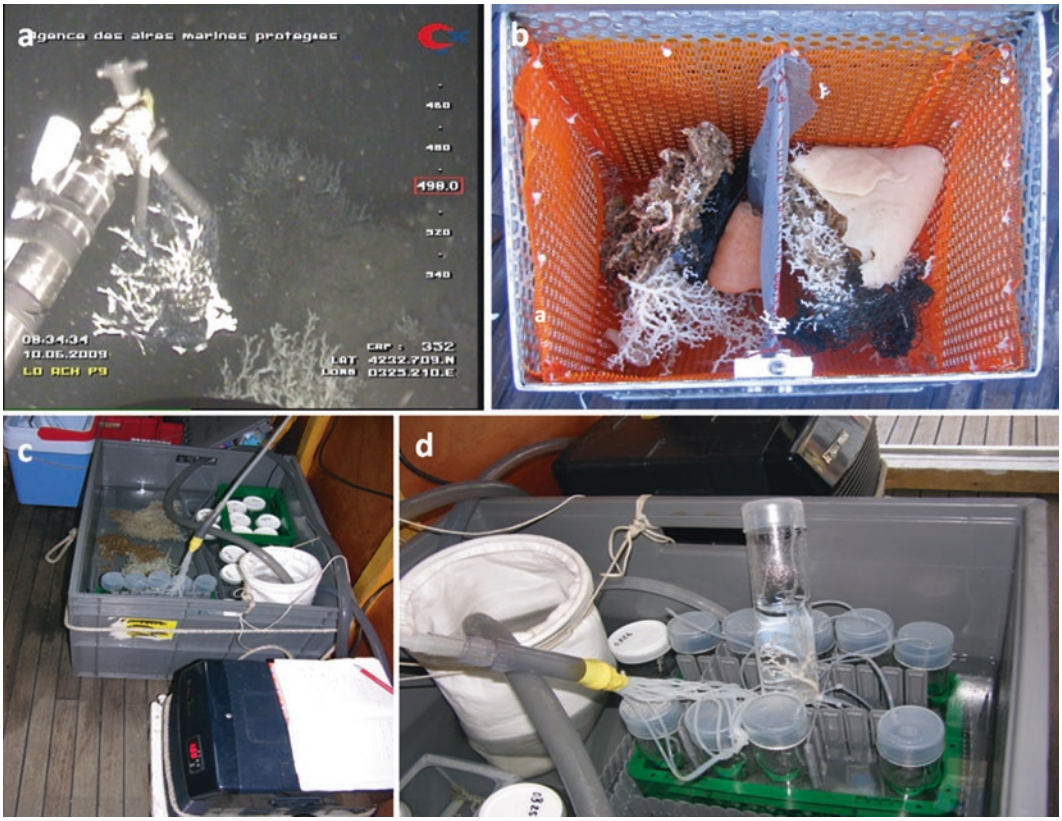

Fig. 38.5 Sampling and on board experiments during Minibex cruises in the Mediterranean. **a**) The ancient sampling gear "Croix St. André" was the inspiration to construct a miniature version to more efficiently sample small CWC colonies with the ROV that was dropped together with the colony entangled in the mesh ends into the buckets on the ROV (**b**). On board maintenance and experiments were conducted in a single container equipped with chilling unit, circulation pumps and a filtration unit consisting of two micron bags with 5 and 1 μm mesh size (**c**, **d**). (Photos: © C. Maier)

branches that may otherwise lost in the soft sediment underneath. On board, the experimental set-up was kept simple using either open (aerated) or closed incubation containers that were kept in the CWC storage container at 13 °C. In closed system incubations, the seawater chemistry can change significantly as a result of coral metabolism, chamber volume and time of incubation (Maier et al. 2009, 2012). Despite the changes in carbonate chemistry, calcification rates derived from closed system incubations proved to be comparable to open system incubations (Maier et al. 2012) and were comparable to those obtained in long-term aquarium experiments (Maier et al. 2013b) and *in situ* measurements (Lartaud et al. 2014, 2017a, b). Closed system incubations are easier (and frequently the only ones) to use on board and might therefore facilitate large scale inter-regional comparisons of CWC calcification growing under different environmental conditions with respect to temperature, salinity and carbonate chemistry. Another advantage of closed system incubations is that both calcification and respiration can be determined in parallel and together with the determination of other parameters (dissolved inorganic carbon, total organic carbon) the CWC carbon (C) and energy budget can be determined from a single incubation (Maier et al. 2016).

38.3 Cold-Water Coral Aquaria Facilities in Research Institutes, Universities and Public Aquaria

This section intends to offer an overview of some of the aquaria facilities currently available in different research institutes, mostly in European laboratories but also from the USA. Even though this book focuses on Mediterranean CWCs, we considered that in such a recent field of research as the maintenance and experimental work with CWCs, any experience in the husbandry of CWCs will be of great use to all researchers (Box 38.2). The facilities of 9 research institutions are presented here as examples of possible approaches which may be employed, and at the end of the chapter we include a list with some of the aquaria infrastructures for CWCs we have been able to identify. We hope we will be able to update this list in future editions of this volume.

Box 38.2: Best Practices on Basic System Requirements

The choice of the most adequate aquaria system to keep CWCs depends on the proximity to the sea, and the amount of money available for system set-up and maintenance. The best aquarium design is an open water system with a continuous intake of seawater. Ideally, seawater should come from the deep to minimise differences in water quality parameters between the aquaria and natural habitat. However, setting up a deep-sea water intake is expensive, and if salinity of a shallow water source does not vary a lot, this is also a good alternative. Having a constant water supply has the advantage of easy removal of waste, avoiding the build-up of toxic nutrient levels, and continuous replenishment of oxygen and consumed minerals (e.g. calcium). Closed system can be efficient too, but are more expensive and technologically complex, requiring an elaborate filtration system.

- Aquaria systems should ideally be mounted inside a temperature controlled room to avoid large temperature variations in the aquaria. Aquaria systems may vary depending on their use (i.e. exhibition or experimentation) but should include stock / quarantine aquaria of at least 50 L capacity in addition to the systems for the actual experiments / research.
- Aquaria and their shelves should be as versatile as possible so this will not limit future experimental designs. There are several options for the aquaria building materials, depending on the budget, the purpose, durability and on maintenance requirements. For example, glass is stronger and cheaper, but also breakable and heavier than plexiglas (acrylic) or polycarbonates, but on the other hand some of these plastics might get slightly opaque or easily scratched with time.
- Seawater refrigeration units should be slightly over dimensioned, considering expected maximum water renewal / turnover / in flow rate, and they should be independent to each separate aquaria system mitigating possible damage / losses from one of the units breaking down.
- For closed aquaria systems the main focus of a basic filtration system is on the water quality in terms of nutrients / organic waste, and similarly to most common seawater aquariums, it should cover first of all the biological filtration, but also mechanical and chemical filtration.
- Biological filtration converts the waste products to a less to non-toxic state. This is mainly attained by various types of bio-filter systems and materials that maximise the growth potential of the naturally occurring nitrifying bacteria. The type or size should be according to the expected maximum bio-load and waste.
- Mechanical filtration serves mainly to collect particles that may be found in suspension in the water (organic and / or inorganic), protecting gears and parts from physical damage or clogging (e.g. sand getting into pumps) and collecting organic matter before it decomposes. But since we are working with filter feeding organisms, this also interferes with / compromises the availability of food.
- Chemical filtration, comprises not only the non-biological removal of dissolved substances from the aquarium (such as using activated carbon), but also other methods such as foam fractioning (or protein skimming), ozonation and ultraviolet sterilisation. Although none of these is absolutely necessary, all of them can be very helpful in the export or mitigation of unwanted inorganic / organic material from the aquaria.
- For open system aquaria the water quality is mostly ensured by a proper water renewal (new water inflow). So, assuming a source of good water quality, the filtration system main focus should be on eliminating or mitigating possible inflow of harmful elements. This mainly includes mechanical filtration of inorganic suspended sediments, and / or organic matter or unwanted and possibly harmful living organism that may be coming along with the new water. Another approach to mitigate the possible inlet of living organisms may be chemical filtration, such as ozonation or ultraviolet sterilisation of the incoming water, thus disabling or even killing them.
- Evaluation of the ideal seawater renewal rate or in flow rate depends on the type of system (open or closed), type of filtration system, and number of corals in relation to volume of water in each aquarium. All these factors will influence nutrients and waste build-up and thus water quality in aquaria. Generally it can be considered good practice to replace 10–50% of seawater weekly or monthly from each aquarium using properly matured bio-filters.
- The type of submersible recirculation pumps (stream or pulsating), direction (laminar or turbulent) and current velocity depend on the coral being maintained (see Sect. 38.4)
- The control / monitoring of parameters usually comprise inorganic nutrients (e.g. ammonia, nitrite, nitrate and phosphates), pH, temperature, salinity

(continued)

Box 38.2 (continued)

and total alkalinity (especially for closed systems). Depending on the experimental design, and objectives of the study, some other parameters might require monitoring.

- Lights should be kept off whenever possible, recreating the coral's natural environmental conditions. The use of red filters on the lights (or red light bulbs) may help reduce possible impacts by the necessary light exposure. In addition, this also helps to avoid unwanted algae proliferations in the aquaria.
- Electrical installation / wiring and plugs should be above water level with some safety distance to minimise the chances of getting water splashed and waterproof parts should be installed whenever possible. Extra plugs should be available, for lab equipment. Each aquaria system should have individual sets of electrical wiring / switches to ensure that an electrical problem on one system does not compromise the others.

38.3.1 Aquaria Facilities for Cold-Water Coral Maintenance at the Benthic Ecogeochemistry Laboratory (LECOB) of Banyuls-sur-Mer, France

The LECOB laboratory at Banyuls-sur-mer marine station (Oceanographical Observatory, Pierre and Marie Curie University) has been equipped with aquaria facilities for cold-water scleractinian and gorgonian corals since 2010. The laboratory is located on the West coast of the Gulf of Lions, in the Mediterranean Sea. This area is close to the Lacaze-Duthiers submarine canyon (canyon head is 23 km off Banyuls-sur-Mer), where *L. pertusa* and *M. oculata* frameworks occur, together with *Desmophyllum dianthus* and *Dendrophyllia cornigera* corals. This canyon and the coral ecosystems are part of the Gulf of Lions Marine Nature Park MPA.

The aquaria facilities include several tanks (Fig. 38.6) installed in thermo-regulated rooms allowing mimicking deep-sea temperatures. The cool-rooms are supplied with natural seawater pumped from 10 m depth. Once the water is transported into the cool-room, a storage tank is filled and temperature is regulated to reach the 13 °C by means of a chiller before filtration by a 5 μm mesh size filtered and after this distributed to the different aquaria. Water is continuously distributed to allow a complete water renewal from 1 to 4 times per day in each tank over 80 L tanks or 50 L recirculating flumes (Purser et al. 2010), depending on the experimental requirements. Corals were maintained in the dark, fed three times a week with live *Artemia* nauplii, and the environmental conditions (temperature, pH, conductivity, oxygen saturation) are continuously monitored. Safety equipment is installed to prevent any problems (water-level sensor, seawater cut-off, temperature anomalies, etc.). This experimental design was developed for medium (months) to long-term (years) experiments.

The experiments conducted in the Banyuls-sur-Mer infrastructures address questions regarding CWC response to environmental changes and anthropogenic threats, the first one in order to forecast the response of Mediterranean CWCs to current and future environmental conditions predicted by the IPCC. Integrative studies are executed at distinct physiological levels including skeleton growth, energy acquisition and coral associated bacterial communities (Lartaud et al. 2013, 2014; Meistertzheim et al. 2016). Conducted experiments aimed at investigate the resilience of reef-building CWCs and their function in canyon ecosystems, particularly regarding the effects of potential changes in temperature, current speed, and organic matter concentrations.

38.3.2 Cold-Water Coral Maintenance Facilities at the Centre Scientifique de Monaco (CSM) (Principality of Monaco)

The CSM has 10 years' experience in maintaining CWC species; specifically, *L. pertusa, M. oculata, D. cornigera, Dendrophyllia ramea* and *D. dianthus* sampled in deep waters

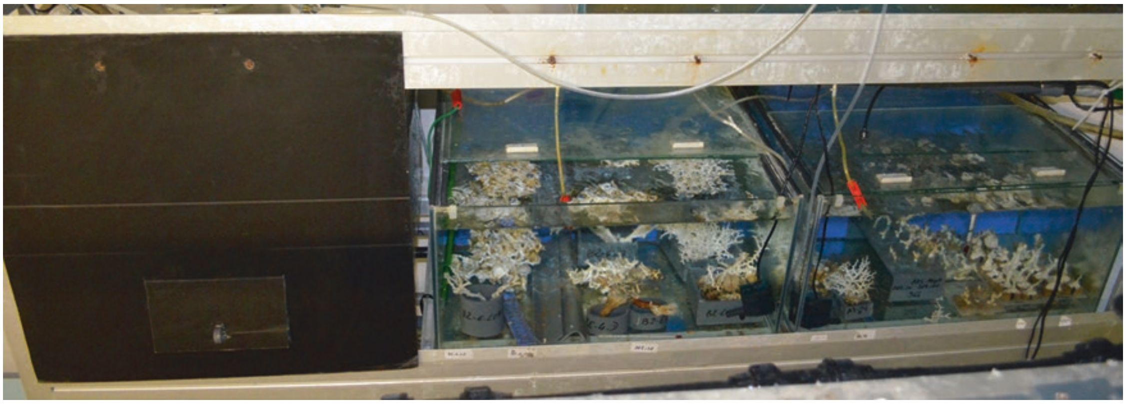

Fig. 38.6 Aquaria facilities in the Marine Laboratory of Banyuls-sur-Mer, France. (Photo: © E. Peru, LECOB)

Fig. 38.7 Coral fragments of *Dendrophyllia ramea* (pink/orange coral) and *Dendrophyllia cornigera* (yellow coral) in the small 30 L aquaria in the aquaria facilities of the CSM. (Photo: © S. Reynaud)

of the Mediterranean Sea, have been maintained in the CSM aquaria infrastructures. Currently, specimens of *D. cornigera* and *D. ramea* have been grown in the CSM aquaria for more than 6 and 2 years, respectively (Fig. 38.7). The corals are maintained in the dark, either in large 100 L aquaria for general maintenance (at 12 °C), or in 30 L aquaria for experimental purposes (at different temperatures). Seawater renewal is provided by a continuous flow of Mediterranean seawater pumped from 50 m depth at a rate of 1 m^3 h^{-1} and pre-cooled at 11 °C. Water temperature is then slightly heated to 12 °C or more using 300 W heaters connected to temperature controllers, or cooled down to lower temperatures using chillers. Submersible pumps with a flow rate of 400 L h^{-1} provide continuous water movement inside each aquarium. Corals are fed 4 times a week with frozen *Mysis* (Crustacea, Eumalacostraca).

38.3.3 Cold-Water Coral Maintenance Facilities at the Institut de Ciències del Mar (ICM-CSIC) (Barcelona, Spain)

Cold-water corals have been maintained at Institut de Ciències del Mar (ICM-CSIC) since 2006 in an updated version of the system developed by Olariaga et al. (2009). The aquaria are located in a 15 m^2 temperature-controlled experimental chamber in the “Area of Experimental Aquaria” (ZAE) of the ICM-CSIC. Air temperature inside the chamber is maintained between 12 ºC and 14 ºC in complete darkness conditions. Corals are kept in four 140 L maintenance aquaria (Fig. 38.8) and twenty-four 25 L experimental aquaria. Seawater is provided by a continuous flow of Mediterranean seawater directly collected in front of the institute facilities and pumped from a depth of 15 m at a maximal inflow capacity of 300 L h^{-1}, then filtered with a 50 μm pore size mesh and cooled at 12 °C. Seawater enters the chamber directly to a 120 L storage tank, from where it is pumped to the 28 aquaria. Continuous water movement inside each aquarium is provided by submersible pumps with a flow rate of 10,000 L h^{-1} in the large maintenance aquaria and 2000 L h^{-1} in the small experimental aquaria. Moreover, in the large maintenance aquaria, flow intensity can be regulated and wave action simulated. As a security measure, in case of malfunctioning of the seawater cooling system, the pumping of water from the storage tank is automatically blocked when seawater temperature exceeds 15 °C. In that case, corals are maintained at 12–14 °C in their aquaria by the air temperature controlled chamber. Currently, the aquaria harbour scleractinian CWCs, as well as gorgonians, black and soft corals and sea pens.

38.3.4 The “DeepSeaLab”, Instituto do Mar (IMAR), University of the Azores in Faial Island (Azores, Portugal)

The DeepSeaLab at IMAR, University of the Azores on Faial Island is an aquaria facility dedicated to research with deep-sea organisms, conceived and designed in collaboration with the Oceanário de Lisboa in 2009 and subsequently renewed and enlarged in 2015. The aquaria facility is composed of 5 independent aquaria systems set-up in a temperature-controlled room at 14 °C in darkness. One semi-closed water system is used for the maintenance of corals and other deep-sea organisms that are not being used in experiments, and four open-water systems used for the experimentation (Fig. 38.9). The existence of a semi-closed water system ensures that in the case of seawater supply failure, corals can still be maintained in a fully closed system. All systems are equipped with a water temperature controller. The temperature sensors have 1 °C accuracy and a minimal hysteresis of 1 °C. The water supply to the aquarium systems is continuously pumped from coastal waters (5 m depth, salinity: 36).

Fig. 38.8 Overview of the CWC aquaria facilities at ICM-CSIC in Barcelona. (Photo: © S. Ambroso)

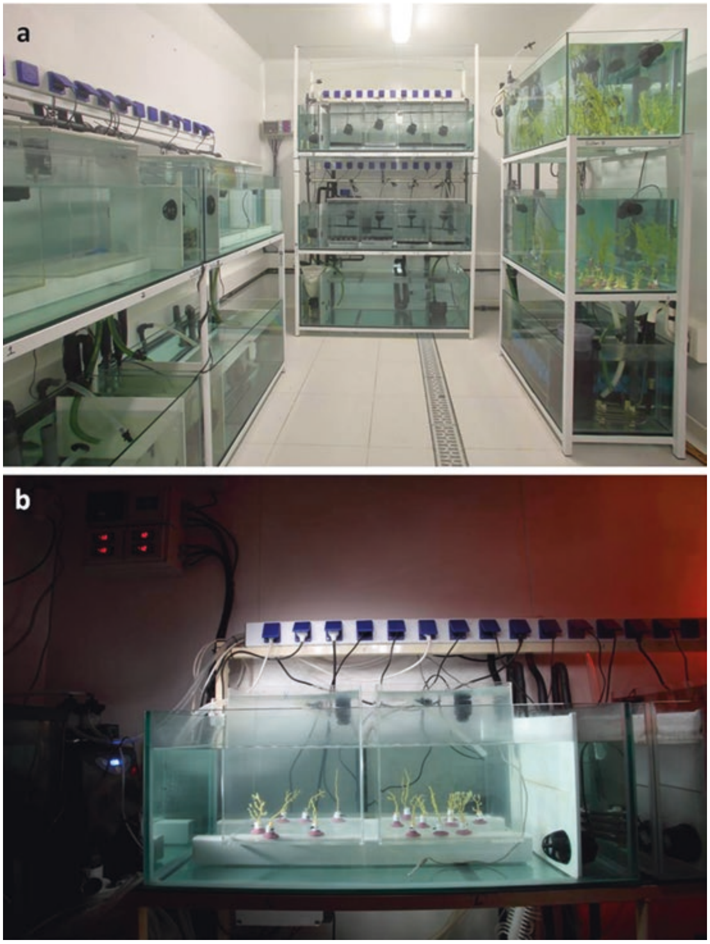

Fig. 38.9 (**a**) Aquaria infrastructures in the DeepSeaLab, (**b**) detail of a tank showing the water bath to minimise fluctuations in seawater temperature between replicate experimental aquaria. (Photos: © R. Sá da Bandeira)

The water is stored in a 410 L storage tank equipped with a cooling unit and a thermostat. Water is filtered first through a 50 um felt filter bag (FSI®) in the storage tank and through an additional 5 um felt filter bag in each experimental system as well as UV sterilised. Water is then pumped into sumps in the individual systems where it is cooled again and subsequently distributed to the individual experimental aquaria. A freshwater water bath equipped with a cooling unit ensures that the water in individual experimental aquaria (e.g. replicate aquaria within the same experimental treatment) is constantly maintained, while maximising space for the experiments. Each aquaria system has the capacity to independently manipulate temperature and pH (through a combination of CO_2 bubbling and/or CO_2 removal through a soda lime filter) enabling the simulation of conditions predicted as consequences of climate change (Carreiro-Silva et al. 2014). In addition, the facility is equipped with 100 L stock tanks and dosing pumps for the delivery of sediments or food particles in different concentrations for feeding and deep-sea mining experiments. Currently, the aquaria maintain cold-water scleractinians, gorgonians, black corals, zoanthids and anemones.

38.3.5 Cold-Water Coral Aquaria Facilities of the "Changing Oceans Group" at the University of Edinburgh (Edinburgh, United Kingdom)

The Changing Oceans Group experimental mesocosm facility was rehoused and refurbished in 2017 to increase capacity and flexibility for conducting CWC and OA experiments, with flexible racking and tank systems. Seawater can either be collected from the East coast of Scotland, or artificially made.

An example set-up used previously (Fig. 38.10) had 20 independent closed-loop systems, each with an additional 4 experimental tanks (5 L each) for separation of biological material. Total volume of each system including the sump is 80 L, and includes individual temperature control and biological filtration. Gas mixing for OA experiments is achieved in house using mixing flasks, and analysed continuously with a Li-820 gas analyser (Licor). Ambient and elevated CO_2 air mixes (e.g. at 750 and 1000 ppm) are plumbed around the room and into sump tanks to modify water carbonate chemistry (Hennige et al. 2015; Gori et al. 2016).

38.3.6 Aquaria Facilities of the University of Gothenburg, Sweden (Sven Lovén Centre for Marine Infrastructure)

The marine station of the University of Gothenburg (UGOT) at Tjärnö offers excellent opportunities for both experimental and field based research on *L. pertusa*. The station is situated on the Swedish west coast in the vicinity (~10 nautical miles) of several shallow coastal *L. pertusa* reefs in the NE Skagerrak. The Tisler reef is the largest of these reefs with living coral extending over an area of ca. 250 ha at a depth of 70–145 m (Lundälv 2003). The facilities include several constant temperature rooms with a flow-through system with seawater taken from 45 m depth in the Koster Fjord, adjacent to the laboratory (Fig. 38.11). The fjord and surrounding areas are fed with deep oceanic water from the Atlantic that is funnelled via the Norwegian Trench allowing for simulation of deep-sea conditions in the laboratory. *L. pertusa* has been successfully reared in these facilities since mid-2000's (see Sect. 38.1).

Fig. 38.10 A previous set-up of the Changing Oceans Group experimental mesocosm facility. (Photo: © S. Hennige)

Fig. 38.11 CWC aquaria facilities at the marine station of the University of Gothenburg, Tjärnö, Sweden. (Photo: © C. Orejas)

38.3.7 Cold-Water Corals Aquaria Facilities at Temple University (Philadelphia, USA)

The aquarium system at Temple University in Philadelphia was first established in 2009 using primarily hobbyist equipment within a temperature-controlled room. In 2010, a second system was added within a standard laboratory room without temperature control, but including a temperature-insulated "lobster tank" paired with an aquaculture-grade recirculating chiller. These two systems, while differing slightly in their mechanism of temperature control, utilise similar designs in terms of waste removal and water flow, and each has continuously supported CWCs from September 2009 up until the present day. A detailed description of this system is available in Lunden et al. (2014a). In support of ongoing research activities in the Gulf of Mexico (GoM), the recirculating aquaria at Temple were designed primarily to maintain scleractinian CWCs for global ocean change and anthropogenic disturbance studies (e.g. Lunden et al. 2014b; Georgian et al. 2016a, b; Kurman et al. 2017). Now, these aquaria house octocorals being used in further studies of OA, and additional *L. pertusa* colonies for use in oil and dispersant exposure experiments.

Other than all previous examples, Temple University uses artificial seawater (ASW) in its facility. In a recirculating system at an institution far from the sea, this is a necessary and ongoing expenditure; however, ASW usage for water changes can be reduced by efficient filtration systems. The filtration system at Temple University includes a protein skimmer, live rock, Jaubert plenum, and UV steriliser (Fig. 38.12). A secondary consequence of utilising ASW is an additional need to modify the total alkalinity of the seawater, due to ASW's high buffering capacity. This is particularly necessary for OA studies. To reduce the total alkalinity, the ASW is treated with strong acid (12.1N HCl) followed by a period of air bubbling to facilitate off gassing of excess CO_2. This method has been effective at producing seawater conditions that approximate the natural environment of deep-water corals (Lunden et al. 2013; Georgian et al. 2016b).

The latest efforts using these systems include maintenance of octocoral species from the GoM. From personal observations, octocorals appear to be much more sensitive to laboratory conditions than scleractinians corals, thus necessitating careful management of water quality, feeding, and flow. Thus far, efforts to sustain octocorals have been successful, aided by the use of improved artificial salts, wave makers, power heads, regular water changes, and target feeding with a variety of food sources.

38.3.8 Aquaria Facilities in the Oregon Institute of Marine Biology (Oregon, USA)

The aquaria system in Oregon was initially conceived at Harbor Branch Oceanographic Institution for studies on deep-sea echinoderms, and was subsequently used to maintain *Oculina varicosa*. The system was housed in an insulated building and comprised four independent sets of five tanks, each with a chiller unit that could be programmed for a specific temperature, and a recirculating pump. Since the facility was located at an estuary, water for the system was brought in from offshore and stored in a large (5678 L) recirculating tank until needed. In 2001, this system was relocated to the Oregon Institute of Marine Biology, which is situated on the Pacific coast and therefore has ready access to natural seawater.

Fig. 38.12 Recirculating aquaria at Temple University for CWCs. Top right: holding tank; top left: TECO recirculating chiller; bottom: sump tank with biological and chemical filtration. Reproduced from Fig. 1 of Lunden et al. 2014a *L&O: Methods.* (Photo: J. Lunden, reproduction of the figure authorised by Wiley. © Wiley)

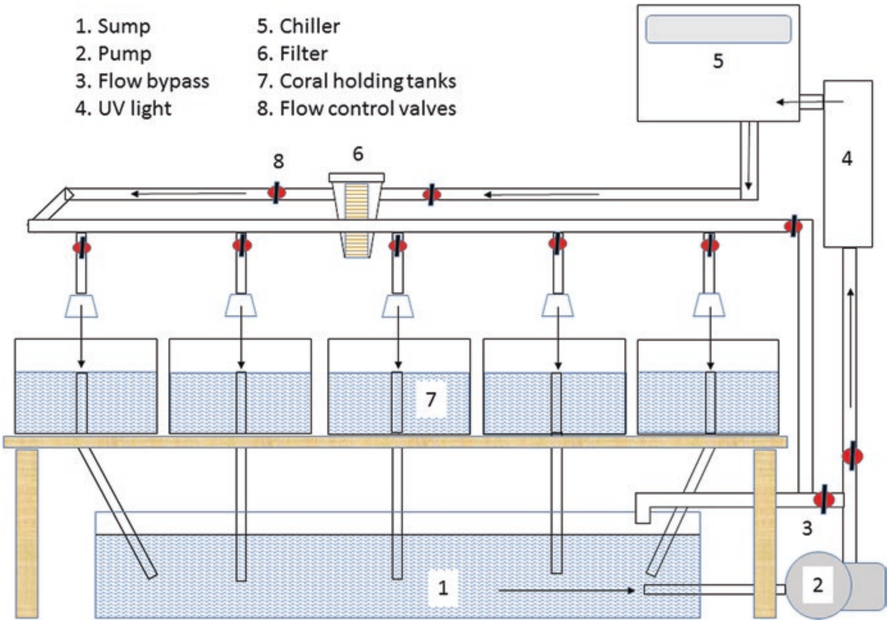

Fig. 38.13 Schematic of a single CWC maintenance tank system operated at Oregon Institute of Marine Biology, showing the lateral view. The different components are labelled and the water flow indicated by arrows. The valves are used to adjust water flow, and for isolating individual tanks for cleaning. (Scheme: © Sandra Brooke)

Each tank series comprises five fibreglass rectangular tanks (1.2 × 0.6 × 0.46 m; 330 L) that are positioned above a larger sump (1.8 × 1.2 × 0.75 m; 1600 L). Water is pumped from the sump through a 0.5 horsepower self-priming pump, through a UV light steriliser and into a chiller. After chilling, the water is pumped into the tanks via a simple filter system, consisting of a household canister style sediment-filter that removes particles >10 μm. Each tank has a feeder line with a pressure disperser on the end to avoid a hard jet of water entering the tank. At the opposite end of the tank, the water leaves through a standpipe and empties into the sump. Valves placed throughout the system are used to control the flow rate, and excess water is bypassed back into the sump (Fig. 38.13). The bottoms of the CWC tanks were covered with a layer of aragonite gravel, and a piece of rigid plastic square mesh (1 × 1 cm × 1 cm deep) was placed on top of the gravel to support the coral fragments and raise them above the substrate. This arrangement also allowed for moving the corals to a clean tank with minimal handling. The gravel served to maintain appropriate carbonate chemistry, captured any waste organic material (which was then removed during cleaning) and provided a substrate for beneficial bacterial growth.

38.3.9 Aquaria Facilities in the Aquarium Finisterrae (A Coruña, Spain)

The public Aquarium Finisterrae has quarantine facilities as well as research tanks. The receipt of the CWC specimens takes place in the quarantine area, where the newly arrived organisms are acclimated to the aquarium water properties (Fig. 38.14a). Acclimation process is slow and carefully avoiding abrupt changes in the physiochemical

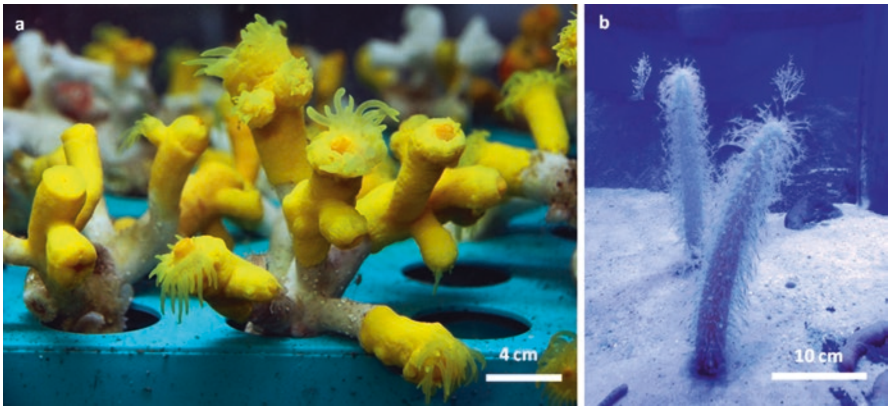

Fig. 38.14 (**a**) *Dendrophyllia cornigera* in a quarantine tank of the Aquarium Finisterrae. The holes on the base are used to provisionally place the colonies to avoid its movement. (**b**) Specimens of *Veretillum cynomorium* in an exhibition tank of the Aquarium Finisterrae. (Photo: © A. Veiga)

water conditions (especially temperature, pH and dissolved oxygen). The quarantine tanks used in the Aquarium Finisterrae for these animals can hold up to 1400 L, and recirculating pumps are usually placed inside them (whose flow depends both on the volume of the tank and the type of hosted animal). Corals are properly fixed in the aquaria to avoid the displacement of the specimens by the currents inside the tank. In case there is need of cold water input, a heat exchanger or a chiller unit can be used. Nevertheless, the choice of the chilling system will depend on the volume of the tank, of the desired final temperature, as well as the temperature and the input rate of the renewal water. In the acclimation tanks usually used in the Aquarium Finisterrae, specimens of both *L. pertusa* and *M. oculata* were kept for several months in the quarantine zone until they were moved to the exhibition aquaria, where they were kept in similar conditions as the aforementioned. At the Aquarium Finisterrae several species of colonial anthozoan have been maintained such as: some species of the genus *Alcyonium*, gorgonians like *Leptogorgia sarmentosa*, or *Eunicella verrucosa*, sea pens such as *Veretillum cynomorium* (Fig. 38.14b), or the CWCs *D. cornigera*, *L. pertusa*, and *M. oculata*, as well as the anthipatarian *Antipathella subpinnata*. It is important to remark that most of these species also inhabit Mediterranean waters.

The specimens collected for scientific research are placed in polycarbonate aquaria of 40 or 80 L, placed in a small isolated room that has its own water supply and an independent filtering system. This way, the studied material can be subjected to different environmental conditions in a controlled setting. The life support used in this installation has a chilling unit capable of keeping the circulating water at a temperature of 10 ± 0.5 °C, a protein fractionator ("skimmer"), a series of cartridge filters capable of filtering water up to 0.30 μm and an ultraviolet unit placed right before the tank's water input.

38.4 Cold-Water Coral Maintenance

This section has been divided in several subsections to present different experiences on the maintenance of different CWC groups (Box 38.3). Maintenance of scleractinian corals, gorgonians, black corals and sea pens are presented here, some correspond to Mediterranean infrastructures, some to infrastructures located in other European countries or in the USA. A final subsection on coral nubbin preparations for experimental purposes is also included.

38.4.1 Maintenance of Scleractinians

38.4.1.1 A Mediterranean Experience: Long Term Maintenance of four Scleractinian Species

Four different species of hexacorals have been maintained alive for more than a decade in the facilities of the Institut de Ciències del Mar (ICM-CSIC) in Barcelona. These species include *Lophelia pertusa*, *Madrepora oculata*, *Dendrophyllia cornigera* and *Desmophyllum dianthus.* All colonies have been kept in tanks with a capacity between 30 L and 150 L in running natural seawater, which is sequentially filtered (5 μm and 50 μm mesh size), constantly renewed and kept in motion using circulation pumps with a flow rate between 2000 and 4000 L/h. Corals are generally glued onto labelled methacrylate holders using a two-component epoxy resin so they can be kept in an upright position, although the type of support used can vary depending on coral size. Scleractinian colonies are fed according to the size of their polyps. Colonies bearing large polyps, such as *D. cornigera* (20–40 mm in diameter) and *D. dianthus* (15–30 mm in diameter), are generally given commercial frozen krill, *Artemia salina* or *Mysis relicta* shrimps on a daily basis, which are directly supplied to each polyp using a plastic Pasteur pipette after they are

Box 38.3: Best Practices for Scleractinian CWC, Gorgonians and Black Corals Maintenance

There is not a single magic recipe for coral maintenance, as depending on the species and its origin (e.g. geographical region, current regime, depth, temperature) the optimum conditions will vary. However some general aspects have to be taking into account for a successful CWCs maintenance.

- Temperature should be in the range of the area where the corals were collected and kept as constant as possible (Box 38.1)
- Flow through systems are highly recommended as they provide continuous clean water (Box 38.1)
- Water chemistry should be checked daily (ammonium and nitrates should be kept at minimum levels) (Box 38.1)
- Tanks should have at least 50-75 L volume. Tank size depend on the number of nubbins / coral fragments per tank
- Different CWC species can share a tank, but enough distance between nubbins / fragments should be allowed in order to avoid any contact among the polyps
- Scleractinians need high flow rates. A flow rate from 2000 to 4000 L/h is recommended
- Feeding can take place daily, every two days or twice a week.
- Food size and type have to be adapted to the polyp size of the species: Generally frozen krill, *Artemia salina* and *Mysis relicta* are suitable for *Desmophyllum dianthus* and *Dendrophyllia cornigera* whereas copepods (*Cyclops* sp.) and *Artemia salina* nauplii are more adequate for *Madrepora oculata,* gorgonians and certain black coral species (*Antipathes dichotoma*). *Lophelia pertusa* can be fed with *Artemia* naupli, *Mysis* sp.,and also, when available with calanoid copepods. Rotifers are an appropriate food source for species with very small polyp size such us the black corals *Bathypathes* sp. and *Leiopathes glaberrima.*
- Prior to feeding the corals polyps have to be open. If possible manual feeding (using a pipette, syringe etc.) is recommended. If polyps are closed chemical stimulation might be necessary, and can be achieved by preparing a “soup” mixing different food types and releasing it in the aquaria.
- After feeding, the remaining food must be removed.
- As CWC live in the aphotic zone, we recommend maintaining the aquaria in darkness (Box 38.1).

defrosted. It is important that the polyps are fully expanded before starting manual feeding. In general terms, colonies tend to extend their polyps daily if fed with regularity. If this is not the case, a solution composed of a wide range of food particles (1–450 μm) can be diluted in the water tanks to induce polyp expansion. Colonies bearing smaller polyps (5–10 mm in diameter), such as *M. oculata*, are given commercial frozen Cyclops alternated with nauplii of live *A. salina*, which are homogeneously distributed in the water tanks for the polyps to actively capture the prey. No issues have been encountered with mixing different species of scleractinian corals in the same aquaria. However, a minimum distance between colonies is required to avoid any possible contact between polyps when in full expansion. Occasionally, it has been observed that foraminifera may attach to the surface of *L. pertusa* and *M. oculata* nubbins. If foraminifera are not manually removed, sediment and particulate matter tend to accumulate in the surface of the colonies and the coenenchyme, which could lead to the death of the tissue and even to the whole colony.

38.4.1.2 Atlantic and Pacific Experiences: Long Term Maintenance of *Lophelia pertusa* and *Oculina varicosa*

Successful maintenance of scleractinians in aquaria demands not only for proper water chemistry to be met, but also sufficient water movement. The rule, drawn from long experience with *L. pertusa*, seems to be that the turbulence should be just below the limit for the polyp’s ability to manage (and thus be able to feed): that is, there should be a noticeable strong flutter of the tentacles due to turbulence, but not so high that the polyp is prevented from positioning it’s tentacles to catch food. If the tentacles flop around fully at the mercy of the water movement, turbulence is too strong. The preferred system used for maintaining water movement at the University of Gothenburg (UGOT) has been the ‘*Mississippi*’ chambers; These are experimental chambers of 12 L volume within which a flow-through system can be maintained to provide corals with an appropriate water supply, with paddlewheels integrated into the tank, to mechanically maintain turbulence within the tank, whilst not simultaneously creating bubbles, following an *in situ* design first described in Tengberg et al. (2003). These paddles, reminiscent of those used on historic *Mississippi* riverboats, consist of a long axle and 8 or more flat panels running the length of the axis. By rotating the axis, the paddles rotate in the same direction, with the paddles each displacing water in the same direction in turn; driving the riverboats on the *Mississippi*, or causing elongated displacement waves in the *Mississippi* chambers. These *Mississippi* paddles are placed in the upper portion of the experimental tank, separated by some cm from experimental coral nubbins. These chambers differ from the initial Tengberg et al. (2003) set-up by facilitating chamber replication with a minimum of mechanical motors. The design of these tanks, and the associated supply systems for dosing tanks continuously with various concentrations of food, pollutants etc. is presented with a schematic drawing in Sects. 38.5.2 and 38.5.4. Although pumps could be used as well, it is important to make sure that no air bubbles are generated since these will stress the corals and trigger mucus production and discharge of cnidae (stinging cells). The pump must also be mounted in a way that minimises vibrations. When using *Mississippi*-type paddles it is important to mount the paddles in a way that minimise surface splashing that also can produce air bubbles and disturbances. The paddles are also a preferred option when corals are kept for breeding, since submerged pumps would destroy the gametes.

Keeping CWCs healthy in aquaria requires a sufficient amount of high quality food, such as calanoid copepods, rich in wax esters and lipids. The brine shrimp *Artemia* sp. is a common food item for corals in aquaria, since they are easily reared and can be served alive. They are, however, probably not sufficiently rich in nutrients (Larsson et al. 2013a) and it is therefore recommended that they be fed with microalgae before feeding them to the corals. There are sources of frozen zooplankton, and at UGOT researchers have used *Calanus* sp., which is a common food source for *L. pertusa* in the North Atlantic (Dodds et al. 2009). Intact frozen copepods have a tendency to float, and therefore the copepods have been homogenised in a blender before feeding. Lipid droplets and carotenoids from the copepods have been observed in histological preparations of mesenterial filaments of recently fed corals (Strömberg and Östman 2016), indicating that they have indeed been feeding on the copepod suspensions.

At UGOT, food is administered twice a week. Too frequent feeding can lead to accumulation of degrading food residues and build-up of biodegrading bacteria and protozoans that can harm the corals, as well as to elevated ammonia and nitrate concentrations, both also harmful for corals. Even though corals potentially can use particulate organic material as a food source, sediment inflow into the aquaria should be minimised to avoid bacterial build-up. Also, the sediments potentially bring other pathogens, such as protozoan parasites or bioeroding organisms. At UGOT researchers use 50- and 5-micron Ametek polypropylene filter cartridges mounted in sequence to filter the incoming water. This system can require frequent filter changes depending on the sediment concentration of the incoming water. A sand filter that is easily back-flushed could probably do the job with less maintenance and at lower cost.

One of the problems when keeping *L. pertusa* in a large aquarium is to perform an efficient feeding of the polyps without altering the water quality due to decaying of accumulated food waste. Mortensen (2001) fed the polyps by adding crushed krill to the water, which rapidly spread with the circulating water through the entire aquarium. In smaller aquaria, it was easier to perform controlled feeding, and to remove food waste after the feeding. Based on this experience, Mortensen considered that the most efficient way of feeding the corals in a small aquarium was to turn off the water supply, and add food above the corals. The food then slowly settles on the polyps. When the polyps have started ingesting the food, the water supply can be turned on again.

In the facilities from the Oregon Institute of Marine Biology, the CWC tanks were maintained at ambient temperature for the target species (16 °C for *Oculina varicosa* and 8 °C for *L. pertusa*). The corals were fed every 3–4 days using live *A. salina* nauplii, which were hatched from cysts in a conical *Artemia* hatchery with seawater and an external light. Prior to feeding, the water flow was reduced to a rate that maintained the appropriate temperature, but did not flush the *Artemia* from the tanks. The corals were allowed to feed for 12–18 h every 4 days, after which time, a Nitex bag (200 μm mesh) was placed over the standpipe outflow to capture unconsumed nauplii, and the water flow was increased. Excess nauplii were removed to maintain low levels of organic material and to prevent formation and accumulation of inorganic wastes, which is particularly important for recirculating systems. This is a simple system with rudimentary water quality control, so in order to maintain healthy animals, every month a 50% water replacement was performed, and a complete system cleaning was done at least every 6 months or more frequently if necessary.

For long term maintenance, flow-through systems are ideal, but not always possible. A series of flow through aquaria have been constructed at the Trondheim Biological Station in Norway (by J. Järnegren, NINA) that are fed by sand-filtered water drawn from 100 m in the Trondheim Fjord. A flow-through system is also available at the UGOT facilities at Tjärnö, Sweden. This system provides a continuous flow of ‘ambient’ water to the corals, and has proven successful for long-term maintenance and research on early life history studies of *L. pertusa* (see Larsson et al. 2014; Järnegren et al. 2017).

It is also worth mentioning the DyMiCo, active sand bed filter used by R. Osinga and collaborators in the University of Wageningen (The Netherlands). This filter was specifically designed to allow maximal plankton feeding while still having a very high water quality. The system is low maintenance and works quite well for sponges and corals. Dr. Osinga and his team currently have two 3000 L systems for work on boreal deep water sponges. Both systems consist of a water storage tank, a DyMiCo filter and 12 replicate 30 L tanks for experimenting, in which temperature and pH can be controlled individually. This facility is run currently at 6 °C in a climate controlled room.

38.4.2 Maintenance of Octocorals (Gorgonians, Soft Corals and Sea Pens)

In the aquaria facilities of Institut de Ciències del Mar (ICM-CSIC) in Barcelona, several gorgonian species (*Acanthogorgia hirsuta*, *Eunicella singularis, Eunicella cavolini*, *Ellisella paraplexauroides*, *Paramuricea macrospina, P. clavata*, and *Spinimuricea klavereni*) and soft coral (*Alcyonium palmatum*, *Nidalia studeri* and *Paralcyonium spinulosum*) of the Mediterranean continental shelf and slope have been successfully maintained for several years. Acclimation of some of these species to aquarium conditions can be challenging. After placing colonies in different aquaria, polyps of some of these species remained contracted. However, it has been observed that if colonies are placed in large aquaria (over 150 L) equipped with submersible pumps that can generate a flow rate of 4000 L h^{-1}, polyps tend to extend more frequently and acclimation occurs faster. The acclimation period may differ between species, lasting less than a week for some of them (e.g. *E. cavolini* and *P. macrospina*), but can last up to several months in others (e.g. *E. paraplexauroides*).

After acclimation, gorgonians are commonly fragmented into several nubbins for experimental purposes (see Sect. 38.4.4, Fig. 38.16). The coenenchyme at the basal end of the nubbin is removed exposing a portion of the axis (1–2 cm). This denuded portion is covered with specific coral epoxy putty (Coralfix Superfast, Grotech) and the nubbins are attached to an acrylic base. Another system, employed by the DeepSeaLab in Azores, consists in the use of sponge pieces that have previously been sterilised in ethanol and rinsed in distilled water to cover the denude portion. It is extremely important not to cover healthy coenenchyme parts with the coral glue as it may rapidly lead to necrosis of the adjacent tissue (more details in Sect. 38.4.4). In the CWC infrastructures in Barcelona, nubbins of species dwelling on hard substrates are maintained in 30 L aquaria equipped with submersible pumps with flow rates of 2000 L h^{-1}. Also in Barcelona, nubbins and colonies of species dwelling in soft sediments, such as *A. palmatum* and *S. klavereni*, are placed over a layer of fine sands (~15 cm in height) in aquaria of 150 L provided with submersible pumps with flow rates of 4000 L h^{-1}.

Recent experiences with the maintenance of gorgonians (e.g. *Viminella flagellum, Dentomuricea* aff. *meteor, Callogorgia verticillata, Paracalypthrophora josephinae, Acanthogorgia armata*) in the DeepSeaLab in Azores revealed that apart from flow speed, flow direction is very important to keep these species alive. Initially, a single pump with a single outflow tube was mounted in the aquaria and the polyps remained closed for days. However, the installation of a pipe with many holes helped to redistribute the flow into a more uniform laminar way and the polyps opened completely and started feeding normally.

Apart from adequate flow conditions, gorgonians maintained in the Azores appear to be quite voracious requiring abundant and frequent feeding. They are fed every day twice a day (20 mL of food / 30 L aquaria) with a mixture of frozen *A. salina* adults and nauplii, mysids, microplakton, and a food supplement composed of proteins, aminoacids, lipids, vitamins, and oligoelements (Marine Active Supplement, Bentos Nutrition) all partially blended with a food processor. Feeding is supplemented with live rotifers (*Branchionus* sp.) and microalgae (*Chaetoceros* sp. and *Nannochloropsis gaditana*) five times a week.

At ICM-CSIC, most octocoral species are fed with commercially frozen cyclops 3 days a week two times per day. However, it has been observed that this diet is not suitable for *A. hirsuta*, as colonies progressively loose polyps and coloration changes from bright orange to pale grey. After feeding live nauplii of *A.salina* enriched with fatty acids and phytoplankton (*Tetraselmis* sp.) to *A. hirsuta* for several months, its original coloration was restored and polyp loss stopped.

Occasionally, researchers from ICM-CSIC have observed that some nubbins, especially of *E. cavolini* and *E. paraplexauroides*, can be plagued by isopods, which can be removed by submerging the nubbins for 5 s in a brackish solution of 50% seawater and 50% distilled water.

38.4.3 Maintenance of Antipatharians (Black Corals)

The species *Antipathes dichotoma*, *Leiopathes glaberrima* and an unidentified species of the genus *Bathypathes* have been maintained in the aquaria facilities at the Institut de Ciències del Mar (ICM-CSIC) in Barcelona during long periods of time (two years for *A. dichotoma* and *Bathypathes* sp. and six months for *L. glaberrima*). Colonies of these three species are kept in a 30 L aquarium equipped with a submersible pump with flow rates of 2000 L h^{-1} and with 50 μm filtered running natural seawater. In these cases, colonies are not divided into nubbins. Because of the small dimensions of their polyps, finding appropriate food sources for antipatharians has been challenging. After unsuccessfully trying different food regimes (cyclops, live nauplii of *A. salina* and red plankton), it was observed that these organisms can capture live rotifera. In order to supplement their diet, rotifera are enriched with phytoplankton (*Tetraselmis* sp.) and yeast. Antipatharians are fed five times a week two times per day.

The species *Leiopathes* sp. and *Antipathella* sp. are currently maintained at the DeepSeaLab in the Azores. Recent observations of the feeding behavior of these species suggest that they have strong nematocysts and capture food particles easily but take a long time to ingest food because of the slow movement of their tentacles. Based on these observations it is advisable to feed them frequently (at least twice a day) with low amounts of food.

38.4.4 Coral Nubbin Preparation for Experimental Purposes

Coral nubbins, the genetically identical replicates (ramets) generated from a single coral genet, have been proposed as preferred source material for biological and molecular studies. The advantages to work with nubbins are several: sizes can be chosen by the researcher depending on the aquaria and experimental chambers used for different kind of measures to be carried out, further they provide several replicates from a single genetic origin, and finally they also minimise environmental impact by reducing the number of coral colonies collected from the wild. As variability among different clones of one species can be larger than variability between species, it is fundamental to work with distinct batches of at least three different genotypes, so that conclusions can be extrapolated to the species level.

The production of coral nubbins relies on the ability of corals to propagate asexually through fragmentation (Highsmith 1982). Corals often fragment because of physical (storms, strong currents) or biological (predators, bioeroders) factors that break off a portion of the colony. Coral fragments can also be formed by fission, the controlled detachment of coral parts as a form of vegetative reproduction (Lasker 1988). The new fragment is able to survive and form a new independent colony. Cutting techniques or fragmentation follow a similar format. A piece of the parent colony is removed using a cutting instrument, and if the cutting is properly removed, it will heal and form a new colony similar to the parent colony (Borneman and Lowrie 2001).

Nubbins of scleractinian corals can be prepared by cutting coral branches of a parent colony with electrician cutters (or bone pliers) previously cleaned in ethanol. Because of their hard skeletons, coral nubbins can be easily placed in an upright position, i.e. with coral polyps facing upwards by using a plastic mesh or egg crate (Fig. 38.15).

Nubbins of octocorals and black coral can also be prepared by cutting fragments with electrician cutters. However, because of their fragile, flexible structure, these nubbins require a sturdier base to keep the nubbins upright in aquaria. When preparing nubbins, the outer ramets should be selected so that there is only one healing point at the base of the nubbin. Care must be taken to remove the tissue around the axis at the base of the cuttings to avoid it to rot when buried in the epoxy putty.

The researchers from the DeepSeaLab in Azores have developed specially designed bases composed by an “argocrete” support (composed of cement and aragonite sand) and epoxy putty that holds a silicone tube in which the coral fragment is placed (Fig. 38.16). A small piece of artificial sponge inside the silicone tube holds the fragment inside the tubing without damaging it. This base was designed to allow the coral to be easily removed and put back in the base. This is particularly useful for experiments that include routine measurements of respiration and buoyant weight, because these measurements can be affected by the biofilm that may form on the holding bases.

Fig. 38.15 Plastic basket and mesh (as the ones used in flower shops) to place the nubbins of the scleractinian corals keeping them in an upright position and make the transport easy; in the image the basket contains *Dendrophyllia cornigera* nubbins. (Photo: ©A. Veiga)

38.5 Experimentation in Aquaria: Increasing the Knowledge on the Physiology and Functioning of Cold-Water Corals

This last section of the chapter includes several case studies to present the experience of researchers working in the Mediterranean region and in the Atlantic with different CWC species in aquaria. Using a variety of techniques, different scientific questions have been addressed, such as how CWCs respond to climate change and other environmental variables, and feeding behaviour and reproduction of CWCs. Each subsection comprises a general description of the most common techniques for different types of ecophysiological research on marine invertebrates, application of these techniques to CWCs and a brief description of the main findings.

Comparative experimental studies of corals require that the environment experienced by each coral fragment is similar, except for the studied factor. In the laboratory, for long term studies of physiological behaviour, capture rates, growth rates or spawning of coral species, it is often necessary to resemble the environmental conditions experienced by the sampled coral as accurately as possible. In addition to supplying a simulated or recirculated flux of water to the corals, temperature controlling this water and ideally the laboratory, there are several mechanical options available to simulate flow conditions.

Fig. 38.16 (**a**) Colony of the gorgonian *Dentomuricea* aff. *meteor* being prepared for fragmentation; (**b**) close up of a nubbin and the bases described in the text. (Photos: (**a**) © A. Godinho, (**b**) © R. Sá da Bandeira)

38.5.1 Measuring Growth and Metabolic Responses of Cold-Water Corals Under Different Environmental Conditions

Biomineralisation is a major parameter when addressing effects on the metabolic responses of calcifying species. Calcification rate, together with other important physiological descriptors such as respiration, energy acquisition, fecundity and gene expression, aim to integrate the organism as a whole in order to characterise the main functions affected under different environmental conditions. Skeletal growth is an energy demanding process, which uses a large proportion of the energy acquired by corals. The dynamic energy budget (DEB) model (Kooijman 1986), is a useful tool to estimate the energy needed for calcification and tissue growth according to the environmental conditions in which the corals live. Analysis of skeleton pieces also offers the opportunity to investigate growth on a longer temporal scale, as biogenic carbonates can archive all events that impacted growth during the skeleton formation (Schöne 2008; Montagna and Taviani, this volume). Following this, the use of growth profiles inferred from sclerochronological analysis can help in a precise dating of growth disturbances after the introduction of new environmental parameters.

For CWCs, several methods are used to measure skeletal growth rates in aquaria. These methods differ according to the types of response required (at a global scale or at local spatial scales on the coral fragments) and the duration of experiments (see chapter by Lartaud et al., this volume). Among the main techniques used, the total alkalinity anomaly (TA; Chisholm and Gattuso 1991), inclusion of radioisotopes (e.g., ^{45}Ca or ^{14}C; Tambutté et al. 1995; Hennige et al. 2014) and the buoyant weight (BW, Jokiel et al. 1978; Davies 1989) provide a quantification of the calcification rate in g $CaCO_3$ g^{-1} skeleton day^{-1} or % day^{-1}, the latter method being suitable for experiments at monthly scales. However, it should be taken into account that in case of exponential growth you cannot use "% day^{-1}" as coral size continuously changes (Leal et al. 2016). One important advantage of TA and BW compared to the use of radioisotopes is that the first two are not destructive whereas the latter one is. Estimation of the linear growth extension and sclerochronological tools allows a spatial quantification of growth (in mm year^{-1}). Those methods generally require long term experiments owing to low growth rates of CWCs (see for experiments with Mediterranean CWCs: Orejas et al. 2011; Naumann et al. 2011, 2013, 2014; Lartaud et al. 2013, 2014; Gori et al. 2014b, 2016), although some species have shown visible extension after 2 to 3 months in aquaria or *in situ* (Orejas et al. 2008, 2011; Lartaud et al. 2017a). Finally, quantification of the budding rate, which corresponds to the rate of new polyps formed, can be applied as a measure for growth. These techniques are more relevant for colonial scleractinians and octocorals than for solitary CWCs, as for the former groups the growth is primarily driven by polyp formation (Lartaud et al. 2017b).

Recent CWC research conducted in the facilities of the CSM in Monaco has greatly improved our knowledge on the ecophysiology of Mediterranean CWC. For example, it was shown that these CWC can tolerate much higher growth temperatures than those experienced *in situ* (12 °C), which suggest that they will be able to cope with summer heat waves due to global warming (Naumann et al. 2013). Indeed, several species were able to maintain high calcification rates when cultured for several weeks at 2 °C–3 °C above their normal, *in situ* growth temperatures (Naumann et al. 2014). Studies have also shown the importance of heterotrophic feeding in sustaining high calcification rates of the CWC,

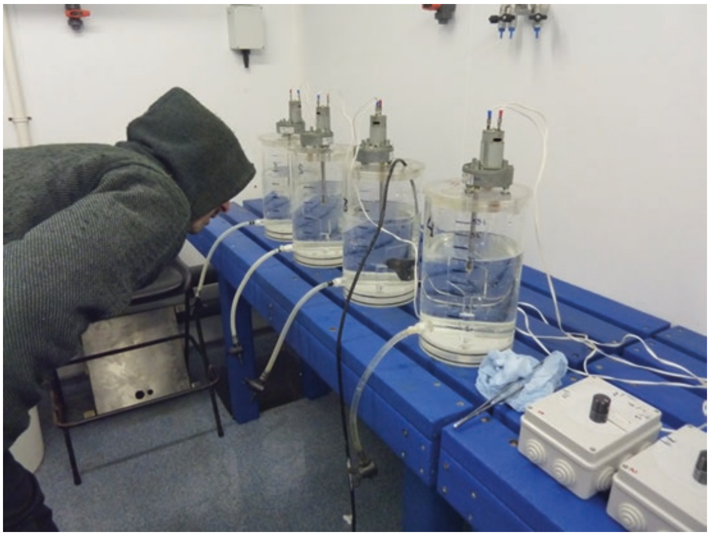

Fig. 38.17 Cylindrical flumes used for feeding experiments. The motor in the top of the chambers is connected to a blade, which keep the water moving at constant flow speed. The speed of the flow can be switched with the controllers (white boxes in the right part of the image). (Photo: © C. Orejas)

also suggesting that CWC are more sensitive to starvation than to temperature increase (Naumann et al. 2011), or the study conducted with *Dendrophyllia cornigera* to evaluate the metabolic response of this coral when it relies on dissolved organic matter as food source (Gori et al. 2014b).

38.5.2 Feeding Experiments with Cold-Water Corals: Closed and Circulating Flumes and 'Mississippi' Chambers

For filter feeding sessile organisms with no algal symbionts, movement within the waters surrounding CWCs is essential for the delivery of food. Flow velocity and reef location influence the food that can be delivered to a reef, given the proximity to a food supply source (such as re-suspended seafloor sediments, fresh phytodetritus or a mixed food supply of phytodetritus and zooplankton). Flow velocity governs the flux and size characteristics of food of different densities or swimming abilities that can be passively transported to a reef, as well as the ease with which particular coral species can collect this carried food from suspension. Passive filter feeders usually show a dome shaped relation between flow speed and capture rate at a given food concentration (e.g. Hunter 1989; Sebens et al. 1997; Allen 1998; Larsson and Jonsson 2006; Wijgerde et al. 2012). With increased flow speed, the flux of food (food per time unit) delivered to the coral increases the feeding efficiency, i.e. the proportion of food particles that can be captured and retained decreases at high flow speeds due to the effect of hydrodynamic forces.

38.5.2.1 Cylindrical Flumes

A modified version of the chambers used by Orejas et al. (2001, 2003) in Antarctica has been utilised by C. Orejas and co-workers in an experiment to find out the ability of *Lophelia pertusa* from the Mingulay Reef (Scotland, NE Atlantic) to capture different type of food (copepods, algae, particulate organic carbon) at different current speeds. The chambers consist in 5 L volume cylindrical aquaria equipped with a paddle which is connected to a motor allowing to switch to different current speeds (Fig. 38.17); results revealed a higher feeding rate for this coral species at low current speeds (2–5 cm s^{-1}) varying the efficiency for the different food types (for detailed information on the results of this experiment, please see Orejas et al. 2016.)

38.5.2.2 Circulation Flumes

To the best of our knowledge, the first feeding experiments performed with Mediterranean CWCs were conducted in the aquaria facilities of the CSM in Monaco in 2008. Four CWC species were used in the experiment: *L. pertusa, Madrepora oculata, Desmophyllum dianthus* and *D. cornigera*. *Artemia salina* nauplii and adults were used as prey items at known concentrations, revealing different feeding efficiencies for the four CWC species depending also on the prey size (Tsounis et al. 2010). These first experiments were done using small (850 mL volume) closed recirculation flumes (Fig. 38.18) with a constant unidirectional flow (1 cm s^{-1}) and they took place simultaneously with the experiments carried on with *L. pertusa* by A.I. Larsson, A. Purser and co-workers in the Tjärnö Marine Laboratory in Sweden.

Purser and co-workers (Purser et al. 2010) considered that rather than placing corals in static aquaria or tiny aquaria with tiny mechanical stirring systems, placing corals in circulating flumes could allow a test section (coral mounting area) to be exposed to unidirectional current at a flow velocity set by the researcher (Fig. 38.19). Flow was maintained within these flumes, as already mentioned, by using a rotary paddle, the speed of which is set manually (Berntsson et al. 2004). Care must be taken in the design to ensure that the paddle and drive

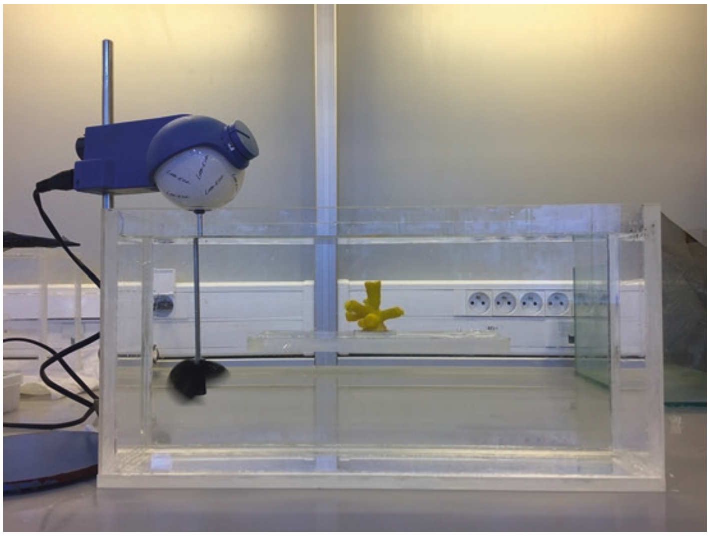

Fig. 38.18 Closed recirculation flume (7 L volume) used at the CSM to conduct feeding experiments. (Photo: © S. Reynaud)

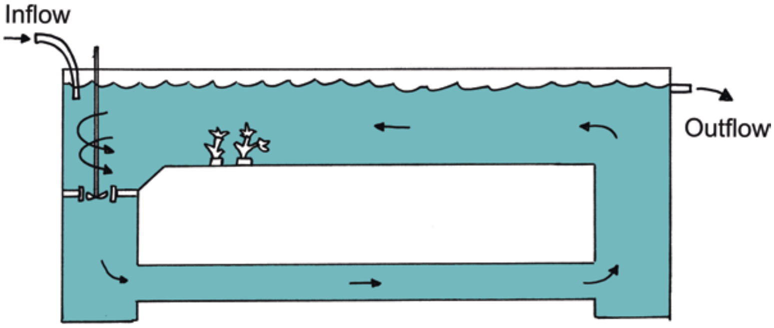

Fig. 38.19 Schematic of a typical 50 L circulation flume. This design offers the possibility for both closed, recirculation functionality and operation as a flow-through system. (Scheme by © A. Purser)

shaft are not constructed of materials that can rust due to the salty seawater used in the experimental runs.

As shown in Fig. 38.19 these flumes can be used as closed systems (as it was the case in Tsounis et al. 2010) or with a continuous flow-through water supply. Commonly, for food uptake studies etc., flumes maintained as flow through systems may have the flow curtailed for the duration of feeding studies, during which the concentrations of food within the 50 L of water are monitored over a known period of time, so that the capture by the corals within the test section can be analysed. Whenever such experiments are based on monitoring the reduction in suspended food over time, it is important to also carry out 'blank' runs, in which comparable 'dead' coral nubbins are used in the place of live corals, to verify that the corals are indeed responsible for suspended food removal over time, rather than a hydrodynamic trapping factor resulting from the coral rugosity. Further, it is also important to consider suspended food removed from suspension by corals may not actually be consumed by the corals (see Sect. 38.5.3). Following an experimental run, the flow-through system can be restarted. Using a circulation flume ensures the flow velocity to be carefully controlled and measured, facilitating comparison of food uptake rates e.g. among flow speeds, within coral species, among different food items at the same flow speeds, and among different species at the same flow velocities. Having well defined and documented flow conditions and food concentrations, is a necessity for comparison of results obtained by independent studies.

These flume designs have been useful in demonstrating that different coral species are able to capture food at varying rates under different flow conditions most optimally (Purser et al. 2010; Tsounis et al. 2010) and that samples of the same coral species, collected from locations with considerably different hydrodynamic and temperature regimes, also collect food at differing rates under differing flow conditions. Larger flumes such as the 1200 L recirculating flume at Tjärnö marine station (described in Jonsson and Johansson 1997) can be used to study flow effects on larger pieces of CWCs or whole coral colonies. This flume has been used to study how *L. pertusa* colonies modify the flow (pattern and velocity) downstream of it, thereby affecting the flux of water and food to neighbouring conspecifics. Further at the CSM, small 7 L volume circulation flumes (Fig. 38.18) have been used in experiments carried out with *D. cornigera* in order to test how the synergy of different factors (e.g. different temperature and flow speed regimes) influence the capture rate ability of this CWC species (Gori et al. 2015).

38.5.2.3 '*Mississippi*' Chambers

Flow conditions surrounding CWCs in the natural situation may be rather chaotic; both as a consequence of the complex relief that may underlie a reef, but also as a result of the complex 3D structure that colonial corals may form with successive generations of growth. The chaotic, turbulent flow can increase feeding rates of corals as the flux and directions of food delivery are varied, and can also help to minimise deposition of material onto coral structure, as may occur under low flow velocity conditions or under unidirectional flow conditions. Turbulent water motion also prevents the development of surface anoxia on fauna and surfaces, an important consideration in long-term or *in situ* experimental studies.

For *in situ* benthic experimental work, experimental chambers deployable as part of lander systems or operated by ROVs, with integrated paddle systems to maintain water movement were developed by the University of Gothenburg for general benthic use (Tengberg et al. 2003). These chambers operate by rotating a '*Mississippi*' type paddlewheel at the top of the chamber by means of a rubber transmission belt, which generates a turbulent flow (see Tengberg et al. 2004). For laboratory work, Jacobs University in Bremen modified the design to allow 5 chambers to be run simultaneously with magnetically linked paddlewheels maintaining equal water movement within 5 separated experimental units (Fig. 38.20). Each chamber contains 12 L of seawater, with either flow-through or static modes possible. Additional experimental functionality is provided by the attachment of peristaltic pumps to each chamber, capable of maintaining the flow of different additional treatments, such as pollutants, food or CO_2 enriched waters (Larsson et al. 2013b). The chambers can also be sealed and used for measurement of respiration rates following treatments. A disadvantage of using this type of chamber is that the flow conditions and hence the flux of food, sediment etc. are not easily measured and defined (will vary with e.g. height of coral, distance from the corners of the chambers), which makes comparisons of results among independent studies difficult.

At the left of Fig. 38.20 the motor block can be seen adjacent to the paddle in the left-most chamber. This motor is connected through the chamber wall by strong magnets to the first paddlewheel, mounted in the left-most aquaria in a small plastic mount. With both ends of the paddlewheel containing magnets, the remaining paddlewheels are attached in a similar fashion via magnetism through the chamber walls. This allows the 5 paddles to be rotated in unison, with a fixed velocity, throughout the 5 chambers making the experimental unit. Commonly the group have employed 3 × 5 chamber *Mississippi* arrays, to allow 4 × 3 chamber treatments and 1 × 3 control chambers for an experimental run, with the various treatments randomised across the 15 chambers. An alternative to using magnets is to use a standard metal bar running through the 5 chambers, with this bar attached directly to the motor block. With this solution, careful sealing is required to exclude inter-chamber transport of treatments, or the use of a lesser volume of water, i.e. 10 L per chamber, to ensure this axle bar remains above the height of the water in each experimental chamber. With this solution there is a possibility of some bubbles forming during operation, which may have relevance for some treatments or experimental investigations. A further, more complex design can be made by placing the paddlewheels at 90° to those illustrated in Fig. 38.20. In this case, each paddle is connected by magnets to magnets mounted on a drive chain mounted on the outside of the 5 aquaria. In this case, the drive chain turns each exterior magnet ring, which turns the paddlewheel within each chamber (Larsson et al. 2014).

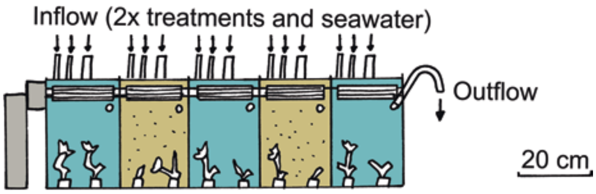

Fig. 38.20 Schematic of an array of replicate 10 L '*Mississippi*' chamber aquaria, within which turbulent flow can be maintained whilst providing a flow-through water supply and timed delivery of experimental treatments (Scheme by © A. Purser). (For a photograph of a typical '*Mississippi*' paddle, see Fig. 38.22)

38.5.3 Carbon and Nitrogen Cycling in Cold-Water Corals – The Use of Stable Isotope Tracers

The quantification of carbon (C) and nitrogen (N) resource utilisation and subsequent processing by CWCs remains a challenging task. Traditional gut content analysis is cumbersome, since scleractinian CWCs are not easy to dissect, and their food resources may consist of small-sized particles, dissolved organic and even inorganic compounds (Orejas et al. 2003; Gori et al. 2014b; Mueller et al. 2014; Middelburg et al. 2015). In experimental feeding studies, CWCs were offered a range of food types and their ingestion was subsequently measured as the decrease in food concentration or as the number of food items caught per polyp (Orejas et al. 2003, 2011, 2016; Tsounis et al. 2010; Purser et al. 2010; Gori et al. 2014b, 2015). Nevertheless, some of the trapped food may be lost due to sloppy feeding (Moeller 2005; Pitt et al. 2009) or cannot be assimilated, and thus food uptake rates may not directly translate to assimilation rates. In addition, the coral utilises the assimilated food in its total energy budget (Fig. 38.21), which includes respiration for maintenance and growth, tissue growth and storage, reproduction (Davies 1984; Kooijman 1986), calcification (Cohen and Holcomb 2009; McCulloch et al. 2012) and the release of coral mucus as particulate and dissolved organic matter

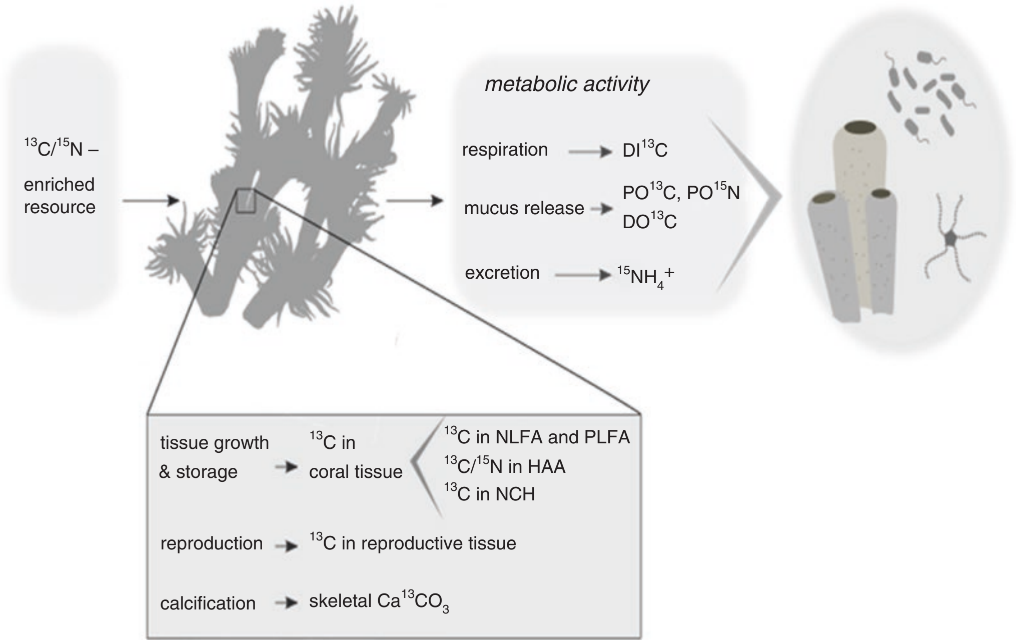

Fig. 38.21 Carbon and nitrogen budget of a cold-water coral feeding on a $^{13}C/^{15}N$ enriched resource, from assimilation to utilisation for metabolic activity, for tissue and skeletal growth and reproductive tissue formation. The resource ^{13}C and ^{15}N can be 'traced back' in metabolic products such as *DIC* dissolved inorganic carbon, *POC/PON* particulate organic carbon/nitrogen, NH_4^+ ammonium, and into coral (reproductive) tissue plus tissue molecules, *NLFA* neutral lipid-derived fatty acids, *PLFA* phospholipid- derived fatty acid, *HAA* hydrolysable amino acids, *NCH* neutral carbohydrates, and in skeletal calcium carbonate. (Scheme by © S.R. Maier)

(POM, DOM; Crossland 1987; Wild et al. 2008; Naumann et al. 2011; Zetsche et al. 2016). The partitioning of the assimilated C and N amongst these components of the energy budget is difficult to determine.

38.5.3.1 Stable Isotope Tracer Experiments to Unravel Organism Physiology

Pulse-chase stable isotope (SI) studies are used to quantitatively follow the uptake and processing of organic and inorganic resources in freshwater and marine organisms (Middelburg 2014) and represent a promising tool to study C and N cycling in CWCs. The general principle is quite straightforward; an (in)organic C or N resource, with a substantially higher than natural ratio of the heavy isotope (e.g. ^{13}C for carbon and ^{15}N for nitrogen) over the lighter isotope (e.g. ^{12}C for carbon and ^{14}N for nitrogen) is offered to the organism and this 'heavy isotope' pulse is used to trace the fate of the resource in the tissue and metabolic products of a consumer (e.g. Middelburg et al. 2000; Moodley et al. 2000).

SI resources can be obtained in various ways: inorganic resources (e.g. $NaH^{13}CO_3$, or $^{15}NH_4Cl$) can be commercially purchased, while organic resources (e.g. phytoplankton or bacteria) can be produced by culturing them in a ^{13}C- or ^{15}N-enriched medium (e.g. Moodley et al. 2000; Mueller et al. 2014). Enriched dissolved organic material (DOM) can be extracted from an enriched algal culture (de Goeij et al. 2008), while herbivorous zooplankton can be grown by feeding them with enriched phytoplankton (Mueller et al. 2014).

38.5.3.2 Studies on Food Sources, Selectivity and Carbon Budgets

SI tracer studies have shed light on CWC physiology in various ways. Mueller et al. (2014) applied SI experiments to test the ability of *L. pertusa* to exploit a wide range of ^{13}C- and ^{15}N-enriched food substrates, including algal-derived amino acids (DOM), bacteria, phytoplankton and zooplankton. C and N of all the tested resources were assimilated into coral tissue, fatty acids, and amino acids, underlining the opportunistic feeding strategy of CWCs as a potential adaptation to their variable trophic environment. In addition, *de novo* synthesis of individual fatty acids by *L. pertusa* was apparent from the ^{13}C enrichment of individual phospholipid-derived fatty acids (PLFAs) in the coral, which were absent in the added food sources. This feature may complicate the interpretation of *in situ* observations on coral nutrition based on lipid composition profiles (Mueller et al. 2014).

van Oevelen et al. (2016) studied selective feeding of *L. pertusa* in a cross-labelling approach, providing corals with ^{13}C-enriched phytoplankton *versus* ^{15}N-enriched bacteria and *vice versa*; they found no selectivity at low food concentrations and a relative preference of phytoplankton over bacteria at higher food concentration.

38.5.3.3 Nitrogen Budgets: From Coral Individuals to the Coral Holobiont

Middelburg et al. (2015) studied the N cycle of the holobiont *L. pertusa* by incubating coral fragments with various inorganic ^{15}N sources (i.e. ammonium, nitrate and N_2).

Surprisingly, the coral holobiont was able to fix N_2 gas, which is an energetically costly process, advantageous in periods of N shortage in the deep-sea. Moreover, ammonia was nitrified to nitrate by nitrifying bacteria that are likely associated with the coral mucus. The nitrifying community used the energy obtained from ammonium oxidation to fix dissolved inorganic carbon into organic carbon, indicating chemoautotrophic activity. Also, denitrification activity was observed, which was associated with anaerobic parts of the coral gut or with the mucus layer (Middelburg et al. 2015).

38.5.3.4 From the CWC Holobiont to CWC Reefs: Trophic and Non-trophic Interactions

Close trophic interactions between reef species, such as facilitation and recycling of metabolic end products (Fig. 38.21), could represent important reef community adaptations to food or nutrient limitation (Levington 1972; Richter et al. 2001; de Goeij et al. 2013; Rix et al. 2016). The application of SI tracers to follow C and N across several trophic levels revealed, amongst others, the assimilation of coral-released DOM by sponges, and their subsequent shedding of cellular debris as food source for detritivores. This sequence of events has been termed the sponge-loop (de Goeij et al. 2013; Rix et al. 2016). Another study found that the CWC-reef associated polychaete *Eunice norvegica* assimilated two to four times more food-^{13}C in the presence of *L. pertusa,* while corals benefitted from the polychaete presence by enhanced calcification (Mueller et al. 2013).

38.5.3.5 Outlook

SI tracer research on CWCs is in its infancy, but can become an important tool, for example to assess changes in energy demand and allocation by CWCs under predicted future ocean scenarios (Cohen and Holcomb 2009). *L. pertusa*'s allocation of food carbon to respiration, mucus production and tissue growth, including the build-up and depletion of carbon stores, has for instance been addressed in a recent SI tracer study (Maier et al. in press.). Studies on OA and temperature rise could apply the SI tracer methodology to investigate both changes in carbon budgets of CWCs and reef-associated species, and changes in their trophic interactions; assessing the reefs' recycling capacity and resilience.

38.5.4 Experimental Research on Cold-Water Coral Reproduction and Larval Rearing

At the University of Gothenburg (UGOT) *L. pertusa* has been reared for spawning and larval production since 2011 (e.g. Larsson et al. 2014), opportunistically starting in 2009 when spawning occurred during respiration measurements in a metabolic experiment (Larsson et al. 2013a). For spawning purposes, the *Mississippi* chambers developed for previous experiments (see Fig. 38.20, Sect. 38.5.2) were modified: individual chambers were made larger to fit the larger coral fragments needed and the back walls of the chambers were made black so that the whitish eggs could be more easily detected (Fig. 38.22a). The high turbulence from the *Mississippi*-type paddles seemed to stimulate spawning behaviour, and kept the corals in general in a good health.

The parental corals were collected in October–November, a couple of months before the estimated local spawning season in January–February. The early collection was done to allow the corals to acclimatise to the laboratory conditions. The collections were carried out with a landing net that was mounted on an ROV.

38.5.4.1 Gamete Collection and Fertilisation

In *L. pertusa* from the NE Atlantic, oogenesis takes a full year, and somewhat less for spermatogenesis (Brooke and Järnegren 2013). Inducing spawning in corals is difficult (Strathmann 1987), probably since corals do not have oviducts or sperm-ducts, but see Miller (1996) who induced spawning in an antipatharian. Dissecting out polyps to collect gametes is futile due to discharge of cnidocysts that results in

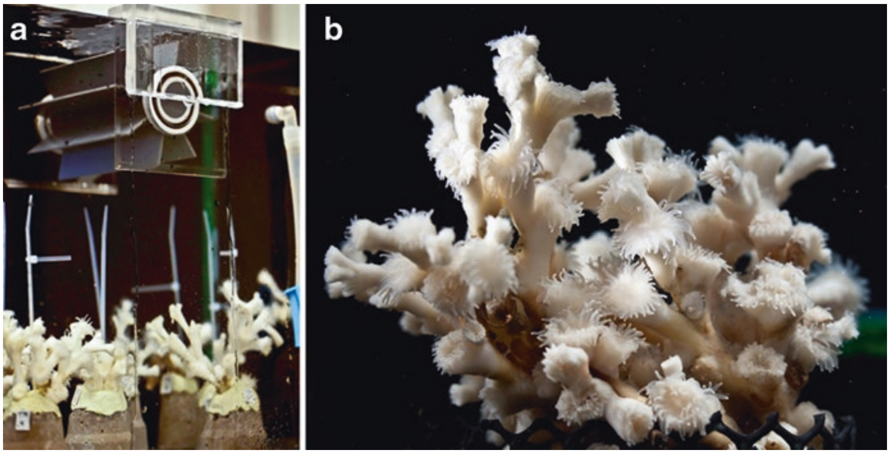

Fig. 38.22 (**a**) Small *Lophelia pertusa* branches in '*Mississippi*' chamber with black wall (**b**) Larger branched colony in darkened '*Mississippi*' chamber. (Photo: © S. Strömberg)

entanglement and destruction. To induce spawning it would probably be necessary to rely on a series of hormones to stimulate final maturation and tissue breakdown, so the best strategy so far is to allow for spontaneous spawning until complete understanding of the reproductive cycle is achieved.

Lophelia pertusa is a broadcast spawner, and spawning in laboratory is protracted over 2 months, possibly with one more intense week during this period. This has yet to be confirmed to also be the case in their natural environment. Spawning by males and females were usually synchronised in chambers where both sexes were combined. Spawning also occurred in chambers where either sex was isolated, although, usually never by both sexes the same day in separate chamber-sets. If isolated eggs and sperm are needed for fertilisation experiments, it is recommended that males and females be placed in adjacent chambers that are interconnected by a membrane or filter that allows chemical signals to pass between them, but not gametes. It is probably conjugated estradiol and testosterone that act as pheromones to synchronise gamete maturation and spawning (Twan et al. 2006); however, this needs further investigation.

Collection of gametes is best done by sucking them up through 5–7 mm tubing, used as a siphon, into large glass bowls for fertilisation and embryo development. The bowl should have a bottom cover of water before transfer. The eggs are approximately 160 μm and barely visible for the naked eye, but they are highly reflective, so with a black background and lateral lighting in an otherwise dark room they are easy to see. Using a sieve to collect the eggs is not possible due to their delicacy; they simply disintegrate in contact with the net, or with surface tension. Eggs and larvae can be handled with glass pipettes, but water motion should always be kept very slow and gentle. Eggs are initially neutrally buoyant and spread out in the entire water mass. After fertilisation they become slightly positively buoyant and start to slowly ascend to just below the surface: usually without getting caught in the surface tension, unless forced into it by too strong turbulence. Larvae will initially actively swim upwards and gather just below the surface as well (Larsson et al. 2014).

If males are less productive and gamete cultures are sperm limited, putting the gamete bowls on a shaking table with gentle motion can increase fertilisation success. The friction of the moving water will increase the water temperature, and development rates will therefore increase if embryos are left on the shaking table as compared with cultures in still water. At UGOT, researchers maintain the cultures, as well as parental corals, at 7–8 °C, since that is the local *in situ* temperatures during the spawning season. They tolerate lower temperatures, however, raising the temperatures to 10 °C or more usually puts the health of cultures at risk due to increased bacterial growth. The *in situ* temperature range for *L. pertusa* and other CWCs is 4–12 °C, however, temperatures above 10 °C have been found to be detrimental in the long run in aquaria.

Besides the work conducted with *L. pertusa,* there are two important papers regarding reproduction and larval ecology of *Oculina varicosa* conducted by Brooke and Young (2003, 2005). Similar data on embryology, larval development, thermal tolerances, and swimming speeds as for *L. pertusa* is thus available also for *O. varicosa*.

38.5.4.2 Larval Rearing

Larval cultures of *L pertusa* have been kept in 2–3 L glass bottles (E-flasks) for maintenance. During the first 3–5 weeks larvae reside in the upper portion of the flasks, swimming underneath the surface, so E-flasks are recommended to be entirely filled up and kept bottom up to give larvae maximum volume. If other types of bottles are used, they can be kept horizontal. Regular changes (e.g. weekly) of a fraction (e.g. 1/3) of the water are sufficient, with occasional larger volumes changed.

After 10 days, larvae are fully developed planulae and good swimmers (see Larsson et al. 2014 and Strömberg 2016 for further details on development). Feeding should start after 20 days—this is when larvae have developed a flexible mouth and are ready for foraging. An oral pore is already visible after 2 weeks, but they are not interested in food at that point. Larvae seem to be opportunistic feeders and prefer a diet similar to adult corals, although, particles of copepods are preferred over live ones. We have homogenised *Calanus* sp., centrifuged the homogenate, and used the fine fraction for feeding. This soup added to cultures has elicited feeding behaviour, that is, larvae swim in a more spiral fashion or stop entirely and move particles towards the mouth by ciliary movements (Strömberg and Larsson 2017). The carotenoids from the copepod fragments are also visible through the body wall of the larvae after feeding, confirming actual intake. Small sized microalgae such as *Isochrysis* sp. and picoplankton have also elicited this behaviour, or trailing of mucus strands that food particles adhere to. Larvae have also been observed to adhere to larger particles of copepods; either feeding directly off the copepod tissues or from the degrading microfauna or picoplankton associated with the tissue.

38.5.4.3 Experiments

The experiments that we have undertaken on *L. pertusa* larvae so far have focused on biological and ecological issues. Specifically, we have tried to establish a timeline for development and ontogenic shifts in behaviour during the pelagic phase of larvae to track what is happening from release to settling. This information is crucial to make adequate projections for larval dispersal, as seen in the work of Fox et al. (2016), where these experimental results were found to contrast with projections based on assumptions of larvae dispersing as passive particles, with fundamentally different outcomes as a result.

To elucidate whether larvae reside in the photic zone during dispersal, we tested if they feed on microalgae, and if they pass through density layers in the water column (Strömberg and Larsson 2017). The latter may be relevant to the Skagerrak area (Northeast Atlantic), where surface waters are affected by the Baltic current, and by outflow from the fjords along the coast, which both give a top layer consisting of less saline water with pronounced haloclines as a result. In most other areas, however, larvae may never encounter lower salinities since offshore oceanic waters usually are not stratified. The larval behaviour in response to salinity gradients was tested in plexiglas aquaria with a bottom slit, allowing for the slow adding of layers of water with different densities. Larvae were then added to the bottom of the aquaria and filmed as they swam upwards. These experiments showed that larvae did not react to salinity differences as high as 5 units between layers, with the top layer salinity as low as 25, instead larvae kept swimming upwards until reaching the surface (Strömberg and Larsson 2017). In addition larvae survived for long even in a salinity of 25 showing that larvae have a broad salinity tolerance range. Tests on feeding preferences also show that larvae might feed on small size microalgae, although this is not fully verified. In summary, we did not find anything that excludes the possibility that larvae spend time in the photic zone during dispersal.

38.5.5 Experiments with Cold-Water Corals under Changing Ocean Conditions

The Changing Ocean Group experimental facility in Edinburgh (Fig. 38.10) has been used for two long-term projects; (1) impacts of ocean acidification (OA) on *L. pertusa* physiology and biomineralisation (Hennige et al. 2015), which ran for 1 year, and (2) impacts of OA on *D. dianthus*, firstly for physiological studies (8 months, Gori et al. 2016) and secondly for biomineralisation research, using pH proxy validation through boron isotopic fractionation (14 months) (Martin et al. 2016). For these experiments, collected corals were fragmented and randomly distributed through all the systems to prevent pseudo-replication. For each of the 5 treatments, there were four replicate systems, each comprising four 5 L tanks connected to a 60 L sump. Each tank was suitable for holding n = 4 live coral fragments and a 'dead' coral skeleton (80 tanks total). Ambient and elevated CO_2 air mixes were bubbled directly into the sump. Experimental conditions for the experiment on *L. pertusa* replicated ambient and predicted future conditions following IPCC emission scenarios. All replicate systems were housed within a temperature-controlled room at ambient reef temperature, and systems at elevated temperatures were controlled through Aqua Medic T-computers and titanium heaters. The bubbled sumps were also equipped with filtration units and powerheads to ensure adequate filtration and water mixing for each replicate system. *L. pertusa* fragments were fed a mixture of live *Artemia* and crushed krill (Gamma frozen blister packs) and *D. dianthus* were fed frozen mysids every 2 days. For more details on the experimental design see Hennige et al. (2015).

Considering the current literature available, experimental time scales are very important when assessing whether or not corals can acclimatise, as short-term experiments may produce results (for example a detrimental impact of OA upon key processes) that may not appear in longer term studies, as organisms have undergone alterations in key regulatory processes to acclimatise. This makes it very useful to compare both short and long term research, and with regard to *L. pertusa,* most significant changes in respiration and calcification occur in the short term (Hennige et al. 2014, 2015), from 24-h experiments to 4 weeks. Beyond 4 weeks, decreases in calcification and respiration have not been observed in studies to date (see Hennige et al. 2015 and references therein). However, even when acclimatisation has been demonstrated, it may come at a cost to other processes and may therefore not be sustainable in the long-term. Research in the Edinburgh Changing Oceans facility demonstrated that although growth rates can continue as normal under low pH conditions over a period of 12 months, skeletal biomineralisation, molecular-scale bonding and skeletal structure all change. Exposed skeleton cannot acclimatise or adapt to future conditions, and its dissolution is a purely biogeochemical process. The dissolution and weakening of the exposed skeleton observed after long term OA exposure (Hennige et al. 2015) when combined with bio-erosion, may mean that reefs of the future may be smaller than currently, and consequently unable to support the large amounts of biodiversity. The breakdown in the relationship between respiration and calcification in long term experiments may also indicate that 'normal' energetic strategies are circumvented in the long-term, possibly due to other processes using energetic reserves (Hennige et al. 2014, 2015).

Further evidence to support this hypothesis was provided from the study on *D. dianthus*. Whilst these corals may be able to tolerate exposure to acidified seawater, when combined with elevated temperature, respiration and calcification rates decreased. Changes in the ratio of respired oxygen to excreted nitrogen (O:N) were recorded, indicating that the main sources of energy being metabolised shifted from mixed use of protein and carbohydrate / lipid as metabolic substrates under control conditions, to less efficient protein-dominated catabolism under both stressors (Gori et al. 2016). These results support a growing literature consensus that CWCs are amongst the most vulnerable of marine ecosystems to global climatic change (Roberts et al. 2016).

In the same line as the experiments conducted in Edinburgh, J. Movilla and co-workers executed aquaria experiments in the aquaria facilities at the ICM-CSIC, in

Barcelona in order to assess the response of the skeletal structure and the tissue composition to OA of four of the most widely distributed CWC species in the Mediterranean (*L. pertusa*, *Madrepora oculata*, *D. cornigera* and *D. dianthus*; Fig. 38.23). The team developed a system for experimental pH manipulation in aquaria that allowed exposing the organisms to different pH conditions, simulating the present values and those expected by the year 2100. Movilla and co-workers assessed the response of the skeletal structure (calcification rate, microstructure, specific microdensity and porosity) and the tissue composition (organic matter amount and lipids content) in each single species (Movilla et al. 2014a, b; Movilla, this volume).

A pH-manipulative experimental system was implemented based on the experimental design described by Reynaud et al. (2003) (Fig. 38.24). The system was installed inside a temperature-controlled room to ensure constant values during the whole experiment. Seawater was continuously supplied to two 150 L tanks where pH is adjusted to the desired experimental values. Treatment 1 consisted of a pH of 8.10 units (total scale), similar to the current natural pH value observed in the sampling area at similar depths and used as control conditions, while treatment 2 consisted of a pH of 7.81 units, simulating the future Mediterranean decline predicted for the year 2100 following an RCP6 scenario (IPCC2013, AR5). In this experimental set-up instead to bubble a CO_2 air mixes directly into the sump (Hennige et al. 2015), CO_2 (99.9% purity) or CO_2-free air (using a filter filled with soda lime, Sigma Aldrich) were bubbled to either increase or reduce pH, respectively. More details in the experimental design and set-up, as well as in the treatments can be found in Movilla et al. (2014a, b).

For this kind of experiments, it is very important to determine the *in situ* values of the carbonate system in the field as well as to make a good monitoring of these parameters throughout the experimental phase to check the accuracy of the treatments. For that purpose, to compare the control treatment with the natural range that the organisms experience in the field, temperature and salinity profiles were obtained with a Seabird CTD911 from surface to 400 m depth, and water samples for pH and total alkalinity (TA) measurements were taken every 30 m with 24 12-L Niskin

Fig. 38.23 Specimens of *Lophelia pertusa* (above left), *Madrepora oculata* (above right), *Desmophyllum dianthus* (below left) and *Dendrophyllia cornigera* (below right) in the experimental aquaria. (Photos from *L. pertusa* and *M. oculata*: © A. Gori; photo from *D. dianthus* and *D. cornigera*: © E. Obis)

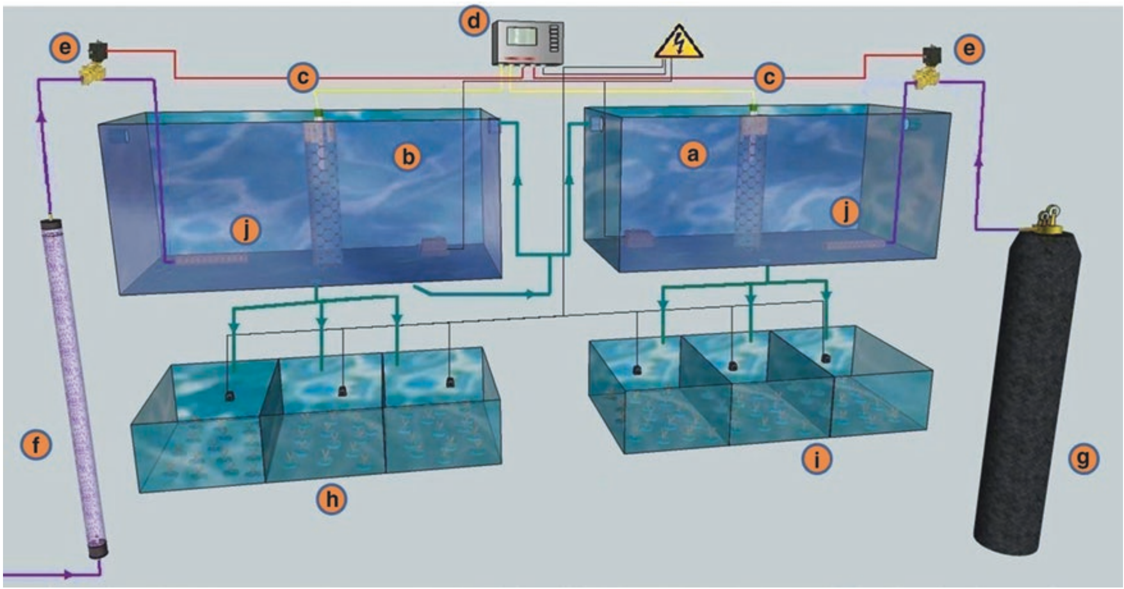

Fig. 38.24 Experimental set-up used to control and modify seawater pH in each aquarium. (**a**) and (**b**) large 150 L tanks for seawater conditioning at pHT 7.81 and 8.10, respectively; (**c**) glass electrodes for pH and PT100 probes for temperature measurements; (**d**) pH controller and data logger; (**e**) solenoid valves; (**f**) soda lime filter; (**g**) 50 kg CO_2 bottle; (**h**) and (**i**) control and low-pH experimental aquaria, respectively (three replicates per treatment); (**j**) Micro bubble diffusers. (Scheme by © J. Movilla)

bottles mounted in a rosette during a research cruise carried out in the sampling area.

In addition, small volumes of water were taken periodically (once a month during the first 3 months and every second month for the rest of the experiment) to analyse TA by potentiometric titration (Pérez and Fraga 1987; Pérez et al. 2000) and pH using spectrophotometry (Clayton and Byrne 1993), which provides better precision than electrodes. These values were used to calculate the rest of parameters of the carbonate system in seawater in both treatments, using the CO_2calc software (Robbins et al. 2010). Results of the experiments have been already published and can be found in Movilla et al. (2014a, b) and Movilla (this volume).

38.5.5.1 Gene Expression Studies with Cold-Water Corals in a Changing Ocean

While the above mentioned studies have mostly focused on studying the effects of OA at organism-level (e.g. growth, calcification, metabolism), only Carreiro-Silva et al. (2014) have looked at the impact of OA at the molecular level of gene expression. For zooxanthellate corals, molecular techniques looking at gene expression have produced useful insights into understanding the physiological pathways involved in the response of corals to OA, by targeting genes involved in the cellular stress response, biomineralisation, and energy metabolism (e.g., Kaniewska et al. 2012; Moya et al. 2012; Vidal-Dupiol et al. 2013). Indeed, the studies of Carreiro-Silva et al. (2014) on the impact of OA on *D. dianthus* have shown that although elevated pCO_2 did not cause significant changes in calcification or respiration rates measured at the level of the organism, gene expression profiles revealed considerable changes in response to OA at the cellular level. The study showed upregulation of genes involved in important cellular processes related to calcification and metabolism as a mechanism to counteract the negative effect of pH on the coral's calcification process. This indicates that CWCs may be able to adjust their physiology in response to environmental changes as a potential mechanism of acclimation or adaptation of CWC to OA.

Consequently, understanding the molecular mechanisms behind the physiological processes involved in a coral's response to elevated pCO_2 is critical to assess the ability of CWCs to acclimate or adapt to future OA conditions.

38.5.6 Measuring Effects of Drilling and Oil Spills in Cold-Water Corals

Cold-water corals are often found in association with hydrocarbon drilling areas. Offshore drilling activities discharge large amounts of waste materials into the water column that cause increased sedimentation around oil and gas installations. The discharged drill cutting material is made up of the rock cuttings generated during drilling and attached added drilling fluids (Holdway 2002). For CWC reef fauna, there is great concern is over the potential for drill-cuttings to cause smothering (Roberts et al. 2006), and coral mortality has been observed in the immediate vicinity of drilling discharge points (Gass and Roberts 2006). Another evident risk is oil spills, which, unlike drill cutting discharges, are accidental.

Following the 2010 *Deepwater Horizon* disaster in the Gulf of Mexico, where an amount of oil equal to approximately 4.4 million barrels of oil was released (Camilli et al. 2010), several oil-impacted coral communities were studied *in situ* (White et al. 2012; Fisher et al. 2014). Except for the crude oil, coral communities were also exposed to a chemical dispersant added into the wellhead in order to mitigate the consequences of the oil spill (DeLeo et al. 2016).

There are two main ways of exposing corals to sediments, either by letting the sediment settle onto coral surfaces in water with low or no movement (e.g. Larsson and Purser 2011; Allers et al. 2013) or by (periodically or continuously) exposing the corals to suspended sediment particles in moving water (e.g. Brooke et al. 2009; Larsson et al. 2013b). In the first case with settled sediments, only ordinary aquaria or jars are needed for exposure. Since the surface area of the aquarium floor is known, a slurry of sediment can be added for targeted exposure of sediment mass per unit area. If a certain burial depth is aimed for, pre-tests of resulting sediment depth on the aquarium floor from known sediment loads may be necessary. Flow through of water is turned on after the sediment has settled. Such aquaria experiments have shown that *L. pertusa* actively removes both natural sediment particles and drill cuttings through ciliary movements on the tentacles (Zetsche et al. 2016) and through mucous shedding on tissue covered parts of the skeleton (Allers et al. 2013; Zetsche et al. 2016). Repeated exposure does not affect the cleaning efficiency but sediment can accumulate on tissue-free (bare) skeleton and after repeated exposure cause smothering of adjacent tissue and polyps (Larsson and Purser 2011).

When corals are exposed to suspended sediment particles in moving water, the degree of exposure is depending on the sediment flux, i.e. on the concentration of sediment particles times the flow velocity. For the same sediment concentration, the exposure in the flow direction is hence twice as high when the flow velocity is doubled. The amount of sediment that will end up on vertically and horizontally oriented parts of the coral will depend on the coral morphology, the weight and stickiness of the sediment particles, and the water velocity with more sediment particles settling from above at lower flow velocities. Exposure to suspended sediment particles for a period of time requires appropriate equipment. Brooke et al. (2009) exposed *L. pertusa* fragments to suspended sediments in closed recirculating systems for 2 weeks. Slurry of sediment was introduced at the start of the experiment and the water with suspended sediment was pumped from the conical bottom of the experimental aquarium to the top ensuring water circulation and that sediment particles were kept in suspension. Both Brooke et al. (2009) and Larsson et al. (2013b) regularly monitored the sediment concentration in the experimental aquaria. In Larsson et al. (2013b), *L. pertusa* was exposed to natural benthic sediments and drill cuttings continuously during a period of 3 months (Fig. 38.25). The corals were kept in constant flow through of water in "*Mississippi*" chamber aquaria (Fig. 38.20) and sediments were added to the aquaria by the use of peristaltic pumps from stock solutions with specific concentrations. Sediment particles in the stock solution were kept in suspension by circulation pumps. Constant sediment exposure in the aquaria was reached by balancing the flow through rate of water with the delivery rate of sediment stock solution. The internal circulation of water in the aquaria was governed by the paddlewheels (Fig. 38.20). By maintaining sufficient flow through of water and sediment, the settlement of particles onto corals and other structure in the aquaria was comparatively very small and the particle concentration could be kept constant. Results showed that sediment accumulates also onto vertically oriented surfaces of coral fragments, starting at tissue-free parts, which may result in smothering of polyps. Skeletal growth can correspondingly be slightly adversely affected after months of exposure (Larsson et al. 2013b).

Fig. 38.25 Experimental set-up for long-term exposure of *Lophelia pertusa* to suspended benthic sediments and drill cuttings. Experiment performed at the University of Gothenburg marine station at Tjärnö, Sweden. (Photo: © A. I. Larsson)

38.5.7 The Fragile Chemical Equilibrium in Cold-Water Corals Maintenance: An Example from the Levantine Mediterranean Sea

This section reports a few notes and comments on how an almost catastrophic and irreversible loss of tissue of *Dendrophyllia ramea* colonies kept at the Ocean Aquarium in Cyprus was prevented. The coral colonies were collected off Cyprus at around 150 m depth in a soft bottom habitat. This is the first time that *D. ramea* has been recorded in the Mediterranean Sea at such a remarkable depth and in a sedimentary environment (Orejas et al. 2017).

The aquarium hosting the coral colonies had one ton of seawater with a "sump filtration system". This particular set-up allows for efficient filtration of the aquarium water in a way that the chemical and biological parameters are precisely and fully controlled. Technicians in charge of the coral exhibition performed daily routine checks, such as chemical water analysis and temperature control, to ensure the right aquarium conditions for the corals. Feeding was performed with a syringe, separately to each colony, to minimise food waste and to increase the feeding efficiency of the polyps. Despite the efforts of technicians, 4 months after the corals were on display, an outbreak of filamentous algae was noticed, which infested the whole aquarium within a matter of days. Later on, technicians also observed a sudden and significant regression of live tissue and polyp size and the expansion of filamentous algae on the bare skeleton (Fig. 38.26a, b). An experienced aquarist revealed that the infestation and tissue loss was the result of a sequence of events that occurred due to poor water quality, incorrect lighting (that favors algae proliferation) and insufficient nutrition. The corals were exposed to increased levels of phosphates, and insufficient nutrition, which may have affected growth and calcification. The contracted polyps suggested a weakening of the polyps. Concurrently, increased levels of nutrients (phosphate and nitrate) and excessive illumination exposure of the aquarium promoted the growth of filamentous algae. With the corals weakened and the filamentous algae proliferating in the aquarium, it was a matter of time for the filamentous algae to aggressively colonise the coral skeleton and lead to noticeable coral tissue loss. Once corals reached this health status, it was almost irreversible and the death of the coral colonies was apparently imminent. Technicians, always in close collaboration with the specialist, attempted to limit the infestation using simple, non-invasive techniques. By increasing the frequency of water changes, water quality was rapidly increased with minimal impact on the corals. Although the outbreak was prevented from further infestation, filamentous algae were still present in the aquarium exhibition and the health state of the corals did not change. Improved water quality on its own proved to be a weak treatment and time was running out as more coral tissue was lost during this process.

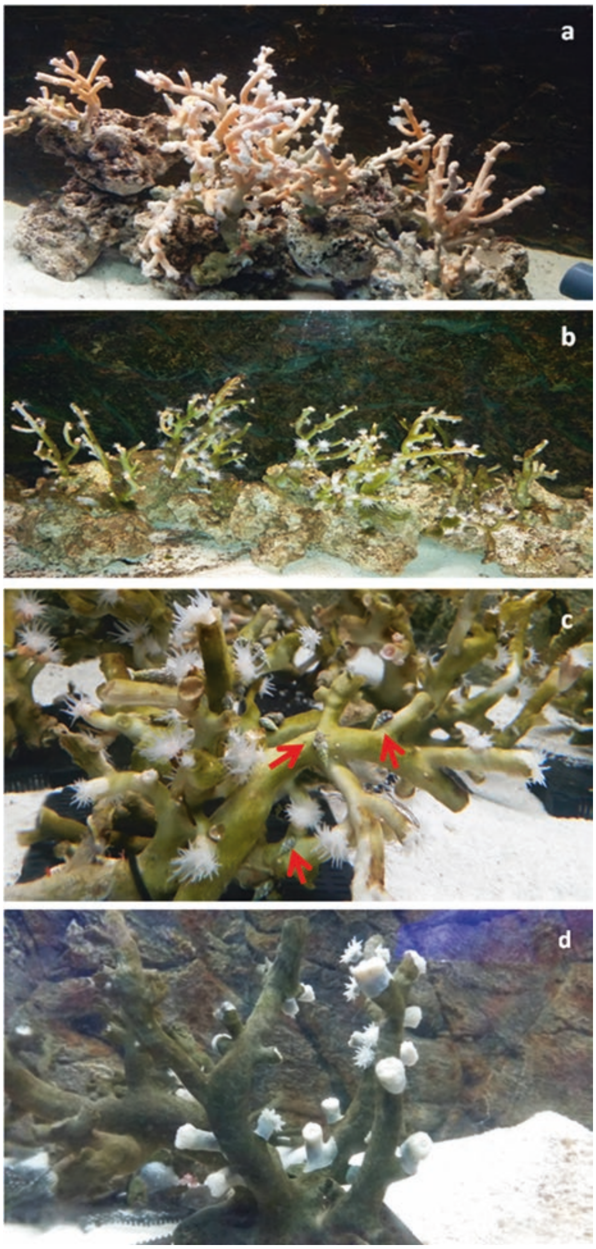

Fig. 38.26 The evolution of the *Dendrophyllia ramea* colonies in the public aquarium of Protaras after an infection event. **a**) healthy *D. ramea* colonies when first transferred in the aquarium facility (June 2015), **b**) colonies already highly infected by the filamentous alga invasion, **c**) *Cerithium* spp. gastropods were introduced in the aquaria to graze the algae, **d**) polyps of *D. ramea* covering again the coral skeleton. (Photos: © V. Andreou)

Hence, it was decided to place the corals in a quarantine tank while the main exhibition tank was disinfected using chemical agents (Fig. 38.26c) to remove the filamentous algae that were still present. This procedure was followed as most of the chemical agents that could be used to eliminate filamentous algae are harmful to most invertebrates and corals in particular. After completion of the disinfection procedure, corals were transferred back to the main exhibition aquarium. Since many variables may have played a role in the development of the filamentous algae, changes in the aquarium set-up were also performed in order to avoid similar incidents in the future. The original lighting system was replaced with one of a specific wave length that limits photosynthesis, in order to inhibit filamentous algae growth. Additionally, two “wave maker” pumps that simulate alternate underwater currents were installed in the aquarium and the previous UV filtration system was replaced with a larger unit that can circulate water at a higher rate. These were precautionary measures to further enhance coral health.

Despite the efforts of the technicians and the successful removal from the aquarium system of the filamentous algae and cyanobacteria, at this stage the infestation on the coral skeleton persisted and so was the tissue loss. Once the water quality was optimal and monitored regularly, the persistence of filamentous algae on the coral skeletons can be attributed to surrounding lighting. Despite the fact that the lighting unit of the aquarium hosting the corals was replaced, lighting of the adjacent aquariums and the maintenance area behind the aquarium might have provided sufficient lighting for the sustenance of the filamentous algae.

Not being able to treat coral skeleton in the same way as the aquarium (the disinfection procedure is deleterious to living organisms), it was necessary to identify the algae and bacteria (cyanobacteria) that were progressively expanding on coral skeletons. Once identified, a significant number of *Cerithium* spp. gastropods were introduced into the tank with the corals. These benthic species, which were collected from the rocky shoreline in the vicinities of the aquarium, have a specialised diet consisting of different unicellular algae, particularly diatoms, as well as biofilm forming cyanobacteria. A few days after the introduction of *Cerithium* in the tank, the basal sections and branches of the corals exhibited areas free of algae, corresponding to the areas where the gastropods had gathered and grazed-clean the skeleton without affecting the remaining live tissue (Fig. 38.26).

Because of the significant volume loss experienced by the polyps while they were retracted due to the algal infestation, it was attempted to promote recovery by optimising the coral diet. Different feeding types were tested, as well as an increase in the percentage of mysids (small size crustacean) and copepods in the diet. Both groups are common prey for Dendrophyllidae corals. This alternative diet substituted the regular one based on soft tissue without exoskeletons from other decapods and bivalve molluscs. In order to stimulate polyps’ capture reaction, fluids and micronised tissue of fresh fish with high fatty acids were added to the water in the tank before the actual feeding with the alternative diet. The polyps’ reaction to the fish compounds was positive and immediate: they were ready to capture the mysids that were given individually to each individual polyp with a syringe.

After the successful treatment following the steps mentioned before (regulation of nutrient concentration in the water, lighting, cleaning by the gastropods and a better diet more in agreement with the nature of the Dendrophyllidae species), a significant improvement in the coral colonies was observed. The size of the polyps increased and there was a progressive increase or recovery of lost tissue. At the moment of writing this there is an incipient polyp budding within a few areas of healthy tissue.

Aside from the aspects presented in this chapter regarding the importance of research in aquaria to shed light in the biology, ecology and physiology of CWCs, we would like to stress out the paramount role that exhibitions in public aquaria also have to disseminate the existence and importance of these habitats and communities, and to transmit this message to the society. The dissemination of research is still an unfinished business for many scientist, particularly for the CWC research (see Rossi and Orejas, this volume). Aquaria exhibitions play a fundamental role on this and numerous scientific institutes and public aquaria around the world are starting to contribute to this by planning “open door” days as well as allocating specific areas dedicated to deep-sea fauna.

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Some European Research Institutes and Public Aquaria with Aquaria Facilities for Maintenance and/or Experimental Work with CWCs

Cyprus

Ocean Aquarium. P.O. Box 33845, 5318 Paralimni, Cyprus

France

Sorbonne Universités, UPMC Univ Paris 06, CNRS, Laboratoire d'Ecogéochimie des Environnements Benthiques (LECOB), Observatoire Océanologique, 66650 Banyuls-sur-mer, France

Germany

Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven

GEOMAR Helmholtz Centre for Ocean Research Kiel, Wischhofstr. 1-3, 24148 Kiel, Germany

Italy

Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Napoli, Italy

Acquario di Genova, Ponte Spinola, 16128 Genova GE

DISVA, Marche Polytechnic University, Via Brecce Bianche, 60131 Ancona, Italy

Monaco

Centre Scientifique de Monaco, Equipe ecophysiologie corallienne, 8 Quai Antoine 1er, MC-98000 Principality of Monaco

Norway

Institute of Marine Research, Austevoll Research Station, 5392 Storebø, Norway

Portugal

IMAR – Institute of Marine Research, University of the Azores, Horta, Portugal & OKEANOS – Center of the University of the Azores Horta, Portugal

Spain

Acuario do Grove, Punta Moreiras, s/n, 36988 O Grove, Pontevedra

Aquarium Finisterrae, Paseo Marítimo Alcalde Francisco Vázquez, 34, 15002 A Coruña, Spain

Institut de Ciències del Mar (CSIC), Pg Maritim de la Barceloneta 37-49, 08003 Barcelona, Spain

Estación de Investigación Jaume Ferrer, La Mola, 07700 Mahón, Menorca, Illes Balears, Spain

Sweden

Department of Marine Sciences, University of Gothenburg, Sweden. Field station on Tjärnö, at the west coast of Sweden and at Kristineberg. Both facilities are run by the Sven Lovén Centre for Marine Infrastructure

The Netherlands

Aquaria facilities in the Wageningen University, Department of Aquaculture and Fisheries, Pots code 338, 6700 AH Wageningen, The Netherlands

United Kingdom

School of GeoSciences, University of Edinburgh, Grant Institute, James Hutton Road, Edinburgh EH9 3FE, UK

References

Allen JR (1998) Suspension feeding in the brittle-star *Ophiothrix fragilis*: efficiency of particle retention and implications for the use of encounter-rate models. Mar Biol 132:383–390

Allers E, Abed RM, Wehrmann LM, et al (2013) Resistance of *Lophelia pertusa* to coverage by sediment and petroleum drill cuttings. Mar Poll Bull 74:132–140

Berntsson KM, Jonsson PR, Larsson AI, et al (2004) Rejection of unsuitable substrata as a potential driver of aggregated settlement in the barnacle *Balanus improvisus*. Mar Ecol Prog Ser 275:199–210

Borneman EH, Lowrie J (2001) Advances in captive husbandry: An easily utilized reef replenishment means from the private sector? Bull Mar Sci 69:897–913

Brooke S, Järnegren J (2013) Reproductive periodicity of the scleractinian coral *Lophelia pertusa* from the Trondheim Fjord, Norway. Marine Biology 160:139–153

Brooke S, Young CM (2003) Reproductive ecology of a deep-water scleractinian coral, *Oculina varicosa*. Cont Shelf Res 23:847–858

Brooke S, Young CM (2005) Embryogenesis and larval biology of the ahermatypic scleractinian *Oculina varicosa*. Mar Biol 146:665–675

Brooke S, Young CM (2009) *In situ* measurement of survival and growth of *Lophelia pertusa* in the northern Gulf of Mexico. Mar Ecol Prog Ser 397:153–161

Brooke S, Holmes M, Young CM (2009) Effects of sediment on two morphotypes of *Lophelia pertusa* from the Gulf of Mexico. Mar Ecol Prog Ser 390:137–144

Camilli R, Reddy CM, Yoerger DR, et al (2010) Tracking hydrocarbon plume transport and biodegradation at Deepwater Horizon. Science 330:201–204. https://doi.org/10.1126/science.1195223

Carreiro-Silva M, Cerqueira T, Godinho A, et al (2014) Molecular mechanisms underlying the physiological responses of the cold-water coral *Desmophyllum dianthus* to ocean acidification. Coral Reefs 33:465–476

Chisholm JRM, Gattuso JP (1991) Validation of the alkalinity anomaly technique for investigating calcification of photosynthesis in coral reef communities. Limnol Oceanogr 36:1232–1239

Clayton TD, Byrne RH (1993) Spectrophotometric seawater pH measurements: total hydrogen ion con- centration scale calibration of m-cresol purple and at-sea results. Deep-Sea Res Part 1 Oceanogr Res Pap 40:2115–2129

Cohen AL, Holcomb M (2009) Why corals care about ocean acidification: Uncovering the mechanism. Oceanography 22:118–127

Crossland C (1987) *In situ* release of mucus and DOC-lipid from the corals *Acropora variabilis* and *Stylophora pistillata* in different light regimes. Coral Reefs 6:35–42

Davies PS (1984) The role of zooxanthellae in the nutritional energy requirements of *Pocillopora eydouxi*. Coral Reefs 2:181–186

Davies PS (1989) Short-term growth measurements of corals using an accurate buoyant weighing technique. Mar Biol 101:389–395

de Goeij JM, Moodley L, Houtekamer M, et al (2008) Tracing ^{13}C-enriched dissolved and particulate organic carbon in the bacteria-containing coral reef sponge *Halisarca caerulea*: Evidence for DOM-feeding. Limnol Oceanogr 53:1376–1386

de Goeij JM, van Oevelen D, Vermeij MJA, et al (2013) Surviving in a marine desert: The sponge loop retains resources within coral reefs. Science 342:108–110

DeLeo DM, Ruiz-Ramos DV, Baums IB, et al (2016) Response of deep-water corals to oil and chemical dispersant exposure. Deep-Sea Res Part 2 Top Stud Oceanogr 129:137–147

Dodds LA, Roberts JM, Taylor AC, et al (2007) Metabolic tolerance of the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature and dissolved oxygen change. J Exp Mar Biol Ecol 349:205–214

Dodds LA, Black KD, Orr H, et al (2009) Lipid biomarkers reveal geographical differences in food supply to the cold-water coral *Lophelia pertusa* (Scleractinia). Mar Ecol Prog Ser 397:113–124

Fisher CR, Hsing P-Y, Kaiser CL, et al (2014) Footprint of Deepwater Horizon blowout impact to deep-water coral communities. Proc Natl Acad Sci 111: 11744–11749. https://doi.org/10.1073/pnas.1403492111

Fox AD, Henry LA, Corne DW, et al (2016) Sensitivity of marine protected area network connectivity to atmospheric variability. Roy Soc Open Sci 3:160494

Gass SE, Roberts JM (2006) The occurrence of the cold-water coral *Lophelia pertusa* (Scleractinia) on oil and gas platforms in the North Sea: Colony growth, recruitment and environmental controls on distribution. Mar Poll Bull 52:549–559

Georgian SE, Dupont S, Kurman M, et al (2016a) Biogeographic variability in the physiological response of the cold-water coral *Lophelia pertusa* to ocean acidification. Mar Ecol 37:1345–1359. https://doi.org/10.1111/maec.12373

Georgian SE, Deleo D, Durkin A, et al (2016b) Oceanographic patterns and carbonate chemistry in the vicinity of cold-water coral reefs in the Gulf of Mexico: Implications for resilience in a changing ocean. Limnol Oceanogr 61:648–665. https://doi.org/10.1002/lno.10242

Gori A, Reynaud S, Orejas C, et al (2014a) Physiological performance of the cold-water coral *Dendrophyllia cornigera* reveals its preferences for temperate environments. Coral Reefs 33:665–674

Gori A, Grover R, Orejas C, et al (2014b) Uptake of dissolved free amino acids by four cold-water coral species from the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 99:42–50

Gori A, Reynaud S, Orejas C, et al (2015) The influence of flow velocity and temperature on zooplankton capture rates by the cold-water coral *Dendrophyllia cornigera*. J Exp Mar Bio Ecol 466:92–97

Gori A, Ferrier-Pagès C, Hennige SJ, et al (2016) Physiological response of the cold-water coral *Desmophyllum dianthus* to thermal stress and ocean acidification. Peer J 4:e1606

Hennige SJ, Wicks LC, Kamenos NA, et al (2014) Short-term metabolic and growth responses of the cold-water coral *Lophelia pertusa* to ocean acidification. Deep-Sea Res Part 2 Top Stud Oceanogr 99:27–35

Hennige SJ, Wicks LC, Kamenos NA, et al (2015) Hidden impacts of ocean acidification to live and dead coral framework. Proc R Soc B 282:20150990

Highsmith RC (1982) Reproduction by fragmentation in corals. Mar Ecol Prog Ser 7:207–226

Holdway DA (2002) The acute and chronic effects of wastes associated with offshore oil and gas production on temperate and tropical marine ecological processes. Mar Poll Bull 44:185–203

Hunter T (1989) Suspension feeding in oscillating flow – the effect of colony morphology and flow regime on plankton capture by the hydroid *Obelia longissima*. Biol Bull 176:41–49

Järnegren J, Brooke S, Jensen H (2017) Effects of drill cuttings on larvae of the cold-water coral *Lophelia pertusa*. Deep-Sea Res Part 2 Top Stud Oceanogr 137:454–462

Jokiel PL, Maragos JE, Franzisket L (1978) Coral growth: buoyant weight technique. In: Coral reefs: research methods. UNESCO, Paris, pp 529–541

Jonsson PR, Johansson M (1997) Swimming behaviour, patch exploitation and dispersal capacity of a marine benthic ciliate in flume flow. J Exp Mar Biol Ecol 215:135–153

Kaniewska P, Campbell PR, Kline DI, et al (2012) Major cellular and physiological impacts of ocean acidification on a reef building coral. PLoS One 7:e34659

Kooijman S (1986) Energy budgets can explain body size relations. J Theor Biol 121:269–282

Kurman MD, Gomez CE, Georgian SE, et al (2017) Intra-specific variation reveals potential for adaptation to ocean acidification in a cold-water coral from the Gulf of Mexico. Front Mar Sci 4:111. https://doi.org/10.3389/fmars.2017.00111

Larsson AI, Jonsson PR (2006) Barnacle larvae actively select flow environments supporting post-settlement growth and survival. Ecology 87:1960–1966

Larsson AI, Purser A (2011) Sedimentation on the cold-water coral *Lophelia pertusa*: Cleaning efficiency from natural sediments and drill cuttings. Mar Poll Bull 62:1159–1168

Larsson AI, Lundälv T, van Oevelen D (2013a) Skeletal growth, respiration rate and fatty acid composition in the cold-water coral *Lophelia pertusa* under varying food conditions. Mar Ecol Prog Ser 483:169–184

Larsson AI, van Oevelen D, Purser A, et al (2013b) Tolerance to long-term exposure of suspended benthic sediments and drill cuttings in the cold-water coral *Lophelia pertusa*. Mar Poll Bull 70:176–188

Larsson AI, Järnegren J, Strömberg SM, et al (2014) Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*. PloS One 9:e102222

Lartaud F, Pareige S, de Rafelis M, et al (2013) A new approach for assessing cold-water coral growth *in situ* using fluorescent calcein staining. Aquat Living Resour 26:187–196

Lartaud F, Pareige S, de Rafelis M, et al (2014) Temporal changes in the growth of two Mediterranean cold-water coral species, *in situ* and in aquaria. Deep-Sea Res Part 2 Top Stud Oceanogr 99:64–70

Lartaud F, Meistertzheim AL, Peru E, et al (2017a) *In situ* growth experiments of reef-building cold-water corals: the good, the bad and the ugly. Deep-Sea Res Part 1 Oceanogr Res Pap 121:70–78

Lartaud F, Galli G, Raza A, et al (2017b) Growth patterns in long-lived coral species. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forest: The Ecology of Benthic Biodiversity Hotspots. Springer, Cham, pp 595–626

Lasker HR (1988) The incidence and rate of vegetative propagation among coral reef alcyonarians. In: Proceedings of the 6th international coral reef symposium, vol 2, Australia, pp 763–768

Leal MC, Ferrier-Pagès C, Petersen D, et al (2016) Coral aquaculture: applying scientific knowledge to ex situ production. Rev Aquacult 8:136–153

Levington J (1972) Stability and trophic structure in deposit feeding and suspension feeding communities. Am Nat 106:472–486

Lundälv T (2003) Kartläggning av marina habitat i Yttre Hvaler, nordöstra Skagerrak. En pilotstudie. Rapport till Fylkesmannen i Østfold och Nordiska Ministerrådet, 16 p

Lunden JJ, Georgian SE, Cordes EE (2013) Aragonite saturation states at cold-water coral reefs structured by *Lophelia pertusa* in the northern Gulf of Mexico. Limnol Oceanogr 58:354–362. https://doi.org/10.4319/lo.2013.58.1.0354

Lunden JJ, Turner JM, Mcnicholl CG, et al (2014a) Design, development, and implementation of recirculating aquaria for maintenance and experimentation of deep-sea corals and associated fauna. Limnol Oceanogr Methods 12:363–372. https://doi.org/10.4319/lom.2014.12.363

Lunden JJ, McNicholl CG, Sears CR, et al (2014b) Acute survivorship of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico under acidification, warming, and deoxygenation. Front Mar Sci 1:1–12. https://doi.org/10.3389/fmars.2014.00078

Maier C (2008) High recovery potential of the cold-water coral *Lophelia pertusa*. Coral Reefs 27:821–821

Maier C, Soest Rv, Hühnerbach V, et al (2006) Biology and ecosystem functioning of cold water coral bioherms at Mingulay, NE Atlantic. Cruise Report R/V Pelagia, cruise 64PE250, 63 pp. http://melia.nioz.nl/public/dmg/rpt/crs/64pe250.pdf

Maier C, Weinbauer MG, Soest RV, et al (2007) Sponge diversity in cold water coral bioherms and calcification rate and prokaryote-coral associations of *Lophelia pertusa* (Skagerrak, North Sea). Cruise Report R/V Pelagia, cruise 64PE263, 30 pp. http://melia.nioz.nl/public/dmg/rpt/crs/64pe263.pdf

Maier C, Hegeman J, Weinbauer MG, et al (2009) Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. Biogeosciences 6:1671–1680

Maier C, Kluijver A, Agis M, et al (2011) Dynamics of nutrients, total organic carbon, prokaryotes and viruses in onboard incubations of cold-water corals. Biogeosciences 8:2609–2620

Maier C, Watremez P, Taviani M, et al (2012) Calcification rates and the effect of ocean acidification on Mediterranean cold-water corals. Proc R Soc B 279:1716–1723

Maier C, Bils F, Weinbauer MG, et al (2013a) Respiration of Mediterranean cold-water corals is not affected by ocean acidification as projected for the end of the century. Biogeosciences 10:5671–5680

Maier C, Schubert A, Sanchez MMB, et al (2013b) End of the century pCO_2 levels do not impact calcification in Mediterranean cold-water corals. PloS One 8:e62655

Maier C, Popp P, Sollfrank N, et al (2016) Effects of elevated pCO_2 and feeding on net calcification and energy budget of the Mediterranean cold-water coral *Madrepora oculata*. J Exp Biol 219:3208–3217

Maier S, Kutti T, Bannister RJ, van Breugel P, van Rijswijk P, van Oevelen D (in press) Survival under conditions of variable food availability: resource utilization and storage in the cold-water coral *Lophelia pertusa*. Limnol Oceanogr. https://doi.org/10.1002/lno.11142

Martin P, Goodkin NF, Stewart JA, et al (2016) Deep-sea coral $d^{13}C$: A tool to reconstruct the difference between seawater pH and $d^{11}B$-derived calcification site pH. Geophy Res Lett 43:299–308

McCulloch M, Trotter J, Montagna P, et al (2012) Resilience of cold-water scleractinian corals to ocean acidification: boron isotopic systematics of pH and saturation state up-regulation. Geochim Cosmochim Acta 87:21–34

Meistertzheim AL, Lartaud F, Arnaud-Haond S, et al (2016) Patterns of bacteria- host associations suggest different ecological strategies between two reef building cold-water coral species. Deep-Sea Res Part 1 Oceanogr Res Pap 114:12–22

Middelburg JJ (2014) Stable isotopes dissect aquatic food webs from the top to the bottom. Biogeosciences 11:2357–2371

Middelburg JJ, Barranguet C, Boschker HTS, et al (2000) The fate of intertidal microphytobenthos carbon: An *in situ* ^{13}C-labeling study. Limnol Oceanogr 45:1224–1234

Middelburg JJ, Mueller CE, Veuger B, et al (2015) Discovery of symbiotic nitrogen fixation and chemoautotrophy in cold-water corals. Sci Rep 5:9. https://doi.org/10.1038/srep17962

Miller K (1996) Piecing together the reproductive habits of New Zealand's endemic black corals. Water Atmos 4:18–19

Moeller EF (2005) Sloppy feeding in marine copepods: Prey-size-dependent production of dissolved organic carbon. J Plankton Res 27:27–35

Moodley L, Boschker HTS, Middelburg JJ, et al (2000) Ecological significance of benthic foraminifera: ^{13}C labelling experiments. Mar Ecol Prog Ser 202:289–295

Mortensen PB (2001) Aquarium observations on the deep-water coral *Lophelia pertusa* (L., 1758) (scleractinia) and selected associated invertebrates. Ophelia 54:83–104

Mortensen PB, Rapp HT (1998) Oxygen and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia pertusa* (L) (Anthoza, Scleractinia) implications for determination of linear extension rates. Sarsia 83:433–446

Movilla J, Gori A, Calvo E, et al (2014a) Resistance of two Mediterranean cold-water coral species to low-pH conditions. Water 6:59–67

Movilla J, Orejas C, Calvo E, et al (2014b) Differential response of two Mediterranean cold-water coral species to ocean acidification. Coral Reefs 33:675–686

Moya A, Huisman L, Ball EE, et al (2012) Whole transcriptome analysis of the coral *Acropora millepora* reveals complex responses to CO_2-driven acidification during the initiation of calcification. Mol Ecol 21:2440–2454

Mueller CE, Lundälv T, Middelburg JJ, et al (2013) The symbiosis between *Lophelia pertusa* and *Eunice norvegica* stimulates coral calcification and worm assimilation. PLoS One 8:1–9

Mueller CE, Larsson AI, Veuger B, et al (2014) Opportunistic feeding on various organic food sources by the cold-water coral *Lophelia pertusa*. Biogeosciences 11:123–133

Naumann MS, Orejas C, Wild C, et al (2011) First evidence for zooplankton feeding sustaining key physiological processes in a scleractinian cold-water coral. J Exp Biol 214:3570–3576

Naumann M, Orejas C, Ferrier-Pagès C (2013) High thermal tolerance of two Mediterranean cold-water coral species maintained in aquaria. Coral Reefs:1–6

Naumann MS, Orejas C, Ferrier-Pagès C (2014) Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. Deep-Sea Res Part 2 Top Stud Oceanogr 99:36–41

Olariaga A, Gori A, Orejas C, Gili JM (2009) Development of an autonomous Aquarium system for maintaining deep corals. Oceanography 22:44–45

Orejas C, Gili JM, López-González PJ, et al (2001) Feeding strategies and diet composition of four Antarctic cnidarian species. Pol Biol 24:620–627

Orejas C, Gili JM, Arntz W (2003) Role of small-plankton communities in the diet of two Antarctic octocorals (*Primnoisis antarctica* and *Primnoella* sp.). Mar Ecol Prog Ser 250:105–116

Orejas C, Gori A, Gili JM (2008) Growth rates of live *Lophelia pertusa* and *Madrepora oculata* from the Mediterranean Sea maintained in aquaria. Coral Reefs 27:255

Orejas C, Ferrier-Pagès C, Reynaud S, et al (2011) Long-term growth rates of four Mediterranean cold-water coral species maintained in aquaria. Mar Ecol Prog Ser 429:57–65

Orejas C, Gori A, Rad-Menéndez C, et al (2016) The effect of flow speed and food size on the capture efficiency and feeding behaviour of the cold-water coral *Lophelia pertusa*. J Exp Mar Bio Ecol 481:34–40

Orejas C, Gori A, Jiménez C, et al (2017) First *in situ* documentation of a population of the coral *Dendrophyllia ramea* off Cyprus (Levantine Sea) and evidence of human impacts. Galaxea J Coral Reef Studies 19:15–16

Perez FF, Fraga F (1987) A precise and rapid analytical procedure for alkalinity determination. Mar Chem 21:169–182

Pérez FF, Rios AF, Rellán T, et al (2000) Improvements in a fast potentiometric seawater alkalinity determination. Ciencias Mar 26:463–478

Pitt KA, Welsh DT, Condon RH (2009) Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. Hydrobiologia 616:133–149

Purser A, Larsson AI, Thomsen L, et al (2010) The influence of flow velocity and food concentration on *Lophelia pertusa* (Scleractinia) zooplankton capture rates. J Exp Mar Bio Ecol 395:55–62

Reynaud S, Leclercq N, Romaine-Lioud S, et al (2003) Interacting effects of CO_2 partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. Glob Chang Biol 9:1660–1668

Richter C, Wunsch M, Rasheed M, et al (2001) Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. Nature 413:726–730

Rix L, Naumann MS, de Goeij JM, et al (2016) Coral mucus fuels the sponge loop in warm- and cold-water coral reef ecosystems. Sci Rep 6:18715 https://doi. org/10.1038/srep187151

Robbins LL, Hansen ME, Kleypas JA, et al (2010) CO2calc – a user-friendly seawater carbon calculator for Windows, Max OS X, and iOS (iPhone): US Geological Survey Open-File Report. 2010–1280, 17 pp

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Roberts JM, Murray F, Anagnostou E, et al (2016) Cold-water corals in an era of rapid global change: are these the deep ocean's most vulnerable ecosystems? In Goffredo S, Dubinsky Z (eds) The Cnidaria, past, present and future. Springer, Cham, pp 53–606

Roik A, Rothig T, Roder C, et al (2015) Captive rearing of the deep-sea coral *Eguchipsammia fistula* from the Red Sea demonstrates remarkable physiological plasticity. PeerJ 3:e734

Sampaio Í, Braga-Henriques A, Pham C, et al (2012) Cold-water corals landed by bottom longline fisheries in the Azores (north eastern Atlantic). J Mar Biol Assoc UK 92:1547–1555

Schöne BR (2008) The curse of physiology-challenges and opportunities in the interpretation of geochemical data from mollusk shells. Geo-Mar Lett 28:269–285

Sebens KP, Witting J, Helmuth B (1997) Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). J Exp Mar Biol Ecol 211:1–28

Shelton GAB (1980) *Lophelia pertusa* (L.): Electrical conduction and behaviour in a deep-water coral. J Mar Biol Ass UK 60:517–528

Strathmann MF (1987) Reproduction and development of marine invertebrates of the northern Pacific coast: data and methods for the study of eggs, embryos, and larvae. University of Washington Press, Seattle, 670 p

Strömberg SM (2016) Early life history of the cold-water coral *Lophelia pertusa* – with implications for dispersal. Thesis. University of Gothenburg, 53 pp. https://gupea.ub.gu.se/handle/2077/42046

Strömberg SM, Larsson AI (2017) Larval behavior and longevity in the cold-water coral *Lophelia pertusa* indicate potential for long-distance dispersal. Front Marine Sci 4(411). https://doi.org/10.3389/fmars.2017.00411

Strömberg SM, Östman C (2016) The cnidome and internal morphology of *Lophelia pertusa* (Linnaeus, 1758) (Cnidaria, Anthozoa). Acta Zool 92:191–213

Tambutté E, Allemand D, Bourge I, et al (1995) An improved ^{45}Ca protocol for investigating physiological mechanisms in coral calcification. Mar Biol 122:453–459

Taviani M, Angeletti L, Antolini B, et al (2011) Geo-biology of Mediterranean deep-water coral ecosystems. In: Brugnoli E, Cavarretta G, et al (eds) Marine research at CNR, Dipartimento Terra e Ambiente. Consiglio Nazionale delle Ricerche, Roma, pp 705–720

Tengberg A, Almroth E, Hall P (2003) Resuspension and its effects on organic carbon recycling and nutrient exchange in coastal sediments: *in situ* measurements using new experimental technology. J Exp Mar Biol Ecol 285–286:119–142

Tengberg A, Stahl H, Gust G, et al (2004) Intercalibration of benthic flux chambers I. Accuracy of flux measurements and influence of chamber hydrodynamics. Progr Oceanogr 60:1–28

Tsounis G, Orejas C, Reynaud S, et al (2010) Prey-capture rates in four Mediterranean cold water corals. Mar Ecol Prog Ser 398:149–155

Twan WH, Hwang JS, Lee YH, et al (2006) Hormones and reproduction in scleractinian corals. Comp Bioch Physiol Part A 144:247–253

van Duyl F, Duineveld G (2005) Biodiversity, ecosystem functioning and food web complexity of deep water coral reefs in the NE Atlantic (Rockall Bank and Porcupine Bank). Cruise report, R/V Pelagia, cruise 64PE238, 96 pp. http://www.nioznl/public/dmg/rpt/crs/64pe238pdf

van Duyl FC, Hegeman J, Hoogstraten A, et al (2008) Dissolved carbon fixation by sponge-microbe consortia of deep water coral mounds in the northeastern Atlantic Ocean. Mar Ecol Prog Ser 358:137–150

van Oevelen D, Mueller CE, Lundalv T, et al (2016) Food selectivity and processing by the cold-water coral *Lophelia pertusa*. Biogeosciences 13:5789–5798

Vidal-Dupiol J, Zoccola D, Tambutté E, et al (2013) Genes related to ion-transport and energy production are upregulated in response to CO_2-driven pH decrease in corals:new insights from transcriptome analysis. PLoS One 8:e58652

Weinbauer M, Ogier J, Maier C (2012) Microbial abundance in the coelenteron and mucus of the cold-water coral *Lophelia pertusa* and in bottom water of the reef environment. Aquat Biol 16:209–216

White HK, Hsing P-Y, Cho W, et al (2012) Impact of the Deepwater Horizon oil spill on a deep-water coral community in the Gulf of Mexico. Proc Nat Acad Sci 109:20303–20308

Wijgerde T, Spijkers P, Karruppannan E, et al (2012) Water flow affects zooplankton feeding by the scleractinian coral *Galaxea fascicularison* a polyp and colony level. J Mar Biol 2012:1–7

Wild C, Mayr C, Wehrmann L, et al (2008) Organic matter release by cold water corals and its implication for fauna-microbe interaction. Mar Ecol Prog Ser 372:67–75

Zetsche EM, Baussant T, Meysman FJR, et al (2016) Direct visualization of mucus production by the cold-water coral *Lophelia pertusa* with digital holographic microscopy. PLoS One 11:1–17

Cross References

Lartaud F, Mouchi V, Chapron L, et al (this volume) Growth patterns of Mediterranean calcifying cold-water corals

Maier C, Weinbauer MG, Gattuso JP (this volume) Fate of Mediterranean scleractinian cold-water corals as a result of global climate change. A synthesis

Montagna P, Taviani M (this volume) Mediterranean cold-water corals as paleoclimate archives

Movilla J (this volume) A case study: variability in the calcification response of Mediterranean cold-water corals to ocean acidification

Reynaud S, Ferrier-Pagès C (this volume) Biology and ecophysiology of Mediterranean cold-water corals

Rossi S, Orejas C (this volume) Approaching cold-water corals to the society: novel ways to transfer knowledge

39

Drop Chapter Approaching Cold-Water Corals to the Society: Novel Ways to Transfer Knowledge

Sergio Rossi and Covadonga Orejas

Abstract

Outreach is fundamental to disseminate scientific knowledge and approach the general public. The cold-water coral ecosystems are not an exception. During the last 15 years many efforts have been made to make more familiar these complex ecosystems to the society. Technology (which allow the possibility to reach deepest locations) but also the engagement of scientists made this approach possible. In this short contribution we highlight several ways to promote the knowledge and the sensitisation on these fragile deep water ecosystems, showing previous experiences and discussing some ways to effectively transfer the information needed to protect and manage these fragile ecosystems.

Keywords

Scientific knowledge · Dissemination · Cold-water corals · Mediterranean · Outreach · General public · Ocean literacy

The Discovery of Cold-Water Corals to the Society

Until the middle of last century almost no one (but see the old work by Pontoppidan 1755) was talking about cold-water corals (CWC), and indeed the general image of the deep-sea was a vast underwater desert. CWC ecosystems have been one of the most neglected ecosystems on earth, being its functioning and role unknown for decades. For most people, the biodiversity, complexity, biomass and the life explosion in the surroundings of these live three dimensional structures was unexpected; although CWC are possibly one of the more widespread ecosystems of the world, comparable in distribution and biomass to shallow coral reefs (Roberts et al. 2006). Only in the last three decades the scientific research field on CWC started to be relevant. The attention paid to these communities was associated from the beginning to the fact these fragile ecosystems are being deeply transformed by humans and these changes are taking place faster than the proper identification and mapping of these ecosystems (Hinz 2017). Indeed, the animal forests living on the deep (formed by scleractinians, gorgonians, sponges, bryozoans, etc.), are being damaged and sometimes completely devastated at a rhythm that we, scientist, cannot overtake with our surveys and studies (Koslow et al. 2001; Rossi 2013). The direct and powerful actions of scientific outreach opened a window to the society, allowing a better interpretation of the role and functioning of CWC, offering in an easy way basic information, fundamental for undertake a sustainable management and conservation for the present and for the future.

Some Examples on Cold-Water Coral Scientific Outreach

During the last decade, the number of outreach outputs on CWC has grown exponentially (Fig. 39.1). Different research groups made a huge effort to make available visual and "easy to manage" information for the general public. In Alaska, Canada and the West Coast of the United States for example, pioneering institutions made an important attempt to widespread images and information through different actions. In

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Fig. 39.1 Different dissemination materials of the Cold-water coral (CWC) ecosystems. (**a**) brochure published by OCEANA to disseminate the need of protection for the Mediterranean CWCs, (credits: © OCEANA) (**b**) the web page www.lophelia.org, which aim to disseminate scientific knowledge, news and provide education material about CWCs (credits: © lophelia.org), (**c**) cover of the publication "Cold-water corals- Out of sight not longer out of mind" (UNEP), this was one of the first publications to disseminate the basic knowledge on the CWC communities, (credits: © UNEP) (**d**) Model of a scientific submarine constructed by the scientist from the ICM-CSIC (Credits: © Project "El Mar a Fondo", www.elmarafondo.com)

Alaska, the MESA program promoted by the NOAA (e.g. https://www.afsc.noaa.gov/ABL/MESA/mesa_me_cor.php) made visible their results about the impacts on CWCs in this area, and in Canada also the government made a direct effort to make more visual the existence and the threats to CWC (e.g. http://science.gc.ca/eic/site/063.nsf/eng/h_EE39B64D.html). The Monterrey Bay Aquarium was one of the first institutions to make an exhibition of sessile and mobile species of the Monterrey submarine canyon, adapting aquaria to the deep-sea species (Sims 1998), being actually very successful (Sims pers. comm.). The positive response of the public encourages other aquaria in Europe to follow the same example (Laterveer et al. 2008).

In some cases, dynamic internet blogs in which people could directly ask basic questions about the deep-sea communities were also very successful. For example, the rapid changes that polar areas experience as a consequence of climate change, together with the possible expansion of oil exploitation in these areas, are problems which have been quickly disseminated thanks to such blogs, which have been essential to contribute to the sensitisation of local and non-local people toward the conservation of these deep communities, which became very urgent. A clear example is the Arctic Sea Ice Forum (https://forum.arctic-sea-ice.net/) where posts of different specialist and non-specialists show different views in different formats about the rapid changes in the Arctic areas. A similar strategy (blogs and outreach papers) was also recently used for the dissemination of the Mediterranean CWC in the INDEMARES Life + project (http://icmdivulga.icm.csic.es/) and the CYCLAMEN project (http://cyclamen.cyi.ac.cy/), explaining the threats and the recent discover of some of these CWC communities (see Gori et al., this volume; Orejas et al., this volume) as well as their relevance to the general public. Also within

INDEMARES it is worthy to mention the very nice (and very successful) initiative promoting the vision (with a real size model) of a scientific submarine. In this project, people could get inside this submersible and visualise underwater videos recorded on CWC communities from the Mediterranean (Fig. 39.1d).

The effort made by scientists has been the key to make visible the problems and the conservation initiatives to maintain the CWC ecosystems. Former European projects as ACES, HERMES, HERMIONE or CORALFISH, among others, were fundamental to increase the knowledge on these ecosystems and in some cases also for the declaration of protected areas beyond the coastal zones. These "pioneer" initiatives working in deep-sea areas, were an important basis for current European projects such as, for instance, ATLAS and SPONGES. The European large projects are deeply committed contributing to enlarge the number of mapped areas in the deep-sea as well as providing the know-how on different aspects of the biology and ecology of these fragile ecosystems. All these efforts have been translated in updated and fully informative web-pages in which scientific information, but also outreach and new ideas are presented including a high visual and aesthetic component (e.g. www.lophelia.org/, Fig. 39.1b). In the United States, there are also many and very good examples of outreach programs. For instance the NOAA used also a good informative vector (reports but also easy to visualise web pages) that helped the general public to understand not only the CWC of US waters but also the functioning and potential/current threats derived from different anthropogenic impacts (Lumsden et al. 2007). For instance the inputs of NOAA scientists in the web pages (e.g. http://ocean.si.edu/ocean-news/deep-sea-corals-noaa-education-plans-activities) are a valuable information source for conservation organisations as well as for other research institutes (https://blog.marine-conservation.org/2017/05/the-hunt-for-a-super-coral-can-cold-water-corals-adapt-to-ocean-acidification.html).

YouTube has become one of the probably most powerful tools to reach the general public, and especially to target young people. The implementation of videos including very short (2–4 min) stories contribute to "put in the map" the presence, biodiversity and fragility of these systems. Frequently scientists are reluctant in using "funny" and visual tools to show their findings, since they are concerned that these activities might trivialise the scientific results. However, this step has become essential to reach many people who are interested in to learn but are used to obtain information through "fast channels". Further the use of other ways to transmit knowledge, as art, is a powerful tool which works not at the level of "facts" but at the "emotional" level. Humans are sensible to beauty and the use of other channels needs to be further explored. A recent dissemination project called Ways of the Waves (WoW) explores the visual and artistic way as a new manner to transfer knowledge (Fig. 39.2, https://medwavesblog.wordpress.com/wow/).

Non Governmental Organisations (NGOs) like Greenpeace, OCEANA or the World Wildlife Found (WWF) are very active disseminating the scientific knowledge on CWC communities. They made an excellent work showing the impacts of the trawlers in these seafloor communities, giving the chance to the people to see what we cannot (and sometimes we do not want…) see. These actions carried out by NGO's which implies the display of fantastic videos and photos showing the beauty of the corals which act as architects of these deep-sea communities are very effective tools to make people aware on the existence of these communities and to sensitise for their protection. Further quite a lot of the dissemination activities to present the CWCs to the society are a join action between scientist and NGOs, as it can be seen in pioneer documents as the "Cold-water coral reef. Out of sight – no longer out of mind" (Fig. 39.1), which was a collaborative work between a large group of scientists, governmental agencies and NGOs (Freiwald et al. 2004).

Contributing to increase the relevance and impact of the outreach actions is an important task which is being taken seriously by many CWC researchers as well as by governmental organisations and NGOs. We present here two cases which exemplify different way to act and present to the general public some of the threats that put the CWC ecosystems in risk. The first case we present here deal with the effects of bottom trawling in these communities, and the second one with the effects of oil exploitation in the oceans.

Deep-sea fisheries industry has grown almost exponentially during the last two decades (FAO 2016), especially in the bottom trawling sector. Sound scientific background produced by different universities and research institutes as well as surveys and explorations conducted by NGOs have been playing over the years an equally fundamental role presenting the CWC and its paramount role as ecosystem engineers to the society. These actions have highly influenced governments and institutions of a high political level, as it is the case of the EU parliamentary which undertook actions towards trawling ban at the beginning of this decade. Indeed after a long debate, the EU supported the banning of bottom trawling beyond 800 meters depth in most of the EU waters (MEPs ban deep-sea fishing below 800 meters in the North-East Atlantic, December 2016). This achievement has been the result of a long process which started in 2005 and reaches the first agreements in 2011 for depths below 1000 meters; however this is still the allowed limit for bottom trawling in Mediterranean waters, which means that many species are still under threat as confirmed in the recent publication by the IUCN presenting the current status of the Mediterranean anthozoans (Otero et al. 2017; see also Otero and Marin, this volume). Especially the bamboo coral

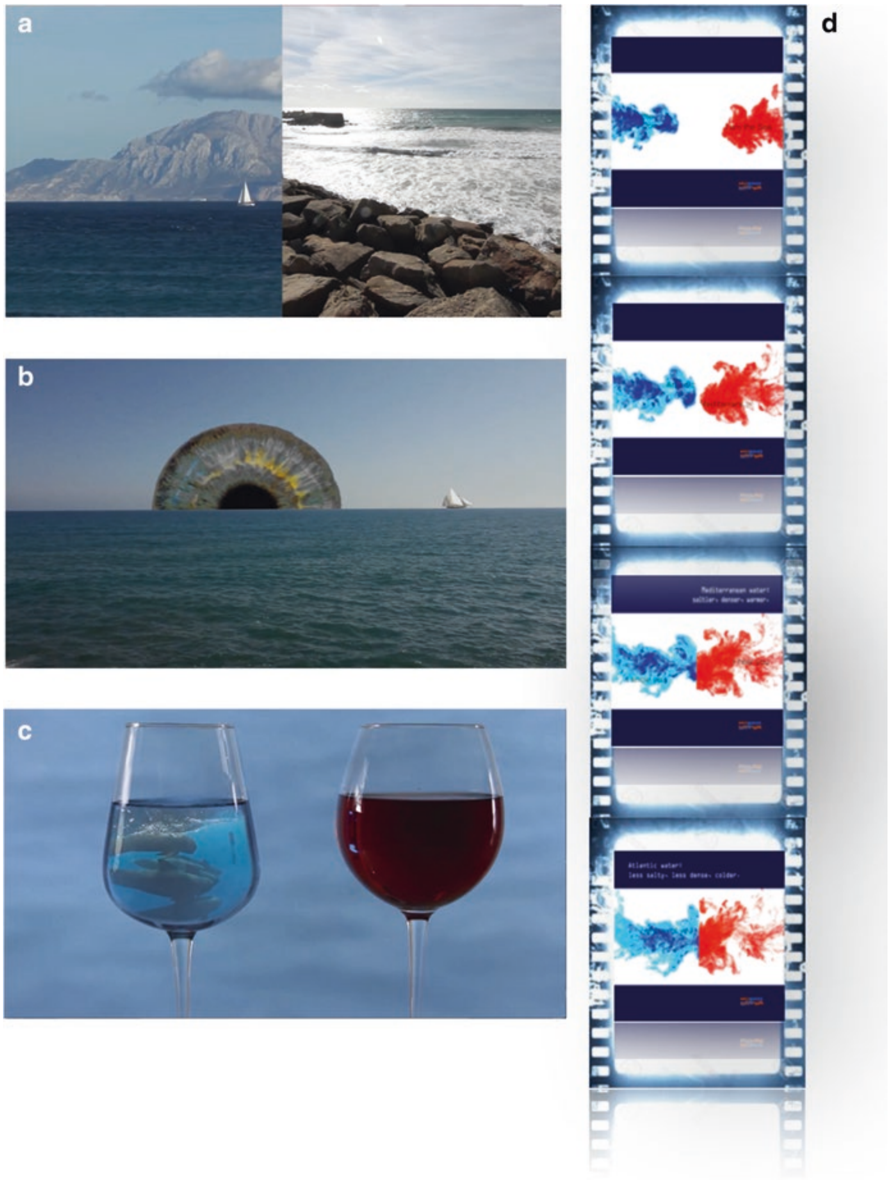

Fig. 39.2 Outreach-artistic project to disseminate scientific knowledge gain during the scientific cruise MEDWAVES, conducted in frame of the European project ATLAS. Images (**a**–**c**) correspond to fotograms from different video clips which can be visualised under https://medwavesblog.wordpress.com/wow/, (**d**) correspond to a series photograms from one of the video clips which represent in an artistic and poetic way the relation between the water masses from the Mediterranean and the Atlantic. (Credits: Images by © Martha Zein and © José Luis Matoso)

Isidella elongata has been categorises as "critically endangered" (www.iucnredlist.org/initiatives/mediterranean), the species has also been recently included in the Annex II of Barcelona Convention. The depth limit for bottom trawling has been changed and moved to shallower waters over the years. In these negotiations, there has been a clear influence of the sound scientific evidence of mismanagement in deep areas, as well as by the dissemination made by several NGOs on the consequences of this mismanagement of the deep-sea ecosystems (Aguilar et al. 2017). The ban of bottom trawling at certain depths and in certain areas is an excellent example of how the synergy of different actions from different groups and at different levels contribute to make people aware about the importance of an ecosystem as the one dominated by CWCs, making evident the threats which endanger these communities and the need of mitigation actions (Figs. 39.3 and 39.4).

Exploration of the deep-sea floor to extract oil and minerals is a potential threat for CWC (Clarke et al. 2010) which is currently taking place in many locations, included the Mediterranean, and it would not stop during the next years (Murton 2013; see also Otero and Marin, this volume). Dissemination of the consequences of oil spills in the ocean has been a fundamental tool to show to the public the consequences of accidents as the one originated by the "Deep Sea Horizon oil spill" in the Gulf of Mexico (GoM). Beside the tragic human casualties, a strong negative impact of this oil spill on the coast and the deep-sea communities was documented (Prouty et al. 2016). The already available information on the CWC communities of the GoM thanks to

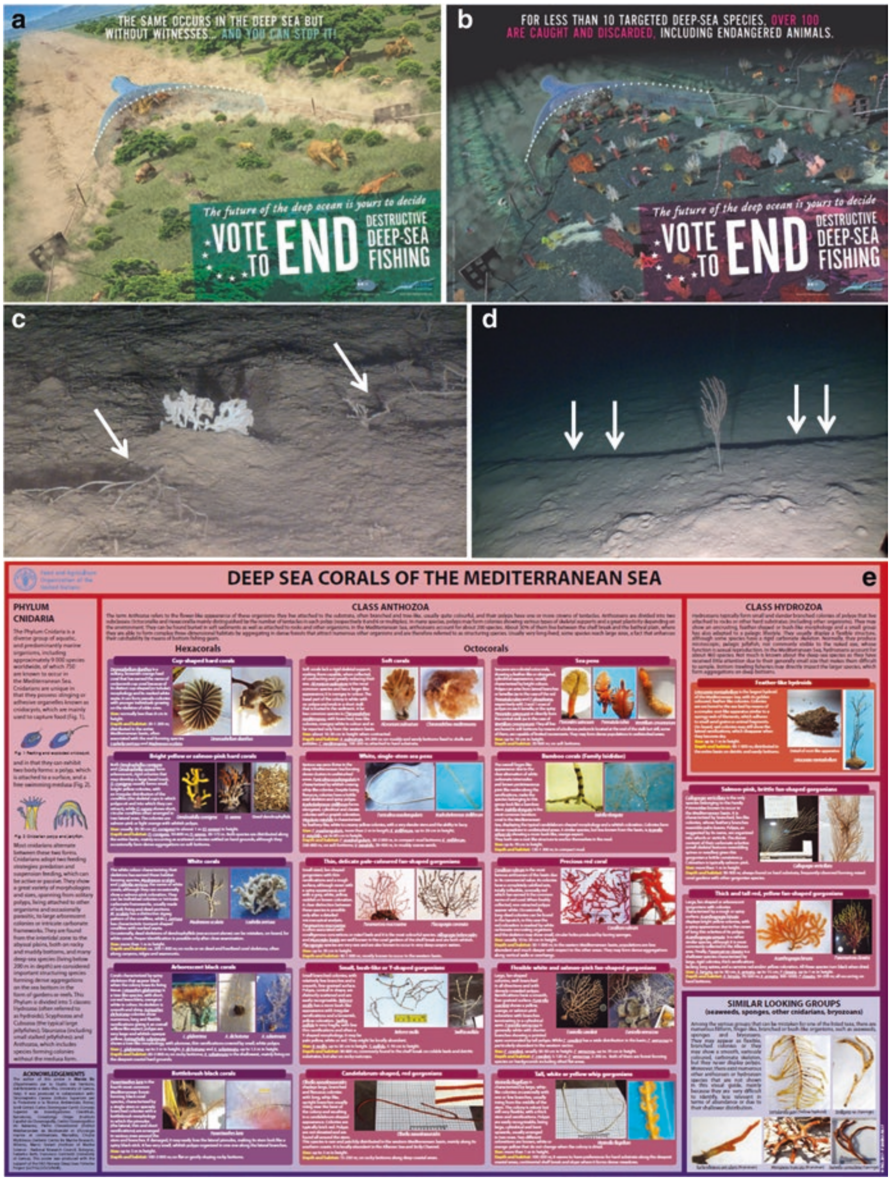

Fig. 39.3 Different ways to disseminate the effects of bottom trawling in the seafloor. (**a**, **b**) campaign by "Bloom association" to promote the ban of bottom trawling (credits: © Bloom); (**c**, **d**) images from the Mediterranean Sea where the effects of bottom trawling in the bamboo coral *Isidella elongata* populations can be observed, white arrows show in image "c" colonies dislodged from the substrate and image "d" the path of a trawl mark an a single *I. elongata* which survive (credits: © OCEANA); (**e**) poster published by FAO to help fishermen and scientist to recognise the most frequent CWC species from the Mediterranean. The poster is freely available by FAO webpage (credits: © FAO)

previous published investigations (e.g. Brooke and Schroeder 2007; Cordes et al. 2008; Brooke and Ross 2013) and the currently available technology to revisit the deep benthic ecosystems of the GoM, allowed to obtain precise information of the catastrophic scenario and obtain visual documentation of it which was obviously the best "weapon" to engage stakeholders, government and society to undertake immediate research activities and mitigation actions. The already existent background information on these CWC ecosystems was essential to obtain the quick response from the society and the sensitisation of the people of the area (see for example www.lophelia.org/latest/338-dwh, and http://response.restoration.noaa.gov/about/media/bottom-gulf-mexico-corals-and-diversity-suffered-after-deepwater-horizon-oil-spill.html).

Some Thoughts About Scientific Outreach

The lack of awareness by the general public on the deep-sea ecosystems in general and CWC ecosystems in particular is due to the remoteness of these ecosystems which have been elusive to most people, more than any other ecosystems of our planet. It cannot be forgotten that the technology needed to get access to these deep-sea areas is expensive and accessible just for a small groups of researchers and some NGOs, making difficult to have a "feeling", for these areas as a citizen. Nevertheless, these aspects cannot be the only reason for being not well informed...a common problem is also the lack of interest from many people and the failure from the scientist to transfer in a proper way the knowledge.

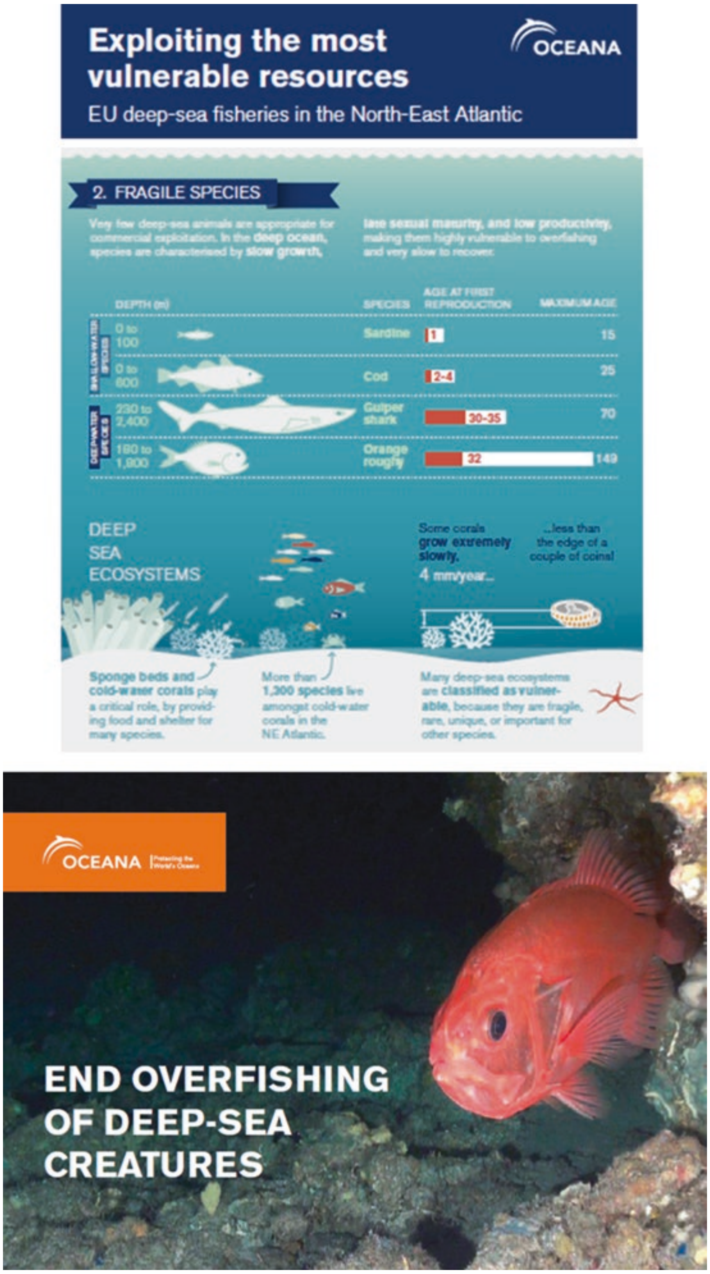

Fig. 39.4 Two different campaigns to disseminate the effects on the ecosystems of the exploitation of the deep-sea species. (Credits: © OCEANA)

This lack of interest is frequent regarding many scientific fields. It is not easy to find the "magic formula" to do good and high quality dissemination, creative and precise at the same time, but nowadays is evident, as demonstrate by the two specific cases we presented before, that public awareness is essential. A deep knowledge of the current status of the CWC communities as well as the problems and threats they are experienced today is necessary to develop outreach strategies that can reach stakeholders and policy makers, but also the citizens. Everyone should be targeted when planning outreach actions and we can identify three specific groups which required different efforts, focus, and ways to envisage outreach from our side, as scientists: (1) children and young people who are the "future society" and will need to cope with the world we are leaving them...they will need to cope with the threats to the CWC communities and they will have to develop the proper tools to solve it...all impossible without proper information; (2) those who "pay the taxes"...hence... every citizen which at the end rely on sound scientific information which will help to build their own opinion in front of the importance of these communities, their sustainable management and the associated threats and conservation problems, and (3) the policy makers which also need the scientific information but in an highly and feasible applied way which can help them to put "numbers" and "facts" to the issues, as these are the tools they can use to define management and protection strategies. There are many actions on CWC outreach targeting the first two groups: one of the pioneer and very visual, intuitive and high quality webpage for CWC dissemination: www.lophelia.org/fun-stuff, or www.earthrangers.com/wildwire/bbtw_updates/why-you-should-protect-cold-water-coral/). These kinds of initiatives are increasing at different regional levels, from the local ones to country and also European level (Helvarg 2006). Regarding dissemination activities addressing policymakers, the approach need to be necessarily different. The idea behind considering that the only possible economic and social model is continuous human growth population and expansion is based on a very "western byassed conception" of our environment (Jacques et al. 2008). At the end of the day, nothing has unlimited grow (maybe with the exception of corals?), economist will have much more to say about that, than we, simple biologists. Our perception is that the current model is destined to fail (Rossi 2019). Taking the CWC as an example, and especially in such a restricted environment as it is the Mediterranean, a system where exploitation of the oceans (e.g. high fishing effort, bottom contact fishing gears, mining and drilling) and direct indirect anthropogenic effects (e.g. presence of microplastics everywhere, global change including ocean acidification) does not have a proper management, it has no chances to survive. Consequently, it is urgent to change our mind, and contribute to change the mind of the society as CWC ecosystems are especially complex, diverse and fragile.

Scientists have to undertake actions at local and country level first, not only to make policy makers aware but also any sectors directly related to these ecosystems as for instance fisheries and oil industry. Promote the organisation of working groups and participative processes where scientists, all stakeholders, policy makers and citizens participation will enhance the sharing of knowledge, opinions, thoughts and experiences.

We believe that the final message would be that a more holistic way of thinking is needed and this is that we need to transmit. The message should be "conserve your home" as the deep-sea is just another part of it, of this planet earth that we share with our con-specifics, but also with millions of other species.

Naturalist and observers are fairly disregarded in this society where the hurry and competitiveness is an important part of our "way of thinking". The role of the naturalist and observer … as well as the role of the scientists needs maybe to be "reset". Sometimes is useful to look backwards and recover traditional scientific methods as long-term observations which supply valuable information on changes in ecosystems; this is still challenging in CWC ecosystems but the current technology is highly contributing to make this possible. In general, the vision of management taking into account the genuine observation of nature is essential to address the current problems that threat the planet (Dayton and Sala 2001). The new generations of scientists frequently focus in a very specific research question or topic, which make sometimes difficult to understand the "big" question behind their small spot of study. We talk about recovery and stability of habitats, but do we really know when they are stable, when and how they can recover? (Bianchi et al. 2017). We need to be prepared to try to ask the right questions, which come from a deep and unhurried observation of ecosystems and nature. We need to transmit to the new generations this approach. Undoubtedly, the exploration of the deep ocean in general and the CWC in particular will be a vast field to find inspiration.

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References

Aguilar R, Perry AL, López J (2017) Conservation and management of vulnerable marine benthic ecosystems. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1165–1207

Bianchi CN, Morri C, Lasagna R, et al (2017) Resilience of the marine animal forest: lessons from Maldivian Coral Reefs after the mass mortality of 1998. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, 1241–1270. https://doi.org/10.1007/978-3-319-17001-5_35-1

Brooke S, Ross SW (2013) First observations of the cold-water coral *Lophelia pertusa* in mid-Atlantic canyons of the USA. Deep-Sea Res Part 2 Top Stud Oceanogr 104:245–251

Brooke S, Schroeder WW (2007) State of deep coral ecosystems in the Gulf of Mexico region: Texas to the Florida Straits. The state of deep coral ecosystems of the United States. NOAA Technical Memorandum CRCP-3, Silver Spring, pp 271–306

Clarke MR, Rowden AA, Schlacher T, et al (2010) The ecology of seamounts: structure, function, and human impacts. Annu Rev Mar Sci 2:253–278

Cordes EE, McGinley MP, Podowski EL, et al (2008) Coral communities of the deep Gulf of Mexico. Deep-Sea Res Part 1 Oceanogr Res Pap 55:777–787

Dayton PK, Sala E (2001) Natural history: the sense of wonder, creativity and progress in ecology. Sci Mar 65:199–206

FAO (2016) The state of world fisheries and aquaculture 2015. FAO Fisheries Department, Rome

Freiwald A, Fosså JH, Grehan A, et al (2004) Cold-water coral reefs. UNEP-WCMC, Cambridge, 86 p

Helvarg D (2006) 50 ways to save the ocean. Inner Ocean Publishing Inc., Maui, 183 p

Hinz (2017) Impact of bottom fishing on animal forests: science, conservation, and fisheries management. In: Rossi S, Bramanti L, Gori A, et al (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1041–1059. https://doi.org/10.1007/978-3-319-17001-5_37-1

Jacques PJ, Dunlap RE, Freeman M (2008) The organization of denial: conservative think tanks and environmental scepticism. Environ Polit 17:349–385

Koslow JA, Gowlett-Holmes K, Lowry JK, et al (2001) Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. Mar Ecol Progr Ser 213:111–125

Laterveer M, Hill G, Petersen D, et al (2008) Cold-water coral reefs – a new topic for aquarium exhibition to enhance public awareness on a threatened ecosystem. Conference paper. 7th international aquarium congress, 19–24 October 2008 Shanghai, China, B42–B51

Lumsden SE, Hourigan TF, Bruckner AW, et al (eds) (2007) The state of deep coral ecosystems of the United States. NOAA Technical Memorandum CRCP-3, Silver Spring

Murton B (2013) Seafloor mining: the future or just another pipe dream? Int J Soc Underw Technol 31:53–54

Otero MM, Numa C, Bo M et al (2017) Overview of the conservation status of Mediterranean anthozoans. UICN. Málaga, Spain, 73 pp

Pontoppidan E (1755) The natural history of Norway. A. Linde, London, 304 pp

Prouty NG, Fisher CR, Demopoulos AWJ, et al (2016) Growth rates and ages of deep-sea corals impacted by the Deepwater Horizon oil spill. Deep-Sea Res Part 2 Top Stud Oceanogr 129:196–212

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Rossi S (2013) The destruction of the ‘animal forests’ in the oceans: towards an over-simplification of the benthic ecosystems. Ocean Coast Manag 84:77–85

Rossi S (2019) Oceans in decline. Copernicus series. Springer Nature Switzerland AG, ISBN: 978-3-030-02513-7, 352 pp

Sims C (1998) From depths of obscurity, Aquarium’s new stars. December 22, 1998, New York Times/Science section

Cross References

Gori A, Grinyó J, Dominguez-Carrió C, et al (this volume) Gorgonian and black coral assemblages in deep coastal bottoms and continental shelves of the Mediterranean Sea

Orejas C, Jiménez C, Gori A, et al (this volume) Corals of Aphrodite: *Dendrophyllia ramea* populations of Cyprus

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

Part III

Future

40

Perspectives of Biophysical Modelling with Implications on Biological Connectivity of Mediterranean Cold-Water Corals

Matthew W. Johnston and Ann I. Larsson

Abstract

Biological connectivity of marine organisms that reproduce via planktonic larvae, such as cold-water corals, is regulated by the reproductive and life history traits of the organism and by physical characteristics of the marine environment into which offspring are released. Connectivity across vast seascapes enables the persistence of metapopulations over ecological and evolutionary timescales and is important when planning the conservation and management of vulnerable species impacted by overfishing, habitat destruction, or invasive species. To study marine connectivity of these organisms, researchers typically measure genetic population structure or use computer modeling, the latter often using biophysical models which integrate both the physical processes of the ocean and the biological traits of the study species. Herein, a broad overview of biophysical modeling topics will be presented including source-sink dynamics and model parameterisation, paradigms, uses, and examples. Unfortunately, there is limited availability of basic life history data on Mediterranean cold-water corals, which are required to implement such models. Known biological traits that are important for dispersal and connectivity are therefore here summarised for cold-water corals found in the Mediterranean and elsewhere. The traits are discussed in context of dispersal potential and their potential use as parameters in biophysical modeling studies of dispersal. Very few such studies of cold-water corals have to date been performed and none of them in the Mediterranean, therefore as a complement global modeling examples will be given for species that reproduce in a similar fashion. It is hoped that these examples can provide insight into the future usage of biophysical modeling to study Mediterranean cold-water corals as their characteristics and the physical influences that shape their population connectivity are better understood.

Keywords

Biophysical models · Connectivity · Population connectivity · Source-sink dynamics · Modeling · Larval dispersal · CWCs · Life history traits

40.1 Introduction

The life cycle of many marine benthic organisms includes a pelagic larval stage that in part enables their connectivity among populations. Connectivity across vast seascapes enables the persistence of metapopulations over ecological and evolutionary timescales (e.g. Gaines et al. 2007) and knowledge of the biological and hydrodynamic factors that determine connectivity are fundamental when planning the conservation and management of vulnerable species impacted by overfishing, habitat destruction, or invasive species (Treml et al. 2012; Andrello et al. 2013; Johnston and Purkis 2015). For populations in the deep-sea, knowledge of these factors is especially important. Methods used for some shallow water species, e.g. marking and recapture of larvae, are not possible to use in the deep-sea and sampling of material for e.g. genetic structuring is logistically difficult and very expensive. In the case of cold-water corals (CWCs), understanding connectivity may be particularly important to, for example, predict the potential for recovery of reefs following mechanical destruction by deep-water dredging from fishers and to establish marine protected area (MPAs) networks. Although there is a great demand for biophysical

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model studies of CWC connectivity, only a few recent studies have been performed (Cardona et al. 2016; Fox et al. 2016; Ross et al. 2017). This can largely be explained by lack of biological data for deep-sea organisms that can inform the dispersal models (Davies and Guinotte 2011; Hilario et al. 2015).

There are numerous biological factors controlling population connectivity of benthic marine species such as CWCs including the pelagic larval duration of the offspring (hereafter PLD – the period of time a larva remains in the water column from spawn until recruitment), reproductive strategy, larval buoyancy and motility behavior, and life-stage mortality (Cowen et al. 2006; Treml et al. 2012, 2015; Boavida et al., this volume; Reynaud and Ferrier-Pagès, this volume). Physical environmental conditions, such as the speed and direction of water flow, salinity, and water temperature, are also important drivers of connectivity and enable the persistence of metapopulations over time (Guizien et al. 2012; Treml et al. 2012; Johnston and Purkis 2015; Fox et al. 2016). Methods used to study connectivity in the marine environment include larval marking and recapture (Jones et al. 2005), otolith microchemistry (Swearer et al. 2003), genetics (Hedgecock et al. 2007; Boavida et al., this volume and references therein), and biophysical modeling (Verdier-Bonnet et al. 1997; Cowen et al. 2000; Guizien et al. 2006; Kool et al. 2010; Johnston and Purkis 2015; Fox et al. 2016), which is the focus of this chapter. Each of these methods has predictive strengths and weaknesses and when considering CWCs, only genetic data and biophysical modeling are plausible methods to use. In particular, genomics are often relied upon by biologists as a method of studying marine organism connectivity and provide an overarching understanding of how populations are connected over evolutionary timescales (Hellberg et al. 2002; Palumbi 2003; Boavida et al., this volume). For e.g. colony-forming CWCs where individuals can be very long-lived, the connectivity patterns found may however be purely historical (further elaborated under Sect. 40.1.1 below). Biophysical dispersal models have the advantage of using present known distributions of organisms and contemporary oceanographic conditions to predict connectivity, given present habitat layout or changes in habitat structure in the future. Biophysical modeling of an organism over multiple generations can also be useful to elucidate decadal connectivity patterns of populations and infer biological and genetic connectivity. Results from generational models can be contrasted with genetic population connectivity studies (Liggins et al. 2013); however, models over multiple cohorts are generally uncommon as optimising model parameters is highly complex and only a few solutions have been proposed (Guizien and Bramanti 2014; Hernandez et al. 2014).

The focus of this book is Mediterranean CWCs, which are deep-water cnidarians that live mostly at aphotic depths between 350–600 m (Taviani et al. 2011). These corals are sessile as adults and the to-date studied species propagate via current-diffused sexually produced larvae (Waller and Tyler 2005; Larsson et al. 2014; Feehan 2016; Martinez-Quintana et al. 2015). Unfortunately, there is limited information on the reproductive behaviors, larval traits, and general life histories of CWCs in the Mediterranean, therefore the known biological traits that are important for dispersal and connectivity of CWCs found in the Mediterranean are here summarised and complemented with information on CWCs found elsewhere on the globe. Data of this kind are needed to adequately parameterise biophysical models that can be used to study connectivity of CWCs. Very few such studies have been performed to date and none of them in the Mediterranean.

To recognise the usefulness of biophysical modeling as it pertains to the understanding of connectivity of CWCs, it is first necessary to gain an understanding of (1) the aim of biophysical models themselves, (2) population 'sources' and 'sinks', and (3) the drivers behind biological connectivity. Given the paucity of studies specific to CWCs, referenced here are interwoven global examples of biophysical models used to study other marine organisms. These examples can illustrate the importance of biophysical models in understanding marine connectivity and the implications of various biotic and physical processes on model results. They also demonstrate how the models may be useful to study CWCs in the Mediterranean as more becomes known about these inhabitants of the deep.

40.1.1 The Aim of Biophysical Models

The deep CWC ecosystem and their population complexity necessitate an understanding of both the biological and physical realms in order to emulate their marine seascape niche and their dispersed populations. Individually, biological and physical models aim to reproduce natural conditions and to provide insight into the function of natural systems through synthetic simulation. In a strictly physical model that may examine CWC connectivity for example, information about water flow and source location would be incorporated but the larvae would be treated as passively-diffused particles, while biological influences, such as planulae movement, would be discounted or not considered (e.g. Siegel et al. 2003; Rossi et al. 2014). Subsequently, the data produced by such a model would be limited and not fully descriptive of the true state of nature, given that larval movement (i.e. directional behavior, especially vertical migration) may influence connectivity (Paris et al. 2007). Biological connectivity models in contrast largely ignore the physics of water motion and instead focus solely on the biological drivers of connectivity such as reproductive traits, suitable habitat congruity, and various life-stage mortalities (e.g. Thorrold et al. 2002). Neither method is complete.

Moreover, many biologists measure connectivity derived solely from DNA studies. Genetic connectivity studies though do not reveal the intricate mechanics of dispersal and instead evaluate the status of a population over various time scales, depending on the genetic markers used (Cowen and Sponaugle 2009). In the context of many marine populations (including CWCs) that may be under duress from multiple immediate stressors such as disease, environmental damage, or invasive species (Galil, this volume), understanding connectivity over decadal or sub-decadal timescales is important. Since populations of many CWC species expand through colonial growth and asexual reproduction through fragmentation, genets (genetic individuals) can be very long-lived, i.e. thousands of years (Dahl et al. 2012). By occupying space, these individuals limit new recruitment, resulting in gene flow blockage (Padrón and Guizien 2016). As such, it is difficult to discern between contemporary and historical genetic connectivity, although present technical development will improve this possibility (Boavida et al., this volume). Understandably, for long lived species like CWCs, genetic connectivity estimates could mirror historical patterns with extinct stepping-stone populations that previously connected geographically distant populations, and to e.g. establish MPA networks based only on such connectivity estimates could be disastrous. The aim of biophysical models in the context of CWCs would be therefore to integrate biological and physical methods, given that both are likely equitable drivers of connectivity, to deliver a more realistic representation of the functionality of CWCs in the short- and long-term perspective. Ideally, these seascape genetic studies could then incorporate biophysical modeling to provide a more holistic picture of connectivity of CWCs (Liggins et al. 2013; Buonomo et al. 2017).

Advances in computational power now allow researchers to approach the subject matter of marine population connectivity using computing power to run complex particle tracking algorithms – something not possible just a few decades ago. Indeed, with decent simplification of intricate mechanics, it is possible to run complex models on a modest laptop computer. However, complexity also increases uncertainty in interpreting the results and introduces potential error. Given this, modern biophysical models are prone to model assumptions and so most models integrate a limited number of physical and biological components that are deemed the most critical from each discipline in an attempt to simulate a natural system (Hernandez et al. 2014). Attempting to account for all variables is unreasonable and can introduce bias to the synthetic model system by including components that may not be biologically or physically relevant (Warren and Seifert 2011). To mitigate such errors, an important component to any study implementing a biophysical model is to sensitivity-test the model by varying the biological and physical parameter values to test model assumptions. Section 40.3 discusses the various implementations of marine biophysical models, but first a dialog on population sources and sinks and biological and physical drivers of biological connectivity provided next is prudent to establish context.

40.1.2 Population Sources and Sinks

A population source, when considering the biological connectivity of benthic marine organisms such as CWCs, is a population of organisms in a location that produces propagules (i.e. spores, eggs, coral planulae, etc.) that are subsequently dispersed via water flow to other locations. These propagules from a source population may be carried either short or long distances on ocean currents or be retained near the natal organism, resulting in relatively open or closed populations (Cowen et al. 2000). In corals, traits such as brooding and crawling planulae (e.g. the cold-water octocorallian *Drifa glomerata*, Sun et al. 2010a) will promote retention and aid in local population self-recruitment whereas traits such as broadcast spawning, vertical migration of larvae, and a long PLD (e.g. the cold-water scleractinian *Lophelia pertusa*, Strömberg and Larsson 2017) will increase dispersal distance by taking advantage of water flow gradients (Paris et al. 2013). Effects of reproductive strategy and larval traits on dispersal will be further discussed in Sect. 40.2.1 below.

A population sink is a location that receives propagules from a nearby or distant source population. Once arriving at a sink location either via passive or active transport, propagules of sessile organisms that recruit to the benthos usually remain there throughout their lifetime. It is important to understand that source and sink locations may be the same (i.e. self-recruitment), a location may be solely a source or a sink, or a location may function as both a source for one location and a sink for another. For example, a CWC inhabiting a deep-water escarpment off of Cyprus may retain 100% of its larvae through nearshore eddies, may export all propagules offshore and solely rely on distant coral colonies to recruit to the ledge, or there may be a gradient of bi-directional exchange between two locations.

40.2 Drivers of Marine Biological Connectivity

To understand biophysical models, it is imperative also to discuss the biological and physical drivers of marine biological connectivity and especially those which researchers use to parameterise biophysical models. Marine benthic organisms such as CWCs exhibit a significant range of fecundities, reproduction modes, propagule behaviors, mortalities and lifespans that help enable the persistence of populations over generations. These life history traits compose one primary driver of biological connectivity in ocean systems. A primary driver of connectivity is also the physical environment itself, such as ocean water flow, temperatures, salinity, bathymetric composition, and water depth. While the physical and biological components are an intricately woven tapestry and their individual influences cannot always be easily extracted, they will be treated separately here to aid in explanation and interpretation. Additionally, the traits and conditions below are not an exhaustive list; they were selected based on those parameters that are predominately used in biophysical modeling at the time of this writing.

40.2.1 Biological Traits

40.2.1.1 Fecundity and Maturity

Organisms that produce large quantities of larvae may show greater biological connectivity between source and sink locations than those organisms which produce fewer offspring or breed only sporadically. This is because, on the balance of probabilities, a greater number of offspring that are produced increases the chances of successful recruitment, assuming equal predatory pressures on planktonic larvae of all species. Still, there exists a vast knowledge gap about larval predation and how this may affect model uncertainty. Note also that metapopulation growth and persistence increase with reproductive output, though dispersal distance may not (Treml et al. 2015). Concordantly, organisms that mature at an earlier age also may contribute offspring to the larval pool sooner and perhaps greater quantities over their lifespan than those that mature later (Johnston and Purkis 2016). Similar to increased fecundity, early maturity may enhance biological connectivity between regions for species exhibiting this trait, at least in the short term. It must be bore in mind, however, that some late-maturing species produce copious amount of eggs after sexual maturity and are long-lived, perhaps offsetting the disadvantage of late maturity when contrasted with quick-maturing species (Johnston and Bernard 2017).

The age of maturity is to our knowledge not estimated for any true CWCs but there are some indications that polyps need to reach a certain size before becoming reproductive (e.g. Feehan 2016) and that larger colonies have more fertile polyps (Sun et al. 2010b). However for deep-water alcyonacean octocorals of the genus *Drifa*, Sun et al. (2010a) report that colonies only a few centimeters in size are fertile. The youngest fertile colonies of the Mediterranean octocoral *Corallium rubrum* sampled at 40 m depth by Torrents et al. (2005) were 7–10 years old.

The fecundity of a few CWC species that appear in the Mediterranean have been investigated. Populations of *Desmophyllum dianthus* in Chilean Patagonian fjords show high fecundity compared to other deep-sea scleractinians, with an average number of eggs per polyp ranging from 2500 to 170,000 among fjords (Feehan 2016). In northeast Atlantic populations, Waller and Tyler (2005) measured the fecundity in *Lophelia pertusa* as 3300 oozytes per cm^2 skeletal area which was an order of magnitude higher than 256 oocytes per cm^2 in *Madrepora oculata*. Preferably, the fecundity should be investigated in several different geographical areas since optimal environmental conditions may differ between CWC-species and fecundity will vary accordingly.

40.2.1.2 Mode of Reproduction and Time of Spawning

Corals have two sexual reproductive modes which largely determine their dispersal potential. Scleractinian reef-forming CWCs studied to date, i.e. *Oculina varicosa*, *Solenosmilia variabilis*, *Goniocorella dumosa*, *Enallopsammia rostrata*, *L. pertusa*, *M. oculata*, and *D. dianthus,* are broadcast spawners (Brooke and Young 2003; Burgess and Babcock 2005; Waller and Tyler 2005; Larsson et al. 2014; Pires et al. 2014; Feehan 2016) – i.e. eggs and sperm are released into the water column where fertilisation and embryo development take place. Most solitary CWC scleractinians (Waller 2005; Waller and Tyler 2011; Mercier et al. 2011; Waller and Feehan 2013) and perhaps a majority of cold-water octocorals including all deep-sea sea pens (Rice et al. 1992; Tyler et al. 1995; Eckelbarger et al. 1998; Orejas et al. 2002, 2007; Pires et al. 2009, Mercier and Hamel 2011, Beazley and Kenchington 2012; Baillon et al. 2014; Feehan and Waller 2015; Rossina et al. 2017) are also broadcast spawners. In contrast, for brooding species, fertilisation of eggs occurs either in or on the surface of maternal colonies and larvae are mature before released. Among studied CWCs, hydrocorals (Brooke and Stone 2007), some solitary scleractinians (Waller et al. 2008) and some octocorals (Cordes et al. 2001; Orejas et al. 2007; Sun et al. 2009, 2010a, b; Mercier and Hamel 2011; Grinyó 2016) are brooders. The larvae of broadcast spawning corals generally have greater potential to disperse widely outside their natal reef whereas brooding corals release mature larvae directly that are ready to settle within much shorter periods (Harrison and Wallace 1990; Underwood et al. 2009). Although “mode of reproduction” cannot be fed directly into a biophysical dispersal model, it is a proxy for the length of the larval precompetency period – i.e. the minimum period of time that larvae disperse in the water column before settlement. For brooded larvae, this period is very short, from a few hours to a few days in tropical species (Harii et al. 2002 and references therein). Generally, brooders also exhibit shorter median PLDs (Underwood et al. 2009). The effect on dispersal of larval pre-competency period and PLD is further discussed below. Only recently, the reproduction mode of two deep living Mediterranean gorgonian octocorals has been investigated. Both *Paramuricea macrospina* (Grinyó 2016) and *Eunicella cavolini* collected at 70–100 m depth are internal brooders. The previously investigated gorgonians *C. rubrum* and the facultative zooxanthellae *Eunicella singularis* which have both shallow and deep populations are also internal brooders (Gori et al. 2012; Martinez-Quintana et al. 2015).

Knowledge about the time of spawning is also crucial to model coral larvae dispersal since the circulation of water masses within a sea basin differs with seasons (e.g. Hayes et al., this volume). For seasonally reproducing CWCs, spawning is speculated to be coupled to seasonal fluctuations in quality and quantity of food (Burgess and Babcock 2005; Waller and Tyler 2005; Sun et al. 2010a, b; Mercier et al. 2011; Brooke and Järnegren 2013). *Lophelia pertusa* reproduces annually, with differences in timing depending on geographical location. Spawning occurs in Jan-March in the NE Atlantic (Waller and Tyler 2005; Brooke and Järnegren 2013; Larsson et al. 2014), in Sept-Nov in the south-eastern US and Gulf of Mexico (Brooke et al. 2007; Brooke and Järnegren 2013), and in May–July in Campos Basin off Brazil (Pires et al. 2014). Reproduction of *D. dianthus* has only been studied in Chilean fjords but also shows strong seasonality with gametes likely spawned in August – i.e. at the end of the austral winter (Feehan 2016). Contrasting to *L. pertusa* and *D. dianthus*, *M. oculata* produces multiple cohorts annually (Waller and Tyler 2005; Pires et al. 2014). Although these three species are common in the Mediterranean, reproduction in these corals is not yet studied here. The deep living Mediterranean gorgonians *E. cavolini* and *P. macrospina* (Grinyó 2016) reproduce annually and earliest in July and August respectively.

40.2.1.3 Precompetency-Period and Pelagic Larval Duration (PLD)

The larval precompetency-period determines the minimum amount of time that embryos and larvae, after being released, spend in the water column before maturing to settle. The precompetency-period is hence equal to the minimum pelagic larval duration (PLD) period for coral planulae. Considering the chances of larvae settling locally – i.e. in the vicinity of the natal reef – the pre-competency period is more instrumental than the maximum length of the PLD. A short pre-competency period will increase the proportion of larvae recruiting locally (e.g. Harrison and Wallace 1990; Underwood et al. 2009; Treml et al. 2015). The dispersal potential outside the natal area increase with PLD and for both median and maximum dispersal distance, PLD is most important (Treml et al. 2015). As discussed above, planulae of brooding corals generally have shorter pre-competency periods than those of their broadcast spawning relatives and shorter pre-competency periods are coupled to shorter median PLDs (Underwood et al. 2009). Some brooded larvae are however also capable of settling after many weeks (reviewed by Harrison and Wallace 1990), so the maximum PLD can still be quite long enabling occasional long distance dispersal in brooding coral species (Underwood et al. 2007, 2009).

There are very few studies of CWC larval biology. Planulae of two brooding NW Atlantic octocorals of the genus *Drifa* settle from 1 day up to 3 months after release in temperatures of −0.5 to 8.5 °C (Sun et al. 2010a). Brooke and Young (2003) studied larval development of the broadcast-spawning facultative zooxanthellate coral *O. varicosa* that forms extensive reef systems along the edge of the Florida shelf at 70–100 m depth. Larvae in this study were reared at 25 °C and a ciliated planula formed 9 h after fertilisation. The larvae initially swam upwards but started to show benthic-probing or creeping behavior after 1–2 weeks signaling maturity to settle, and settling was observed after 3–4 weeks. Larval development was comparatively much slower in *L. pertusa* from the northeast Atlantic with a fully developed swimming planulae formed 9 days after spawning (Larsson et al. 2014). Larvae were reared at *in situ* temperatures of 8 °C and a recent study show that when the rearing temperature is increased to 11–12 °C, the development rate approximately doubles (Strömberg and Larsson 2017). The difference is likely caused by an upturn in metabolic rate with temperature, and highlights caution when inserting available data of pre-competency periods and PLD into biophysical dispersal models. *Lophelia pertusa* is a cosmopolitan species found at various depths and at both low and high latitudes and consequently its embryos and larvae may encounter a large range of temperatures. This species typically thrives at 4–12 °C (Rogers 1999), but appears in water masses of ca. 13 °C in the Mediterranean (Taviani et al. 2017). Since larvae also exhibit ontogenetic vertical migration and possibly migrate into surface waters (Strömberg and Larsson 2017), the temperature span encountered may be even larger. In conclusion, it is important to consider the ambient temperatures at various reef sites and the effect it may have on larval development rate and larval duration.

The precompetency period of *L. pertusa* planulae reared at 7–8 °C is at least 3 weeks as indicated by the observation of cnidocyst discharge starting 20 days after spawning, and the use of these for temporary attachment to the substrate (Strömberg 2016). Earliest notation of bottom probing behavior is also at 3 weeks of age (Larsson et al. 2014) but the majority of larvae start showing this behavior at 4–5 weeks or later (Larsson et al. 2014; Strömberg and Larsson 2017). No settling of *L. pertusa* planulae is yet observed but larvae can survive for a full year in laboratory cultures indicating a possibly very long PLD in this species (Strömberg and Larsson 2017).

Larval ecology of deep water corals in the Mediterranean is poorly investigated but Martinez-Quintana et al. (2015) studied planulae from shallow populations (25–30 m) of the brooding octocoral *C. rubrum*. This coral has been found to 800 m depth in the Mediterranean (Freiwald et al. 2009). Larvae maintained at 19–21 °C had a maximum PLD of 42 days (Martinez-Quintana et al. 2015). Since larvae also were active swimmers with a clear upward swimming behavior, the authors conclude that the dispersal potential in open waters should be high. This hypothesis is contradicted by molecular studies of shallow populations showing significant gene flow only on very limited spatial scales (Costantini et al. 2007; Ledoux et al. 2010). This pattern may however be explained by that *C. rubrum* is a heavily harvested species fragmenting the metapopulation (e.g. Tsounis et al. 2013).

40.2.1.4 Embryo and Larval Behavior

In addition to pre-competency period and PLD, the realised dispersal distance can be significantly influenced by embryo and larval behavior. Traits such as embryo and larval buoyancy, larval type (crawling or swimming) and swimming behavior will decide where in the water column larvae are transported during their different life phases. Some brooding corals release non-swimming planulae (crawlers) that depending on the ambient current strength may be transported a very short distance before they settle from the water column and become demersal. Such an example is the deep-sea alcyonacean octocoral *Drifa glomerata* (Sun et al. 2010a). With crawling larvae, recruitment is often restricted to within a few hundred meters from the parental colonies (e.g. Harii and Kayenne 2003). For broadcast spawning corals, embryo density dictates if they are positively or negatively buoyant, which for CWCs can be extra critical since the development to swimming larvae can take several days (Larsson et al. 2014). Brooke and Young (2003), noted that eggs of *O. varicosa* are negatively buoyant. In contrast, eggs of *L. pertusa* appear to be neutrally buoyant, and embryos from one-day old, positively buoyant (Larsson et al. 2014). In addition, *L. pertusa* embryos start developing cilia three days after fertilisation and are slowly ascending swimming blastulae after five days. After an inactive phase when gastrulation occurs, larvae are competent swimmers at the age of 7–9 days (Larsson et al. 2014).

Although most marine larvae are weak swimmers, many of them are able to regulate their vertical position in the water column, which may change over time (ontogenetic shifts) or with diel or tidal cycles. Other determinants of vertical position are larval buoyancy and vertical water flow. Since both the current direction and velocity normally differ with depth (Sponaugle et al. 2002), knowledge of the position of larvae in the water column is crucial for more accurate biophysical modelling of larval dispersal. Several studies have found major effects of vertical migration on both dispersal distance and connectivity (e.g. Fiksen et al. 2007; Paris et al. 2007; Corell et al. 2012; Moksnes et al. 2014; Fox et al. 2016), and for deep-sea organisms the effect of being transported in the surface layer compared to deeper layers can be dramatic (Young et al. 2012; Fox et al. 2016). The most direct and accurate way of finding out where in the water column larvae reside is to collect larvae in the field at different depths as done by Arellano et al. (2014) for deep-sea molluscs. While this is possible, it involves extensive sampling efforts in expensive field surveys, during the period when larvae are in the plankton. Unlike mollusc larvae that wear a shell, deep-sea coral planulae are soft-bodied and prone to disintegrate when filtered out from the seawater. It would therefore demand genetic screening of species-specific DNA sequences to verify presence, a scientific methodology still in its infancy. Amplification and characterisation of genomic DNA from tissue of *L. pertusa* planulae has previously been successfully performed (Larsson et al. 2014) indicating such sampling could be feasible.

As an alternative, the probable *in situ* depth distribution during different larval phases can be deduced from larval behavior in laboratory experiments – i.e. the tendency of positive or negative buoyancy, active vertical swimming and onset of bottom probing behaviour. Using data and observations from Larsson et al. (2014), Ross et al. (2017) made a “vertical migration profile” for *L. pertusa* planulae, which they used as input to model the dispersal among a network of MPAs in NE Atlantic. Larsson et al. (2014) observed that *L. pertusa* larvae accumulate in the upper part of aquaria until 3–5 weeks old and Strömberg and Larsson (2017) (see also Orejas et al., Chap. 38, this volume) further showed that 4–5 weeks old planulae that were introduced at the bottom of aquaria consistently reacted by swimming upwards until reaching the surface. The larvae also passed salinity gradients with a maximum tested difference of 5 with no hesitation (Strömberg and Larsson 2017). Larvae were further observed to feed and survived for months also at salinities typical for surface waters above coastal populations in the Skagerrak (25). This indicates that the larvae may spend a period of their pelagic phase in the photic zone, being transported in the relatively faster surface currents, before descending to settle. Ontogenetic shift in vertical positioning was also observed by Brooke and Young (2003) in *O. varicosa*. When planulae became ciliated they swam to the surface of the water where they resided for about a day before turning to swimming actively throughout the water column during 1–2 weeks. The above findings suggest that CWCs may take advantage of surface currents for dispersal (similar to many marine benthic organisms) and therefore is an integral behavioural component that should be included when using a biophysical model to examine CWC connectivity.

40.2.1.5 Mortality

Natural life stage mortality is likely the second most influential to PLD in the context of maintaining biological connectivity of benthic marine species between regions in biophysical models (Johnston and Purkis 2016). Marine organisms are arguably most vulnerable to predation (i.e. the 'wall of mouths' theory – Hamner et al. 1988), disease, and simply death in the larval stages of their life – perhaps reflected by the large number of offspring that most small marine fauna produce. Even a small percentage reduction in mortality during the egg or larval phases can produce a much more robust next generation cohort (Johnston and Purkis 2016). This is because reduced larval mortality allows a greater number of individuals to have the opportunity to successfully colonise, likely increasing biological connectivity between regions. We suggest that decreased larval mortality is perhaps a partial explanation for the success of non-native species, whereas larvae 'released' from predation in their introduced range allows a large percentage of spawned larvae to reach adulthood. Natural mortality (i.e. not including fishing pressure) generally peaks during recruitment and is commonly at its lowest point after full maturity (Ware 1975).

Unfortunately, empirical measures of larval mortality under natural conditions for most marine organisms including CWCs are scarce despite its high importance for dispersal outcomes (Treml et al. 2015). Mortality rates of larvae under laboratory conditions will not reflect mortality rates in the field where e.g. predation is an important controlling factor. On the other hand, many bacteria and parasites flourish in closed laboratory cultures, artificially shortening the life span (Strömberg and Larsson 2017). In laboratory cultures, these authors noted a 60% survival rate of developed *L. pertusa* planulae during a 3-month period, though it is unknown how representative this is of mortality in the wild.

40.2.1.6 Reproductive and Larval Traits, and Implications for CWC Connectivity

The importance of differences in reproductive and larval traits is highlighted by genetic estimates of connectivity among deep-sea coral populations, which have shown species-specific variation. Miller et al. (2010) assessed connectivity among nine deep-sea coral species populations on seamounts and slopes in the Australian and New Zealand region spanning thousands of kilometers. They found conflicting estimates of connectivity with evidence of genetic subdivision among regions for three of the species whereas levels of genetic variation were low for the remaining species. The authors hypothesise that differences in larval biology of which virtually nothing is known for the studied species may explain the observed differences in connectivity patterns. For the estimated low connectivity in *D. dianthus*, Miller et al. (2010) also suggest that differences in sampling depth of this coral may have contributed to the observed genetic differentiation among the regions provided that larvae are primarily dispersed by currents at the depth where they are spawned. This hypothesis was corroborated in a later study by Miller and Gunasekera (2017) where populations of *D. dianthus* were clearly genetically structured by depth rather than by geographical location. These results suggest planulae of *D. dianthus* may not migrate vertically as planulae of *L. pertusa* do (Strömberg and Larsson 2017) but there are no larval observations available for *D. dianthus*.

Similar to Miller et al. (2010), Becheler et al. (2017) found contrasting patterns of connectivity between the CWC species *L. pertusa* and *M. oculata*. These two reef-building species often occur together in the northeast Atlantic and were here studied in continental slope canyons of the Bay of Biscay. Genetic structuring was detected among the five canyons spanning a distance of ~500 km for populations of *M. oculata* whereas *L. pertusa* was panmictic on this scale. Because the coral species co-occur in all the canyons studied by Becheler et al. (2017) hence sharing the hydrodynamic environment, and sampling of corals has been conducted in a similar way, it is likely that one or several of the biological parameters important for dispersal of larvae differ between these species. Since both species are broadcast spawners, other traits must underlie the difference. There is a large difference in fecundity between these species with *L. pertusa* having more than 10 times higher fecundity than *M. oculata* in studied northeast Atlantic populations (Waller and Tyler 2005). Given the genetic structuration of *M. oculata* occurring at a smaller scale than in *L. pertusa* populations, we may hypothesise that planulae of *M. oculata* (which are not yet studied) have a shorter pre-competency period, and/or a shorter pelagic larval duration period (PLD). But other explanations could be a different vertical migration pattern (if any) or the time of spawning (Treml et al. 2015) due to e.g. differences in hydrodynamical conditions among seasons, since *L. pertusa* reproduces seasonally whereas *M. oculata* produces two cohorts annually in northeast Atlantic waters (Waller and Tyler 2005). Hopefully the larval biology of many more deep-sea coral species can be studied in the future to help explain such differences in connectivity patterns among CWCs and that can be integrated into future biophysical modeling efforts.

40.2.2 Physical Ocean Conditions

The physical environment into which the offspring are released is equally as important as species traits in driving population connectivity. Following is an audit of environmental ocean conditions that influence biological connectivity and that are commonly used to parameterise biophysical models. We also direct the reader to chapters Hayes et al., this volume and Chimienti et al., this volume, which contain a comprehensive review of biogeography of CWCs and physical ocean conditions in the Mediterranean that are important drivers of CWC populations.

40.2.2.1 Ocean Currents

The predominant physical driver of biological connectivity for benthic organisms that reproduce via pelagic marine larvae is water flow (Treml et al. 2008; Cowen and Sponaugle 2009). In some regions such as the western Atlantic and Gulf of Mexico, dispersal is heavily influenced by very swift and persistent surface currents such as the Loop Current and Gulf Stream. Many marine larvae including some CWCs (e.g. *L. pertusa* – see Sect. 40.2.1) vertically migrate, or are buoyant and float, into the upper layers of the water column as a dispersal strategy (Paris and Cowen 2004; Martinez-Quintana et al. 2015; Ross et al. 2017). As a result, strong surface flow in such regions is capable of consistently dispersing propagules great distances (Johnston and Purkis 2015; Ross et al. 2017). Conversely, in regions such as the tropical eastern Pacific and closed ocean basins/gulfs such as the Mediterranean Sea and Persian Gulf, surface water flow is generally much weaker and sometimes seasonal or influenced by meteorology (Pinardi and Masetti 2000; Estournel et al. 2003; Hayes et al., this volume). In the latter case, dispersal of larvae may be more radial or gradual, such as demonstrated by Andrello et al. (2013) and Johnston and Purkis (2014) in the Mediterranean and Johnston and Purkis (2016) in the Hawaiian Islands.

In the deep intermediate waters of the Mediterranean Sea – i.e. where CWCs reside – water flow is largely driven by thermohaline mixing and overturning circulation and is generally weaker and more intermittent than at the surface, except in locations near submarine canyons and cascades (Pinardi and Masetti 2000; Hayes et al., this volume). Bottom topography, such as seamounts and escarpments, and baroclinic eddies also influence the direction and speed of water flow (Cherubin et al. 2000; Freiwald et al. 2009; Taviani et al. 2015), which can be significantly different, directionally than at the surface. Intermediate waters of the Levantine (Levantine Intermediate Water – LIW) spread through the Mediterranean at depths of 0–500 m in complex cyclonic and anticyclonic eddy fields (e.g. the Rhodes Gyre, the Cyprus Eddy), with a general trend of cyclonic rotation in the eastern Mediterranean basin and anticyclonic in the west ern Mediterranean basin (Hayes et al., this volume). Salty LIW exits through the Sicily Channel and balances the net inflow of lower salinity water into the Mediterranean from the Atlantic through the Straights of Gibraltar. West of the Sicily Channel, some flow of LIW flanks the northern African coast, eventually leaving the Sea through the straights of Gibraltar. To the north, mesoscale anti- and cyclonic eddies (e.g. Western and Eastern Algerian Gyres, Algerian Eddies and Sardinian Eddies) and along-coast currents (West coast of Italy, the Northern Current along France and Spain) dominate the circulation pattern.

As it pertains to general trends that would be seen in a biophysical modeling study of CWCs, typical intermediate water circulation in the Mediterranean suggests that connectivity should increase from east to west across the basin for CWCs with neutrally or negatively buoyant larvae. However, surface water flow, where larvae of the CWC *L. pertusa* may be contained, does not necessarily reflect deep flow, particularity in the western Mediterranean where biophysical models have suggested an eastward flow of buoyant larvae (Johnston and Purkis 2015).

Notably, and very important in the context of biophysical modeling, very few sensing platforms measure ocean currents directly at any depth in the Mediterranean or elsewhere (Hayes et al., this volume), making characterisation of deep water circulation difficult, especially for ocean models such as HyCOM, MFS, and NEMOMED12 that aim to emulate Mediterranean and global deep-sea environments. Sea level anomaly from satellite altimeters is often used to estimate surface and approximate deep water flow, but stratification makes this method unreliable at best and is most suitable for measuring surface water characteristics. Nevertheless, data assimilated ocean models are gaining traction that integrate *in situ* data such as CTD profiles and satellite-derived surface flow measurements to more accurately simulate ocean dynamics in surface waters and the deep.

40.2.2.2 Habitat Suitability

Benthic substratum is an important driver of connectivity of CWCs in that offspring must encounter a location suitable for recruitment concluding the PLD. For example, given a tropical reef broadcast spawning coral such as *Acropora millepora*, a planula that reaches competency is not able to recruit to aphotic benthos or to a location where the benthic composition is outside of their tolerances such as mud or silt (Jones et al. 2016; Ricardo et al. 2017). Mediterranean CWCs, in contrast, are found at deep, aphotic depths and primarily live on steeply inclined submarine walls and escarpments beneath bedrock overhangs and secondarily on subtly inclined shelves (Freiwald et al. 2009; Orejas et al. 2009; Gori et al. 2012; Chimienti et al., this volume). Often CWC colonies are found in the vicinity of canyons, troughs, and shelf edges which deliver nutrients and plankton on cascading or upwelling LIW that bath the colonies (Thiem et al. 2006; Freiwald et al. 2009; D'Onghia et al. 2015). Microhabitats preferred by the corals include bedrock lithologies containing overhangs and fissures that dissect the bedrock (Freiwald et al. 2009; Chimienti et al. this volume). Planulae settling in such regions would likewise have a greater success as surviving to maturity than those that may recruit to abyssal plains, for example.

Similar to unsuitable benthic structure and aphotic depths, low water temperatures limit the distribution of some fauna both at high latitudes and also perhaps at depth, though typically the latter limitation is due to attenuation of sunlight (e.g. photosynthetic corals). Important to consider is overwintering, especially for shallow corals or deep CWCs such as *L. pertusa* whose larvae may migrate vertically and be dispersed in surface waters (Strömberg and Larsson 2017). As the Mediterranean Sea is a marginal environment given its high latitude, shallow and surface waters are colder in the winter than deep water (Millot 1999), the latter perhaps serving as refugia for some marine organisms. Marine species accustomed to warmer temperatures and that successfully recruit to shallow Mediterranean waters in northerly latitudes during summer months are likely ephemeral due to overwintering temperatures that drop below their thermal tolerances (Johnston and Purkis 2014; Jimenez, pers. communication). This may help limit the spread of some warm-water Lessepsian migrants from the Red Sea, but is probably not a limiting factor to those native biota that are accustomed to water temperature fluctuations, such as *L. pertusa* which is found at both high and low latitudes and whose larvae likely encounter and tolerate a large range of temperatures. Interestingly and conversely, the Mediterranean seems to be a marginal environment for some deep CWCs because the water may be too warm during some parts of the year. For example, *L. pertusa* thrives in a thermal envelope of 4 to 13 °C (Rogers 1999; Freiwald 2002; Taviani et al. 2017) and peak Mediterranean water temperatures at 300 m sometimes reach >15 °C (Palanques et al. 2006). Furthermore, it is thought that warming climatic conditions at the start of the Holocene may have holistically increased the temperature the Mediterranean and subsequently promoted the recession of all CWC species in the sea (McCulloch et al. 2010; see chapters of the Past section in this volume).

Salinity is not typically a physiologically limiting factor in the dispersal of marine organisms, aside from exceptional locations where freshwater plumes may significantly lower salinity to below marine levels or in estuarine environments (Luiz et al. 2013). Such conditions in the Mediterranean occur in limited locations such as the Rhone River delta and river discharges in the Adriatic, however freshwater inflows are uncommon since the construction of the Aswan High Dam across the Nile River in the 1960s that reduced the inflow of freshwater into the Sea (Skliris this volume). Studies have also shown however that CWC larvae can tolerate quite low salinities and readily cross pycnoclines (Strömberg and Larsson 2017) without increased mortality of their planulae. It is unknown, however how an increasingly saline Mediterranean may affect larval and adult mortality of CWCs, though salinity fluctuations in the LIW layer throughout the basin strongly influence CWC growth (Skliris, this volume).

While likely physiologically tolerable, salinity gradients in the Mediterranean may physically restrict CWC larval exchange to outside of the basin. The Mediterranean is a relatively salty sea with an average salinity of ~38 (Borghin et al. 2014) due to its largely closed nature and high rates of evaporation (Skliris, this volume). At the Sea's connection with the Atlantic Ocean through the Straights of Gibraltar, lower salinity water of the Atlantic (salinity of ~ 35) flows over higher-density Mediterranean water, resulting in a net influx of water (Bryden et al. 1994). This zone, known as the Almeria-Oran front is thought to act as a barrier to gene flow in the Mediterranean, driven by different water densities that extend deep into the water column (Catarino et al. 2017). Furthermore, this net flow of surface water may prevent floating pelagic larvae such as those of *L. pertusa* from exiting the Sea into the Atlantic and serve as a biogeographic barrier to CWCs. Such water flow would be an integral component to include in any biophysical modeling effort in the context of understanding CWC connectivity between the Mediterranean basin and the Atlantic. In any case, a three-dimensional representation of ocean conditions is requisite for modeling the dispersal of Mediterranean CWCs, given their variable position throughout the water column spanning larval through adult life stages.

40.3 Biophysical Modeling

40.3.1 Integrating the Physical

The physical construct of a biophysical model is primarily a virtual two- or three-dimensional model grid which represents a real-world study domain such as the Mediterranean Sea. The domain is a matrix of grid cells where each cell represents a discrete physical area of the ocean, which may be of fixed or variable dimensions across the grid, and is characterised by ocean conditions relevant to the species being modeled. For Mediterranean CWCs, such data could comprise the speed and direction of water flow, salinity, ocean temperature, and bathymetry. The temporal and spatial resolution of the grid is entirely dependent upon the data that are used to parameterise the model. Often, nested grids of different resolutions are used that reflect different temporal and spatial resolutions of available ocean condition data. Ocean forecast data from computer models such as the HYbrid Coordinate Ocean Model (HyCOM), Region Ocean Model System (ROMS), Nucleus for European Modelling of the Ocean (NEMO), Mediterranean Ocean Forecasting System (MFS) are often used (e.g. Paris et al. 2013; Andrello et al. 2013; Rossi et al. 2014; Johnston and Purkis 2016) to characterise the model grid and are available at spatial resolutions from <1 km to >100 km. The temporal resolution of these ocean models ranges from hours to climactic averages computed over years. Understandably, biophysical models that use high resolution ocean data to parameterise the physical component are computationally expensive and therefore parameters are chosen based on the science question that is being asked. For example, some studies use very high resolution data to analyse microscale processes such as inter-reef connectivity (e.g. Paris et al. 2013) and some models use more broad resolution data to answer questions about connectivity over longer time periods and spatial spans (e.g. Andrello et al. 2013; Johnston and Purkis 2015). Also important is the consideration of strong land-ocean interaction, which is a characteristic of the Mediterranean Sea due to its high temporal and spatial variability as a closed basin.

The transport of marine particles, e.g. CWC larvae, in Individual Based biophysical Models (i.e. IBMs, where individual particles are tracked, as opposed to some Eulerian models that simply track concentrations) typically can be binned into one of two fluid dynamics categories: Eulerian models or Lagrangian models, referring the method that the larvae are transported within the model grid (Cowen et al. 2000; Zhang and Chen 2007). In an Eulerian IBM, larvae diffuse from cell-center to cell-center in a straight line and in a trajectory that reflects the velocity and direction of water flow of the source cell. The passive trajectories are sometimes modified by stochastic processes, such as planulae swimming behavior, which are included in the model algorithm (e.g. Treml et al. 2008; Hernandez et al. 2014; Johnston and Purkis 2015). This method is computationally swift and allows the production of simulations over long timespans. Larval trajectories in Eulerian IBMs generally mirror the time- and space-averaged direction and speed of water flow at somewhat lower resolution than a Lagrangian algorithm (Johnston and Purkis 2015). By contrast, in a Lagrangian model, larvae are transported through the model grid using an algorithm which uses weighted averaging to diffuse the larvae at discrete time-steps (e.g. 1 h) over the simulation time period (e.g. Lett et al. 2008; Paris et al. 2013; Johnston and Bernard 2017). The position of each larvae at each time-step is corrected using either an iterative bi- or tri-linear interpolation equation (i.e. 2D versus 3D models, respectively). Some Lagrangian models, especially those that are used to simulate high-resolution processes with fine spatial or temporal resolution ocean condition inputs, use a Runge–Kutta 4th-order calculation which integrates a four-step correction process to further refine larval diffusion at each time-step (e.g. Paris et al. 2013). The Runge–Kutta method increases computational overhead but may be desirable for resolving fine-scale processes such as those occurring, for example, along deep ocean escarpments or mouths of canyons when modeling CWCs. Lagrangian and Eulerian IBMs are widely accepted (though Lagrangian IBMs are becoming more common) and robust simulations of particle movement in a fluid and can integrate sub grid-scale processes intended to reflect biological or physical components outside of passive particle transport (Liggins et al. 2013).

40.3.2 Two-Versus Three-Dimensional and Eulerian Versus Lagrangian

Both two-dimensional and three-dimensional Eulerian and Lagrangian IBMs have been used in biophysical modeling studies within and outside of the Mediterranean (e.g. Cowen et al. 2000; Treml et al. 2008; Kool et al. 2010; Andrello et al. 2013; Hernandez et al. 2014; Johnston and Purkis 2015) and each method has strengths and weaknesses. Two-dimensional IBMs (e.g. Treml et al. 2008; Johnston and Purkis 2015) are usually faster computationally, easier to construct and arguable do an acceptable job of simulating the dispersal of organisms whose larvae are typically constrained to the upper layers of the water column (i.e. due to buoyancy and/or lack of vertical water flow), such as many coral larvae including, for part of their pelagic time, those of the CWC *Lophelia pertusa* (Treml et al. 2008; Johnston and Purkis 2015). Still, three-dimensional models are becoming more commonplace as computing technology evolves (i.e. eliminating the need for a super computer) and model algorithms and ocean forecasts are refined. In the deep ocean where CWCs reside, three-dimensional models are requisite as deep ocean circulation does not intrinsically reflect surface conditions and CWC larvae may either vertically migrate/float (e.g. *L. pertusa*) or be neutrally or negatively buoyant transported within deep ocean currents.

Speed and accuracy tradeoffs perhaps exist between Eulerian and Lagrangian IBMs. Many times the end results are similar between the two model paradigms (e.g. Kool et al. 2010 in contraposition to Johnston and Purkis 2015), especially at large spatial and temporal scales. For broad-scale studies, Eulerian IBM algorithms have a speed advantage over Lagrangian, despite their lower resolution, because they integrate fewer parameters for the transport model, which greatly optimises the model algorithm (Hernandez et al. 2014). In contrast, high resolution Lagrangian IBMs more accurately mimic the physics as they relate to larval transport in water. In the end, the resolution compromises inherent to each method must be decided upon given the specific scientific question and available computing power (Liggins et al. 2013).

40.3.3 Integrating the Biological

Biophysical model algorithms integrate the biology of an organism such as a CWC by assimilating the life history characteristics over the model run timespan. For instance, many generic models use 30 days as a typical PLD for marine larvae, tracking the origination, diffusion, and recruitment positions of larvae (e.g. Kool et al. 2010; Paris et al. 2013). Most biophysical models include stochasticity to more realistically integrate sub-grid scale processes that are not otherwise resolved by the model algorithm and also the random nature of animal movements (e.g. Guizien et al. 2006; Paris et al. 2013; Johnston and Purkis 2015). These random processes may represent micro-eddy diffusion or active migration by the larvae, the latter of which is poorly understood for most marine larvae including CWCs. Some models try to mimic diel migrations of larvae and also 'sensory zones', the latter where larvae are capable of actively seeking substrate when passing within a certain distance of suitable habitat such as a reef tract or deep water escarpment (e.g. Kool et al. 2010; Paris et al. 2013; Johnston and Purkis 2015). As these processes are largely untested *in situ*, care must be taken to sensitivity test such integrated sub processes so that error is not unintentionally introduced to the algorithm.

A small subset of biophysical models integrate post-recruitment processes such as adult mortality, maturity, and subsequent reproduction at maturity of successful recruits (e.g. Johnston and Bernard 2017). These 'generational' biophysical models are a further attempt to recreate the natural process and may have utility in forecasting population structure over many years or decades, especially in long-lived species such as CWCs. The outputs of these models can be compared to more traditional and literature-accepted biological connectivity measures such as genetic population structure. Prudence is appropriate when interpreting the results of such models however as empirical abundance data is usually not available for many model species. Forecasted densities and connections between regions thus should be perceived as potential metrics given ocean conditions and model conditioning parameters (i.e. population size, locations, etc.). Still, generational models have advantages in that emergent population structure can be measured over long temporal scopes.

40.3.4 Biophysical Model Products

Given that individual larvae are usually tracked from spawn until recruitment in IBMs, it is possible to quantify not only the connections between release sites and settlement sites, but also the interim and along-path trajectories, for example, of individual CWC larvae. These spatial-temporal data are useful to quantify diffusion probabilities of the particles over space and time and can be illustrated with larval diffusion maps and kernel density heat maps (Fig. 40.1). Both types of maps are useful to visually interpret and quantify spatial patterns of larvae over the simulation time period. As the sources and sinks of propagules are also recorded, kernel density plots can also be used to illustrate source versus sink probabilities (sometimes referred to as densities). As precise empirical abundance data for marine organisms are many times severely lacking, models make assumptions about population size or simply use a fixed population size at specific locations throughout the model grid. The simulations are then initiated using an estimated larval emission rate based on the chosen population size (e.g. Johnston et al. 2017). In such cases, source/sink probabilities cannot be interpolated to natural abundance and should normally be interpreted as potential source (sometimes reported as exporters) and sink (sometimes reported as importers) ratios given the starting conditions of the model and physical characteristics of the synthetic model domain.

Often useful for illustrating transfer probabilities between release and settlement sites are transition or connectivity matrices. Transition matrices are valuable data visualisation tools to help interpret the spatial connectivity of a population as the connections between sources and sinks and simply graphed on an X/Y plot (Fig. 40.2). Each location within the study domain – i.e. a tangible, real world location – is represented by a corresponding position on both the X and Y axes. In the case of IBMs, individual settlement positions are plotted. Alternately, the recruitment positions can be summed and represented as relative densities that are color-coded transfer probabilities that lie on the center diagonal represent self-recruitment – i.e. the source and sink locations are identical or within the same general area. The farther away the positions plot from the diagonal, the greater distance larvae are transported away from the source population on most matrices. Transition matrices are a standardised way of illustrating biological connectivity from biophysical models and can be scaled to any spatial domain.

40.3.5 Limitations of Biophysical Models

Biophysical models are inherently restricted by a paucity of empirically-derived life history traits for many modeled species included CWCs. As such, life history data are often substituted with similar data from a congener or generic species (e.g, Kool et al. 2010; Cardona et al. 2016; Johnston et al. 2017). This situation adds an error factor that can be mitigated by sensitivity testing the biological parameters (Treml et al. 2012). Likewise, life history traits, even if measured empirically, are gradients and so sensitivity testing is also prudent in such cases to establish the likely biological envelope that may be witnessed *in situ* by the model species. The same is true for integrating larval behavior and homing instincts. Much of the science on these components is in infancy. Data are not well verified with empirical studies to a species level and therefore may not be applicable to marine organisms with a passive dispersal strategy, or those that presumably float in surface waters for a majority of the PLD (Treml et al. 2008). Understandably, much care must be

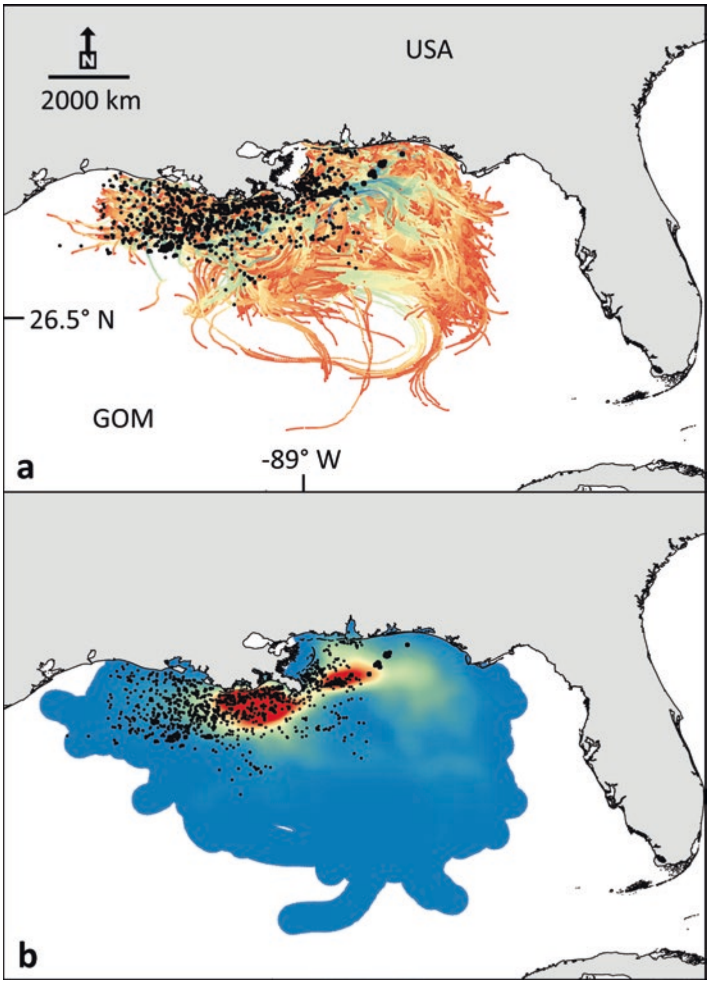

Fig. 40.1 Example diffusion and recruitment pattern (**a**) of the benthic brooding coral *Tubastrea micrantha* on oil platforms in the Gulf of Mexico. Larval diffusion paths are color-colored from cool (blue) to hot (red) spanning the PLD of 14 days. Recruitment positions noted by black dots. Heat map (**b**) demonstrating larval dispersal densities, color coded from blue (low) to red (high). Recruitment positions are black dots (© Matthew Johnston 2018)

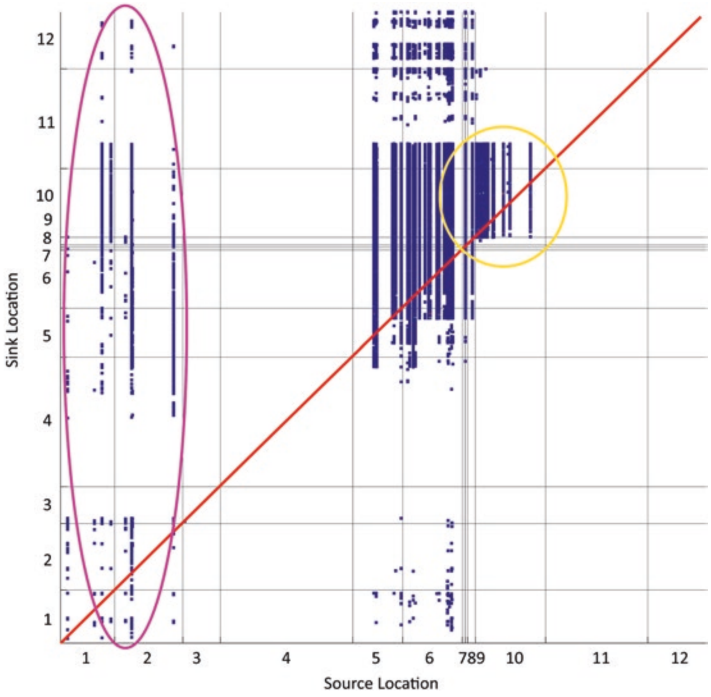

Fig. 40.2 Sample Transition Matrix. Transition matrix illustrating connectivity between 12 regions. Source locations are on the x-axis and sink locations are on the y-axis. Square symbols relay locations of larvae that successfully recruit. Squares near the red diagonal line indicate self-recruitment. Circled in pink are two locations (regions 1 and 2) with high connectivity to other locations. Circled in yellow is a location with high self-recruitment (region 10). (© Matthew Johnston 2018)

given to explain the caveats of including larval behaviors until empirical evidence suggests otherwise.

The physical conditions used to parameterise models are also not typically measured *in situ*, with the exception of bathymetry data which has been historically measured quite accurately with acoustics and does not change appreciably over time. Contemporaneous *in situ* measurements are not typically used for ocean currents and sea surface temperature when modeling because ultra-high resolution, empirical measurements are simply not available at the spatial and temporal scale needed. Most biophysical modelers therefore rely on ocean hindcast models that assimilate data from satellite imagery, drifters, and stationary buoys to supplement the model algorithm (i.e. it is an 'assimilated' model). HyCOM is one of the most utilised global ocean condition models (in the Mediterranean NEMO-MFS and NEMOMED12 are commonly used) by biophysical modelers and the forecasts produced by HyCOM typically mimic real-world conditions to a high level of certainty, especially large scale ocean processes and surface waters. Indeed, cross-validation of HyCOM outputs against *in situ* measurements has shown good correspondence on both a seasonal and annual scales (Kourafalou et al. 2009). Still, HyCOM data are estimates and as such, introduce another level of complexity and error into biophysical model forecasts (HyCOM data are available freely to the public at www.hycom.org).

Beyond parameterisation errors, inaccuracies can be introduced inadvertently into model algorithms by simple human error, which may negatively affect the output produced by the model. Mitigation of these types of systemic errors can be reduced and avoided by having multiple individuals review the algorithm logic and computer code, using sensitivity analysis, and stress testing the model. Still, implicit error must be acknowledged as one of the limitations of aiming to synthetically reproduce a sea-scape such as the Mediterranean Sea within the confines of a virtual, computerised domain.

40.3.6 The Future of Biophysical Modeling

Empirically-measured physical and biological phenomenon and ocean model forecasts continue to improve in spatial and temporal resolution. Accordingly, the biophysical models that ingest these data continue to progress in resolution. Processing times also continue to decrease with technological advances that speed computation time. Both will allow biophysical models to increase the scope of their hindcasts and forecasts over space and time. Though theoretical in nature, biophysical models rely heavily on empirical studies to correctly parameterise the models in both the physical and biological dimensions. As such, field data that can be used to parameterise models are a necessity going forward.

Perhaps the weakest link when parameterising biophysical models is a paucity of studies that accurately document biological drivers of connectivity such as PLD, natural mortality, population sizes, and larval movements of marine organisms. For deep-sea organisms such as CWCs, such information is particularly challenging to obtain and only available for a few species (Davies and Guinotte 2011; Hilário et al. 2015). Ongoing work to quantify the length of PLD, mortality rates, and also movements of planktonic larvae is of particular importance (Treml et al. 2008). Additionally, very few biophysical models integrate a comprehensive suite of post-settlement demographics, including active movement of adults and anthropogenic-induced mortality (Hernandez et al. 2014). Integration of such demographics can provide a clearer picture of overall population structure over time.

In addition to a lack of empirically-derived data on life history traits of model species, there is a challenge yet to be addressed when modeling organisms such as CWCs in the deep layers of the ocean. This is because oceanographic models such as HyCOM produce estimates (i.e. not real measurements) of water flow, salinity, and temperature and while they generally perform well in surface waters, they are largely untested in the deep ocean. Limitations of these estimates impose a challenge enough in the surface layers and are an acknowledged caveat of using model instead of *in situ* data. This challenge is exacerbated in the deep oceans simply because not enough is known about their dynamics and it is difficult and costly to obtain *in situ* measurements of the deep ocean which may be then used to tune ocean models such as HyCOM. Still, progress is being made by the author and others to validate and make recommendations on how ocean models such as HyCOM compare to *in situ* data in an effort to help them more realistically emulate the deep ocean environment. In conclusion, accurate physical and biological components are critical to properly condition biophysical models and are areas of future research that are in continued need to advance the science of biophysical modeling in both the surface and deep layers of the World's oceans, both of which likely are influential environments for Mediterranean CWCs.

References

Andrello M, Mouillot D, Beuvier J, et al (2013) Low connectivity between Mediterranean marine protected areas: a biophysical modeling approach for the dusky grouper *Epinephelus marginatus*. PLoS One 8:e68564

Arellano SM, Van Gaest AL, Johnson SB, et al (2014) Larvae from deep-sea methane seeps disperse in surface waters. Proc R Soc B 281:20133276

Baillon S, Hamel JF, Wareham VE, et al (2014) Seasonality in reproduction of the deep-water pennatulacean coral *Anthoptilum grandiflorum*. Mar Biol 161:29–43

Beazley LI, Kenchington EL (2012) Reproductive biology of the deep-water coral *Acanella arbuscula* (phylum Cnidaria: class Anthozoa: order Alcyonacea), Northwest Atlantic. Deep-Sea Res Part 1 Oceanogr Res Pap 68:92–104

Becheler R, Cassone AL, Noël P, et al (2017) Low incidence of clonality in cold water corals revealed through the novel use of a standardized protocol adapted to deep-sea sampling. Deep-Sea Res Part 2 Top Stud Oceanogr 145:120–130

Borghin M, Bryden H, Schroeder K, et al (2014) The Mediterranean is becoming saltier. Ocean Sci 10:693–700

Brooke S, Järnegren J (2013) Reproductive periodicity of the scleractinian coral *Lophelia pertusa* from the Trondheim Fjord, Norway. Mar Biol 160:139–153

Brooke S, Stone R (2007) Reproduction of deep-water hydrocorals (family Stylasteridae) from the Aleutian Islands, Alaska. Bull Mar Sci 81:519–532

Brooke S, Young CM (2003) Reproductive ecology of a deep-water scleractinian coral, *Oculina varicosa*, from the Southeast Florida shelf. Cont Shelf Res 23:847–858

Brooke S, Young CM, Holmes M (2007) Ch 6. Biological characterization and studies. In: Continental shelf associates. Characterization of northern Gulf of Mexico Deepwater hard bottom communities with emphasis on *Lophelia* coral. Final report to US Dept interior, minerals management service, Gulf of Mexico region. OCS Study 2007-044:119–147

Bryden HL, Candela J, Kinder TH (1994) Exchange through the strait of Gibraltar. Progr Oceanogr 33:201–248

Buonomo R, Assis J, Fernandes F, et al (2017) Habitat continuity and stepping-stone oceanographic distances explain population genetic connectivity of the brown alga *Cystoseira amentacea*. Mol Ecol 26:766–780

Burgess S, Babcock RC (2005) Reproductive ecology of three reef-forming, deep-sea corals in the New Zealand region. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 701–713

Cardona Y, Ruiz-Ramos D, Baums IB, et al (2016) Potential connectivity of Coldwater black coral communities in the northern Gulf of Mexico. PLoS One 11:e0156257

Catarino D, Stefanni S, Jorde PE, et al (2017) The role of the strait of Gibraltar in shaping the genetic structure of the Mediterranean grenadier, *Coryphaenoides mediterraneus*, between the Atlantic and Mediterranean Sea. PLoS One 12:e0174988

Cherubin L, Carton X, Paillet J, et al (2000) Instability of the Mediterranean water undercurrents southwest of Portugal: effects of baroclinicity and of topography. Oceanol Acta 23:551–573

Cordes EE, Nybakken JW, VanDykhuizen G (2001) Reproduction and growth of *Anthomastus ritteri* (Octocorallia : Alcyonacea) from Monterey Bay, California, USA. Mar Biol 138:491–501

Corell H, Moksnes PO, Engqvist A, et al (2012) Depth distribution of larvae critically affects their dispersal and the efficiency of marine protected areas. Mar Ecol Progr Ser 467:29–46

Costantini F, Fauvelot C, Abbiati M (2007) Fine-scale genetic structuring in *Corallium rubrum*: evidence of inbreeding and limited effects of larval dispersal. Mar Ecol Progr Ser 340:100–119

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annu Rev Mar Sci 1:443–466

Cowen RK, Lwiza KM, Sponaugle S, et al (2000) Connectivity of marine populations: open or closed? Science 287(5454):857–859

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311:522–527

D'Onghia G, Capezzuto F, Cardone F, et al (2015) Macro- and megafauna recorded in the submarine Bari canyon (southern Adriatic, Mediterranean Sea) using different tools. Mediterr Mar Sci 16:180–196. https://doi.org/10.12681/mms.1082

Dahl MP, Pereyra RT, Lundälv T, et al (2012) Fine-scale spatial genetic structure and clonal distribution of the cold-water coral *Lophelia pertusa*. Coral Reefs 31:1135–1148

Davies AJ, Guinotte JM (2011) Global habitat suitability for framework-forming cold-water corals. PLoS One 6:e18483

Eckelbarger KJ, Tyler PA, Langton RW (1998) Gonadal morphology and gametogenesis in the sea pen *Pennatula aculeata* (Anthozoa: Pennatulacea) from the Gulf of Maine. Mar Biol 132:677−690

Estournel C, Durrieu de Madron X, Marsaleix P, et al (2003) Observation and modeling of the winter coastal oceanic circulation in the Gulf of lion under wind conditions influenced by the continental orography (FETCH experiment). J Geophys Res Oceans 108(C3)

Feehan K (2016) Highly seasonal reproduction in *Desmophyllum dianthus* from the northern Patagonian fjords. In: Electronic theses and dissertations: 2433. University of Maine. http://digitalcommons.library.umaine.edu/etd/2433

Feehan KA, Waller RG (2015) Notes on reproduction of eight species of eastern Pacific cold-water octocorals. J Mar Biol Assoc UK 95:691–696

Fiksen Ø, Jørgensen C, Kristiansen T, et al (2007) Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. Mar Ecol Progr Ser 347:195–205

Fox AD, Henry LA, Corne DW, et al (2016) Sensitivity of marine protected area network connectivity to atmospheric variability. R Soc Open Sci 3:160494

Freiwald A (2002) Reef-forming CWCs. In: Wefer G, Billet D, Hebbeln D, et al (eds) Ocean margin systems. Springer, Berlin, pp 365–385

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Gaines SD, Gaylord B, Gerber LR, et al (2007) Connecting places: the ecological consequences of dispersal in the sea. Oceanography 20:90–99

Gori A, Bramanti L, Lopez-Gonzalez P, et al (2012) Characterization of the zooxanthellate and azooxanthellate morphotypes of the Mediterranean gorgonian *Eunicella singularis*. Mar Biol 159:1485–1496

Grinyó J (2016) Ecological study of benthic communities in the continental shelf and upper slope in the Menorca Channel (North Western Mediterranean). PhD thesis, Polytechnic University of Catalonia, 170 p. https://doi.org/10.13140/RG.2.2.24275.78885

Guizien K, Bramanti L (2014) Modelling ecological complexity for marine species conservation: the effect of variable connectivity on species spatial distribution and age-structure. Theor Biol Forum 107:47–56

Guizien K, Brochier T, Duchêne JC, et al (2006) Dispersal of *Owenia fusiformis* larvae by wind-driven currents: turbulence, swimming behaviour and mortality in a three-dimensional stochastic model. Mar Ecol Progr Ser 311:47–66

Guizien K, Belharet M, Marsaleix P, et al (2012) Using larval dispersal simulations for marine protected area design: application to the Gulf of lions (Northwest Mediterranean). Limnol Oceanogr 57:1099–1112

Hamner WM, Jones MS, Carleton JH, et al (1988) Zooplankton, planktivorous fish, and water currents on a windward reef face: great barrier reef. Aust Bull Mar Sci 42:459–479

Harii S, Kayanne H (2003) Larval dispersal, recruitment, and adult distribution of the brooding stony octocoral *Heliopora coerulea* on Ishigaki Island, Southwest Japan. Coral Reefs 22:188–196

Harii S, Kayanne H, Takigawa H, et al (2002) Larval survivorship, competency periods and settlement of two brooding corals, *Heliopora coerulea* and *Pocillopora damicornis*. Mar Biol 141:39–46

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Ecosystems of the world: coral reefs. Elsevier, New York, pp 133–207

Hedgecock D, Barber PH, Edmands S (2007) Genetic approaches to measuring connectivity. Oceanography. Spec issue marine Populat conn, vol 20, pp 70–79

Hellberg ME, Burton RS, Neigel JE, et al (2002) Genetic assessment of connectivity among marine populations. Bull Mar Sci 70:273–290

Hernandez O, Lehodey P, Senina I, et al (2014) Understanding mechanisms that control fish spawning and larval recruitment: parameter optimization of an Eulerian model (SEAPODYM-SP) with Peruvian anchovy and sardine eggs and larvae data. Progr Oceanogr 123:105–122

Hilário A, Metaxas A, Gaudron S, et al (2015) Estimating dispersal distance in the deep sea: challenges and applications to marine reserves. Front Mar Sci 2:6

Johnston MW, Bernard AM (2017) A bank divided: quantifying a spatial and temporal connectivity break between the Campeche Bank and the northeastern Gulf of Mexico. Mar Biol 164:12

Johnston MW, Purkis SJ (2014) Are lionfish set for a Mediterranean invasion? Modelling explains why this is unlikely to occur. Mar Pollut Bull 88:138–147. https://doi.org/10.1016/j.marpolbul.2014.09.013

Johnston MW, Purkis SJ (2015) A coordinated and sustained international strategy is required to turn the tide on the Atlantic lionfish invasion. Mar Ecol Progr Ser 533:219–235. https://doi.org/10.3354/meps11399

Johnston MW, Purkis SJ (2016) Forecasting the success of invasive marine species; lessons learned from purposeful reef fish releases in the Hawaiian islands. Fish Res 174:190–200

Johnston MW, Bernard AM, Shivji MS (2017) Forecasting lionfish sources and sinks in the Atlantic: are Gulf of Mexico reef fisheries at risk? Coral Reefs 36:169–181

Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. Curr Biol 1:1314–1318

Jones R, Ricardo GF, Negri AP (2016) Effects of sediments on the reproductive cycle of corals. Mar Pollut Bull 100:13–33

Kool JT, Paris CB, Andréfouët S, et al (2010) Complex migration and the development of genetic structure in subdivided populations: an example from Caribbean coral reef ecosystems. Ecography 33:597–606

Kourafalou VH, Peng G, Kang H, et al (2009) Evaluation of global ocean data assimilation experiment products on South Florida nested simulations with the Hybrid Coordinate Ocean model. Ocean Dyn 59:47–66

Larsson AI, Järnegren J, Strömberg SM, et al (2014) Embryogenesis and larval biology of the cold-water coral Lophelia pertusa. PLoS One 9:e102222

Ledoux J, Garrabou J, Bianchimani O, et al (2010) Fine-scale genetic structure and inferences on population biology in the threatened Mediterranean red coral, *Corallium rubrum*. Mol Ecol 19:4204–4216

Lett C, Verley P, Mullon C, et al (2008) A Lagrangian tool for modelling ichthyoplankton dynamics. Environ Model Softw 23:1210–1214

Liggins L, Treml EA, Riginos C (2013) Taking the plunge: an introduction to undertaking seascape genetic studies and using biophysical models. Geogr Compass 7:173–196

Luiz OJ, Floeter SR, Rocha LA, et al (2013) Perspectives for the lionfish invasion in the South Atlantic: are Brazilian reefs protected by the currents? Mar Ecol Progr Ser 485:1–7

Martinez-Quintana A, Bramanti L, Viladrich N, et al (2015) Quantification of larval traits driving connectivity: the case of *Corallium rubrum* (L. 1758). Mar Biol 162:309–318

McCulloch M, Taviani M, Montagna P, et al (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the younger Dryas. Earth Planet Sci Lett 298:143–152

Mercier A, Hamel JF (2011) Contrasting reproductive strategies in three deep-sea octocorals from eastern Canada: *Primnoa resedaeformis; Keratoisis ornata,* and *Anthomastus grandiflorus*. Coral Reefs 30:337−350

Mercier A, Sun Z, Hamel J-F (2011) Reproductive periodicity, spawning and development of the deep-sea scleractinian coral *Flabellum angulare*. Mar Biol 158:371–380

Miller KJ, Gunasekera RM (2017) A comparison of genetic connectivity in two deep sea corals to examine whether seamounts are isolated islands or stepping stones for dispersal. Sci Rep 7:46103

Miller K, Williams A, Rowden AA, et al (2010) Conflicting estimates of connectivity among deep-sea coral populations. Mar Ecol Evol Perspect 31:144–157

Millot C (1999) Circulation in the western Mediterranean Sea. J Mar Syst 20:423–442

Moksnes PO, Corell H, Tryman K, et al (2014) Larval behavior and dispersal mechanisms in shore crab larvae (*Carcinus maenas*): local adaptations to different tidal environments? Limnol Oceanogr 59:588–602

Orejas C, López-González PJ, Gili JM, et al (2002) Distribution and reproductive ecology of the Antarctic octocoral *Ainigmaptilon antarcticum* in the Weddell Sea. Mar Ecol Progr Ser 231:101–114

Orejas C, Gili JM, López-González PJ, et al (2007) Reproduction patterns of four Antarctic octocorals in the Weddell Sea: an interspecific, shape, and latitudinal comparison. Mar Biol 150:551–563

Orejas C, Gori A, Iacono CL, et al (2009) CWCs in the cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51

Padrón M, Guizien K (2016) Modelling the effect of demographic traits and connectivity on the genetic structuration of marine metapopulations of sedentary benthic invertebrates. ICES J Mar Sci 73:1935–1945

Palanques A, Durrieu de Madron X, Puig P, et al (2006) Suspended sediment fluxes and transport processes in the Gulf of lions submarine canyons. The role of storms and dense water cascading. Mar Geol 234:43–61

Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. Ecol Appl:S146–S158

Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limnol Oceanogr 49:1964–1979

Paris CB, Chérubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. Mar Ecol Progr Ser 347:285–300

Paris CB, Helgers J, Van Sebille E, et al (2013) Connectivity modeling system: a probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. Environ Model Softw 42:47–54

Pinardi N, Masetti E (2000) Variability of the large scale general circulation of the Mediterranean Sea from observations and modelling: a review. Palaeogeogr Palaeoclimatol Palaeoecol 158:153–173

Pires DO, Castro CB, Silva JC (2009) Reproductive biology of the deep-sea pennatulacean *Anthoptilum murrayi* (Cnidaria, Octocorallia). Mar Ecol Progr Ser 397:103–112

Pires DO, Silva JC, Bastos ND (2014) Reproduction of deep-sea reef-building corals from the southwestern Atlantic. Deep-Sea Res Part 2 Top Stud Oceanogr 99:51–63. https://doi.org/10.1016/j.dsr2.2013.07.008

Ricardo GF, Jones RJ, Nordborg M, et al (2017) Settlement patterns of the coral *Acropora millepora* on sediment-laden surfaces. Sci Total Environ 609:277–288

Rice AL, Tyler PA, Paterson GIL (1992) The Pennatulid *Kophobelemnon stelliferum* (Cnidaria, Octocorallia) in the porcupine Seabight (north-East Atlantic Ocean). J Mar Biol Assoc UK 72:417–434

Rogers AD (1999) The biology of *Lophelia pertusa* (LINNAEUS 1758) and other deep-water reef-forming corals and impacts from human activities. Int Rev Hydrobiol 84:315–406

Ross RE, Nimmo-Smith WAM, Howell KL (2017) Towards 'ecological coherence': assessing larval dispersal within a network of existing marine protected areas. Deep-Sea Res Part 1 Oceanogr Res Pap 126:128–138

Rossi V, Ser-Giacomi E, López C, et al (2014) Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves. Geophys Res Lett 41:2883–2891

Rossina AM, Waller RG, Försterra G (2017) Reproduction of the cold-water coral *Primnoella chilensis* (Philippi, 1894). Cont Shelf Res 144:31–37

Siegel DA, Kinlan BP, Gaylord B, et al (2003) Lagrangian descriptions of marine larval dispersion. Mar Ecol Progr Ser 260:83–96

Sponaugle S, Cowen RK, Shanks A, et al (2002) Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. Bull Mar Sci 70:341–375

Strömberg (2016) Early Life History of the Cold-Water Coral *Lophelia pertusa* – with implications for dispersal. PhD thesis, University of Gothenburg, 53 p

Strömberg SM, Larsson AI (2017) Larval behavior and longevity in the cold-water coral *Lophelia pertusa* indicate potential for long distance dispersal. Front Mar Sci 4:411. https://doi.org/10.3389/fmars.2017.00411

Sun Z, Hamel JF, Mercier A (2009) Planulation of deep-sea octocorals in the NW Atlantic. Coral Reefs 28:781

Sun Z, Hamel JF, Mercier A (2010a) Planulation periodicity, settlement preferences and growth of two deep-sea octocorals from the Northwest Atlantic. Mar Ecol Progr Ser 410:71–87

Sun Z, Hamel J-F, Edinger E, et al (2010b) Reproductive biology of the deep-sea octocoral *Drifa glomerata* in the Northwest Atlantic. Mar Biol 157:863–873

Swearer SE, Forrester GE, Steele MA, et al (2003) Spatio-temporal and interspecific variation in otolith trace-elemental fingerprints in a temperate estuarine fish assemblage. Estuar Coast Shelf Sci 56:1111–1123

Taviani M, Angeletti L, Antolini B, et al (2011) Geo-biology of Mediterranean deep-water coral Ecosystems. Marine Research at CNR 6:705–719

Taviani M, Freiwald A, Zibrowius H (2015) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78. https://doi.org/10.1016/j.dsr2.2015.12.008

Thiem Ø, Ravagnan E, Fosså JH, et al (2006) Food supply mechanisms for cold-water corals along a continental shelf edge. J Mar Syst 60:207–219

Thorrold SR, Jones GP, Hellberg ME, et al (2002) Quantifying larval retention and connectivity in marine populations with artificial and natural markers. Bull Mar Sci 70:291–308

Torrents O, Garrabou J, Marschal C, et al (2005) Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L.) in the Marseilles area (France, NW Mediterranean). Biol Conserv 121:391–397

Treml EA, Halpin PN, Urban DL, et al (2008) Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. Landsc Ecol 23:19–36

Treml EA, Roberts JJ, Chao Y, et al (2012) Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. Integr Comp Biol 52:525–537

Treml EA, Ford JR, Black KP, et al (2015) Identifying the key biophysical drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the sea. Mov Ecol 3:1–16

Tsounis G, Rossi S, Bramanti L, et al (2013) Management hurdles for sustainable harvesting of *Corallium rubrum*. Mar Policy 39:361–364

Tyler PA, Bronsdon SK, Young CM, et al (1995) Ecology and gametogenic biology of the genus *Umbellula* (Pennatulacea) in the North Atlantic Ocean. Int Rev Gesamten Hydrobiol Hydrograph 80:187−199

Underwood JN, Smith LD, van Oppen MJH, et al (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Mol Ecol 16:771–784

Underwood JN, Smith LD, van Oppen MJH, et al (2009) Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience. Ecol Appl 19:18–29

Verdier-Bonnet C, Carlotti F, Rey C, et al (1997) A model of larval dispersion coupling wind-driven currents and vertical larval behaviour: application to the recruitment of the annelid *Owenia fusiformis* in Banyuls Bay, France. Mar Ecol Progr Ser 160:217–231

Waller RG (2005) Deep-water Scleractinia (Cnidaria: Anthozoa): current knowledge of reproductive processes. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 691–700

Waller RG, Feehan KA (2013) Reproductive ecology of a polar deep-sea scleractinian, *Fungiacyathus marenzelleri* (Vaughan, 1906). Deep-Sea Res Part 2 Top Stud Oceanogr 92:201–206

Waller RG, Tyler PA (2005) The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic ocean. Coral Reefs 24:514–522

Waller RG, Tyler PA (2011) Reproductive patterns in two deep-water solitary corals from the north-East Atlantic— *Flabellum alabastrum* and *F. angulare* (Cnidaria: Anthozoa: Scleractinia). J Mar Biol Assoc UK 91:669–675

Waller RG, Tyler PA, Smith CR (2008) Fecundity and embryo development of three Antarctic deep-water scleractinians: *Flabellum thouarsii, F. curvatum and F. impensum*. Deep-Sea Res Part 2 Top Stud Oceanogr 55:2527–2534

Ware DM (1975) Relation between egg size, growth, and natural mortality of larval fish. J Fish Board Can 32:2503–2512

Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol Appl 21:335–342

Young C, He R, Emlet R, et al (2012) Dispersal of deep-sea larvae from the intra-American seas: simulations of trajectories using ocean models. Integr Comp Biol 52:483–496

Zhang Z, Chen Q (2007) Comparison of the Eulerian and Lagrangian methods for predicting particle transport in enclosed spaces. Atmos Environ 41:5236–5248

Cross References

Boavida J, Becheler R, Addamo A, et al (this volume) Past, present and future connectivity of Mediterranean cold-water corals: patterns, drivers and fate in a technically and environmentally changing world

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Galil BS (this volume) The spread of non-indigenous species in the Mediterranean – a threat to cold-water corals?

Hayes D, Schoeder K, Poulain PM, et al (this volume) Review of the circulation and characteristics of intermediate water masses of the Mediterranean –implications for cold-water coral habitats

Reynaud S, Ferrier-Pagès C (this volume) Biology and ecophysiology of Mediterranean cold-water corals

Skliris N (this volume) The Mediterranean is getting saltier: from the past to the future

41

Drop Chapter The Interface Between Tectonic Evolution and Cold-Water Coral Dynamics in the Mediterranean

Rinus Wortel and Paul Meijer

Abstract

Circulation and water properties in the Mediterranean basin, and thus the living conditions for marine biota, including cold-water corals, are a strong function of the connectivity of the basin with neighbouring water masses. The configuration of the basin and its connections with adjacent basins are governed by the interplay of large scale and regional scale geodynamical (or tectonic) processes within the Mediterranean region. As to surface area, it appears that the Mediterranean basin as a whole is closing whereas some of its sub-basins are opening, at the expense of the eastern Mediterranean basin. More important are opening or closure of gateway connections. The pertinent Mediterranean gateways to the Atlantic Ocean and the Black Sea are potentially subject to minor changes resulting from tectonics. However, the impact of such possible changes on marine conditions, including those for cold-water corals, would be slow and of minor magnitude compared to the effects of climate change. Typical aspects of cold-water coral occurrences in the Mediterranean region, notably the uplift and outcrops of Plio-Pleistocene communities and the presence of steep faults (with steered fluid seeps providing nutrients) as preferred production areas, are accounted for by vertical motions in subduction zone evolution.

Keywords

Mediterranean Sea · Cold-water corals · Tectonics · Gateways · Marine conditions

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Introduction

We analyse elements of the geodynamics (or, equivalently: tectonics) of the Mediterranean region envisaged to be relevant to the dynamics of cold-water corals (CWCs) and their habitats. Some tectonic effects appear to be direct geosphere-biosphere connections (in particular, the formation of faults scarps as possible habitats, in combination with fluid seeps providing nutrients), whereas others are indirect, with the geosphere-hydrosphere interactions affecting the circulation and marine conditions of the Mediterranean Sea.

The Mediterranean Sea is a marginal basin to the Atlantic Ocean (e.g., Fusco et al. 2008; Lionello et al. 2012), which implies relevant differences of marine conditions, in particular salinity and temperature, between these two basins. In light of the future evolution of CWC habitats, the principal question to address concerns the nature and stability of the Gibraltar Strait which represents the gateway connection between the two basins, and largely controls water masses interchanges. Thus: Is the Mediterranean Basin opening or closing? Whereas relative motion of the large Eurasian and African plates (a slow convergence) primarily seems to control the future of the Mediterranean Sea, we will argue that tectonic processes within the Mediterranean Basin are likely to be of more importance.

Geodynamics of the Mediterranean Region

Africa-Eurasia Convergence and Continental Collision

As its name indicates, the Mediterranean Sea is surrounded by land, or continents. It acquired this so-called *landlocked basin* configuration as a result of the relative motion of the African and Eurasian plates, which in turn is part of the global pattern of relative plate motions as described in plate

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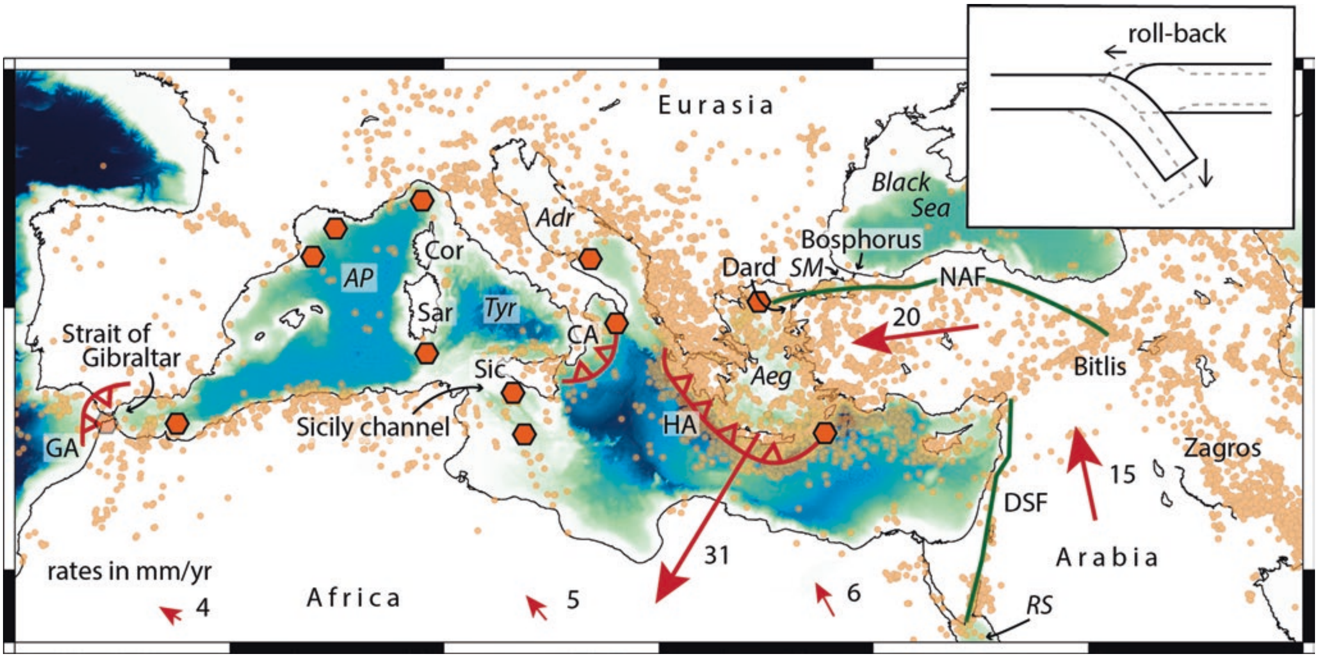

Fig. 41.1 Active tectonics of the Mediterranean. Epicentres of shallow earthquakes (1992–2016, magnitude >4, NEIC catalogue) outline the often diffuse southern boundary of Eurasia. Arrows give motions with respect to Eurasia; rates in mm/year (Reilinger and McClusky, 2011; Nocquet 2012). Discrete faults mentioned in the text are shown in green. Key: *Adr* Adriatic Sea, *Aeg* Aegean Sea, *AP* Alghero-Provençal basin, *CA* Calabrian Arc, *Cor* Corsica, *Dard* Dardanelles, *DSF* Dead Sea Fault, *GA* Gibraltar Arc, *HA* Hellenic Arc, *NAF* North Anatolian Fault, *RS* Red Sea, *Sar* Sardinia, *Sic* Sicily, *SM* Sea of Marmara, *Tyr* Tyrrhenian Sea
Three sites of active or recent subduction (GA, CA, HA) are indicated by the red lines in the main figure. The triangles (dents) along these lines indicate the direction of underthrusting, i.e. the dip direction of the subducted slab (see inset).
Hexagons indicate living occurrences of framework-forming cold-water corals *Lophelia pertusa* and *Madrepora oculata* (compiled from Fink et al. 2015, and Taviani et al. 2017).
Inset: Schematic cross-section of the plate contact region in a subduction zone. In a subduction zone one plate is subducted (underthrust) below another plate. The ocean-floor at the site of downwarping is often marked by a deep-sea trench (which may, however, be filled by sediments). In case of low relative convergence velocities of the plates (less than a few cm/yr) the gravitational forces acting on the cold and, hence, dense subducting plate ("slab") lead to vertical sinking of the slab (indicated by vertical arrow), from the solid line geometry towards the dashed line geometry. This is accompanied by horizontal motion of the trench or hinge zone at the surface ("roll-back", indicated by horizontal arrow, also referred to as "trench migration" or "arc migration"), in the direction opposite to that of underthrusting. The lithosphere above the subducted slab and behind the arc adjacent to the plate contact (cf. the Hellenic, Calabrian and Gibraltar Arcs) is extended ("back-arc extension", towards the dashed line geometry), leading to subsidence of the Earth surface or seafloor. (© Faculty of Geosciences, Utrecht University)

tectonics. The lithosphere is the outer rather strong shell of the Earth, with a thickness characteristically in the order of 100 km. The lithosphere of the Earth is divided in a few tens of large and somewhat smaller units: the "plates". Since about 80 Ma (i.e., 80 million years ago), the large lithospheric plates Eurasia and Africa, the latter encompassing Arabia until approximately 20 Ma, have been converging in an approximately NNW-SSE direction (Fig. 41.1; see Nocquet 2012 for an overview). The oceanic areas between these continents – collectively referred to as Tethys Oceans – gradually decreased in size through the subduction (see Fig. 41.1, inset) of the Tethys lithosphere in a complex subduction (trench) system along the southern margins of Eurasia.

To first order, the subducted lithosphere was oceanic in nature, i.e. the lithosphere was formed by seafloor spreading, at a spreading centre similar to the present-day Mid-Atlantic Ridge. Relative to oceanic lithosphere, continental lithosphere, in particular its upper crustal part, is made up of different rocks, with a lower average density. This tends to hamper the downward motion of subduction when – after an episode of oceanic lithosphere subduction – continental lithosphere approaches and enters the trench of a subduction zone at the margin of a continent, resulting in *continental collision,* which eventually leaves an imprint in the geological structure in the form of a usually complex mountain belt, the *suture zone.* The continuing motion of Africa and Eurasia led to such a process in the region of present-day southeastern Turkey-northern Iran-Irak (in the Bitlis and Zagros suture zone; Fig. 41.1), in the Oligo-Miocene (from ~30 Ma to ~20 Ma; Okay et al. 2010). This was followed by opening of the Red Sea and formation of the Dead Sea Fault, giving rise to the splitting-off of Arabia from the African plate, to form a new separate plate, the Arabian plate. In terms of the underlying oceanic lithospheric basement, the present-day eastern Mediterranean (east of Sicily) is a remnant of the nearly completely lost Tethys Oceans.

Continental collision does not immediately lead to complete closure of all connections between adjacent marine realms; a moderate-depth or shallow connection may remain open for several million years. In case of the Arabia-Eurasia collision, the closure of the Mediterranean-Indian Ocean gateway, at least as a deep marine connection, was probably completed in the Early Tortonian (Miocene), at about 11 Ma (Hüsing et al. 2009). This left the Mediterranean basin with a (composite) gateway to the Atlantic in the west and with connections to the Paratethys – an assemblage of predominantly shallow seas in central and eastern Europe – to the north of it (e.g., Palcu et al. 2015). Of the latter connections, the one to the Black Sea, through the Dardanelles/Sea of Marmara/Bosphorus (Fig. 41.1), is the only one existing at present.

Internal Mediterranean Tectonics

After continental collision between Africa/Arabia and Eurasia in the Oligo-Miocene, the convergence velocity of the two plates decreased by approximately 50%, to the current low values indicated in Fig. 41.1. In that situation, the downward directed gravitational forces acting on the subducted slabs along the northern boundary of the African plate led to roll-back (see Fig. 41.1, inset), the oceanward migration of the subduction zones and their trench systems (Jolivet and Faccenna 2000; Wortel and Spakman 2000). In the western-central Mediterranean the trench migration was in a SE (later E-SE) direction, in the direction of the present-day Calabrian Arc, and also in W direction towards the present-day Gibraltar region (Fig. 41.1). It gave rise to the motion of Corsica, Sardinia and the Calabrian block away from Iberia and (present-day) southern France, from about 30 Ma onward. In the wake of the migrating slab segments, back-arc extension occurred (Fig. 41.1, inset), resulting in subsidence (with velocities of less than 1 mm/year, but nevertheless producing a total subsidence of 1 km or more over a period of a few million years), the formation of oceanic lithosphere and the corresponding opening of the Algero-Provençal basin between Iberia/Southern France and Corsica-Sardinia (which stopped in the Langhian, about 15 Ma) and later the Tyrrhenian Sea. The back-arc extension process in the western Mediterranean is essentially identical, albeit of a smaller spatial scale, to the process of opening by seafloor spreading of a large oceanic basin such as the Atlantic Ocean. The continental margins created by such extensional tectonic processes (seafloor spreading, rifting, back-arc extension) are named *passive continental margins* (active/passive used in the sense of "with/without subduction zones and related geodynamic activity"). Their usual expression is that of a faulted slope with variable gradient, from the coastal region to the deep parts of the basin, possibly with canyon-type of features.

After considerable activity in the Neogene, with (horizontal) velocities of up to ~ 6 cm/year (Faccenna et al. 2001), arc migration and back-arc extension in the central Mediterranean virtually came to an end at ~0.8–0.5 Ma (Goes et al. 2004); the current (GPS) motion of the Calabrian Arc, the last active segment in this region, relative to stable Eurasia is less than 5 mm/year in a NNE direction (Nocquet 2012).

Gutscher et al. (2012) have explored the recent tectonic activity of the Gibraltar Arc region, in the westernmost Mediterranean; they concluded that very slow, ongoing subduction most likely is the underlying process. Also, GPS data testify to the active motion (~5–6 mm/year, relative to Iberia and Africa) of the arc region (Nocquet 2012). The Strait of Gibraltar gateway has known stages with a distinctly restricted connectivity, which gave rise to the Messinian Salinity Crisis (Flecker et al. 2015; Freiwald, this volume).

This "internal" roll-back process in the western-central Mediterranean thus developed into a final stage in which only two relatively narrow slab segments, the east dipping Gibraltar arc segment and the WNW dipping Calabrian arc segment (Fig. 41.1), continued to migrate to the west and east-southeast, respectively (Jolivet and Faccenna 2000; Wortel and Spakman 2000; Spakman and Wortel 2004). Of these two, the Gibraltar segment is particularly relevant for assessing future developments in the circulation and marine conditions of the Mediterranean, since it plays a key role in shaping the gateway to the Atlantic Ocean.

The currently most active trench migration in the region occurs in the eastern Mediterranean, along the Hellenic Arc (Fig. 41.1), at a velocity of about 30 mm/year. It is accompanied by back-arc extension in the Aegean Sea, which, as yet, has not reached the stage of oceanic lithosphere formation.

Influence of Tectonics on Cold-Water Corals

Direct Effects: Vertical Motions of the Ocean-Floor and the Formation of Fault Scarps

Two kinematic aspects of the subduction zone evolution in the Calabrian, Gibraltar and Hellenic Arcs are directly relevant to the past and modern habitats of CWCs in the Mediterranean and to understanding that they are even exposed on outcrops, a truly remarkable feature in the Mediterranean region (Taviani et al. 2005; Roberts et al. 2009, pp 190–191):

(i) At the lateral edges of the migrating slab segments, the roll-back process in the Mediterranean was accompanied by near-vertical faulting (tearing) of the lithosphere (Govers and Wortel 2005) in the Gibraltar area, a significant part of the coastal regions in the central Mediterranean (Tyrrhenian Sea-Sicily-Calabrian arc; Polonia et al. 2016), and in the eastern part of the Hellenic Arc (Özbakir et al. 2013). Probably even the rifting in the Sicily Channel (Fig. 41.1) is caused by the roll-back-process, in this case of the slab in the Calabrian arc (Argnani 2009). We propose that – as a direct effect of tectonics – this may have produced the steeply inclined fault scarps, steep bathymetry gradients and (hard) substrates, apparently favourable as (although not necessary for) CWC growth habitats (Titschack and Freiwald 2005; Titschack et al. 2005; Roberts et al. 2009; Titschack, this volume). Primary productivity being another governing factor crucial for CWC distribution, the interplay between complex seafloor bathymetry and water masses in highly productive areas promotes suitable environmental conditions for CWC habitats (e.g., White et al. 2005; Mienis et al. 2007; Tracey et al. 2011).

(ii) The subduction zone background of the arcs implies that – even in case the horizontal convergence velocities are very low (<10 mm/year) – vertical motions in the arc region are possible, resulting from the evolution of the subducted slab (Govers 2009). From the well-studied Calabrian Arc, it is known that uplift rates may reach values of about 1 mm/year, with maxima of ~ 2.5 mm/year (Antonioli et al. 2006; Faccenna et al. 2011). Such motions are neither an expression of postglacial rebound nor of regional compression or collision (see Taviani et al. 2005); instead they are considered to be intrinsic elements of the subduction process in a transient, terminal stage of activity, possibly including flow of mantle material around slab edges (Faccenna et al. 2011) and breaking-off and sinking of the deep part of a subducting slab (Fig. 41.1, inset; Wortel and Spakman 2000).

The time scale at which Mediterranean CWCs are analysed, determines the perception of the impact of such vertical motions. Also, the time scale of interest for future activity may well differ from that for past activity. Whereas a 1 mm/year uplift rate during a period of 1–2 million years in recent geological history, resulting in a 1–2 km uplift, adequately accounts for the remarkable outcrops of Plio-Pleistocene CWCs in the NE Sicily-Calabria region (Di Geronimo et al. 2005) and Rhodes (Titschack et al. 2005; Titschack and Freiwald 2005; Titschack, this volume), continuing uplift at the same rate integrated over a significantly shorter future period (say 1000 years) would produce a correspondingly small uplift of only 1 m. At present, finally, any tectonic-rate uplift would incur only a minor effect on water depth because sea level rises at a similar pace (Zerbini et al. 2017).

It should be noted that hard substrates and steep bathymetry are not exclusively caused by tectonic activity in or near subduction zones; similar seafloor conditions can be the result of extensional tectonics accompanied by vertical motions, e.g., in rift zones and along the slopes of continental margins. This is evidenced in many CWC occurrences in the Atlantic realm (e.g., Freiwald and Roberts 2005; Roberts et al. 2009) and – to a lesser extent – also in the Mediterranean (see Fig. 41.1), along the Spanish and French margins in the N-NW part of the western Mediterranean, in the rift zone of the Sicily Channel, off the South coast of Sardinia, and probably also in the Adriatic Sea and the northern Aegean Sea (e.g., Taviani et al. 2017, this volume).

The above effects of tectonics on CWC dynamics are direct not only in a causal sense, but also spatially. They are localised at or near places where tectonic processes occur(red), and their spatial scale is local to regional. With respect to differences and similarities in CWC habitats between the Atlantic Ocean and the Mediterranean Sea, we note that extensional tectonic processes inherent to the formation of passive continental margins (see Sect. *Internal Mediterranean Tectonics*) have been extremely prominent in the Atlantic Ocean (passive continental margins are often termed “Atlantic margins”) where they form elongated belts, parallel to the strike of the continental margins. These are readily identified in the distribution of CWC occurrences in the Atlantic Ocean (Roberts et al. 2009, pp 28–29, their Figs. 2.3 and 2.5). In the smaller and more variable setting of the Mediterranean basin the passive margins are of more restricted dimensions, and less dominant. Hence, in the CWC distribution in the Mediterranean both passive margins and subduction zones (at active margins) play a role and, jointly, contribute to a more irregular distribution pattern than in the Atlantic Ocean, even including surface exposure.

Indirect Effects: The Control of Tectonics on Marine Conditions

A widespread, basin-scale influence due to tectonics is possible through tectonic control on the shape of the gateways. This represents an indirect effect of tectonics on CWCs: Changes in gateway depth and width may critically affect the connectivity between the basins involved and potentially result in changes in the temperature, salinity, nutrient availability and ventilation which are all thought to impact on CWC development (Freiwald and Roberts 2005; Alvarez-Perez et al. 2005; Roberts et al. 2006; Fink et al. 2012, 2015; see Smith et al. (2000) for a relationship proposed to use CWC properties to infer paleotemperatures). The literature on the role of gateways is vast; in the context of the past circulation of the Mediterranean, see e.g. Rogerson et al. (2010, 2012), Meijer (2012), Simon and Meijer (2015), de la Vara et al. (2015), de la Vara and Meijer (2016); for the present-day Mediterranean, see also Hayes et al. (this volume) and references therein. For the earlier Paratethys evolution this is a subject of active research (Palcu et al. 2015), aiming at unravelling the Middle Miocene extinction of marine species in the central Paratethys (the eastern part, present-day Romania). This prompts the question: Is the present gateway configuration stable? To answer this question, we briefly explore the stability of the gateways (once) connecting the Mediterranean Sea to the outside, in particular the now closed one in the east (Bitlis), and the only now existing gateway connection with the Paratethys, the Dardanelles/Sea of Marmara/Bosphorus gateway, or briefly, the Bosphorus (Fig. 41.1). In the previous section, we already reviewed the subduction zone background of the Gibraltar Arc and the corresponding open gateway to the Atlantic, the Strait of Gibraltar, including its current horizontal and possible vertical motions.

Eastern Gateway (Bitlis) Continental collision hampers subduction but does not necessarily terminate it. If the forces driving the converging plates can overcome the increased resistance, subduction continues albeit at an often significantly reduced rate. This appears to be the case for the Africa-Eurasia motion: for the Bitlis suture zone, along the Arabia-Eurasia plate boundary high resolution GPS measurements indicate a 15–20 mm/year motion of Arabia relative to Eurasia, in NNW direction (Reilinger and McClusky 2011). Thus, in this region the former gateway to the Indian Ocean is firmly closed and continuing plate motion will maintain this condition.

Bosphorus In contrast with the Gibraltar gateway, the Bosphorus gateway to the Black Sea is not associated with a retreating slab segment in a subduction zone (roll-back). It is, however, located near the active North Anatolian Fault (NAF) and its extensions into the Sea of Marmara (Fig. 41.1). Oktay et al. (2002) proposed that the present Bosphorus connection resulted from the propagation of the NAF into the Sea of Marmara region; new rupturing of the right-lateral NAF in the Sea of Marmara region, with clockwise rotations of the two blocks on each side of the Bosphorus, was accompanied by left-lateral NNE trending faults affecting the area of the strait and the structure of the strait itself ("book shelf faulting").

In the past century, seismic activity along the NAF has been very considerable, with a distinct east-to-west migration, approaching the Istanbul area. In the context of possible further westward migration, recent analyses of seismicity and GPS observations led to the identification of a distinct seismic gap (with a length of 30–45 km) in the fault segments in the central and eastern Sea of Marmara (Bohnhoff et al. 2013; Ergintav et al. 2014; Schmittbuhl et al. 2016). The seismic gap is an indication of delayed earthquake activity. The length of the gap and the estimated present slip deficit of ~ 2.5 m are considered to be sufficient to generate a magnitude ~ 7 earthquake. The time scale for possible long-term changes, however, is governed by the long- term (horizontal) relative motion along the North Anatolian Fault (about 23–25 mm/year; Nocquet 2012; Schmittbuhl et al. 2016).

Both the Bosphorus and the Strait of Gibraltar provide the Mediterranean Sea with an outlet for its relatively salty waters and both act as a source ("inlet") of water of lower salinity. Tectonically induced further constriction of these gateways would thus raise Mediterranean average salinity, and vice-versa. The Strait of Gibraltar also affects mean water temperature in that it compensates the loss of heat incurred from the exchange of heat between the sea and the atmosphere. Of the internal processes, perhaps the continuing migration of the Hellenic Arc may entail a small change in the deep circulation, given that the arc accommodates the passage (east and west of Crete) of dense waters formed in the Aegean Sea.

Any tectonically induced change in marine conditions is likely to be slow and best considered a long-term trend (100 kyr to 1 Myr) overprinted by the higher frequency change due to, among others, orbital-induced climate variation (Skliris this volume, discusses the current rise in salinity related to changes in the water cycle). Of course, the very fact that the Mediterranean basin is sensitive to these climatic changes is due to its gateway-controlled landlocked nature and thus, ultimately, a consequence of tectonics.

Conclusions

The ongoing large-scale motion of the Eurasian and African plates drives active and continuing *closing* (i.e., decrease of surface area) of the Mediterranean Sea basin as a whole. Within the Mediterranean basin, arc migration and back-arc extension continue to lead to changing configurations of sub-basins, implying that the basins, notably the Aegean Sea and possibly – to a very minor extent – the Tyrrhenian Sea, are *opening*, i.e. increasing in size, at the expense of the Eastern Mediterranean basin. More importantly than a reduction in surface dimensions of the Mediterranean Sea, tectonic processes may lead to changes in the width and/or depth of the Strait of the Gibraltar and Bosphorus gateways. The impact of such possible changes on marine conditions relevant for CWCs, however, would be slow and of minor magnitude compared to the effects of climate change.

Typical aspects of CWC occurrences in the Mediterranean region, notably the presence of steep fault scarps (as preferred production areas) and the (long-term) uplift and surface exposure of Plio-Pleistocene CWCs, are accounted for by faulting processes and vertical motions characteristic for the terminal stage the Mediterranean subduction zones are in.

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References

Alvarez-Perez G, Busquets P, de Mol B, et al (2005) Deep-water coral occurrences in the Strait of Gibraltar. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 207–221

Antonioli F, Ferranti L, Lambeck K, et al (2006) Late Pleistocene to Holocene record of changing uplift rates in southern Calabria and northeastern Sicily (southern Italy, Central Mediterranean Sea). Tectonophysics 422:23–40

Argnani A (2009) Evolution of the southern Tyrrhenian slab tear and active tectonics along the western edge of the Tyrrhenian subducted slab. In: van Hinsbergen DJJ, Edwards M, Govers R (eds) Collision and collapse at the Africa–Arabia–Eurasia subduction zone. The Geological Society, London, Special Publications 311:193–212

Bohnhoff M, Bult F, Dresen G, et al (2013) An earthquake gap south of Istanbul. Nat Commun 4:1999. https://doi.org/10.1038/ncomms2999

de la Vara A, Meijer P (2016) Response of Mediterranean circulation to Miocene shoaling and closure of the Indian gateway – a model study. Palaeogeogr Palaeoclimatol Palaeoecol 442:96–109

de la Vara A, Topper RPM, Meijer PT, et al (2015) Water exchange through the Betic and Rifian corridors prior to the Messinian salinity crisis: a model study. Paleoceanography 30. https://doi.org/10.1002/2014PA00271

di Geronimo J, Messina C, Rosso A, et al (2005) Enhanced biodiversity in the deep: early Pleistocene coral communities from southern Italy. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 61–86

Ergintav S, Reilinger RE, Çakmak R, et al (2014) Istanbul's earthquake hot spots: geodetic constraints on strain accumulation along faults in the Marmara seismic gap. Geophys Res Lett 41:5783–5788

Faccenna C, Funiciello F, Giardini D, et al (2001) Episodic backarc extension during restricted mantle convection in the Central Mediterranean. Earth Planet Sci Lett 187:105–116

Faccenna C, Molin P, Orecchio B, et al (2011) Topography of the Calabria subduction zone (southern Italy): clues for the origin of Mt. Etna. Tectonics 30. https://doi.org/10.1029/2010TC002694

Fink HG, Wienberg C, Hebbeln D, et al (2012) Oxygen control on Holocene cold-water coral development in the eastern Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 62:89–96

Fink HG, Wienberg C, De Pol-Holz R, et al (2015) Spatio-temporal distribution patterns of Mediterranean cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) during the past 14,000 years. Deep-Sea Res Part 1 Oceanogr Res Pap 103:37–48

Flecker R, MEDGATE team (2015) Evolution of the late Miocene Mediterranean-Atlantic gateways and their impact on regional and global environmental change. Earth-Sci Rev 150:365–392

Freiwald A, Roberts JM (eds) (2005) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, 1243 p

Fusco G, Artale V, Cotroneo Y, et al (2008) Thermohaline variability of Mediterranean water in the Gulf of Cadiz, 1948–1999. Deep-Sea Res Part 1 Oceanogr Res Pap 55:1624–1638

Goes S, Giardini D, Jenny S, et al (2004) A recent tectonic reorganization in the south-central Mediterranean. Earth Planet Sci Lett 226:335–345

Govers R (2009) Choking the Mediterranean to dehydration: the Messinian salinity crisis. Geology 37:167–170

Govers R, Wortel MJR (2005) Lithosphere tearing at STEP faults: response to edges of subduction zones. Earth Planet Sci Lett 236:505–523

Gutscher MA, Dominguez S, Westbrook GK, et al (2012) The Gibraltar subduction: a decade of new geophysical data. Tectonophysics 574-575:72–91

Hüsing SK, Zachariasse WJ, van Hinsbergen DJJ, et al (2009) Oligocene-Miocene basin evolution in SE Anatolia: constraints on the closure of the eastern Tethys gateway. Geol Soc Lond Spec Publ 311:107–132

Jolivet L, Faccenna C (2000) Mediterranean extension and the Africa-Eurasia collision. Tectonics 19:1095–1106

Lionello P, Abrantes F, Congedi L, et al (2012) Introduction: Mediterranean climate—background information. In: Lionello P (ed) The climate of the Mediterranean region: from the past to the future. Elsevier, pp xxxv–xc

Meijer PT (2012) Hydraulic theory of sea straits applied to the onset of the Messinian salinity crisis. Mar Geol 326–328:131–139

Mienis F, de Stigter HC, White M, et al (2007) Hydrodynamic controls on cold-water coral growth and carbonate-mound development at the SW and SE Rockall Trough Margin, NE Atlantic Ocean. Deep-Sea Res Part 1 Oceanogr Res Pap 54:1655–1674

Nocquet JM (2012) Present-day kinematics of the Mediterranean: a comprehensive overview of GPS results. Tectonophysics 579:220–242

Okay AI, Zattin M, Cavazza W (2010) Apatite fission track data for the Miocene Arabia-Eurasia collision. Geology 38:35–38

Oktay FY, Gökasan E, Sakinc M, et al (2002) The effects of the North Anatolian Fault Zone on the latest connection between Black Sea and Sea of Marmara. Mar Geol 190:367–382

Özbakir AD, Şengör AMC, Wortel MJR, et al (2013) The Pliny – Strabo trench region: a large shear zone resulting from slab tearing. Earth Planet Sci Lett 37:188–195

Palcu DV, Tulbure M, Bartol M, et al (2015) The Badenian-Sarmatian extinction event in the Carpathian foredeep basin of Romania: paleogeographic changes in the paratethys domain. Glob Planet Chang 133:346–358

Polonia A, Torelli L, Artoni A, et al (2016) The Ionian and Alfeo-Etna fault zones: new segments of an evolving plate boundary in the central Mediterranean Sea? Tectonophysics 675:69–90

Reilinger R, McClusky S (2011) Nubia-Arabia-Eurasia plate motions and the dynamics of Mediterranean and Middle East tectonics. Geophys J Int 186:971–979

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Roberts JM, Wheeler A, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, p 334. https://doi.org/10.1017/CBO9780511581588

Rogerson M, Colmenero-Hidalgo E, Levine RC, et al (2010) Enhanced Mediterranean-Atlantic exchange during Atlantic freshening phases. Geochem Geophys Geosyst 11:Q08013. https://doi.org/10.1029/2009GC002931

Rogerson M, Rohling EJ, Bigg GR, et al (2012) Paleoceanography of the Atlantic- Mediterranean exchange: overview and first quantitative assessment of climatic forcing. Rev Geophys 50:RG2003. https://doi.org/10.1029/2011RG000376

Schmittbuhl J, Karabulut H, Lenglin O, et al (2016) Seismicity distribution and locking depth along the Main Marmara Fault, Turkey. Geochem Geophys Geosyst 17:954–965. https://doi.org/10.1002/2015GC006120

Simon D, Meijer P (2015) Dimensions of the Atlantic-Mediterranean connection that caused the Messinian Salinity Crisis. Mar Geol 364:53–64

Smith JE, Schwarcz HO, Risk MJ, et al (2000) Paleo temperatures from deep-sea corals: overcoming “vital effects”. Palaios 15:25–32

Spakman W, Wortel R (2004) A tomographic view on Western Mediterranean geodynamics. In: Cavazza W, Roure F, Spakman W, et al (eds) The TRANSMED Atlas: the Mediterranean region from crust to mantle. Springer, Berlin, Heidelberg, pp 31–52

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Taviani M, Angeletti L, Canese S, et al (2017) The “Sardinian cold-water province” in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78

Titschack J, Freiwald A (2005) Growth, deposition and facies of Pleistocene bathyal coral communities from Rhodes, Greece. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 41–59

Titschack J, Bromley RG, Freiwald A (2005) Plio-Pleistocene cliff-bound, wedge-shaped, warm-temperate carbonate deposits from Rhodes (Greece): sedimentology and facies. Sediment Geol 180:29–56

Tracey DM, Rowden AA, Mackay KA, et al (2011) Habitat-forming cold-waters show affinity for seamounts in the New Zealand region. Mar Ecol Progr Ser 430:1–22

White M, Mohn C, de Stigter H, et al (2005) Deep-water coral development as a function of hydrodynamics and surface productivity around submarine banks of the Rockall Trough, NE Atlantic. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 503–514

Wortel MJR, Spakman W (2000) Subduction and slab detachment in the Mediterranean-Carpathian region. Science 290:1910–1917

Zerbini S, Raicich F, Prati CM, et al (2017) Sea-level change in the Northern Mediterranean Sea from long-period tide gauge time series. Earth-Sci Rev 167:72–87

Cross References

Freiwald A (this volume) Messinian salinity crisis: what happened to cold-water corals?

Hayes DR, Schroeder K, Poulain PM, et al (this volume) Review of the circulation and characteristics of intermediate water masses of the Mediterranean – implications for cold-water coral habitats

Skliris N (this volume) The Mediterranean is getting saltier: from the past to the future

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals

Titschack J (this volume) Bathyal corals within the Aegean Sea and the adjacent Hellenic trench

42

Drop Chapter
The Mediterranean Is Getting Saltier: From the Past to the Future

Nikolaos Skliris

Abstract

The Mediterranean region is getting drier. Evaporation has been steadily increasing over the last few decades driven by the rapid surface warming implying an increase of latent heat loss from the sea surface. A long-term decrease of river freshwater discharge has been also observed since the early 1960s, reflecting the impact of both river damming and recent climate change. As a result of the net evaporation increasing rate, the salt content of the basin has been also strongly increasing over the last four to five decades with this salinification signal rapidly travelling from the surface into the deep layers via the intense Mediterranean overturning circulation. Long-term increases were also observed in the salinity of the Levantine Intermediate Water layer throughout the basin, which strongly influences cold-water coral habitats and distribution. Climate models predict that the present warming and salinification trends will be accelerated over this century and they are expected to have strong impacts on marine ecosystems and biodiversity.

Keywords

Mediterranean Sea · Salinity · Water cycle · Evaporation · River runoff · Cold-water corals

The Mediterranean is a semi-enclosed strongly evaporative basin, i.e. evaporation exceeds precipitation and river runoff. Therefore, it functions as a concentration basin which is evidenced from the transformation of the inflowing low salinity Atlantic surface waters (i.e. with a salinity of about 36.2 at the Strait of Gibraltar) into very saline Mediterranean intermediate and deep waters (with a deep water salinity of about 38.4 and 38.7 in the western and eastern subbasins, respectively). The density contrast between the highly saline Mediterranean water and the relatively fresh Atlantic Water (AW) drives an inverse estuarine circulation with Mediterranean water of high salinity exiting through the bottom of the Gibraltar Strait into the Atlantic Ocean.

The high salt content plays a key role in mixing and dense water formation processes. The Mediterranean has a very active thermohaline (overturning) circulation (see Hayes et al., this volume) with very strong intermediate and deep water formation in various sites of the basin (Fig. 42.1), and for this reason, it is often described as a laboratory model to study the global overturning circulation and to investigate its impacts on marine ecosystems and the earth's climate system (e.g. Malanotte-Rizzoli and Eremeev 1999). Northern parts of the basin, such as the Gulf of Lions, the Adriatic Sea and the Aegean Sea, are characterised by continental very dry and cold winds during winter inducing strong cooling and salting of the surface layer and thus increasing its density, which, in combination with local intense cyclonic circulation features strongly favour deep water formation. In addition, the Levantine Intermediate Water (LIW) a very salty water mass formed through excessive evaporation in the northeastern Levantine basin, spreading at intermediate depths (200–600 m) throughout the whole basin, enhances mixing and strongly preconditions the water column for deep water formation (Hayes et al., this volume). The intensity of the overturning has major impacts on Mediterranean ecosystems as it controls deep-water renewal, oxygenation and nutrient replenishment of the upper layers. Moreover, LIW strongly influences cold-water coral (CWC) habitats. The CWC living grounds are usually found at depths ranging 350–600 m with maximum growth typically taking place close to the LIW core (Taviani et al. 2017; Chimienti et al., this volume; Hayes et al., this volume; Lo Iacono et al., this volume; Vertino et al., this volume).

Another important feature of the Mediterranean is that it is very sensitive to environmental and climate perturbations

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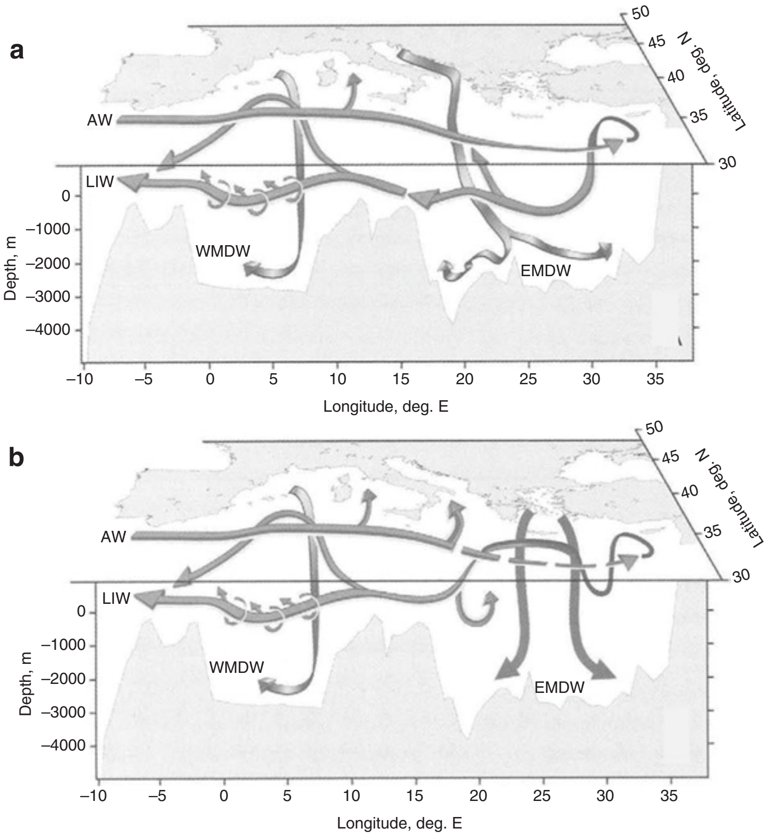

Fig. 42.1 (**a**) Mediterranean thermohaline circulation schematic prior to the Eastern Mediterranean Transient (*EMT*) and (**b**) during the *EMT*. Pathways of main water masses including Atlantic Water (*AW*), Levantine Intermediate Water (*LIW*), Eastern Mediterranean Deep Water (*EMDW*) and Western Mediterranean Deep Water (*WMDW*) are depicted. (From Tsimplis et al. 2006. © Elsevier)

and it is considered to be a "hotspot" for climate change (Giorgi 2006; Maier et al., this volume). Large industrial and population agglomerations surrounding the Mediterranean Sea severely impact its marine ecosystems (Belkin 2009; Macias et al. 2014). The Mediterranean is a temperate transition region influenced by both the North African climate, characterised by warmer and drier conditions, and the European climate, characterised by cooler and wetter conditions. In addition, due to its shape and limited exchange with adjacent basins, changes in the surface heat and freshwater budgets cannot be compensated for by changes in the exchange flows at the straits but mainly by changes in the hydrological properties of the basin (Bethoux and Gentilli 1999), which in turn strongly affect its overturning circulation and ecosystems (Skliris et al. 2007).

In a steady-state balance of the salt budget, the salinity increase in the basin due to intense net evaporation (evaporation-precipitation-river runoff) is compensated for by net freshwater inputs at the straits connecting the Mediterranean with the adjacent basins, i.e. the Gibraltar Strait and to a lesser extent the Dardanelles Straits (exchange with the Black Sea). However, in the geological past, the Mediterranean salt budget was far from being close to a balance with drastic changes being observed in its thermohaline and ecosystem properties. Over the so-called Messinian Salinity Crisis (Krijgsman et al. 1999), a geological event that occurred around 6 million years ago, the precursor of the Gibraltar Strait was closed, and the strong evaporative conditions in the absence of the fresh Atlantic inflow dramatically increased salinity at levels not tolerated by many organisms, including corals, strongly reducing biodiversity of the basin (Freiwald, this volume; Wortel and Meijer, this volume). Large changes in the Mediterranean hydrological properties also took place in the recent geological past with dire consequences for the CWC habitats (Taviani et al., this volume; Vertino et al., this volume). The Younger Dryas period (11,700–12,900 years ago) was the driest interval of the past 20,000 years (Kotthoff et al. 2008) with almost glacial conditions and strong salting of the basin. On the contrary, the Holocene Climatic Optimum (~6000–10,000 years ago) was a very warm and humid period for the Mediterranean region resulting in an intense freshening of the basin. The burial of the Tyrrhenian coral mounds under a thin veneer of silt, c. 11,000 years ago, seems to be related to increased continental runoff that reached its maximum between 6000 and 9000 years ago (Remia and Taviani 2005). In particular, surface salinity was drastically reduced by four to seven below the present values in the Levantine Basin (Emeis et al. 2000). As a consequence of lighter surface waters, the overturning circulation and deep-water renewal were considerably reduced. This in turn led to the development of deep-sea water anoxia with severe implications for the Mediterranean ecosystems (Emeis et al. 2000; Rohling et al. 2015).

Before the 1990s, it was assumed that in the present era the Mediterranean freshwater budget was close to a balance with small variations in the salt content of the basin. However, recent research demonstrated that the Mediterranean is getting saltier following the rapid warming over the last few decades. For example, thermodynamics indicate that the global water cycle is amplifying in a warming climate with dry regions getting drier and wet regions getting wetter (Held and Soden 2006). Although changes in evaporation and precipitation are very hard to measure (Hegerl et al. 2015), recent droughts in the Mediterranean region have been already associated with anthropogenically forced drying trends (Kelley et al. 2012). The last drought in the Levant (1998–2012) was probably the driest in the 900-year record (Cook et al. 2016). Observational studies indicate a continuous increase in evaporation over the Mediterranean Sea driven by the rapid surface warming during the last three to four decades implying an increase of latent heat loss from the sea surface (Mariotti 2010; Romanou et al. 2010; Skliris et al. 2012, 2018).

A large decrease in precipitation has also been observed over the second half of the twentieth century (Krahman and Schott 1998; Tsimplis and Josey 2001). However, the precipitation rate over the Mediterranean is also controlled by natural variability related to the northern hemisphere atmospheric circulation that is mainly expressed by the so-called North Atlantic Oscillation (NAO) (Hurrell 1995). The long-term increase of the NAO index from the late 1960s to the mid-1990s was suggested to be a key factor contributing to the reduced precipitation over the Mediterranean Sea during this period (Krahman and Schott 1998; Tsimplis and Josey 2001).

A long-term decrease of freshwater input in the Mediterranean is associated with decreasing river freshwater discharge, reflecting the impact of both river damming and recent climate change. A decrease larger than 50% in the freshwater discharge of rivers feeding directly or indirectly (i.e. the Black Sea rivers through the Dardanelles inflow) the Mediterranean Sea was estimated since the second half of the nineteenth century due to damming (Poulos and Drakopoulos 2001). Ludwig et al. (2009) estimated a reduction in the river freshwater discharge in the Mediterranean basin of at least 20% between 1960 and 2000. After the construction of the Aswan Dam in the early 1960s, the Nile river runoff was drastically reduced affecting the salt budget and the thermohaline circulation of the whole basin for several decades (Rohling and Bryden 1992; Skliris and Lascaratos 2004; Skliris et al. 2007). Although the effects of these thermohaline circulation changes on deepwater corals are still unknown, negative consequences are reported for deep marine ecosystems, such as the drop in abundance of deep-sea shrimp (Cartes et al. 2011) as well as in sharks and other top predators of the Mediterranean Sea (Cartes et al. 2013).

Atmospheric model reanalysis products, based on the assimilation of various observational data, also show a strong increase in net evaporation over the Mediterranean Sea surface over the last few decades (Mariotti et al. 2015), largely exceeding estimations of global water cycle amplification. This finding is also supported by coupled climate model historical simulations, although the obtained evaporation increases are much less pronounced as compared to atmospheric reanalyses and observations (Mariotti et al. 2015).

With the global ocean receiving about 80% of surface freshwater fluxes, the three-dimensional ocean salinity field is considered to be an integrator of changes in the global water cycle. In contrast with air-sea freshwater fluxes, salinity is a well-measured parameter, especially over the last few decades. Surface salinity observations clearly indicate that precipitation-dominated oceanic regions such as the tropical and subpolar regions are getting less saline and evaporation-dominated oceanic regions such as the subtropical gyres and evaporative marginal seas, such as the Mediterranean, are getting saltier (Durack and Wijffels 2010; Skliris et al. 2014). Recent studies inferring water cycle changes from salinity observations indicate a global water cycle amplification ranging 2–4% over the last 50–60 years (Durack et al. 2012; Skliris et al. 2014, 2016). Salinity-inferred net evaporation increase is estimated to be much larger over the Mediterranean Sea at 8–12% over 1950–2010 (Skliris et al. 2018).

Together with warming, coherent and robust trends of increased salinity are evidenced in key Mediterranean water masses since the 1950s, consistent with the strong net evaporation increase (Rohling and Bryden 1992; Krahman and Schott 1998; Bethoux and Gentili 1999; Rixen et al. 2005; Vargas-Yanez et al. 2010; Borghini et al. 2014; Schroeder et al. 2016). The deep waters of the western basin have become saltier for at least the past 40 years at rates of about 0.015 per decade (Borghini et al. 2014). Below 1000 m depth, the Mediterranean basin exhibited the strongest salinity gain in the World Ocean since 1950 (Skliris et al. 2014). Long-term increasing trends in the LIW core salinity are also reported throughout the basin (Rohling and Bryden 1992; Skliris and Lascaratos 2004; Borghini et al. 2014). Salinity increases at intermediate layers were partially attributed to the Nile outflow drastic reduction after the mid-1960s when induced an enhanced salt preconditioning for LIW formation and a large increase in the salinity of the newly formed intermediate waters (Skliris and Lascaratos 2004; Skliris et al. 2007). The LIW circulation spread this salinification signal westward and through the Sicily Strait into the western Mediterranean basin (Hayes et al., this

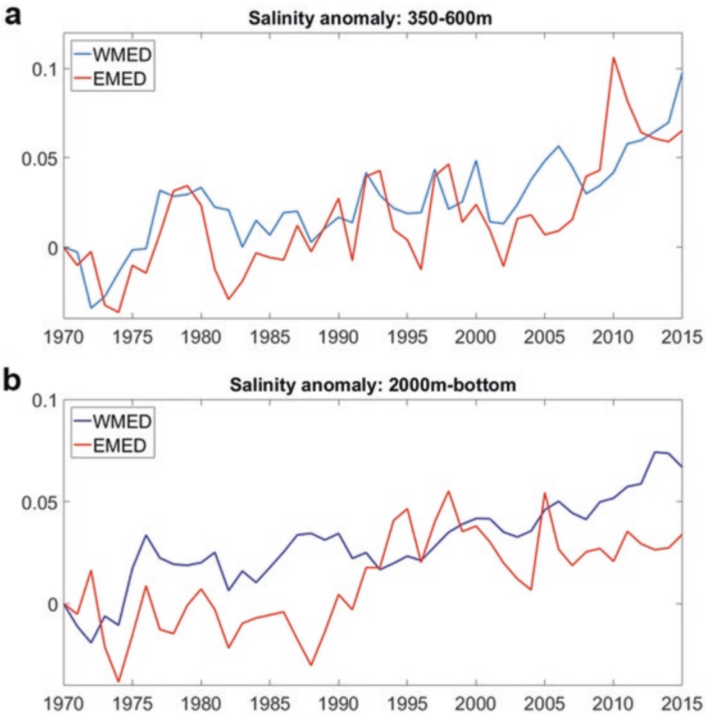

Fig. 42.2 (**a**) Volume-averaged salinity anomaly annual time series over 1970–2015 for the Western Mediterranean (*WMED, blue lines*) and Eastern Mediterranean (*EMED, red lines*) subbasins and for the 350–600 m layer and (**b**) the 2000 m - bottom layer. Salinity data are derived from the Enhanced Ocean Data Assimilation and Climate prediction (ENACT) archive version 4 (EN4, subversion En4.1.1, http://www.metoffice.gov.uk/hadobs/en4) objectively analysed monthly observational dataset. (Good et al. 2013)

volume). These large changes in LIW formation rate, hydrological properties and circulation are expected to affect occurrence and distribution patterns of CWC habitats as well as corals' biology and physiology. The effects of hypersaline or hyposaline conditions on shallow-water corals are found to be in general negative (e.g. Jokiel et al. 1993; Ferrier-Pagès et al. 1999; Kuanui et al. 2015) or positive in other cnidarians where salinity interacts with other factors, such as temperature (Gegner et al. 2017). Salt content of the 350–600 m layer, where maximum CWC growth is typically observed (Taviani et al. 2017), increased in both the eastern and western Mediterranean subbasins since the early 1970s at rates of about 0.02 per decade (Fig. 42.2).

The increasing salinity rate in the intermediate and deep layers seems to be accelerated over recent extreme climate transient events (i.e. abrupt shifts of the "ocean climate" with large changes in the thermohaline circulation and hydrological properties, see Fig. 42.2), i.e. the Eastern Mediterranean Transient (EMT) during the 1990s (e.g. Klein et al. 1999) and the Western Mediterranean Transient (WMT), which started in the mid-2000s (e.g. Schroeder et al. 2016; Hayes et al., this volume). These abrupt salinity changes seem to be superimposed on the longer-term quasilinear increases in salinity due to changes in surface freshwater fluxes associated with global warming and/or natural variability. Such climate transient events may be more frequent and extreme in the future as the salinity of the basin continues to increase inducing a more efficient salt preconditioning of the water column for deep water formation.

The long-term increased Mediterranean salinity signal is also evidenced in the Mediterranean Outflow Water (MOW) exiting into the Atlantic ocean, and it is clearly depicted at intermediate depths (1000–1500 m) in the subtropical Northeast Atlantic (Curry et al. 2003; Potter and Lozier 2004; Skliris et al. 2014). The MOW salty vein reaching the northern Atlantic is a very important factor impacting deep water formation processes in the North Atlantic (Reid 1979; McCartney and Mauritzen 2001). Hydrological observations show that warming almost compensates for the salting effect resulting in no significant change in density in MOW over the second half of the twentieth century (Potter and Lozier 2004). However, over the last 15 years, a strong density increase is observed in the deep layer of the western Mediterranean basin driven by the accelerated salinity increase (Borghini et al. 2014; Hayes et al., this volume). A saltier and denser MOW may enhance deep water formation in the northern North Atlantic with strong implications for the global overturning circulation and subsequently for the earth's climate system and marine ecosystems. An intensification of the Atlantic meridional overturning circulation (AMOC), partially driven by MOW after the Younger Dryas 11,600 years ago, led to the fastest postglacial CWC range expansion ever recorded (Henry et al. 2014).

Coupled climate models predict excessive drying and warming of the Mediterranean region during the twenty-first century (Mariotti et al. 2008, 2015; Somot et al. 2008). Following the strong net evaporation increase, large salinity gains are predicted throughout the basin (Macias et al. 2015; Adloff et al. 2015; Maier et al., this volume). Regional climate model projections under high greenhouse gas emission scenarios show very large average Mediterranean surface salinity increases of the order of 1 at the end of the twenty-first century (e.g. Macias et al. 2015). The LIW, circulating around the whole Mediterranean basin at depths ranging 200–600 m, controlling occurrence and distribution of CWC habitats (Taviani et al. 2017), is also projected to become considerably more saline over this century (Adloff et al. 2015; Maier et al., this volume).

So, are we heading towards a new salinity crisis in the Mediterranean Sea? Although salinity changes and their impacts on ecosystems are far from being as dramatic as over the Messinian Salinity Crisis or the Holocene Climatic Optimum periods, the observed salting over the last few decades and the projected salting by climate models over the twenty-first century are quite pronounced considering the relatively short timescales. Over the recent historical period, both warming and salinity gain in the Mediterranean basin are much stronger than global ocean average trends (Belkin 2009; Skliris et al. 2014). Taking into account the high sensitivity of the climate system and the overturning circulation of the Mediterranean Sea, relatively small climatic perturbations may exert strong pressures in its marine ecosystems. The Mediterranean is considered to be one of the large marine ecosystems (LMEs) which is already strongly affected by the rapid surface warming with large effects on marine biodiversity (Belkin 2009). How drastically the projected strong salting combined with warming and acidification of the basin will affect Mediterranean CWC communities over this century remains an open question.

References

Adloff F, Somot S, Sevault F, et al (2015) Mediterranean Sea response to climate change in an ensemble of twenty first century scenarios. Clim Dyn 45:2775–2802. https://doi.org/10.1007/s00382-015-2507-3

Belkin M (2009) Rapid warming of Large Marine Ecosystems. Progr Oceanogr 81: 207–213

Bethoux JP, Gentili B (1999) Functioning of the Mediterranean Sea: past and present changes related to freshwater input and climate changes. J Mar Syst 20:33–47

Borghini M, Bryden H, Schroeder K, et al (2014) The Mediterranean is becoming saltier. Ocean Sci 10:693–700

Cartes JE, Maynou F, Fanelli E (2011) Nile damming as plausible cause of extinction and drop in abundance of deep-sea shrimp in the western Mediterranean over broad spatial scales. Progr Oceanogr 91:286–294

Cartes JE, Fanelli E, Lloris D, et al (2013) Effect of environmental variations on sharks and other top predators in the deep Mediterranean Sea over the last 60 years. Clim Res 55:239–251. https://doi.org/10.3354/cr01137

Cook BI, Anchukaitis KJ, Touchan R, et al (2016) Spatiotemporal drought variability in the Mediterranean over the last 900 years. J Geophys Res Atmos 121:2060–2074. https://doi.org/10.1002/2015JD023929

Curry R, Dickson B, Yashayaev I (2003) A change in the freshwater balance of the Atlantic Ocean over the past four decades. Nature 426:826–828

Durack PJ, Wijffels SE (2010) Fifty-year trends in global ocean salinities and their relationship to broad-scale warming. J Clim 23:4342–4362

Durack PJ, Wijffels SE, Matear RJ (2012) Ocean salinities reveal strong global water cycle intensification during 1950 to 2000. Science 336:455–458. https://doi.org/10.1126/science.1212222

Emeis KC, Struck U, Schulz HM, et al (2000) Temperature and salinity variations of Mediterranean Sea surface waters over the last 16,000 years from records of planktonic stable oxygen isotopes and alkenone unsaturation ratios. Palaeogeogr Palaeoclimatol Palaeoecol 158:259–280

Ferrier-Pagès C, Gattuso JP, Jaubert J (1999) Effect of small variations in salinity on the rates of photosynthesis and respiration of the zooxanthellate coral *Stylopora pistillata*. Mar Ecol Progr Ser 181:309–314

Gegner HM, Ziegler M, Rädecker N, et al (2017) High salinity conveys thermotolerance in the coral model Aiptasia. Biol Open: bio.028878. https://doi.org/10.1242/bio.028878

Giorgi F (2006) Climate change hot spots. Geophys Res Lett 33:L08707. https://doi.org/10.1029/2006GL025734

Good SA, Martin MJ, Rayner NA (2013) Quality controlled ocean temperature and salinity profiles and monthly objective analyses with uncertainty estimates. J Geophys Res Oceans 118:6704–6716

Hegerl G, Black E, Alan RP, et al (2015) Challenges in quantifying changes in the global water cycle. Bull Am Meteor Soc 96:1097–1115. https://doi.org/10.1175/BAMS-D-13-00212.1

Held IM, Soden BJ (2006) Robust responses of the hydrological cycle to global warming. J Clim 19:5686–5699

Henry LA, Frank N, Hebbeln D, et al (2014) Global Ocean conveyor lowers extinction risk in the deep sea. Deep-Sea Res Part 1 Oceanogr Res Pap 88:8–16

Hurrell JW (1995) Decadal trends in the North Atlantic oscillation, regional temperatures and precipitation. Science 269:676–679

Jokiel PL, Hunter CL, Taguchi S, et al (1993) Ecological impact of a fresh-water “reef kill” in Kaneohe Bay, Oahu, Hawaii. Coral Reefs 12:177–184

Kelley C, Ting M, Seager R, et al (2012) The relative contributions of radiative forcing and internal climate variability to the late 20th century winter drying of the Mediterranean region. Clim Dyn 38:2001–2015. https://doi.org/10.1007/s00382-011-1221-z

Klein B, Roether W, Manca BB, et al (1999) The large deep water transient in the Eastern Mediterranean. Deep-Sea Res Part 1 Oceanogr Res Pap 46:371–414

Kotthoff U, Müller UC, Pross J, et al (2008) Lateglacial and Holocene vegetation dynamics in the Aegean region: an integrated view based on pollen data from marine and terrestrial archives. The Holocene 18:1019–1032. https://doi.org/10.1177/0959683608095573

Krahman G, Schott F (1998) Longterm increases in Western Mediterranean salinities and temperatures: anthropogenic and climatic sources. Geophys Res Lett 25:4209–4212

Krijgsman W, Hilgen FJ, Raffi I, et al (1999) Chronology, causes and progression of the Messinian salinity crisis. Nature 400:652–655

Kuanui P, Chavanich S, Voranop Viyakarn V, et al (2015) Effects of temperature and salinity on survival rate of cultured corals and photosynthetic efficiency of zooxanthellae in coral tissues. Ocean Sci J 50:263–268. https://doi.org/10.1007/s12601-015-0023-3

Ludwig L, Dumont E, Meybeck M, et al (2009) River discharges of water and nutrients to the Mediterranean and Black Sea: major drivers for ecosystem changes during past and future decades? Progr Oceanogr 80:199–217

Macias D, García-Gorríz E, Piroddi C, et al (2014) Biogeochemical control of marine productivity in the Mediterranean Sea during the last 50 years. Glob Biochem Cycles 28:897–907. https://doi.org/10.1002/2014GB004846

Macias DM, Garcia-Gorriz E, Stips A (2015) Productivity changes in the Mediterranean Sea for the twenty-first century in response to changes in the regional atmospheric forcing. Front Mar Sci 2:79. https://doi.org/10.3389/fmars.2015.00079

Malanotte-Rizzoli P, Eremeev VN (eds) (1999) The Eastern Mediterranean as a laboratory basin for the assessment of contrasting ecosystems. Nato Science series, vol 51. Springer, Heidelberg

Mariotti A (2010) Recent changes in the Mediterranean water cycle: a pathway toward long-term regional hydroclimatic change? J Clim 23:1513–1525

Mariotti A, Zeng N, Yoon J, et al (2008) Mediterranean water cycle changes: transition to drier 21st century conditions in observations and CMIP3 simulations. Environ Res Lett 3:044001. https://doi.org/10.1088/1748-9326/3/044001

Mariotti A, Pan Y, Zeng N, et al (2015) Long-term climate change in the Mediterranean region in the midst of decadal variability. Clim Dyn 44:1437–1456

McCartney MS, Mauritzen C (2001) On the origin of the warm inflow to the Nordic seas. Progr Oceanogr 51:125–214

Potter R, Lozier S (2004) On the warming and salinification of the Mediterranean outflow waters in the North Atlantic. Geophys Res Lett 31:L01202. https://doi.org/10.1029/2003GL018161

Poulos SE, Drakopoulos PG (2001) A reassessment of the Mediterranean river runoff. Rapp Comm Int Mer Mediterr 36:76

Reid JL (1979) On the contribution of the Mediterranean Sea outflow to the Norwegian-Greenland Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 26:1199–1223

Remia A, Taviani M (2005) Shallow-buried Pleistocene Madrepora-dominated coral mounds on a muddy continental slope, Tuscan Archipelago, NE Tyrrhenian Sea. Facies 50:419–425. https://doi.org/10.1007/s10347-004-0029-2

Rixen M, Beckers J-M, Levitus S, et al (2005) The Western Mediterranean deep water: a proxy for climate change. Geophys Res Lett 32:L12608. https://doi.org/10.1029/2005GL022702

Rohling EJ, Bryden HL (1992) Man-induced salinity and temperature increases in western Mediterranean water. J Geophys Res 97:11191–11198

Rohling EJ, Marino G, Grant KM (2015) Mediterranean climate and oceanography, and the periodic development of anoxic events (sapropels). Earth Sci Rev 143:62–97. https://doi.org/10.1016/j.earscirev.2015.01.008

Romanou A, Tselioudis G, Zerefos CS, et al (2010) Evaporation-precipitation variability over the Mediterranean and the Black Seas from satellite and reanalysis estimates. J Clim 23:5268–5287

Schroeder K, Chiggiato J, Bryden HL, et al (2016) Abrupt climate shift in the Western Mediterranean Sea. Sci Rep 6:23009. https://doi.org/10.1038/srep23009

Skliris N, Lascaratos A (2004) Impacts of the Nile River damming on the thermohaline circulation and water mass characteristics of the Mediterranean Sea. J Mar Syst 52:121–143

Skliris N, Sofianos S, Lascaratos A (2007) Hydrological changes in the Mediterranean Sea in relation to changes in the freshwater budget: a numerical modelling study. J Mar Syst 65:400–416

Skliris N, Sofianos S, Gkanasos A, et al (2012) Decadal scale variability of sea surface temperature in the Mediterranean Sea in relation to atmospheric variability. Ocean Dyn 62:13–30

Skliris N, Marsh R, Josey SA, et al (2014) Salinity changes in the World Ocean since 1950 in relation to changing surface freshwater fluxes. Clim Dyn 43:709–736

Skliris N, Zika JD, Nurser G, et al (2016) Global water cycle amplifying at less than the Clausius-Clapeyron rate. Sci Rep 6:38752. https://doi.org/10.1038/srep38752

Skliris N, Zika JD, Herold L, et al (2018) Mediterranean Sea water budget long-term trend inferred from salinity observations. Clim Dyn. https://doi.org/10.1007/s00382-017-4053-7

Somot S, Sevault F, Déqué M, et al (2008) 21st century climate change scenario for the Mediterranean using a coupled atmosphere–ocean regional climate model. Glob Planet Chang 63:112–126

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part 2 Top Stud Oceanogr 145:61–78. https://doi.org/10.1016/j.dsr2.2015.12.008

Tsimplis MN, Josey SA (2001) Forcing of the Mediterranean Sea by atmospheric oscillations over the North Atlantic. Geophys Res Lett 28:803–806

Tsimplis MN, Zervakis V, Josey SA, et al (2006) Changes in the oceanography of the Mediterranean Sea and their link to climate variability. In: Lionello P, Malanotte-Rizzoli P, Boscolo R (eds) Developments in earth & environmental sciences. Mediterranean climate variability, vol 4. Elsevier, Amsterdam, pp 227–282

Vargas-Yanez M, Zunino P, Benali A, et al (2010) How much is the western Mediterranean really warming and salting? J Geophys Res 115:C04001. https://doi.org/10.1029/2009JC005816

Cross References

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Freiwald A (this volume) Messinian salinity crisis: what happened to cold-water corals?

Hayes D, Schroeder K, Poulain PM, et al (this volume) Review of the circulation and characteristics of intermediate water masses of the Mediterranean – implications for cold-water coral habitats

Lo Iacono C, Savini A, Huvenne VAI, et al (this volume) Habitat mapping of cold-water corals in the Mediterranean Sea

Maier C, Weinbauer MG, Gattuso JP (this volume) Fate of Mediterranean scleractinian cold-water corals as a result of global climate change. A synthesis

Taviani M, Vertino A, Angeletti L, et al (this volume) Paleoecology of Mediterranean cold-water corals

Vertino A, Taviani M, Corselli C (this volume) Spatio-temporal distribution of Mediterranean cold-water corals

Wortel R, Meijer P (this volume) The interface between tectonic evolution and cold-water coral dynamics in the Mediterranean

Drop Chapter The Spread of Non-indigenous Species in the Mediterranean – A Threat to Cold-Water Corals?

43

Bella S. Galil

Abstract

Only few live records of cold-water corals are known from the Aegean and Levant seas, though antipatharians, ceriantharians, zoantharians, gorgonians and pennatulaceans have been recorded from their continental shelf and upper slope. These mesophotic coral communities, including the *Corallium rubrum* (Linnaeus, 1758) colonies in Crete and southeast Turkey, are already within the depth range of disruptive carnivorous and omnivorous non-indigenous species introduced though the Suez Canal. The recent enlargement of the Suez Canal has raised concern over increasing propagule pressure of deeper living species. In fact, the recently observed "descent" of Erythraean non-indigenous species from the upper to lower continental shelf and upper slope may be also a harbinger of temperature-dependent range expansion, both horizontal and vertical. As mesophotic coral communities in the easternmost Mediterranean have barely been documented, it is impossible to predict the possibility of degradation and loss of native populations, habitats and ecosystem services. However, preliminary studies on impacts of the invasive Indo-Pacific lionfish on Caribbean mesophotic reef communities suggested a shift in community structure. The spread of non-indigenous species to mesophotic depths requires a concerted effort to map these habitats and study their communities.

Keywords

Bathymetric range expansion · Mesophotic coral assemblages · Suez Canal · Ecological impact

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The spread of non-indigenous species (NIS) is one aspect of global change and is considered to be among the main direct drivers of biodiversity loss, affecting environmental and economic damage. The negative effects of NIS are exacerbated by climate change, pollution, habitat loss and human-induced disturbance. The most harmful NIS displace native species, alter community structure and food webs, and change ecosystem functioning. Non-indigenous species have transformed marine coastal habitats worldwide and their impact has been increasing inexorably (Millenium Ecosystem Assessment 2005).

Complex and fundamental alterations to the Mediterranean Sea, including increases in NIS, have affected the structure and functioning of the sea and the consequent provision of goods and services (Micheli et al. 2013; European Environmental Agency 2015). The number of recorded metazoan NIS in the Mediterranean Sea (over 800) is far higher than in other European seas – nearly triple the number of records known from the western European margin – and it doubled between 1980 and 2016 (Galil et al. 2014). From those species, 470 were introduced through the Suez Canal (Erythraean NIS), the balance were primarily introduced by shipping and mariculture. The number and abundance of Erythraean NIS are substantially greater in the Levant where they are prominent in many coastal habitats (Steinitz 1970; Por 1978; Galil 2007; Galil et al. 2014). Vectors determine the choice of introduced taxa, their geographical origin and propagule pressure: where the Suez Canal is the main vector, most NIS are of tropical Indo-Pacific origin and comprise taxa actively spreading as adults or passively transported as larvae; where vessels and aquaculture are the prevailing vectors, the taxonomic composition and native ranges of NIS are more diverse and depend on shipping routes and mariculture transfers. As these activities were confined to the shallow shelf, it was assumed that so would the NIS. Indeed, until the millennium NIS records were largely limited to the coastal zone. That was about to change.

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Recent findings of NIS populations established in deeper waters have upended this paradigm – a growing number of NIS have been collected on the deeper shelf, even beyond the shelf break and well into the upper slope. The Erythraean portunid crab *Charybdis longicollis* (Leene, 1938), recorded in the Mediterranean since 1954, and its sacculinid parasite, *Heterosaccus dollfusi* Boschma, 1960, were collected off Israel as deep as 250 m (Innocenti et al. 2017). Off the Mediterranean coast of Israel in 1960–1962 *C. longicollis* was abundant at 36 m depth, but at a depth of 82 m "only single specimens were taken" (Gilat 1964: 14, fig. 4). In the late 1970s 3.5 times as many individuals were collected in 35 m as in 50 m, and only two specimens were collected in 80 m (Galil and Lewinsohn 1981). However, in recent surveys (2008–2012) the highest numbers of specimens were collected between 40 and 80 m, but specimens were also collected also at 100, 120 and 250 m depth (Innocenti et al. 2017). The goldband goatfish *Upeneus moluccensis* (Bleeker, 1855) and the lessepsian lizardfish *Saurida lessepsianus* Russell, Golani and Tikochinski, 2015, first recorded in the Mediterranean in 1935 and 1952 respectively, constitute a significant component of the local trawl fisheries and have been common in trawls hauled from depths of 100 and 120 m (Levitt 2012). *Charybdis longicollis*, *U. moluccensis* and *S. lessepsianus* are widespread and abundant throughout the eastern Mediterranean Sea, and the latter has spread westwards to Albania and Tunisia (Rakaj 1995; Ben Souissi et al. 2005). In 2004 the bathydemersal spiny blaasop *Tylerius spinosissimus* (Regan, 1908) was collected off Rhodes at 90 m, and again in 2009 in 50–80 m (Corsini et al. 2005, 2010a, b), and in 2010 off Israel at 120–140 m (Golani et al. 2011). In 2010, specimens of the spotfin cardinal *Apogon queketti* Gilchrist, 1903 were collected at depths of 140–150 m in the gulf of Antalya, Turkey (Gökoğlu et al. 2011). In the same year a portunid crab, *Gonioinfradens giardi* (Nobili, 1905), was collected off Rodos Island on biogenic debris at 200 m (Corsini-Foka et al. 2010a, b, as G. *paucidentatus* (A. Milne Edwards, 1861) (Fig. 43.1). In 2010 and 2011, large numbers of Randall's threadfin bream *Nemipterus randalli* Russell 1986 were collected at depths of 100 and 120 m off the Israeli coastline (fig 5a in Stern et al. 2014,). Nuttal et al. (2014) documented the occurrence of *Pterois volitans* (Linnaeus, 1758) and *P. miles* (Bennett, 1828) to depth of 112 m in the northwestern Gulf of Mexico, with the greatest abundance between 80 and 90 m, whereas Lesser and Slattery (2011) suggested a shift to algal dominated communities in Bahamian mesophotic reefs is associated with the invasion of the Indo-Pacific lionfish. *Pterois miles* has been spreading rapidly also in the Mediterranean Sea (Ounifi-Ben Amor et al. 2015; Azzuro et al. 2017) (Fig. 43.2).


Fig. 43.1 *Gonioinfradens giardi* (A. Milne Edwards, 1861), Rosh HaNikra marine nature reserve, Israel, 2015. (Photographed by © Oren Klein)


Fig. 43.2 *Pterois miles* (Bennett, 1828), Rosh HaNikra marine nature reserve, Israel, 2014. (Photographed by © Oren Klein)

All these species have in common their mode of introduction through the Suez Canal. The implications of the successive enlargements of the Suez Canal combined with higher through-current velocities on propagule pressure of Erythraean NIS are all too clear – increasing the delivery of multiple species and in particular deeper living ones. As the sea is warming, the expansion of their bathymetric range may be accelerating. In fact, the recently observed "descent" of Erythraean NIS (references given above) from the upper to lower continental shelf and upper slope may be a harbinger of temperature-dependent range expansion, both horizontal and vertical.

With few exceptions, the ecological impact of NIS on the indigenous Mediterranean biota is poorly known (Zibrowius 1992; Boudouresque 2004; Katsanevakis et al. 2014), although some species have caused major degradation and loss of native populations, habitats and ecosystem services (Galil 2007). The individual and cumulative impacts of these species affect the conservation status of native species and critical habitats, as well as the structure and function of ecosystems and the availability of natural resources. A century worth of surveys has provided ample evidence that a significant number of Erythraean NIS have high potential for spread, either rapid on arrival or following decades of residency time lag called "invasion debt", and that once established they can not be contained or controlled. Their impacts are irreversible.

Mediterranean Sea cold-water corals (CWCs) were considered rare and nearly extinct until relatively recent expeditions documented banks of living *Madrepora oculata* Linnaeus, 1758, *Desmophyllum dianthus* (Esper, 1794) and *Lophelia pertusa* (Linnaeus, 1758) in the Ionian Sea, southwestern Adriatic Sea, Strait of Sicily, Catalan-Provençal margin and Alborán Sea, some at depths shallower than 250 m (e.g. Freiwald et al. 2009; Orejas et al. 2009; Vertino et al. 2010; Gori et al. 2013; Michez et al. 2014, and several chapters in this volume). Only three live records are known in the Levant Sea (*D. dianthus* from Eratosthenes seamount, *Dendrophyllia cornigera* (Lamarck 1816) south of Crete, *Dendrophyllia ramea* (Linnaeus, 1758) (Galil and Zibrowius 1998; Smith et al. 2009) and off Cyprus (Orejas et al. 2017, this volume; http://www.medmpaforum2012.org/sites/default/files/pres.fsob1a_marin.pdf accessed 3 Aug 2017). Though samples collected during the GECO cruise off Crete, Karpathos, and Rhodes comprised mostly late Pleistocene fossils, the authors suggested "…it is possible that like *D. dianthus*, the *Lophelia*-*Madrepora* communities also persist in some areas of the easternmost sector of the Mediterranean Basin" (Taviani et al. 2011). Yet, antipatharians, ceriantharians, zoantharians, gorgonians and pennatulaceans have been recorded from the shelf and upper slope in the Aegean and Levant seas (mainly <250 m depth) (Zibrowius 1979a, b; Chintiroglou et al. 1989; Vafidis et al. 1994, 1997; Vafidis and Koukouras 1998 [2002]; Vafidis 2009; Abdelsalam 2014; Altuna and Poliseno, this volume; Chimienti et al., this volume). Thus some of the mesophotic coral communities in the Levant and southern Aegean Sea (including *Corallium rubrum* (Linnaeus, 1758) colonies in Crete and southeast Turkey) are already within the depth range of disruptive carnivorous and omnivorous NIS. The trophic ecology of the eastern Mediterranean mesophotic coral communities is unknown, so that NIS impacts and risk analysis is infeasible. Mediterranean CWCs are already threatened by human activities and climate change (Roberts and Cairns 2014; Otero and Marin, this volume; Maier et al., this volume; Movilla, this volume). The spread of NIS to depths where these unique assemblages occur bodes ill to the already beleaguered and fragile communities.

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References

Abdelsalam KM (2014) Faunistic study of benthic Pennatulacea (Cnidaria, Octocorallia) from the Northern coast of Egypt. Egypt J Aquat Res 40:261–268

Azzurro E, Stancanelli B, Di Martino V, et al (2017) Range expansion of the common lionfish *Pterois miles* (Bennett, 1828) in the Mediterranean Sea: an unwanted new guest for Italian waters. BioInvasions Rec 6:95–98

Ben Souissi J, El Menif NT, Mahjoub MS, et al (2005) On the recent occurrence of marine exotic species in the Tunisian waters. In: Proceedings of the seventh international conference on the Mediterranean coastal environment, Turkey, pp 529–540

Boudouresque CF (2004) Marine biodiversity in the Mediterranean: status of species, populations and communities. Sci Rep Port-Cros Natl Park 20:319–323

Chintiroglou H, Dounas C, Koukouras A (1989) The presence of *Corallium rubrum* (Linnaeus, 1758) in the eastern Mediterranean Sea. Mitt Zool Mus Berl 65:145–149

Corsini M, Margies P, Kondilatos G, et al (2005) Lessepsian migration in Aegean Sea: *Tylerius spinosissimus* (Pisces, Tetraodontidae) new for the Mediterranean, and six more fish records from Rhodes. Cybium 29:347–354

Corsini-Foka M, Margies P, Kondilatos G, et al (2010a) Tetraodontid colonizers in the Aegean Sea; second record of the spiny blaasop, *Tylerius spinosissimus* (Actinopterygii: Tetraodontiformes: Tetraodontidae). Acta Ichthy Pisc 40:71–74

Corsini-Foka M, Pancucci-Papadopoulo A, Kondilatos G, et al (2010b) *Gonioinfradens paucidentatus* (A. Milne Edwards, 1861) (Crustacea, Decapoda, Portunidae): a new alien crab in the Mediterranean Sea. Med Mar Sci 11:331–340

Ernesto Azzurro E, Stancanelli B, Di Martino V, et al (2017) Range expansion of the common lionfish *Pterois miles* (Bennett, 1828) in the Mediterranean Sea: an unwanted new guest for Italian waters. BioInvasions Rec 6:95–98

European Environment Agency (2015) State of Europe's Seas, Technical report No. 2/2015, European Environment Agency, Copenhagen. 220 pp. http://www.eea.europa.eu/publications/state-of-europes-seas

Freiwald A, Beuck L, Ruggerberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74

Galil BS (2007) Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. Mar Poll Bull 55:314–322

Galil BS, Lewinsohn C (1981) Macrobenthic communities of the Eastern Mediterranean continental shelf. Mar Ecol 2:343–352

Galil B, Zibrowius H (1998) First benthos samples from Eratosthenes seamount, Eastern Mediterranean. Senck Marit 28:111–121

Galil BS, Marchini A, Occhipinti-Ambrogi A, et al (2014) International arrivals: widespread bioinvasions in European seas. Ethol Ecol Evol 26:152–171

Gilat E (1964) The macrobenthic invertebrate communities on the Mediterranean continental shelf of Israel. IAEA radioactivity in the sea. Publication no. 8. Bull Inst Océanogr Monaco 62:1–46

Gökoğlu M, Ünlüsayin M, Balci BA, et al (2011) Two alien fish in the Gulf of Antalya: *Apogon queketti* Gilchrist, 1903 (Apogonidae) and *Champsodon nudivittis* (Ogilby, 1895) (Champsodontidae). Zool Middle East 54:138–140

Golani D, Sonin O, Edelist D (2011) Second records of the Lessepsian fish migrants *Priacanthus sagittarius* and *Platax teira* in the Mediterranean and distribution extension of *Tylerius spinosissimus*. Aquat Invasions 6:S7–S11

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de

Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Innocenti G, Goren M, Stern N, et al (2017) Going down together: invasive host, *Charybdis longicollis* (Leene, 1938) (Decapoda: Brachyura: Portunidae) and invasive parasite, *Heterosaccus dollfusi* Boschma, 1960 (Cirripedia: Rhizocephala: Sacculinidae) on the upper slope off the Mediterranean coast of Israel. Mar Biol Res 13:229–236

Katsanevakis S, Wallentinus I, Zenetos A, et al (2014) Impacts of marine invasive alien species on ecosystem services and biodiversity: a pan-European review. Aquat Invasions 9:391–423

Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. Biol Invasions 13:1855–1868

Levitt Y (2012) The impact of depth gradient on the status of alien species along the Mediterranean coast of Israel. MSc thesis [Hebrew, English abstract], 90 pp

Micheli F, Halpern BS, Walbridge S, et al (2013) Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: assessing current pressures and opportunities. PLoS One 8:e79889

Michez N, Fourt M, Aish A, et al (2014) Typologie des biocénoses benthiques de Méditerranée Version 2. Rapport SPN 2014-33. MNHN, Paris, 26 pp

Millenium Ecosystem Assessment (2005) Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, DC

Nuttal MF, Johnston MA, Eckert RJ (2014) Lionfish (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) records within mesophotic depth ranges on natural banks in the Northwestern Gulf of Mexico. BioInvasions Rec 3:111–115

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51

Orejas C, Gori A, Jiménez C, et al (2017) First in situ documentation of a population of the coral *Dendrophyllia ramea* off Cyprus (Levantine Sea) and evidence of human impacts. Galaxea 19:15–16

Ounifi-Ben Amor K, Rifi M, Ghanem R, et al (2015) Update of alien fauna and new records from Tunisian marine waters. Mediterr Mar Sci 17:124–143

Por FD (1978) Lessepsian Migration – the influx of Red Sea Biota into the Mediterranean by way of the Suez Canal. Ecological studies, vol 23, Springer, Berlin, Heidelberg, New York, 228 pp

Rakaj N (1995) Iktiofauna e Shqipërisë [Ichthyofauna of Albania]. Shtëpia Botuese “Libri universitar”, Tiranë, 700 p

Roberts JM, Cairns SD (2014) Cold water corals in a changing ocean. Curr Opin Environ Sustain 7:118–126

Smith C, Sakellariou D, McCoy F, et al (2009) Deep coral environments south of Crete. 9o Πανελλήνιο Συμπόσιο Ωκεανογραφίας & Αλιείας 2009—Πρακτικά. Τόμος 1:665–668

Steinitz H (1970) A critical list of immigrants via the Suez Canal. Biota of the Red Sea and Eastern Mediterranean. In: The Hebrew University–Smithsonian Institution Joint Program: biota of the Red Sea and the eastern Mediterranean, progress report. Department of Zoology, Hebrew University Jerusalem, pp 64–74 [mimeo]

Stern N, Levitt Y, Galil BS, et al (2014) Distribution and population structure of the alien indo-Pacific Randall's threadfin bream *Nemipterus randalli* in the eastern Mediterranean Sea. J Fish Biol 85:394–406

Taviani M, Vertino A, López-Correa M, et al (2011) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603

Vafidis D (2009) First record of *Leptogorgia sarmentosa* (Octocorallia: Gorgoniidae) from the eastern Mediterranean Sea. Mar Biodivers Rec 2:e17

Vafidis D, Koukouras A (1998) [2002] Antipatharia, Ceriantharia and Zoantharia (Hexacorallia, Anthozoa) of the Aegean Sea with a checklist of the Mediterranean and Black Sea species. Ann Inst Océanogr Paris 74:115–126

Vafidis D, Koukouras A, Voultsiadou-Koukoura E (1994) Octocoral fauna of the Aegean Sea with a check list of the Mediterranean species: new information, faunal comparisons. Ann Inst Océanogr Paris 70:217–229

Vafidis D, Koukouras A, Voultsiadou-Koukoura E (1997) Actiniaria, Corallimorpharia, and Scleractinia (Hexacorallia, Anthozoa) of the Aegean Sea, with a checklist of the eastern Mediterranean and Black Sea species. Isr J Zool 43:55–70

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396

Zibrowius H (1979a) A propos du corail rouge en Méditerranée orientale. Rapp Comm Int Mer Médit 25/26:121–122

Zibrowius H (1979b) Campagne de la Calypso en Méditerranée nord-orientale (1955, 1956, 1960, 1964 (suite). 7. Scleractiniaires. Ann Inst Océanogr, Paris 55:7–28(Suppl)

Zibrowius H (1992) Ongoing modification of the Mediterranean marine fauna and flora by the establishment of exotic species. Mésogée 51:83–107

Cross References

Altuna A, Poliseno A (this volume) Taxonomy, genetics and biodiversity of Mediterranean deep-sea corals and cold-water corals

Chimienti G, Bo M, Taviani M, et al (this volume) Occurrence and biogeography of Mediterranean cold-water corals

Maier C, Weinbauer MG, Gattuso JP (this volume) Fate of Mediterranean scleractinian cold-water corals as a result of global climate change. A synthesis

Movilla J (this volume) A case study: variability in the calcification response of Mediterranean cold-water corals to ocean acidification

Orejas C, Jiménez C, Gori A, et al (this volume) Corals of Aphrodite: *Dendrophyllia ramea* populations of Cyprus

Otero M, Marin P (this volume) Conservation of cold-water corals in the Mediterranean: current status and future prospects for improvement

44

Fate of Mediterranean Scleractinian Cold-Water Corals as a Result of Global Climate Change. A Synthesis

Cornelia Maier, Markus G. Weinbauer,
and Jean-Pierre Gattuso

Abstract

This chapter addresses the question as to how Mediterranean cold-water corals might fare in the future under anthropogenically-induced global climate change. The focus on three most prominent scleractinian cold-water corals species, the two branching and habitat-forming forms *Madrepora oculata, Lophelia pertusa* and the solitary cup coral *Desmophyllum dianthus.* We provide an introduction to climate change principals, highlight the current status of the marine environment with regard to global climate change, and describe how climate change impacts such as ocean acidification are predicted to affect key calcifiers such as scleractinian cold-water corals in the Mediterranean region. A synthesis of the experimental cold-water coral studies conducted to date on climate change impacts: The present state of knowledge reviewed in this chapter takes into account the number of experiments that have been carried out in the Mediterranean as well as for comparative purposes in other parts of the world, to examine the effects of climate change on the corals. We assess the statistical robustness of these experiments and what challenges the presented experiments. A comprehensive multi-study comparison is provided in order to inform on the present state of knowledge, and knowledge gaps, in understanding the effects of global climate change on cold-water corals. Finally we describe what the fate could be for the important scleractinian coral group in the Mediterranean region.

Keywords
Mediterranean cold-water coral · Climate change · Ocean acidification · Temperature · Calcification · Respiration

44.1 Introduction

44.1.1 Global Climate Change

Climate change refers to a change in weather conditions over a longer period of time, taking place from decades to millions of years and usually referring to (regional) rise or fall of mean temperatures, changes in precipitation and parameters such as the frequency of extreme weather events. Throughout Earth's history long-term climate change and climate events have taken place as a consequence of internal or external forcing of the naturally occurring climate system. The most recent, relatively short-term change in the global climate however, has been more dramatic and due to anthropogenically produced greenhouse gases that have acted on the climate system by reducing the heat radiation to space. Anthropogenically induced global warming trend had already been described in the late nineteenth century (Arrhenius 1896). At that time, the contribution of industrially produced CO_2 was thought to have minor effects with respect to the overall natural climate dynamics and it was believed that the observed warming would at least be partially beneficial to human prosperity: "*…there is good mixed with the evil. …, we may hope to enjoy ages with more equable and better climates, especially as regards the colder regions of the earth…*" (Arrhenius 1908). Since this time research to investigate climate change impacts has intensified and there is now strong evidence, that besides the increase in temperature, our global climate has become less stable with more frequent and intense weather events due to the present day atmospheric levels of CO_2 concentration being higher than at any time during the last 2.6 million

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years (Lewandowsky et al. 2016). Since pre-industrial times, atmospheric CO_2 increased from 280 to 400 ppm and a further doubling is projected until the end of the century (IPCC 2013). This rate of change is unprecedented with a anthropogenic CO_2 release rate being 14,000 times faster than the natural net release of CO_2 (Zeebe et al. 2016).

44.1.2 The Role of the Oceans

The oceans play an important role in global climate through gas and heat exchange and it is this thermal capacity of the oceans that moderates the climate and slows down global warming. Heat exchange with the ocean affects the upper ocean layers more strongly than the deep ocean and up to 90% of the additional heat and about one third of anthropogenic CO_2 released since pre-industrial times has been absorbed by the oceans. Since the 1970s ocean temperatures too have increased by 0.11 °C per decade in the upper 75 m and by 0.015 °C at 700 m water depth (Levitus et al. 2012; Rhein et al. 2013). An apparent 'hiatus' in global warming and sea surface heat uptake during the last 15 years had been identified (IPCC 2013), while the deeper ocean has contributed significantly to an additional and recent heat sequestration. This factor explains the observed slowing down of atmospheric warming during the last decade (Hansen et al. 2011; Meehl et al. 2011; Chen and Tung 2014; Cheng et al. 2015; Yan et al. 2016; Desbruyères et al. 2016; Bova et al. 2016), with recent research substantiating the ongoing ocean warming trend (Kosaka and Xie 2013; Karl et al. 2015; Lewandowsky et al. 2016; Fyfe et al. 2016; Song et al. 2016; Hausfather et al. 2017). Global change not only affects the general heat content and warming of the oceans, but has widespread consequences related to the temperature dependent state of water as solid ice, liquid or vapour. Changes in sea level, salinity and freshwater content show strong regional trends dependent on the ratio of evaporation, precipitation, river discharge and melting of glaciers and ice caps (Church et al. 2011; Pierce et al. 2012; Levermann et al. 2013; Rhein et al. 2013). Since the 1950s the contrast between high- and low-salinity regions has increased by 0.13 (Rhein et al. 2013). These changes in seawater temperature and salinity affect the density and volume of seawater causing changes to the steric sea level (Antonov et al. 2002; Llovel et al. 2014), circulation of water masses and to ocean currents (Purkey and Johnson 2010; England et al. 2014; McGregor et al. 2014).

44.1.3 Ocean Acidification

Anthropogenic CO_2 released to the atmosphere is partially taken up by the oceans and acts as a major net sink for anthropogenic carbon (Revelle and Suess 1957; Orr et al. 2001; Sabine et al. 2004; Landschützer et al. 2016). Since pre-industrial times about 25–30% of atmospheric CO_2 has been absorbed by the oceans. The rising partial pressure of CO_2 (pCO_2) has major consequences as CO_2 reacts to carbonic acid in solution resulting in the reduction of ocean pH termed ocean acidification (OA). There is an increasing awareness that climate change is altering the physical and biogeochemical status of the surface ocean and with the simultaneous increase of hydrogen and bicarbonate ions and a decrease in carbonate ions the seawater pH will decline by an average 0.3 units by the end of the century (Caldeira and Wickett 2003; Cicerone et al. 2004; Feely et al. 2004; Sabine et al. 2004; Orr et al. 2005b; Gattuso et al. 2015). This change also affects the calcium carbonate saturation state (Ω) in seawater which is the discriminant parameter with respect to the precipitation and solution of calcium carbonates. Solubility increases at higher pressure and lower temperature, which means that Ω decreases with increasing water depths and at higher latitudes. OA has been postulated to be of a major concern for various calcifying organisms as they depend on the surrounding seawater to build their shells or in the case of cold-water corals (CWCs), their skeletons (Orr et al. 2005a, b; Kleypas et al. 2006). Over the last decade research on the effects of OA on marine organisms has intensified and new priorities for future research identified. OA impacts have highlighted the urgent need to study keystone species, ecosystem engineers and those ecosystems considered most vulnerable or most resilient to global climate change (Riebesell and Gattuso 2015). Like their tropical counterparts, scleractinian CWCs grow an aragonitic 3-D matrix like exoskeleton, and as such are susceptible to changes in the seawater carbonate chemistry. The surface ocean is currently supersaturated in aragonite and calcite, the two forms of carbonate that marine calcifiers use to form their shells or skeletons. The ongoing absorption of atmospheric CO_2 by the oceans results in a shallowing of the aragonite saturation horizon (ASH), the critical depth between precipitation and dissolution of aragonitic calcium carbonate. Work by Feely et al. (2012) showed that the offset in the ASH in the South Pacific between the 1990s and the 2000s had shifted by 10 m. In the New Zealand region estimates suggest that the ASH may have already shoaled by an order of 50 to 100 m (Bostock et al. 2013, 2015; Law et al. 2016). This places the deep-sea aragonitic scleractinian CWCs, being confined to the deep waters and to colder regions at great risk with 70% of the CWC habitats becoming exposed to undersaturated conditions (Guinotte et al. 2006; Mikaloff-Fletcher et al. 2006; Bostock et al. 2015). Scleractinian CWC ecosystems are thought to be one of the most vulnerable groups that will be impacted by global climate change. This factor and additional anthropogenic stressors such as deep-sea trawling, mineral exploration, mining, and marine pollution (Turley et al. 2007; Roberts et al. 2016), add to the vulnerability of CWCs in a high CO_2 world.

44.1.4 Cold-Water Corals

While the biology of shallow-water tropical corals and their response to global change (warming and OA) has been studied for many decades, research on the biology and physiology of deep-sea CWCs such as the abundant scleractinian coral group is still in its infancy (but see Reynaud and Ferrier-Pagès, this volume and references therein). Until a decade ago knowledge was based on few studies providing some insights on skeletal extension (Bell and Smith 1999; Mortensen 2001), food capture (Mortensen 2001), potential food sources (Kiriakoulakis et al. 2005; Duineveld et al. 2007), the respiratory response to temperature change or hypoxia (Dodds et al. 2007) and reproductive ecology (Waller and Tyler 2005; Waller et al. 2005). However, the knowledge on the abundance and distribution of CWCs has advanced rapidly since the 1990s due to several factors such as an increase in deep-sea biodiversity surveys (e.g. Zibrowius and Gili 1990; Rogers 1999; Roberts et al. 2009; Buhl-Mortensen et al. 2010; Mastrototaro et al. 2010; Tittensor et al. 2010; Gori et al. 2013; Smith and Williams 2015); access to more sophisticated deep-sea technology facilitating surveys in deeper water over larger areas (e.g. Hovland et al. 2002; Sumida et al. 2004; Taviani et al. 2005; Wheeler et al. 2007; Freiwald et al. 2009; Orejas et al. 2009; De Mol et al. 2011; Gori et al. 2013; Savini et al. 2014; Clippele et al. 2016; see also Angeletti et al., this volume; Lo Iacono et al., this volume), and in several regions, primarily due to fishing activity and fisheries research surveys where the bycatch of deep-sea corals has occurred (e.g. Fosså et al. 2002; Gass and Willison 2005; Hourigan 2009; Tracey et al. 2011; Clark et al. 2015). This growing knowledge of the presence and spatial distribution of CWCs allowed to model and identify the most important parameters supporting or limiting CWC distribution and habitat suitability (Davies et al. 2008; Davies and Guinotte 2011; Tracey et al. 2011; Rowden et al. 2013; Anderson et al. 2016). Among a multitude of environmental and geographic variables taken into consideration depth, temperature, salinity and aragonite saturation state (Ω_a) appear to be some of the most important factors controlling the abundance and distribution of CWCs. Additionally, the knowledge on the physiology and growth of CWCs has rapidly advanced during the last decade (Lartaud et al., this volume; Reynaud and Ferrier-Pagès, this volume) owing to an increased effort in sampling live CWCs and in establishing aquarium facilities that allow to maintain CWCs for an extended time in the laboratory (see Orejas et al., this volume and references therein).

44.1.5 Climate Change in the Mediterranean Region

The Mediterranean region has been identified as one among the most important climate change Hot-Spots world-wide as it has become warmer and drier throughout the twenty-first century (Giorgi 2006). The variability in warming during summer is twice the global standard deviation (Hansen and Sato 2016). With this large increase in variability and a decrease in mean precipitation during the dry, warm seasons the Mediterranean constitutes one of the most responsive and affected regions with respect to global change (Giorgi et al. 2001; Giorgi and Lionello 2008; Mariotti et al. 2008; Alessandri et al. 2014).

The Mediterranean Sea is nearly land-locked, connected to the Atlantic by the shallow (300 m) Strait of Gibraltar. Evaporation greatly exceeds precipitation which drives the thermohaline circulation with deep and intermediate dense water convection in several basins and a unique open upper thermohaline cell that acts in a similar way as the global conveyer belt while it is characterised by a much shorter residence time of ca. 100 years (Malanotte-Rizzoli et al. 2014; Hayes et al., this volume). Therefore, the waters respond faster and are more sensitive to environmental change and thus can be regarded as a miniature model ocean (Bethoux et al. 1990, 1998; Bethoux and Gentili 1996; Turley 1999). Over the last decades, the trends of long-term warming and saltening have been evidenced throughout the Mediterranean Sea (Bethoux et al. 1990; Rixen et al. 2005; Nykjaer 2009; Vargas-Yáñez et al. 2009). Based on model simulations, an increase in sea surface temperature and sea surface salinity (SST and SSS) by 2 to 3 °C and 0.48 to 0.89 are predicted for 2070–2099. This is in comparison to ~30 years of SST and SSS data measured between 1961–1990 (Adloff et al. 2015). The trend has also increased at depth, where a temperature and salinity increase of 0.93–1.35 °C and 0.28 to 0.52 respectively has occurred throughout the water column. At the depths that scleractinian CWCs occur in the Mediterranean (below 200 m), the predicted temperature rise may increase by up to 2 °C and the salinity by ~0.5. Accordingly, Mediterranean CWCs might be exposed to a temperature between 15.5 to 16 °C and a salinity of 39.5 to 40 by the end of the century.

The Mediterranean Sea is characterised by a high total alkalinity (A_T) of ca 2600 μmol kg^{-1} with a high buffering capacity absorbing more CO_2 than the open ocean (CIESM 2008). It is a small to medium sink for CO_2 absorbing ca. 0.24 Gt C year^{-1} (D'Ortenzio et al. 2008) while the reduction of ocean pH is relatively fast with −0.14 to −0.05 pH units year^{-1} (Touratier and Goyet 2009, 2011). Despite this, the Ω remains higher in the deep Mediterranean waters compared to the deep waters of the North Atlantic (Millero et al. 1979), and even at the deepest water depths the seawater is not likely to become undersaturated with respect to Ω_a (Hassoun et al. 2015; Goyet et al. 2016). Present day Ω_a reported in the vicinity of Mediterranean CWCs are relatively high ranging between 2.3 and 3.0 (Rodolfo-Metalpa et al. 2015; Maier et al. 2016) but will drastically decrease to ca. 1.5 by the end of the century (Maier et al. 2016).

44.1.6 Effect of Climate Change Parameters on Cold-Water Corals

To date 24 experimental studies have been published on the physiological response of scleractinian CWCs to climate change and these studies, from both the Mediterranean and elsewhere, are summarised in Table 44.1. Nineteen of these studies addressed the effect of OA, eight the effect of temperature, four took into account the combined effect of OA and temperature. No studies are available on the effect on CWCs to changes in salinity. Interestingly, 40% of the studies were conducted using CWCs from the Mediterranean Sea region. The studies comprise five scleractinian coral species (*Madrepora oculata, Lophelia pertusa, Desmophyllum dianthus, Dendrophyllia cornigera and Caryophyllia smithii),* while most of the non-Mediterranean CWC studies were confined to the species *L. pertusa* (Table 44.1). The studies were distinct with respect to the time allowed for acclimation, replication and the use of single (Fig. 44.1), consecutive (Fig. 44.2) or repeated (Fig. 44.3) measure designs. Most studies were carried out in the laboratory, some short-term experiments were conducted at sea using freshly collected specimens and seawater from the actual sampling site (Maier et al. 2009, 2012; Hennige et al. 2014) and one other Mediterranean study included *in situ* experiments where coral fragments were transplanted to the close vicinity of a natural CO_2 vent site (Rodolfo-Metalpa et al. 2015). To provide an indication on the statistical robustness of the experimental studies a point system was introduced ("SR"; Table 44.1) taking into account criteria such as the number of replication, number of repeated measurements and the type of controls. Theoretically, a minimum point score of 3 and a maximum of 11 was possible, and an average SR of 5.7 points (±1.4 S.D) was typical for the studies (Table 44.1). This point system is not exclusive with respect to other criteria that may be important to evaluate the robustness of a study (e.g. handling stress, sampling and analytical procedures, adequacy of maintenance conditions), however, these criteria are difficult to judge in a scoring system.

44.2 Ocean Acidification Studies

The pCO_2 used in most of the OA experimental studies ranged between ambient (ca. 400 µatm) and 800–1000 µatm, corresponding to current and future conditions in 2100 using a business-as-usual CO_2 emission scenario. The exception was for two short-term experiments where pCO_2 levels in which pCO_2 values outside this range were used: 280 µatm to represent pre-industrial times (Maier et al. 2012) and 1725 µatm (Maier et al. 2016). The first studies of the effect of OA were performed on *Lophelia pertusa*. They revealed a negative response of calcification to increasing pCO_2 during short-term exposure (Maier et al. 2009; Form and Riebesell 2012) while no effect was detected when exposed for several months to elevated pCO_2 (Form and Riebesell 2012). These two studies show that *L. pertusa* is able to maintain positive calcification rates despite being exposed to undersaturated Ω_a (Maier et al. 2009; Form and Riebesell 2012). Subsequent studies have demonstrated that calcification remains constant for pCO_2 levels corresponding to those between present-day (~400 µatm) and those projected until the end of the century (~800–1000 µatm) (Figs. 44.1, 44.2, and 44.3). This was found for both short- and long-term exposure and for most CWC species studied, suggesting that no long-term acclimation occurs (Maier et al. 2012, 2013b, 2016; Carreiro-Silva et al. 2014; Hennige et al. 2014; Movilla et al. 2014a, b; Rodolfo-Metalpa et al. 2015). However, some recent literature states that CWCs may exhibit a long-term acclimation response in calcification to OA (Hennige et al. 2015; Roberts et al. 2016). Evidently, calcification is negatively affected in short-term experiments when Ω_a is below a certain threshold level (Figs. 44.1a, c and 44.2b, c; Maier et al. 2009; Lunden et al. 2014; Georgian et al. 2016b, Maier et al. 2016) but the same is true in long-term experiments (Fig. 44.3d, Hennige et al. 2015). Furthermore, using a repeated measures experimental design, Movilla et al. (2014b) showed a decline in calcification for the Mediterranean coral *Desmophyllum dianthus* after 314 days of exposure to elevated pCO_2 (800 µatm), while no effect at shorter exposure times was observed (Fig. 44.3c; Movilla et al. 2014b). This response might be species-specific, as none of the other three species (*L. pertusa, Madrepora oculata* and *Dendrophyllia cornigera*) studied in parallel revealed any significant effect between control and elevated pCO_2 treatments, neither during short- nor long-term exposure (Movilla et al. 2014a,b). It would have been interesting to see, if calcification of *D. dianthus* remains at the lower level it revealed after 314 days, restores calcification to normal rates or in the worst case scenario, further reduces calcification with increasing exposure time. A result such as this could be indicative of an eventual break down in calcification as a consequence of extended and continuous exposure to elevated pCO_2. For *D. dianthus* it has been shown that genes involved in stress response, metabolism or calcification

Table 44.1 Summary of experimental studies on the effects of climate change on cold-water corals (CWCs)

	Reference	Region	Factors					Species						Physiol. functions						Experimental design								Replication		
#			T	OA	TxOA	F	S	LP	MO	DE	DC	CS	SV	G	R	Sk	GE	OT	†	ST	LT	SM	RM	CM	IC	PC	FC	n	Tanks/n	*SR*
1	Dodds et al. (2007)	N-A	+	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–	–	+	–	+	–	–	–	+	–	4–6	n	*5*
2	Maier et al. (2009)	Skag	–	+	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	+	–	+	–	–	–	+	–	2x8	n	*6*
3	Form and Riebesell (2012)	N-A	–	+	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	+	–	+	–	–	–	+	–	4	n	*4*
																				–	+	+	–	–	–	–	–	5	n	*4*
4	Maier et al. (2012)	MED	–	+	–	–	–	–	+	–	–	–	–	+	+	–	–	–	–	+	–	+	–	+	+	–	–	15	n	*7*
5	Maier et al. (2013b)	MED	–	+	–	–	–	+	+	–	–	–	–	+	–	–	–	–	–	+	+	+	+	–	+	+	–	4	n	*7*
6	Maier et al. (2013a)	MED	+	+	+	–		+	+	–	–	–	–	–	+	–	–	–	–	+	+	+	+	–	+	+	–	4	n	*7*
7	Brooke et al. (2013)	GoM	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	+	+	–	+	+	–	–	+	–	5	n	*6*
8	Naumann et al. (2013b)	MED	+	–	–	–	–	+	+	–	–	–	–	+	+	–	–	DOC	–	–	+	+	+	–	–	+	–	5	1/n	*5*
9	Naumann et al. (2013a)	MED	+	–	–	–	–	–	–	+	+	–	–	+	–	–	–	–	–	–	+	+	–	–	–	+	–	5	1/n	*4*
10	Carreiro-Silva et al. (2014)	N-A	–	+	–	–	–	–	–	+	–	–	–	+	+	–	+	NUTS GE	–	–	+	+	+	–	–	+	–	6	2/n	*6*
11	Hennige et al. (2014)	N-A	–	+	–	–	–	+	–	–	–	–	–	+	+	–	–	–	–	+	–	+	+	–	+	+	–	8	1/n	*6*
12	Lunden et al. (2014)	GoM	+	+	–	–	–	+	–	–	–	–	–	+	–	–	–	–	+	+	–	+	–	+	–	+	–	2x8	2/n	*7*
13	Movilla et al. (2014a)	MED	–	+	–	–	–	+	+	–	–	–	–	+	–	+	–	–	–	–	+	+	+	–	–	+	–	12–18	3/n	*7*
14	Movilla et al. (2014b)	MED	–	+	–	–	–	–	–	+	+	–	–	+	–	+	–	OM	–	–	+	+	+	–	+	+	–	9	3/n	*7*
15	Rodolfo-Metalpa et al. (2015)	MED	–	+	–	–	–	–	–	+	+	+	–	+	+	–	–	–	–	–	+	+	–	–	+	+	–	7–23	2/n	*7*
16	Hennige et al. (2015)	N-A	+	+	+	–	–	+	–	–	–	–	–	+	+	+	–	–	–	–	+	+	+	–	–	+	–	4–8	4/n	*6*
17	Wall et al. (2015) (#3)	N-A	–	+	–	–	–	+	–	–	–	–	–	–	–	+	–	d^{11}B	–	–	+	+	–	–	–	+	–	1–4	n	*n/a*
18	Gori et al., (2016)	MED	+	+	+	–	–	–	–	+	–	–	–	+	–	+	–	–	–	–	+	+	–	–	–	+	–	3	n	*4*
19	Maier et al. (2016)	MED	–	+	–	+	–	–	+	–	–	–	–	+	+	–	–	TOC; RQ; E	–	+	–	+	+	+	+	–	+	13	n	*9*
20	Georgian et al. (2016a, b)	GoM Skag	–	+	–	+	–	+	–	–	–	–	–	+	+	–	–	Food uptake	–	+	–	+	–	–	–	+	–	8	2/n	*5*
21	Büscher et al. (2017)	N-A	+	+	+	+	–	+	–	–	–	–	–	+	–	+	–	RNA/DNA	+	–	+	+	–	–	–	+	–	4	n	*4*
22	Kurman et al. (2017)	GoM	–	+	–	–	–	+	–	–	–	–	–	+	–	–	–	GT	–	+	–	+	–	–	–	+	–	12	1/n	*5*
														+	–	–	–	CAA	+	–	+	+	+	–	–	+	–	4	1/n	*4*
23	Burdett et al. (2014)	N-A	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	DMSP	–	+	–	+	–	–	–	+	–	5	1/n	*4*
24	Gammon et al. (2018)	SW-P	–	+	–	–	–	–	–	–	–	–	+	+	+	+	–	CS, pH$_i$	+	–	+	+	+	–	–	+	–	9	*3/n*	*6*
		MED = 10	8	19	4	2	0	17	6	5	3	1	1	16	9	5	2	8	4	10	11	19	9	3	8	16	1			*5.7*

The variables used temperature change (T), ocean acidification (OA), combined effects of T and OA (TxOA) and salinity (S). The study regions were the Mediterranean Sea (MED), the focus region of this Chapter, as well the North-Atlantic (N-A), Skagerrak (Skag), Gulf of Mexico (GoM) and South-West Pacific (SW-P). Study species were *Lophelia pertusa* (LP), *Madrepora oculata* (MO), *Desmophyllum dianthus* spp. (DE), *Dendrophyllia cornigera* (DC), *Caryophyllia smithii* (CS) and *Solenosmilia variabilis* (SV). The measures of calcification (G), respiration (R), skeletal structure (Sk), gene expression (GE), genotypes (GT), polyp mortality (†) and other measurements (OT), like inorganic nutrients (NUTS), dimethylsulfoniopropionate (DMSP), dissolved organic carbon (DOC), organic matter (OM), total organic carbon (TOC), respiratory quotient (RQ), energy requirements (E), boron isotopes (δ^{11}B), carbonic anhydrase activity (CAA), RNA/DNA ratio (RNA/DNA) and loss of coenosarc (CS). Experiments were evaluated according to their statistical robustness (SR) by using a point-system based on experimental duration short- and/or long-term exposure (ST and/or LT), design with a single (SM), repeated (RM) or consecutive (CM) measurements, the type of control(s) used with initial (IC), parallel (PC) and/or final controls (FC). The number of replicates (n), number of tanks per treatment (tanks/n) were taken into consideration. The points for statistical robustness (SR) were attributed as follows: each "+" under Experimental Design was counted as 1. For replication 1 point was given for of 5–9 and 2 points for >10 replicates. If more than 1 tank per treatment for replicates (tanks/n) was used (>1/n) another point was allocated

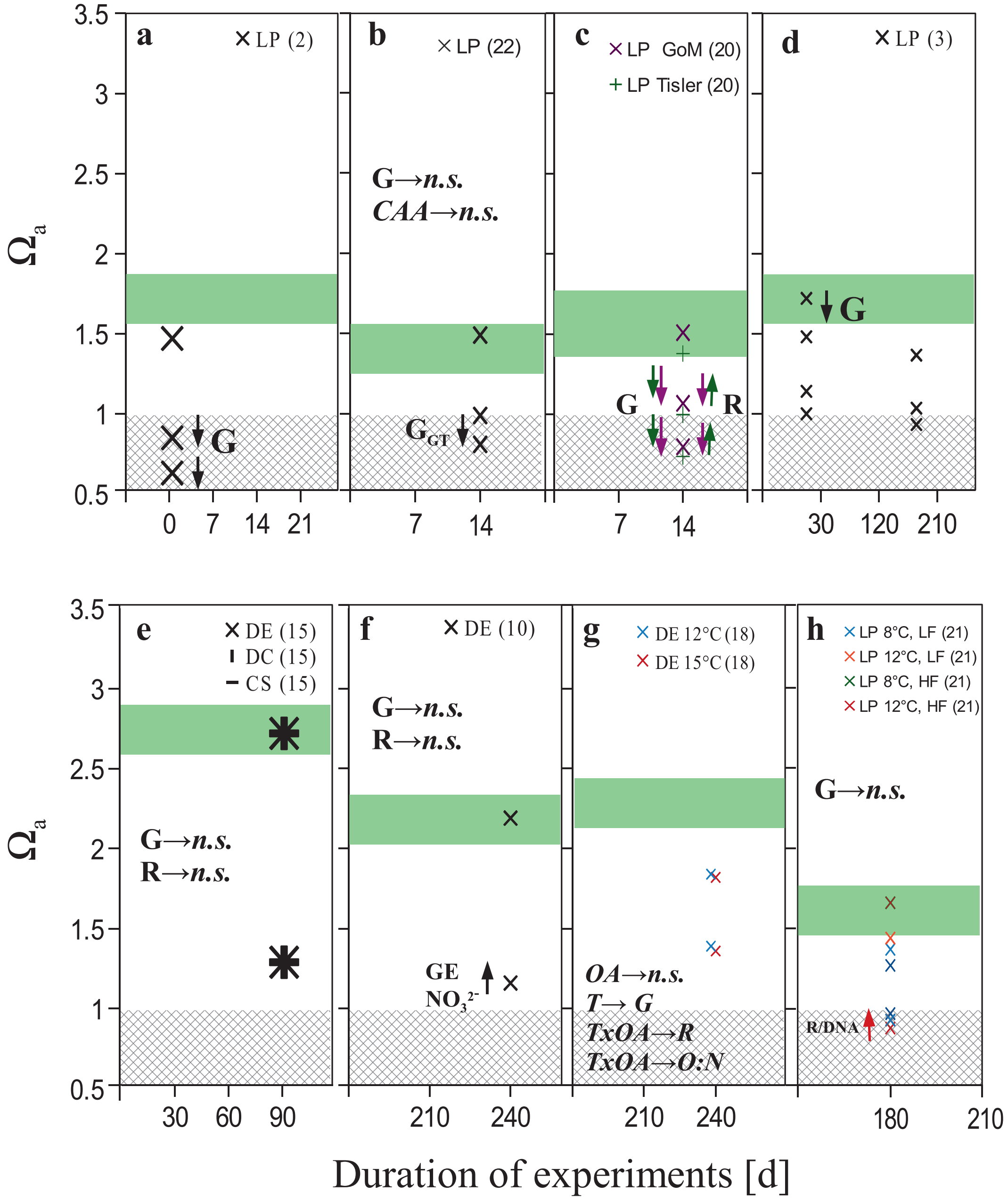

Fig. 44.1 Plot of studies using single-point experimental designs for measurements according to aragonite saturation state (Ω_a) in seawater (y-axis) and acclimation time in days (duration of experiments [d], x axes). The response of physiological functions are shown according to studies (**a–h**) and include calcification (G), calcification of different genotypes (G_{GT}), respiration (R), gene expression (GE), carbonic anhydrase activity (CAA) and nitrate excretion (NO_3^{2-}) for the species *Lophelia pertusa* (LP), *Madrepora oculata* (MO), *Desmophyllum dianthus* (DE), *Dendrophyllia cornigera* (DC), and *Caryophyllia smithii* (CS). Numbers in brackets refer to the publications referenced in Table 44.1. For studies addressing combined effects of OA and temperature (**g**) or OA, temperature and feeding (**h**) coloured symbols were used. The temperature and high or low food supply (HF and LF) are indicated in the symbol legend. According to the region the ambient Ω_a varied and is indicated by the green area. The grey area indicates $\Omega_a < 1$. Numbers in brackets refer to the publications referenced in Table 44.1. Size of symbols is indicative of number of replicates (n), vertical arrows depict where a significant positive (↑) or negative (↓) response was revealed, while *n.s.* indicates that there was no significant effect between treatment levels for the respective variable (© Cornelia Maier)

were upregulated under elevated pCO_2 levels after a 8-month exposure while the rates of calcification and respiration remained stable (Carreiro-Silva et al. 2014). No time-series on gene expression experiments exist for these species to date, and so it is not known whether an up- or down regulation of genes is dependent on the duration of exposure. While calcification rates are relatively constant over a large range of pCO_2 and only decrease after a certain threshold has been reached, faster skeletal linear extension under high pCO_2 has been reported for North Atlantic studies on *L. pertusa*

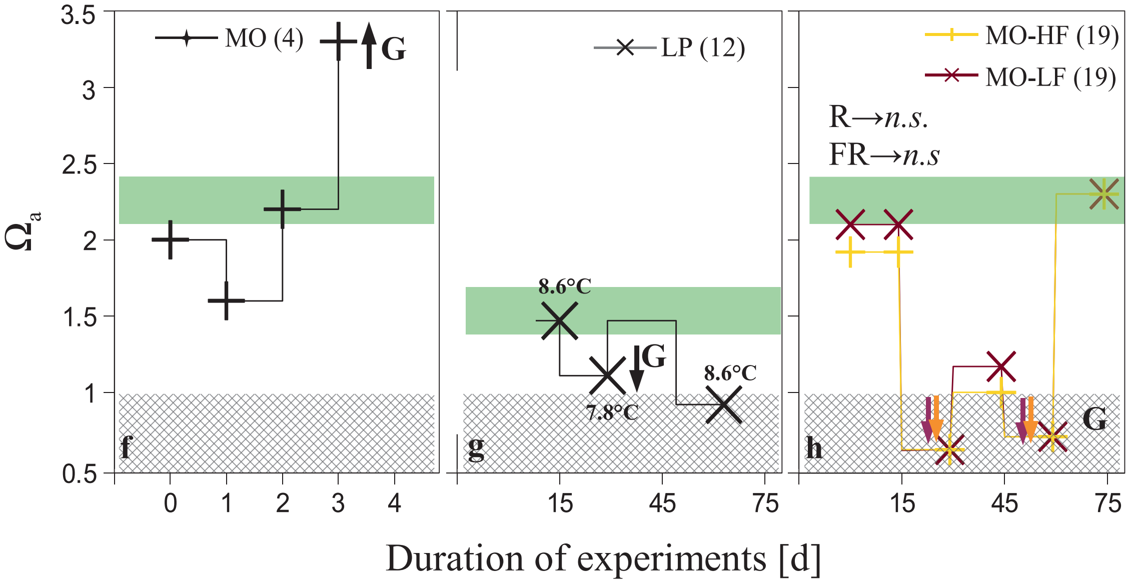

Fig. 44.2 Plot of studies using consecutive experimental designs for measurements according to aragonite saturation state (Ω_a) in seawater (y-axis) and acclimation time in days (duration of experiments [d]; x axes). The symbol lines record changes of Ω_a during experiments with symbols depicting when calcification (G) or respiration (R) of *Lophelia pertusa* (LP) or *Madrepora oculata* (MO) were assessed during the consecutive changes in Ω_a. Numbers in brackets refer to the publications referenced in Table 44.1. Coloured symbols (in **h**) were used to depict the high (HF) and low (LF) food regime. According to the region the ambient Ω_a varied and is indicated by the green area. The grey area indicates $\Omega_a < 1$. Numbers in brackets refer to the publications referenced in Table 44.1. Size of symbols is indicative of number of replicates (n), vertical arrows depict where a significant positive (↑) or negative (↓) response was revealed, while *n.s.* indicates that there was no significant effect between treatment levels or time steps for the respective variable (© Cornelia Maier)

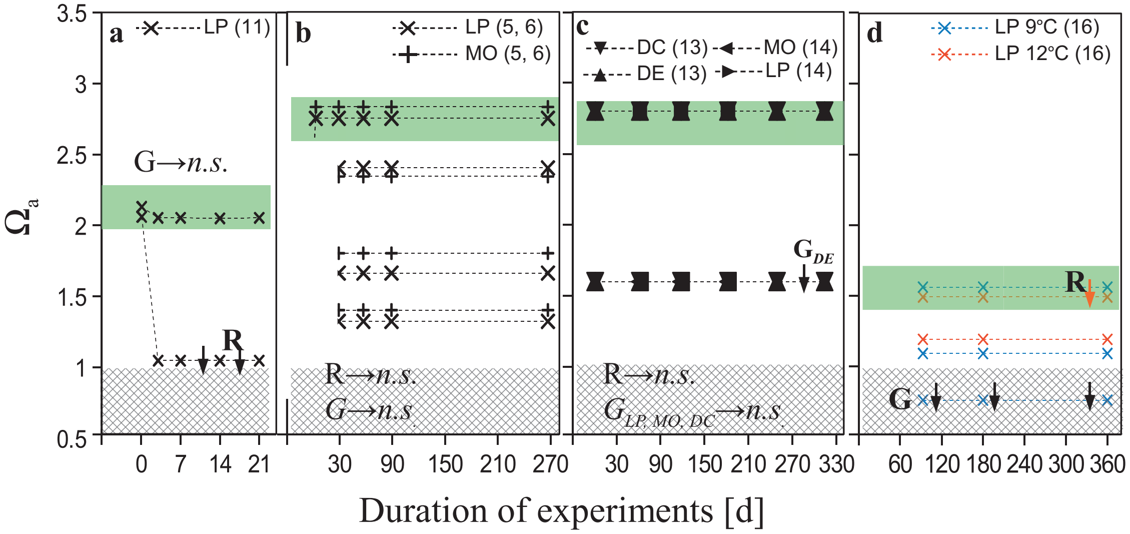

Fig. 44.3 Plot of studies using repeated measurement designs showing measurements points according to aragonite saturation state (Ω_a) in seawater (y-axis) and acclimation time in days (duration of experiments [d]; x-axis). The symbol lines record Ω_a for replicated measurements with symbols depicting when calcification (G) or respiration (R) of *L. pertusa* (LP), *M. oculata* (MO), *D. dianthus* (DE) or *D. cornigera* (DC) were assessed during the consecutive changes in Ω_a. Numbers in brackets refer to the publications referenced in Table 44.1. According to the region the ambient Ω_a varied and is indicated by the green area. The grey area indicates $\Omega_a < 1$. Numbers in brackets refer to the publications referenced in Table 44.1. Coloured symbols were used for the combined effect of OA and temperature (in **d**) with the temperature indicated in the symbol legend. Size of symbols is indicative of number of replicates (n), vertical arrows depict where a significant positive (↑) or negative (↓) response was revealed, while *n.s.* indicates that there was no significant effect between treatment levels or time steps for the respective variable (© Cornelia Maier)

(Hennige et al. 2015). This coincides with thinner and longer corallites and an altered mineral organisation that may impact the stability and breaking strength of the skeleton and the stability of the CWC framework. Despite this, changes in the micro-density and porosity were not reported under similar conditions, neither for North Atlantic *L. pertusa* (Wall et al. 2015) nor Mediterranean CWC species (Movilla et al. 2014a). In a study on a related species *Solenosmilia variabilis* colonies were grown under ambient pH (7.88, Ω_a 0.93) and lower pH (7.65, Ω_a 0.78) for two years (Gammon et al. 2018). Respiration and growth rate were not altered under low pH, although there was a decrease in skeletal colouration attributed to a loss of coenochyme, the tissue connecting neighbouring polyps and covering the outer skeleton, indicating the potential reallocation of energy to other physiological processes such as growth and respiration. While there has been two studies where respiration decreased or increased after two weeks during short-term exposure to higher pCO_2 (Figs. 44.1c and 44.3a; Hennige et al. 2014; Georgian et al. 2016b) no effect on respiration at increased pCO_2 levels has been detected in other studies (Figs. 44.1e–g, 44.2c, and 44.3b, c; Maier et al. 2013a, 2016; Carreiro-Silva et al. 2014; Movilla et al. 2014a, b; Rodolfo-Metalpa et al. 2015; Hennige et al. 2015; Gori et al. 2016; Gammon et al. 2018).

The apparent high resilience of CWCs to OA in both the experimental studies, described here for the Mediterranean and elsewhere, and also observed *in situ* (Thresher et al. 2011; Fillinger and Richter 2013; Jantzen et al. 2013; Bostock et al. 2015; Georgian et al. 2016a; Gammon et al. 2018) has been attributed to pH upregulation of the calicoblastic pH (McCulloch et al. 2012; Wall et al. 2015). The upregulation of calicoblastic pH has been thought to require a high amount of energy and may consequently require high food availability in areas with low Ω_a to maintain calcification constant (McCulloch et al. 2012; Fillinger and Richter 2013; Jantzen et al. 2013). However, a study establishing an energy budget for major physiological functions of Mediterranean *M. oculata* revealed that the energy required for calcification in general and for the upregulation of calicoblastic pH (or Ω_a) in particular only constitutes a minor fraction of about 1 to 3% of overall metabolic requirements (Maier et al. 2016). Despite a four-fold food uptake in the high feeding group and the respiratory quotient indicating starvation in the low-food group, no mitigating effect on calcification or respiration at increased pCO_2 levels due to feeding was reported (Maier et al. 2016). Similarly, in a study on North-Atlantic *L. pertusa* no mitigating effect of feeding has been shown despite a tenfold food availability in the high-food group (Büscher et al. 2017).

However, the need to double the energy allocated to calcification at elevated pCO_2 (Maier et al. 2016) might nevertheless constitute a burden over an extended time and permanent exposure to unfavorable conditions. Specifically in an environment where food is permanently scarce, a shift in energy allocation might occur in favor of other physiological functions that may explain the observed decline in calcification of *D. dianthus* (Movilla et al. 2014b). The decrease in skeletal colouration attributed to a loss of coenochyme seen by Gammon et al. (2018) may have also reflected a food scarcity response.

44.2.1 Temperature

Of the eight studies assessing the response of CWCs to changes in temperature, two measured the survival of *L. pertusa* from the Gulf of Mexico at a temperature range from 8 (ambient) to 15, 20 and 25 °C and an exposure time of 1 and 8 days (Brooke et al. 2013) or by changing temperature in consecutive steps from 8, 10, 12, 14 to 16°, with an adjustment period of 1 day per 2 °C increment (Lunden et al. 2014). Both studies showed significant mortalities at temperatures ≥15 °C and conclude that the upper temperature limit for the survival of *L. pertusa* would be 15 °C. The projected rise in temperature in the Mediterranean Sea could be as detrimental to the Mediterranean CWCs. However, the experimental design used by Brooke et al. (2013) did not allow for longer term acclimation and was in fact designed to reflect specific conditions prevailing in the Gulf of Mexico, where CWCs can experience occasional flushing by warm-water currents and a rapid and dramatic increase in seawater temperature (Brooke et al. 2013). In the Mediterranean Sea, CWCs are not subject to such an abrupt temperature increase, but they are subject to the high temperatures at the extreme reported for all CWCs. It is for this reason that it has been assumed that the Mediterranean CWCs are already at their upper tolerance limit (ca. 13 °C) and any further increase in temperature might therefore be detrimental. Despite this, there is some evidence that Mediterranean CWCs are well adapted to a relatively constant high temperature. In two experiments without prior acclimation phase, a temperature dependent increase or decrease of respiration has been reported for *L. pertusa* from the North Atlantic (Dodds et al. 2007) and Mediterranean Sea (Maier et al. 2013a, Supplement SI_1). At ambient temperature, respiration rates of Mediterranean *L. pertusa* were comparable to those from the North Atlantic region despite the 4 °C temperature difference. The temperature-dependent coefficient of respiration (Q_{10}) was lower for Mediterranean *L. pertusa* than for North-Atlantic specimen further indicating that Mediterranean *L. pertusa* as being well adapted to the higher temperature and potentially less sensitive to a further increase in temperature than specimen from colder regions. This is further substantiated by the finding by Naumann et al. (2013a, b) and Hennige et al. (2015) who found that no significant changes in respiration were observed when Mediterranean or North Atlantic *L. pertusa* were acclimated for 3–6 months to lower or higher than ambient temperatures (Naumann et al. 2013a, b;

Hennige et al. 2015). However, in the study by Hennige et al. (2015) respiration rates decreased significantly after a total of 9 months exposure to 12 °C. This response is difficult to explain, and with the good replication (n = 8, 4 tanks / n) it is not likely caused by experimental constraints such as tank effects. The authors therefore consider "… that normal' energetic strategies are no longer applying, possibly due to other processes using energetic reserves. This could be the result of processes that maybe occurring of which we have poor understanding and/or cannot easily measure" (Hennige et al. 2015). In contrast to *L. pertusa,* respiration of Mediterranean *M. oculata* significantly decreased when temperature was lowered from 12 to 9 and then down to 6 °C after a 3-month acclimation (Naumann et al. 2013b). This result led the authors to speculate that *M. oculata* acclimates at a much slower rate to changes in temperature than *L. pertusa*. The results also provide the variable thermal tolerance range for the two species. *M. oculata* is the dominant species in the Mediterranean, while *L. pertusa* prevails in colder regions like the North Atlantic. This preferred distribution for both species could indicate that *L. pertusa* acclimates faster to colder temperature than *M. oculata* and conversely, that *M. oculata* acclimates more easily to increasing temperatures. To date, no longer term study with respect to increasing temperature tolerance exists for these two species and no final conclusion can be made as to: how these two species may acclimate to the ongoing warming in the Mediterranean Sea. For calcification responses, the Mediterranean *D. cornigera* revealed a significant increase in calcification at 17.5 °C while a slight but non-significant reduction to 83% was reported for *D. dianthus* at 17.5 °C (Naumann et al. 2013a). When the temperature was lowered from 12 to 9 to 6 °C, calcification of *M. oculata* and *L. pertusa* was faster at the higher temperature levels in both species. While calcification of *M. oculata* significantly decreased at each temperature step, calcification of *L. pertusa* was only significantly lower at 6°, and between 12 to 9 °C only a slight, non-significant decrease was observed (Naumann et al. 2013b). For North Atlantic *L. pertusa* the response differed, showing a slight decrease in calcification to 82 and 70% after exposure of 3 and 6 months to higher (12 °C) than ambient (9 °C) temperature, while calcification increased to 1.5 times that at ambient temperature after a total of 9 months (Hennige et al. 2015, Fig. 44.3d). The study on Mediterranean *D. dianthus* by Gori et al. (2016) reported a significant and negative effect on calcification when temperature was increased from 12 to 15 °C. When subjected to both elevated temperature and pCO_2, however, there was no significant calcification effect and the opposite result was found for respiration (Gori et al. 2016). The experimental approach of the Gori et al. (2016) study was interesting and timely as the authors tackled the question of single and combined effects of temperature and OA impacts with the temperature and pCO_2 levels representative of projected changes in the Mediterranean Sea. However, the statistical robustness of the experiment was limited, due to a low number of sample replicates (n = 3) (Table 44.1). The results are useful as they provide a first indication as to how Mediterranean *D. dianthus* would respond to long-term increasing temperature; however the results require some consolidation.

This can also be said for the general perception that CWCs in the Mediterranean Sea are at their upper tolerance limit with respect to temperature. There is evidence that at least some of the species may be able to cope with increasing temperatures but overall there needs to be some caution before drawing this conclusion. It is important to consider in the first instance experimental design (duration of experiments, sample sizes, replication, and controls), as well as other environmental stressors, before any assumptions can be made when assessing the physiological response of these corals to changes in temperature.

44.2.2 Salinity

As a consequence of global change, the salinity in the Mediterranean Sea will increase by ~0.5 at the depths of CWC occurrence (see Skliris, this volume and references herein). Despite this fact, and that the current salinity levels are the highest reported for CWC occurrence in any one area, no studies are available on the physiological response of CWCs to increasing salinity. In addition to this and of significance is that climate change models need to take into account the ever growing need of freshwater in this region as consequence of a growing population and a higher consumption per capita. The construction of desalination plants along Mediterranean shorelines has intensified during the last decades several times over to generate fresh water. While 50% of the seawater is converted to drinking water the other 50% is discharged back into the sea as concentrated brine. For the Mediterranean Sea, it has been estimated that the salinity due to brine discharge will increase by an additional 0.81 g / L until 2050 (Bashitialshaaer et al. 2011). This situation means that together with the salinity increase due to climate change, the salinity may rise to above levels of around 40, which is comparable to the salinity of the Red Sea. The Red Sea is renowned for its thriving tropical coral reefs and one may therefore speculate that this increase in salinity may not impact Mediterranean CWCs. However, a high sensitivity to small changes in salinity has been reported for the tropical coral *S. pistillata* found in the region and that appeared to acclimate more easily to a decline than to an increase in salinity (Ferrier-Pagès et al. 1999). As with temperature, salinity is the highest reported in the Mediterranean region experienced by CWC habitats to date. It will therefore be important to study the response of Mediterranean CWCs to the added stress of an increase in salinity, particularly in light of the additional climate related impacts due to brine discharge that will potentially accelerate the increase in salinity during the coming decades.

44.3 Conclusions

It has been shown in a number of studies that CWCs exhibit a high resilience to OA and may be able to maintain calcification and respiration rates constant over a large gradient in pCO_2. There is robust evidence that with the projected Ω_a remaining above a level of 1, Mediterranean CWC growth might not be as impacted by OA despite the projected and relatively fast decline in seawater pH. The studies summarised in this chapter indicate that there is potentially some hope for some of Mediterranean CWC study species with some groups able to acclimate to an increase in temperature and withstand ocean acidification. However, upper tolerance limits (thresholds) for single climate change parameters still need to be consolidated for each species. This is particularly so for Mediterranean CWCs that are being exposed to additional stressors such as an increase in salinity or pollution. It will be pivotal to address the effect of the concomitant increase in temperature, pCO_2, and salinity to ultimately conclude on the potential fate of Mediterranean CWC species in the near future as both calcification and respiration reveal a strong acclimation response to temperature.

It is acknowledged that further work is required to tease out the impacts of multiple stressors on the CWCs. Some species may appear to be able to tolerate temperature and OA impacts but at what expense of other biological processes. The various aspects of human induced salinity changes need to be investigated, particularly as the availability of water to growing populations and agriculture will grow in demand. Also important will be to quantify the saturation state of aragonite (Ω_a) within the calcifying fluid of corals as this is critical for understanding their biomineralisation process and sensitivity to environmental changes including ocean acidification.

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References

Adloff F, Somot S, Sevault F, et al (2015) Mediterranean Sea response to climate change in an ensemble of twenty first century scenarios. Clim Dyn 45:2775–2802. https://doi.org/10.1007/s00382-00015-02507-00383

Alessandri A, Felice MD, Zeng N, et al (2014) Robust assessment of the expansion and retreat of Mediterranean climate in the 21st century. Sci Rep 4:7211. https://doi.org/10.1038/srep07211

Anderson OF, Guinotte JG, Rowden AA, et al (2016) Habitat suitability models for predicting the occurrence of vulnerable marine ecosystems in the seas around New Zealand. Deep-Sea Res Part 1 Oceanogr Res Pap 115:265–292

Antonov JI, Levitus S, Boyer TP (2002) Steric Sea level variations during 1957–1994: importance of salinity. J Geophys Res 107:8013. https://doi.org/10.1029/2001JC000964

Arrhenius S (1896) On the influence of carbonic acid in the air upon the temperature of the ground. Philos Mag Ser 41:237–276

Arrhenius S (1908) Worlds in the making. The evolution of the Universe, vol. Harper & Brothers Publishers, New York, London, 264 p

Bashitialshaaer RAI, Persson KM, Aljaradin M (2011) Estimated future salinity in the Arabian Gulf, the Mediterranean Sea and the Red Sea. Consequences of brine discharge from desalination. Int J Acad Res 3:133–140

Bell N, Smith J (1999) Coral growing on North Sea oil rigs. Nature 402:601

Bethoux JP, Gentili B (1996) The Mediterranean Sea, coastal and deep-sea signatures of climatic and environmental changes. J Mar Syst 7:383–394

Bethoux JP, Gentili B, Raunet J, et al (1990) Warming trend in the western Mediterranean deep water. Nature 347:660–662

Béthoux J-P, Gentili B, Tailliez D (1998) Warming and freshwater budget changes in the Mediterranean since the 1940s: their possible relation to the greenhouse effect. Geophys Res Lett 25:1023

Bostock HC, Mikaloff-Fletcher SE, Williams MJM (2013) Estimating carbonate parameters from hydrographic data for the intermediate and deep waters of the Southern Hemisphere oceans. Biogeosciences 10:6199–6213

Bostock HC, Tracey DM, Currie KI, et al (2015) The carbonate mineralogy and distribution of habitat-forming deep-sea corals in the Southwest Pacific region. Deep-Sea Res Part 1 Oceanogr Res Pap 100:88–104

Bova SC, Herbert TD, Fox-Kemper B (2016) Rapid variations in deep ocean temperature detected in the Holocene. Geophys Res Lett 43:12190–12198. https://doi.org/10.1002/2016GL071450

Brooke S, Ross SW, Bane JM, et al (2013) Temperature tolerance of the deep-sea coral *Lophelia pertusa* from the southeastern United States. Deep-Sea Res Part 2 Top Stud Oceanogr 92:240–248

Buhl-Mortensen L, Vanreusel A, Gooday AJ, et al (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the open ocean margins. Mar Ecol 31:21–50. https://doi.org/10.1111/j.1439-0485.2010.00359.x

Burdett HL, Carruthers M, Donohue P, et al (2014) Effects of high temperature and CO_2 on intracellular DMSP in the cold-water coral *Lophelia pertusa*. Mar Biol 161:1499–1506

Büscher JV, Form AU, Riebesell U (2017) Interactive effects of ocean acidification and warming on growth, fitness and survival of the cold-water coral *Lophelia pertusa* under different food availabilities. Front Mar Sci 4. https://doi.org/10.3389/fmars.2017.00101

Caldeira K, Wickett ME (2003) Anthropogenic carbon and ocean pH. Nature 425:365–365. https://doi.org/10.1038/425365a

Carreiro-Silva M, Cerqueira T, Godinho A, et al (2014) Molecular mechanisms underlying the physiological responses of the cold-water coral *Desmophyllum dianthus* to ocean acidification. Coral Reefs 33:465–476. https://doi.org/10.1007/s00338-00014-01129-00332

Chen X, Tung K-K (2014) Varying planetary heat sink led to global-warming slowdown and acceleration. Science 345:897–903. https://doi.org/10.1126/science.1254937

Cheng L, Zheng F, Zhu K (2015) Distinctive Ocean interior changes during the recent warming slowdown. Sci Rep 5:14346. https://doi.org/10.11038/srep14346

Church JA, White NJ, Konikow LF, et al (2011) Revisiting the Earth's sea-level and energy budgets from 1961 to 2008. Geophys Res Lett 38:L18601. https://doi.org/10.11029/12011GL048794

Cicerone R, Orr J, Brewer P, et al (2004) The ocean in a high-CO2 world. Oceanography 17:72–78

CIESM (2008) Impacts of ocean acidification on biological, chemical and physical systems in the Mediterranean and black seas. In: Briand F (ed) CIESM workshop monographs, Monaco, p 124

Clark MR, Althaus F, Schlacher TA, et al (2015) The impacts of deep-sea fisheries on benthic communities: a review. ICES J Mar Sci 73:i59–i69. https://doi.org/10.1093/icesjms/fsv1123

Clippele LHD, Gafeira J, Robert K, et al (2016) Using novel acoustic and visual mapping tools to predict the small-scale spatial distribution of live biogenic reef framework in cold-water coral habitats. Coral Reefs 36:255–268

D'Ortenzio F, Antoine D, Marullo S (2008) Satellite-driven modeling of the upper ocean mixed layer and air-sea CO2 flux in the Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 55:405–434

Davies AJ, Guinotte JM (2011) Global habitat suitability for framework-forming cold-water corals. PLoS One 6:e18483. https://doi.org/10.11371/journal.pone.0018483

Davies AJ, Wisshak M, Orr JC, et al (2008) Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). Deep-Sea Res Part 1 Oceanogr Res Pap 55:1048–1062

De Mol L, van Rooij D, Pirlet H, et al (2011) Cold-water coral habitats in the Penmarch and Guilvinec Canyons (Bay of Biscay): Deep-water versus shallow-water settings. Mar Geol 282:40–52

Desbruyères DG, Purkey SG, McDonagh EL, et al (2016) Deep and abyssal ocean warming from 35 years of repeat hydrography. Geophys Res Lett 43. https://doi.org/10.1002/2016GL070413

Dodds LA, Roberts JM, Taylor AC, et al (2007) Metabolic tolerance of the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature and dissolved oxygen change. J Exp Mar Biol Ecol 349:205–214

Duineveld GCA, Lavaleye MSS, Bergman MJN, et al (2007) Trophic structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in relation to the near-bottom particle supply and current regime. Bull Mar Sci 81:449–457

England MH, McGregor S, Spence P, et al (2014) Recent intensification of wind-driven circulation in the Pacific and the ongoing warming hiatus. Nat Clim Chang 4:222–227

Feely RA, Sabine CL, Lee K, et al (2004) Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science 305:362–366

Feely RA, Sabine CL, Byrne RH, et al (2012) Decadal changes in the aragonite and calcite saturation state of the Pacific Ocean. Glob Biogeochem Cycles 26:GB3001

Ferrier-Pagès C, Gattuso J-P, Jaubert J (1999) Effect of small variations in salinity on the rates of photosynthesis and respiration of the zooxanthellate coral *Stylophora pistillata*. Mar Ecol Progr Ser 181:309–314

Fillinger L, Richter C (2013) Vertical and horizontal distribution of *Desmophyllum dianthus* in Comau Fjord, Chile: a cold-water coral thriving at low pH. PeerJ 1:e194. https://doi.org/10.7717/peerj.7194

Form AU, Riebesell U (2012) Acclimation to ocean acidification during long-term CO_2 exposure in the cold-water coral *Lophelia pertusa*. Glob Change Biol 18:843–853. https://doi.org/10.1111/j.1365-2486.2011.02583.x

Fosså JH, Mortensen PB, Furevik DM (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471:1–12

Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:36–52

Fyfe JC, Meehl GA, England MH, et al (2016) Making sense of the early-2000s warming slowdown. Nat Clim Chang 6:224–228. https://doi.org/10.1038/nclimate2938

Gammon MJ, Tracey DM, Marriott PM, et al (2018) The physiological response of the deep-sea coral *Solenosmilia variabilis* to ocean acidification, e5236. PeerJ 6. https://doi.org/10.7717/peerj.5236

Gass SE, Willison JHM (2005) An asessment of the distribution of deep-sea corals in Atlantic Canada by using both scientific and local forms of knowledge. In: Freiwald A, Roberts JM (eds). Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 223–245

Gattuso J-P, Magnan A, Billé R, et al (2015) Contrasting futures for ocean and society from different anthropogenic CO2 emmissions scenarios. Science 349:aac4722. https://doi.org/10.1126/science.aac4722

Georgian SE, DeLeo D, Durkin A, et al (2016a) Oceanographic patterns and carbonate chemistry in the vicinity of cold-water coral reefs in the Gulf of Mexico: implications for resilience in a changing ocean. Limnol Oceanogr 61:648–665

Georgian SE, Dupont S, Kurman M, et al (2016b) Biogeographic variability in the physiological response of the cold-water coral *Lophelia pertusa* to ocean acidification. Mar Ecol 37:1345–1359

Giorgi F (2006) Climate change hot-spots. Geophys Res Lett 33:L08707. https://doi.org/10.01029/02006GL025734

Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. Glob Planet Chang 63:90–104

Giorgi F, Whetton PH, Jones RG, et al (2001) Emerging patterns of simulated regional climatic changes for the 21st century due to anthropogenic forcings. Geophys Res Lett 28:3317–3320

Gori A, Orejas C, Madurell T, Bramanti L, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Bigeosciences 10:2049–2060

Gori A, Ferrier-Pagès C, Hennige SJ, et al (2016) Physiological response of the cold-water coral *Desmophyllum dianthus* to thermal stress and ocean acidification. PeerJ 4:e1606. https://doi.org/10.7717/perj.1606

Goyet C, Hassoun AER, Gemayel E, et al (2016) Thermodynamic forecasts of the Mediterranean Sea acidification. Mediterr Mar Sci 17:508–518

Guinotte JM, Orr J, Cairns S, et al (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? Front Ecol Environ 4:141–146

Hansen J, Sato M (2016) Regional climate change and national responsibilities. Environ Res Lett 11:034009

Hansen J, Sato M, Kharecha P, et al (2011) Earth's energy imbalance and implications. Atmos Chem Phys 11:13421–13449

Hassoun AER, Gemayel E, Krasakopoulou E, et al (2015) Acidification of the Mediterranean Sea from anthropogenic carbon penetration. Deep-Sea Res Part 2 Top Stud Oceanogr 102:1–15

Hausfather Z, Cowtan K, Clarke DC, et al (2017) Assessing recent warming using instrumentally homogeneous sea surface temperature records. Sci Adv 3:e1601201

Hennige SJ, Wicks LC, Kamenos NA, et al (2014) Short-term metabolic and growth responses of the cold-water coral *Lophelia pertusa* to ocean acidification. Deep-Sea Res Part 2 Top Stud Oceanogr 99:27–35. https://doi.org/10.1016/j.dsr1012.2013.1007.1005

Hennige SJ, Wicks LC, Kamenos NA, et al (2015) Hidden impacts of ocean acidification to live and dead coral framework. Proc R Soc B 282:20150990

Hourigan TF (2009) Managing fishery impacts on deep-water coral ecosystems of the USA: emerging best practices. Mar Ecol Progr Ser 397:333–340

Hovland M, Vasshus S, Indreeide A, et al (2002) Mapping and imaging deep-sea coral reefs off Norway, 1982–2000. Hydrobiologia 471:13–17

IPCC (2013) Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In: Stocker TF, Qin D, Plattner G-K, et al (eds) Cambridge University Press, Cambridge

Jantzen C, Häussermann V, Försterra G, et al (2013) Occurrence of a cold-water coral along natural pH gradients (Patagonia, Chile). Mar Biol 160:2597–2607. https://doi.org/10.1007/s00227-00013-02254-00220

Karl TR, Arguez A, Huang B, et al (2015) Possible artifacts of data biases in the recent global surface warming hiatus. Science 348:1469–1472

Kiriakoulakis K, Fisher E, Wolff GA, et al (2005) Lipids and nitrogen isotopes of two deep-water corals from the North-East Atlantic: initial results and implications for their nutrition. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 715–729

Kleypas JA, Feely RA, Fabry VJ, et al (2006) Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide to future research. Report of a workshop sponsored by the National Science Foundation, the National Oceanographic and atmospheric administration, And the US geological survey 96 p. Available at: www.isseucaredu/Florida/

Kosaka Y, Xie S-P (2013) Recent global-warming hiatus tied to equatorial Pacific surface cooling. Nature 501:403–407. https://doi.org/10.1038/nature12534

Kurman MD, Gómez CE, Georgian SE, et al (2017) Intra-specific variation reveals potential for adaptation to ocean acidification in a cold-water coral from the Gulf of Mexico. Front Mar Sci 4:111. https://doi.org/10.3389/fmars.2017.00111

Landschützer P, Gruber N, Bakker DCE (2016) Decadal variations and trends of the global ocean carbon sink. Global Biogeochem Cycles 30:1396. https://doi.org/10.1002/2015GB005359

Law CS, Rickard GJ, Mikaloff-Fletcher SE, et al (2016) The New Zealand EEZ and south West Pacific. Synthesis report RA2, marine case study. Climate Changes, Impacts and Implications (CCII) for New Zealand to 2100. MBIE contract C01X1225, 41pp

Levermann A, Clark PU, Marzeion B, et al (2013) The multimillennial sea-level commitment of global warming. Proc Natl Acad Sci 110:13745–13750

Levitus S, Antonov JI, Boyer RP, et al (2012) World ocean heat content and thermosteric sea level change (0–2000 m), 1955–2010, 1955–2010. Geophys Res Lett 39:L10603 https://doi.org/10.11029/12012GL051106

Lewandowsky S, Cook J, Lloyd E (2016) The 'Alice in Wonderland' mechanics of the rejection of (climate) science: simulating coherence by consiracism. Synthese 195:175–196. https://doi.org/10.1007/s11229-11016-11198-11226

Llovel W, Willis K, Landerer FW, et al (2014) Deep-ocean contribution to sea level and energy budget not detectable over the past decade. Nat Clim Chang 4:1031–1035. https://doi.org/10.1038/nclimate2387

Lunden JJ, Nicholl CGM, Sears CR, et al (2014) Acute survivorship of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico under acidification, warming, and deoxygenation. Fron Mar Sci 1:78. https://doi.org/10.3389/fmars.2014.00078

Maier C, Hegeman J, Weinbauer MG, et al (2009) Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. Biogeosciences 6:1671–1680

Maier C, Watremez P, Taviani M, et al (2012) Calcification rates and the effect of ocean acidification on Mediterranean cold-water corals. Proc R Soc Lond 279:1713–1723. https://doi.org/10.1098/rspb.2011.1763

Maier C, Bils F, Weinbauer M, Watremez P, et al (2013a) Respiration of Mediterranean cold-water corals is not affected by ocean acidification as projected for the end of the century. Biogeosciences 10:5671–5680. https://doi.org/10.5194/bg-5610-5671-2013

Maier C, Schubert A, Berzunza Sànchez MM, et al (2013b) End of the century pCO_2 levels do not impact calcification in Mediterranean cold-water corals. PLoS One 8:e2655. https://doi.org/10.1371/journal.pone.0062655

Maier C, Popp P, Sollfrank N, et al (2016) Effects of elevated pCO_2 and feeding on net calcification and energy budget of the Mediterranean cold-water coral *Madrepora oculata*. J Exp Biol 219:3208

Malanotte-Rizzoli P, Font J, García-Ladona E, et al (2014) Physical forcing and physical/biochemical variability of the Mediterranean Sea: a review of unresolved issues and directions for future research. Ocean Sci 10:281–322

Mariotti A, Zeng N, Yoon J-H, et al (2008) Mediterranean water cycle changes: transition to drier 21st century conditions in observations and CMIP3 simulations. Environ Res Lett 3:044001 10.041088/041748-049326/044003/044004/044001

Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res Part 2 Top Stud Oceanogr 57:412–430

McCulloch M, Trotter J, Montagna P, et al (2012) Resilience of cold-water scleractinian corals to ocean acidification: boron isotopic systematics of pH and saturation state up-regulation. Geochim Cosmochim Acta 87:21–34. https://doi.org/10.1016/j.gca.2012.1003.1027

McGregor S, Timmermann A, Stuecker MF, et al (2014) Recent Walker circulation strengthening and Pacific cooling amplified by Atlantic warming. Nat Clim Chang 4:888–892. https://doi.org/10.1038/nclimate2330

Meehl GA, Arblaster JM, Fasullo JT, et al (2011) Model-based evidence of deep-ocean heat uptake during surface-temperature hiatus periods. Nat Clim Chang 1:360–364. https://doi.org/10.1038/nclimate1229

Mikaloff-Fletcher SE, Gruber N, Jacobson AR, et al (2006) Inverse estimates of anthropogenic CO_2 uptake, transport, and storage by the ocean. Global Biogeochem Cycles 20. https://doi.org/10.1029/2005GB002530

Millero FJ, Morse J, Chen CT (1979) The carbonate system in the western Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 26A:1395–1404

Mortensen PB (2001) Aquarium observations on the deep-water coral *Lophelia pertusa* (L., 1758) (Scleractinia) and selected associated invertebrates. Ophelia 54:83–104

Movilla J, Gori A, Calvo E, et al (2014a) Resistance of two Mediterranean cold-water coral species to low-pH conditions. Water 5:59–67

Movilla J, Orejas C, Calvo E, et al (2014b) Differential response of two Mediterranean cold-water coral species to ocean acidification. Coral Reefs 33:675–686

Naumann MS, Orejas C, Ferrier-Pagès C (2013a) High thermal tolerance of two Mediterranean cold-water coral species maintained in aquaria. Coral Reefs 32:749. https://doi.org/10.1007/s00338-00013-01011-00337

Naumann MS, Orejas C, Ferrier-Pagès C (2013b) Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. Deep-Sea Res Part 2 Top Stud Oceanogr 99:36–41

Nykjaer L (2009) Mediterranean Sea surface warming 1985–2006. Clim Res 39:11–17

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51

Orr JC, Maier-Reimer E, Mikolajewicz U, et al (2001) Estimates of anthropogenic carbon uptake from four three-dimensional global ocean models. Global Biogeochem Cycles 15:43–60

Orr JC, Fabry VJ, Aumont O, et al (2005a) Anthropogenic Ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Orr JC, Pantoja S, Pörtner HO (2005b) Introduction to special section: the ocean in a high-CO_2 world. J Geophys Res 110:C09S01. https://doi.org/10.1029/2005JC003086

Pierce DS, Gleckler PJ, Barnett TP, et al (2012) The fingerprint of human-induced changes in the ocean's salinity and temperature fields. Geophys Res Lett 39:L21704. https://doi.org/10.21029/2012GL053389

Purkey SG, Johnson GC (2010) Warming of global abyssal and deep Southern Ocean waters between the 1990s and 2000s: contributions to global heat and sea level rise budgets. J Clim 23:6336–6351. https://doi.org/10.1175/2010JCLI3682.6331

Revelle R, Suess HE (1957) Carbon dioxide exchange between atmosphere and ocean and the question of an increase of atmospheric CO2 during the past decades. Tellus 9:18–27. https://doi.org/10.3402/tellusa.v9i1.9075

Rhein M, Rintoul SR, Aoki S, et al (2013) Observations: ocean. In: Stocker TF, Qin D, Plattner G-K, et al (eds) Climate change 2013: the physical science basis contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, New York

Riebesell U, Gattuso JP (2015) Lessons learned from ocean acidification research. Nat Clim Chang 5:12–14

Rixen M, Beckers JM, Levitus S, et al (2005) The western Mediterranean deep water: a proxy for climate change. Geophys Res Lett 32:L12608

Roberts JM, Davies AJ, Henry LA, et al (2009) Mingulay reef complex: an interdisciplinary study of cold-water coral habitat, hydrograqphy and biodiversity. Mar Ecol Progr Ser 397:139–151

Roberts JM, Murray F, Anagnostou E, et al (2016) Cold-water corals in an era of rapid global change: are these the deep ocean's most vulnerable ecosystems? In: Goffredo S, Dubinsky Z (eds) The Cnidaria, past, present and future. Springer, Cham, pp 593–606

Rodolfo-Metalpa R, Montagna P, Aliani S, et al (2015) Calcification is not the Achilles' heel of cold-water corals in an acidifying ocean. Glob Chang Biol 21:2238–2248

Rogers AD (1999) The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. Int Rev Hydrobiol 84:315–406

Rowden AA, Guinotte JM, Baird SJ, et al (2013) Developing predictive models for the distribution of vulnerable marine ecosystems in the South Pacific region. New Zealand aquatic environment and biodiversity report 120:70p

Sabine CL, Feely RA, Gruber N, et al (2004) The oceanic sink for anthropogenic CO_2. Science 305:367–371

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the Northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108

Smith AM, Williams MJM (2015) The carbonate mineralogy and distribution of habitat-forming deep-sea corals in the southwest pacific region. Deep-Sea Res Part 1 Oceanogr Res Pap 100:88–104

Song J, Wang Y, Tang J (2016) A hiatus of the greenhouse effect. Sci Rep 6:33315

Sumida PYG, Yoshinaga MY, Madureira LASP, et al (2004) Seabed pockmarks associated with Deepwater corals off SE Brazilian continental slope, Santos Basin. Mar Geol 207:159–167

Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, pp 137–156

Thresher RE, Tilbrook B, Fallon S, et al (2011) Effects of chronic low carbonate saturation levels on the distribution, growth and skeletal chemistry of deep-sea corals and other seamount megabenthos. Mar Ecol Progr Ser 442:87–99

Tittensor DP, Baco AR, Hall-Spencer JM, et al (2010) Seamounts as refugia from ocean acidification for cold-water stony corals. Mar Ecol 31:212–225

Touratier F, Goyet C (2009) Decadal evolution of anthropogenic CO2 in the northwestern Mediterranean Sea from the mid-1990s to the mid-2000s. Deep-Sea Res Part 1 Oceanogr Res Pap 56:1708–1716

Touratier F, Goyet C (2011) Impact of the Eastern Mediterranean Transient on the distribution of anthropogenic CO2 and first estimate of acidification for the Mediterranean Sea. Deep-Sea Res Part 1 Oceanogr Res Pap 58:1–15

Tracey DM, Rowden AA, Mackay KA, et al (2011) Habitat-forming cold-water corals show affinity for seamounts in the New Zealand region. Mar Ecol Progr Ser 430:1–22

Turley CM (1999) The changing Mediterranean Sea – a sensitive ecosystem? Progr Oceanogr 44:387–400

Turley CM, Roberts JM, Guinotte JM (2007) Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? Coral Reefs 26:445–448

Vargas-Yáñez M, Moya F, Tel E, et al (2009) Warming and salting in the western Mediterranean during the second half of the 20th century: inconsistencies, unknown and the effect of data processing. Sci Mar 73:7–28

Wall M, Ragozzola F, Foster LC, et al (2015) pH up-regulation as a potential mechanism for the cold-water coral *Lophelia pertusa* to sustain growth in aragonite undersaturated conditions. Biogeosciences 12:6869–6880

Waller RG, Tyler PA (2005) The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic Ocean. Coral Reefs 24:514–522

Waller RG, Tyler PA, Gage JD (2005) Sexual reproduction in three hermaphroditic deep-sea Caryophyllia species (Anthozoa: Scleractinia) from the NE Atlantic Ocean. Coral Reefs 24:594–602

Wheeler AJ, Beyer A, Freiwald A, et al (2007) Morphology and environment of cold-water coral carbonate mounds on the NW European margin. Int J Earth Sci 96:37–56

Yan X-H, Boyer T, Trenberth K, et al (2016) The global warming hiatus: slowdown or redistribution. Earth's Future 4:472–482. https://doi.org/10.1002/2016EF000417

Zeebe RE, Ridgwell A, Zachos JC (2016) Anthropogenic carbon release rate unprecedented during the past 66 million years. Nat Geosci 9:325–329

Zibrowius H, Gili J-M (1990) Deep-water Scleractinia (Cnidaria: Anthozoa) from Namibia, South Africa, and Walvis ridge, southeastern Atlantic. Sci Mar 54:19–46

Cross References

Angeletti L, Bargain A, Campiani E, et al (this volume) Cold-water coral habitat mapping in the Mediterranean Sea: methodologies and perspectives

Hayes D, Schroeder K, Poulain, PM, et al (this volume) Review of the circulation and characteristics of intermediate water masses of the Mediterranean--implications for cold-water coral habitats

Lartaud F, Mouchi V, Chapron L, et al (this volume) Growth patterns of Mediterranean calcifying cold-water corals

Lo Iacono C, Savini A, Huvenne VAI, et al (this volume) Habitat mapping of cold-water corals in the Mediterranean Sea

Orejas C, Taviani M, Ambroso S, et al (this volume) Cold-water coral in aquaria: advances and challenges. A focus on the Mediterranean

Reynaud S, Ferrier-Pagès C (this volume) Biology and ecophysiology of Mediterranean cold-water corals

Skliris N (this volume) The Mediterranean is getting saltier: from the past to the future

45

Drop Chapter A Case Study: Variability in the Calcification Response of Mediterranean Cold-Water Corals to Ocean Acidification

Juancho Movilla

Abstract

The Mediterranean Sea has certain characteristics that make it especially sensitive and vulnerable to changes in atmospheric CO_2 and its gradual acidification. Some of the organisms that may be the first to be threatened by this impact are the cold-water corals. The few studies carried out up to date with these organisms by simulating in aquarium the acidified conditions expected for the year 2100 revealed a high variability between and within species. This chapter shows this highly variable response in the calcification of four of the most abundant cold-water coral species in the Mediterranean to low-pH conditions and their potential ecological implications.

Keywords

Ocean acidification · Mediterranean · *Lophelia pertusa* · *Madrepora oculata* · *Dendrophyllia cornigera* · *Desmophyllum dianthus*

In the upper bathyal zone of the Mediterranean Sea (between ~200 and 1200 m depth), *Lophelia pertusa*, *Madrepora oculata*, *Dendrophyllia cornigera* and *Desmophyllum dianthus* are the principal cold-water coral (CWC) species, which form three-dimensional structures (especially *Lophelia* and *Madrepora*) that host an enormous variety of associated species (Orejas et al. 2009; Gori et al. 2013; Roberts and Cairns 2014; D'Onghia et al., this volume; Rueda et al., this volume). Regrettably, ocean acidification (OA) could lead to degradation and fragmentation of these deep-sea habitats (Roberts et al. 2006; Cao et al. 2014). Moreover, although it is still under debate if the impact of OA will be stronger in the Mediterranean than in the global ocean (Touratier et al. 2012; Palmiéri et al. 2015), it is expected that this threat will be an added pressure to other anthropogenic influences and extreme natural events taking place at present in this semi-enclosed sea (Calvo et al. 2011).

Given the lack of fundamental information on the biological impacts of OA on CWC communities, experimental manipulations in aquaria will continue to play an important role in improving our knowledge on this topic (Orejas et al., this volume). However, due to the difficulties of sampling in deep-sea areas, only a handful of studies have focused on evaluating such effects in Mediterranean CWC, with rather different results (Maier et al. 2012, 2013; Rodolfo-Metalpa et al. 2015; see Maier et al., this volume for a review). In the following, laboratory experimentation is used to illustrate the high variability between and within Mediterranean CWC species with regard to calcification responses to low-pH conditions.

We conducted experiments simulating the present pH values and those expected by the year 2100 to assess the response to OA of four of the most widely distributed CWC species in the Mediterranean (*L. pertusa*, *M. oculata*, *D. cornigera* and *D. dianthus*; Fig. 45.1). For further details on the experimental setup, see Movilla et al. (2014a, b). Interestingly, no apparent pH-driven effects on the calcification process were observed in *L. pertusa* and *M. oculata* at midterm (6 months) and *D. cornigera* at long-term (11 months) exposure time, compared to control conditions (Fig. 45.2). However, we found a high intraspecific variability in the calcification rate among different colony fragments of *L. pertusa* depending on their initial weight, with small and younger nubbins showing faster skeletal growth rates. It is expected that those younger specimens with high calcification rates may be the most susceptible to the negative effects of OA due to the high-energy demand of this biological process (Cohen and Holcomb 2009; Allemand et al. 2011). This hypothesis was supported by the response observed in *D. dianthus* to low-pH conditions predicted for 2100. Fast-growing young polyps of *D. dianthus* displayed a 70% reduction in their calcification rates after a

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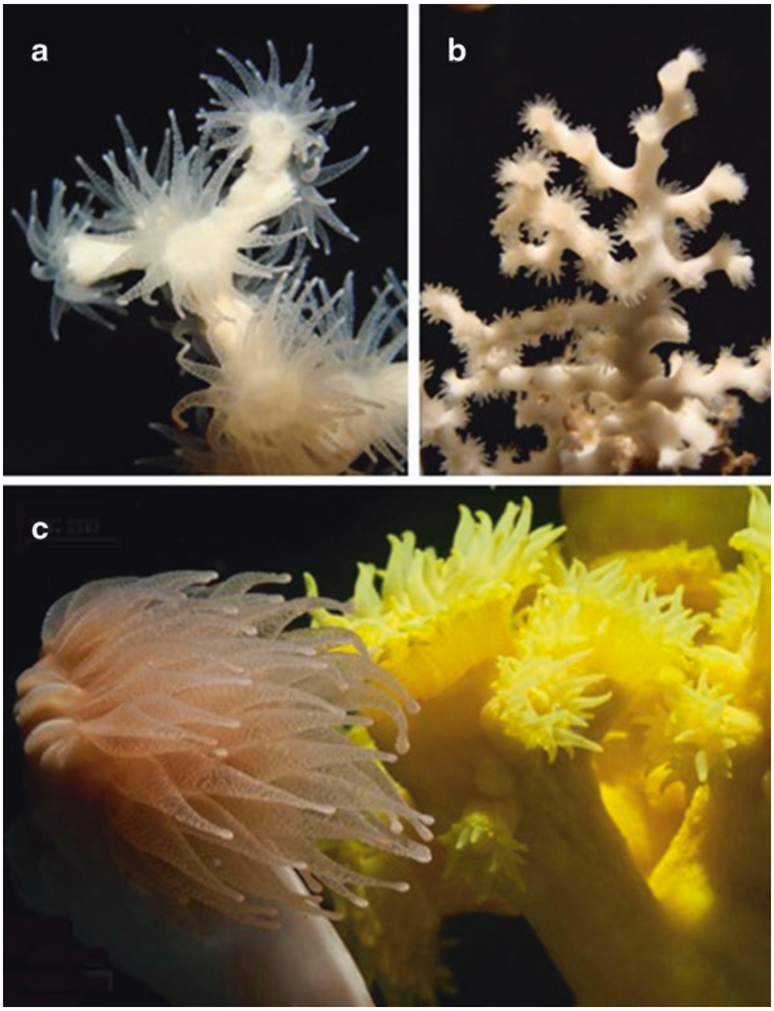

Fig. 45.1 Specimens of *Lophelia pertusa* (**a**), *Madrepora oculata* (**b**), *Desmophyllum dianthus* (**c**, left) and *Dendrophyllia cornigera* (**c**, right) in the experimental aquaria. Photo credits by A. Gori (**a** and **b**) and E. Obis (**c**). Panel (**a**) previously published by MEPS (©Inter-Research 2011)

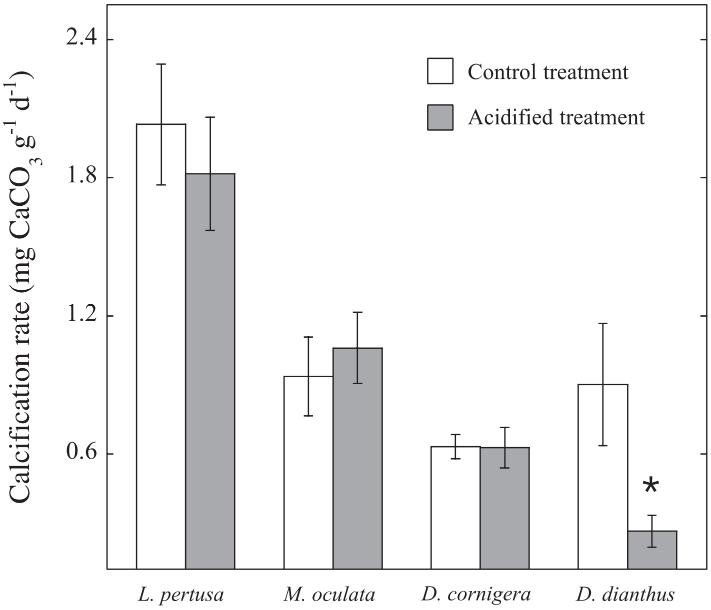

Fig. 45.2 Calcification rates under control (pH ~8.10 units) and acidified conditions (pH ~7.81 units). Results are expressed as mean ± SE. Asterisk indicates significant differences between treatments

long-term (11 months) exposure to acidified conditions, whereas larger and older polyps showed no significant effects to pH reduction.

These results suggest some degree of acclimation in terms of calcification to changes in carbonate chemistry and no mid- to long-term effects of OA in CWC populations when assessing the average overall effect on large adult colonies. However, those CWC populations presenting younger coral colonies with small polyps may be more sensitive to OA. These young, fast-growing polyps ensure, in the case of the branching CWC colonies, the increase in size and complexity of the three-dimensional structures. Similarly, in the case of the solitary corals such as *D. dianthus*, the young polyps are the recruits, which support the maintenance of the populations. Thus, the decreased in calcification of these young polyps could compromise the long-term persistence of CWC communities and the habitats they form in the Mediterranean.

We should keep in mind that although calcification rates did not change between treatments, other adverse effects associated with a lower pH could also be at stake. Indeed, it is known that OA could affect CWC in different ways (e.g. Carreiro-Silva et al. 2014; Hennige et al. 2015; Maier et al., this volume) and that synergies with other stressors could make them more susceptible to other threats (e.g. Wicks and Roberts 2012). On the other hand, even in the case where a given species shows a strong and consistent response to acidification, reactions may be significantly different at the community level. This 'scaling up' from individual to community or ecosystem level is one of the most challenging goals in assessing the effects of OA. It is important to evaluate jointly the physiological response of several key species under future conditions, as well as identify the eventual consequences related with changes on species interaction and energetic flow thorough trophic webs. An integrative understanding how the ecosystem works as a whole is essential to predict the consequences of the different stressors that are affecting the marine biodiversity of the Mediterranean Sea.

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References

Allemand D, Tambutté E, Zoccola D, et al (2011) Coral calcification, cells to reefs. In: Dubinsky Z, Stambler N (eds) Springer, Dordrecht, pp 119–150. https://doi.org/10.1007/978-94-007-0114-4

Calvo E, Simó R, Coma R, et al (2011) Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. Clim Res 50:1–29

Cao L, Zhang H, Zheng M, et al (2014) Response of ocean acidification to a gradual increase and decrease of atmospheric CO_2. Environ Res Lett 9:024012

Carreiro-Silva M, Cerqueira T, Godinho A, et al (2014) Molecular mechanisms underlying the physiological responses of the cold-water coral *Desmophyllum dianthus* to ocean acidification. Coral Reefs 33:465–476

Cohen AL, Holcomb M (2009) Why corals care about ocean acidification: uncovering the mechanism. Oceanography 22:118–127

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Hennige SJ, Wicks LC, Kamenos NA, et al (2015) Hidden impacts of ocean acidification to live and dead coral framework. Proc R Soc B 282:20150990

Maier C, Watremez P, Taviani M, et al (2012) Calcification rates and the effect of ocean acidification on Mediterranean cold-water corals. Proc R Roc B 279:1716–1723

Maier C, Schubert A, Berzunza-Sánchez MM, et al (2013) End of the century pCO_2 levels do not impact calcification in Mediterranean cold-water corals. PLoS One 8:e62655. https://doi.org/10.1371/journal.pone.0062655

Movilla J, Gori A, Calvo E, et al (2014a) Resistance of two Mediterranean cold-water coral species to low-pH conditions. Water 6:59–67

Movilla J, Orejas C, Calvo E, et al (2014b) Differential response of two Mediterranean cold-water coral species to ocean acidification. Coral Reefs 33:675–686

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Progr Ser 397:37–51

Palmiéri J, Orr JC, Dutay JC, et al (2015) Simulated anthropogenic CO_2 storage and acidification of the Mediterranean Sea. Biogeosciences 12:781–802

Roberts JM, Cairns SD (2014) Cold-water corals in a changing ocean. Curr Opin Environ Sustain 7:118–126

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547

Rodolfo-Metalpa R, Montagna P, Aliani S, et al (2015) Calcification is not the Achilles' heel of cold-water corals in an acidifying ocean. Glob Chang Biol 21:2238–2248

Touratier F, Guglielmi V, Goyet C, et al (2012) Distributions of the carbonate system properties, anthropogenic CO_2 and acidification during the 2008 BOUM cruise (Mediterranean Sea). Biogeosci Discuss 9:2709–2753

Wicks L, Roberts JM (2012) Benthic invertebrates in a high-CO2 world. Oceanogr Mar Biol Annu Rev 50:127–188

Cross References

D'Onghia G (this volume) Cold-water coral as shelter, feeding and life-history critical habitats for fish species: ecological interactions and fishing impact

Maier C, Weinbauer MG, Gattuso JP (this volume) Fate of Mediterranean scleractinian cold-water corals as a result of global climate change. A synthesis

Orejas C, Taviani M, Ambroso S, et al (this volume) Cold-water coral in aquaria: advances and challenges. A focus on the Mediterranean

Rueda JL, Urra J, Aguilar R, et al (this volume) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas

Conservation of Cold-Water Corals in the Mediterranean: Current Status and Future Prospects for Improvement

46

Maria del Mar Otero and Pilar Marin

Abstract

The Mediterranean deep-sea contains a mosaic of ecosystems and habitat types. Among them, cold-water corals provide shelter to a large and unique variety of organisms as well as ecosystem services. Scientific findings over the last decade have strengthened this fact and further supported the identification of cold-water corals habitats as sites of conservation interest and high vulnerability. Given the semi-enclosed nature of the Mediterranean basin and the significant anthropogenic pressure on its ecosystems, most, cold-water corals species have been listed as threatened as they are found at areas which are frequently the focus of resource exploitation (e.g. deep-sea fisheries, oil and gas prospections among others) or are affected directly by other human activities (e.g. marine debris, pollution events) as well as by the increasing impacts of climate change including ocean acidification. Nowadays, conservation and protection of such important species and ecosystems largely depend upon the proper development and implementation of marine policies. Here, we analyze the most important policy framework in place to protect these species in the Mediterranean Sea and we consider the most recent developments and opportunities for improving the situation. The management of cold-water corals involves important challenges. This is partly due to their remote location, limited political awareness, as well as incomplete information available on the occurrence, distribution and resilience of these cold-water coral species and their associated fauna, to impacts and disturbances. Specific actions are discussed to increase the protection of deep-sea ecosystems hosting cold-water corals through good governance and to establish effective area-based conservation measures to safeguard Mediterranean deep-sea biodiversity.

Keywords

Cold-water corals · Mediterranean · Marine conservation · Policy · Species protection · Deep-sea

46.1 Introduction

Knowledge of global cold-water coral (CWC) ecosystems has significantly increased over the last two decades. New findings have increased our information on the occurrence and spatial distribution of deep-sea corals (see Altuna and Poliseno, this volume, and references therein; Chimienti et al., this volume, and references therein), leading to a better understanding of their ecological role and functional significance. Even so, public awareness is still a pending issue (see Rossi and Orejas, this volume).

Generally, CWCs refers to azooxanthellate species of scleractinian, antipatharian, gorgonian and stylasterid corals that are not restricted to the photic zone (Roberts et al. 2009), usually found below 200 m. However, there is not a single definition for the term "Cold-water corals" and several authors come out with different definitions, depth and temperature limits (see for instance Cairns 2007; Altuna and Poliseno, this volume, among others). CWCs have been described in the Mediterranean Sea forming a large variety of biotopes with biodiversity and abundance of the dominant and associated species varying with the region, hydrodynamic regime, topography, substrate and bathymetry among others (e.g. Freiwald et al. 2009; Taviani et al. 2011, 2017; Sanfilippo et al. 2013; Gori et al. 2013; Altuna and Poliseno, this volume; Chimienti et al., this volume; Rueda et al., this volume). Mediterranean CWCs are known to occur at the shelf breaks, escarpments and submarine canyon walls, seamounts as well as on top and flanks of coral-formed reliefs or mounds. Whether they are scleractinian frameworks, dense aggregations of antipatharians and/or gorgonians on hard or soft substrates, CWCs could form oasis-like habitats in the

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deep Mediterranean environment providing a physical support, refuge or nursery area for other living organisms (Maynou and Cartes 2011; Baillon et al. 2012; Calcinai et al. 2013; Bo and Bavestrello, this volume; Gori et al., this volume; Rueda et al., this volume).

The discovery of new CWC taxa is still ongoing as exploration of the deep Mediterranean waters continues. New species have been discovered in recent surveys such as the soft corals *Chironephthya mediterranea* and *Nidalia studeri* reported in the shelf break and flanks of a submarine canyon of Menorca Channel, Balearic Islands (López-González et al. 2015; see also Altuna and Poliseno, this volume). Often, explorations indicate also that some deep coral species appear to be much more extensively distributed than previously thought. This is the case of the gorgonian *Dendrobrachia bonsai* reported in various locations along the western coast of Corsica Island between 200 and 500 m depth that establish its northern distribution limits in the western Mediterranean basin (Sartoretto 2012; Altuna and Poliseno, this volume). Similarly, recent findings of *Dendrophyllia ramea* in Cyprus (Orejas et al. 2017, this volume; Altuna and Poliseno, this volume) and Lebanese waters (Aguilar pers. comm.[1]) demonstrate a new depth and geographical limit for this species.

Moreover, molecular identification tools are revealing a much more diverse and evolutionarily complex picture of the Mediterranean coral diversity than previously depicted (Boavida et al., this volume). Debate on taxonomic rearrangement of some taxa, discovery of new species, as well as the possibility of splitting taxa into different groups (such as in the case of the bamboo coral *Acanella arbuscula* from *Isidella elongata*), are still ongoing (Heestand Saucier 2016; Otero et al. 2016). These studies will have a considerable impact on conservation and management efforts and raise the need for a more pro-active approach to safeguard the Mediterranean deep-sea biodiversity.

46.2 Current Impacts and Scenario Trends

Past and ongoing human activities impacting the Mediterranean deep-sea have been increasingly documented and future trends in most maritime sectors indicate that these impacts are on the rise (Pianté and Ody 2015). Mediterranean CWCs face considerable threat from fishing activities particularly from demersal fisheries (Maynou and Cartes 2011). Bottom contact gears directly damage corals (Palanques et al. 2006; D'Onghia et al. 2016; Bo and Bavestrello, this volume; Puig and Gili, this volume) and remobilise soft surface sediments, generating increased turbidity also far from fishing grounds (Puig et al. 2012; Martín et al. 2014; Paradis et al. 2017). The settling of this suspended sediment (added to the natural deposition of sediments) can lead to the smothering of benthic communities as have been already observed at various sites such as La Fonera Canyon on the Catalan margin off the NW Mediterranean (Paradis et al. 2017). Accidental bycatch of black corals and scleractinians with experimental long lines and through trammel nets has also been proved to have a significant impact (D'Onghia et al. 2010, 2012; Mytilineou et al. 2014; Bo et al. 2014; Bo and Bavestrello, this volume; Gori et al., this volume; Orejas et al., this volume). Lost fishing gears can further entangle on scleractinian CWCs and damage colonies which may in turn severely impair their recovery (Reed et al. 2007; Orejas et al. 2009; Huvenne et al. 2016).

Other aspects that are having or will have a high impact in Mediterranean CWC communities are climate change and ocean acidification (OA) (e.g. Maier et al. 2012; Movilla et al. 2014a, b; Maier et al., this volume; Movilla, this volume), as well as the accumulation of marine litter (Savini et al. 2014; Lastras et al. 2016) and chemical pollution (e.g. disposal of solid waste from land-based mines and oil spills) (Larsson and Purser 2011; Fabri et al. 2014; Otero et al. 2016).

Climate change is affecting the Mediterranean biodiversity (e.g. Danovaro et al. 2004; Lejeusne et al. 2010; Crisci et al. 2011; Otero et al. 2013; Parravicini et al. 2015) and it is expected to have a strong effect in the future (Giorgi 2006; IPCC 2007, 2013). Current climate model simulations indicate a significant warming, increasing acidification and temperature stratification, variations in precipitation patterns and terrestrial nutrient loads, as well as changes in plankton phenology and spatial distribution among others (Yang and Rudolf 2010; Lazzari et al. 2014; Lacoue-Labarthe et al. 2016). These changes may shift the carbon balance in the sea and further affect corals' ability to grow as well as enhance their vulnerability to OA (Davies et al. 2017). Ocean acidification causes the depth of carbonate compensation (the specific *depth* at which calcium carbonate minerals dissolve in the water) to rise closer to the sea surface. Consequently this will affect the rate of supply of calcium carbonate needed for the coral's skeletal structures (Harris and Whiteway 2011).

Cold-water corals seem to live close to their upper thermal limits in the Mediterranean Sea (see Maier et al., this volume) and are characterised by slow growth rates and long generation times (Orejas et al. 2008, 2011a, b; Lartaud et al. 2013, 2014, 2017, this volume; Reynaud and Ferrier-Pagès, this volume). The detrimental effects of a potential additional stresses given by a small increase of water temperature, lowered pH and reduced food supply are likely to reduce their resilience and recovery capacity from other impacts (e.g. Gori et al. 2016). Knowledge of the severity of these

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[1] Deep Sea Lebanon Project, a partnership between Oceana, IUCN and UNEP/MAP-RAC/SPA, on behalf of the Ministry of Environment with the support of CNRS-L.

threats is further hampered by the limited knowledge of the occurrence, distribution and habitat requirements of CWCs (Tittensor et al. 2010).

Off-shore oil exploration and exploitation activities are also booming in the Mediterranean basin and could increase by 60% by 2020 as gas production could increase five-folds by 2030 (Pianté and Ody 2015). The scarce scientific information (see Larsson and Purser 2011 work on the NE Atlantic and De Leo et al. 2016 in the Gulf of Mexico) on the ecological consequences and the risks involved in developing some of these activities would likely not be countenanced in a terrestrial environment and there are still significant gaps in our knowledge of anthropogenic impacts on the deep-sea.

Proposals for the commercial mining of deep-sea mineral resources (particularly for sulphide deposits) in the Mediterranean Sea are not yet developed and there is great uncertainty concerning these exploitations. Even if the seafloor mining is not directly developed in the vicinity of CWC communities, it could impact suspension-feeding corals living on rocky seafloors far from the exploitation areas, as already demonstrated by Larsson and Purser (2011) in the NE Atlantic and by Reichelt-Bruschett (2012) in Indonesia.

46.3 Policy Framework in Cold-Water Coral Conservation and Management

To date, Sustainable Development Goals (SDGs) have been defined as the environmental reference for United Nations (UN) during the period 2015–2030. Regarding marine issues, the global framework to develop policies and actions is provided by SDG 14 to "*conserve and sustainably use the oceans, seas and marine resources for sustainable development* (Rees et al. 2018)". Accordingly, SDG 14 has been recently integrated in the different Mediterranean regional seas strategies for their future plans (GFCM Mid-Term Strategy 2017–2020; UNEP-MAP Mediterranean Strategy for Sustainable Development 2016–2025).

The United Nations General Assembly (UNGA) in paragraph 51 of its resolution 58/240 (2003), "*reiterated its call for urgent consideration of ways to integrate and improve, on a scientific basis, the management of risks to the marine biodiversity of seamounts, CWC reefs and other underwater features*". This further relates to the conservation and sustainable use of biodiversity in marine areas beyond the limits of national jurisdiction (ABNJ), in particular since negotiations to develop a new instrument that addresses marine protected areas (MPAs) and environmental impact assessments in these areas, are still ongoing (Druel and Gjerde 2014; Blasiak and Yagi 2016).

In addition, within the Convention on Biological Diversity (CBD) and its Strategic Plan for Biodiversity 2011–2020, the Aichi Target 11 called on Contracting Parties to commit to preserve at least 10% of coastal and marine areas by 2020 (Rees et al. 2018), through especially areas of particular importance for biodiversity and ecosystem services, giving particular emphasis to protect critical ecosystems such as CWC reefs and seamounts (CBD COP11 Decision XI/16). However, the mid-term assessment of progress towards the implementation of Aichi Targets (Global Biodiversity Outlook 4) concluded that regarding Target 11 "*Marine protected areas are accelerating but extrapolations suggest we are not on track to meet the target. With existing commitments, the target would be met for territorial waters but not for exclusive economic zones or high seas*" (Secretariat of the Convention on Biological Diversity 2014). Likewise, the current priority actions to achieve Aichi Target 10 for "*coral reefs and closely associated ecosystems*" are consistent with the previous work plan to avoid the physical degradation and destruction of coral reefs, including CWCs (appendix 1 and 2 of annex I to decision VII/5). Moreover, this work plan aims to minimise the multiple anthropogenic pressures on coral reefs and other fragile ecosystems impacted by climate change, including OA.

Furthermore, within the CBD context, it must be underlined that the Ecologically and Biologically Significant Marine Areas (EBSA) process in the Mediterranean was triggered by a regional workshop in 2014 (CBD 2014). The process culminated at the CBD 12th COP with the endorsement of 15 EBSAs which include a wide coverage of offshore areas, recognising the biological and ecological significance of deep-sea habitats in the Mediterranean basin to define future manage measures that ensure the biodiversity conservation of these areas.

Today, the implementation of such international policies and targets through real management measures in the Mediterranean Sea is still limited. Regional and international bodies have developed instruments and tools towards the achievement of these targets (Table 46.1). Analysis of those efforts and achievements provide the identification of further ways needed to move forward.

At a regional level, within the framework of the Barcelona Convention (Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean), it is the Protocol concerning Specially Protected Areas and Biological Diversity (SPA / BD Protocol) adopted in 1995, which establishes the framework for the protection and conservation of biodiversity of valuable areas and species in the Mediterranean Sea. This Protocol also serves as main tool for implementing the CBD with regards the sustainable management of coastal and marine biodiversity. Since its adoption, several amendments have been adopted by Contracting Parties, bringing the number of species listed as endangered or threatened in Annex II (algae, sponges, fish, mollusks, birds, marine mammals…) up to more than 150, and the number of species listed in Annex III, referring to exploited

Table 46.1 Current policies and framework that includes protection of CWCs in the Mediterranean Sea

Legal or reference instrument	Species protected / Habitat that are or can be considered
FAO/global	
International guidelines for the Management of Deep-sea Fisheries in the high seas	Certain CWCs – communities and habitat forming species that are documented or considered sensitive and potentially vulnerable to deep-sea fisheries in the high-seas, and which may contribute to forming VMEs: stony corals (Scleractinia) alcyonaceans and gorgonians (Octocorallia) black corals (Antipatharia)
Barcelona Convention/Mediterranean region	
Annex II to the SPA/BD protocol	*Callogorgia verticillata* *Lophelia pertusa* *Madrepora oculata* *Antipathella subpinnata* *Antipathes dichotoma* *Leiopathes glaberrima* *Parantipathes larix*
Reference List of marine habitat types for the selection of sites to be included in the National Inventories of natural sites of conservation interest	Facies of soft muds with *Funiculina quadrangularis* and *Aporrhais serresianus* Facies of compact muds with *Isidella elongata* Biocenosis of deep-sea corals
Habitats Directive/European Union	
ANNEX I: Natural habitat types of community interest whose conservation requires the designation of special areas of conservation	1170 reefs. Examples of habitat forming species included under this category: *Callogorgia verticillata* *Dendrophyllia cornigera* *Desmophyllum dianthus* *Lophelia pertusa* *Madrepora oculata*

species in need of regulation, to more than 40. The Cnidaria taxa, initially represented only by *Gerardia savaglia (Savalia savaglia)* and *Antipathes* sp.plur. included in Annex II and by the red coral, *Corallium rubrum* in Annex III, was further updated in 2013 with the inclusion of the following species: *Callogorgia verticillata, Lophelia pertusa, Madrepora oculata, Antipathella subpinnata, Leiopathes glaberrima, Parantipathes larix* and *Antipathes dichotoma*. This was a significant big step forward to improve protection of deep-sea structuring species, as they had never been considered in this context.

In 2016, the IUCN regional Red List assessment classified several anthozoan species with a deep-water distribution as "Threatened" and includes one of them, the bamboo coral *Isidella elongata* as "Critically Endangered", mainly as a result of deep-water bottom trawling (Otero et al. 2017; Table 46.2). The available information on the current status of different Mediterranean CWC populations suggest that similar conditions exist also for other CWC species and that damaging these communities would have dramatic consequences for the ecosystem.

Table 46.2 Deep-sea anthozoan species listed as 'Threatened' at Mediterranean regional level (IUCN Red List, 2016) and included in Annexes of the Protocol SPA/BD to Barcelona Convention (2017)

Species name	IUCN Red List category	Protocol SPA/BD
Isidella elongata	CR	Annex II[a]
Corallium rubrum	EN	Annex III
Leiopathes glaberrima	EN	Annex II
Desmophyllum dianthus	EN	Annex II[a]
Lophelia pertusa	EN	Annex II
Dendrophyllia cornigera	EN	Annex II[a]
Madrepora oculata	EN	Annex II
Funiculina quadrangularis	VU	
Pennatula phosphorea	VU	
Pteroeides spinosum	VU	

CR Critically Endangered, *EN* Endangered, *VU* Vulnerable
[a] Amendment December 2017

As a result of the 2016 IUCN assessment, the Decision[2] to include 3 new deep anthozoans species (*I. elongata*, *Desmophyllum dianthus, Dendrophyllia cornigera*) together with the relatively shallow-water species (*Dendrophyllia ramea)* in Annex II was adopted at the last Contracting Parties meeting to the Barcelona Convention (December 2017) (Fig. 46.1). Despite this, there is an important lack of information for other deep-water species and this is particularly evident for the southern and Levantine basin where more research would help develop management and conservation plans for the entire Mediterranean basin.

At present, very few countries have enacted legislations aimed at protecting CWC taxa in their waters, and these are mostly limited to the decisions adopted by the Conference of Parties, with the exception of the protection of 'Near Threatened' species such as the gold coral *S. savaglia,* the gorgonian *Callogorgia verticillata* or other species of black corals (Otero et al. 2016). Endangered species legislation at national level is also necessary to strengthen protection of species classified as 'threatened', as such legal regulations should aim to control human activities that lead to species declines. Listing species under national legislation should further trigger actions towards enhancing their protection status (e.g. recovery plans), enforcement of regulations to reduce threats and / or identifying habitats for protection.

Likewise, the reference List of Marine Habitat Types under the Barcelona Convention also aims to assist Mediterranean countries in the selection of sites to be

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[2] Draft Decision IG.23/10: Amendments to Annex II to the Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean (UNEP(DEPI)/MED IG.23/13). 20th Ordinary Meeting of the Contracting Parties to the Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean and its Protocols. Tirana, Albania, 17–20 December 2017.

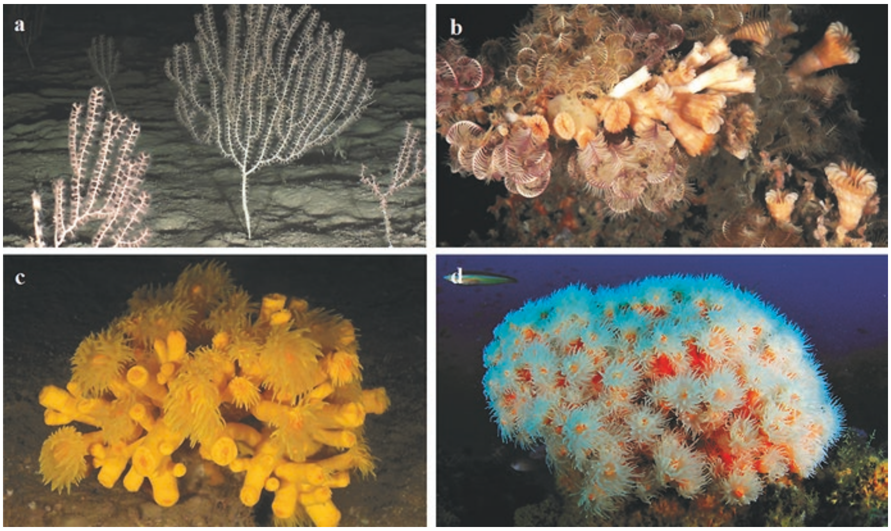

Fig. 46.1 Mediterranean anthozoan species recently included in Annex II of the SPA/BD Protocol to the Barcelona Convention (**a**) *Isidella elongata;* (**b**) *Desmophyllum dianthus;* (**c**) *Dendrophyllia cornigera;* (**d**) *Dendrophyllia ramea*. (Photo credits (a,b,c) © OCEANA; d © OCEANA/Carlos Minguell)

included in the national inventories of Natural Sites of Conservation Interest. This tool is being currently updated[3] to also include deep-sea habitats and will also be reflected in activities within the Dark Habitats Action Plan (Action Plan for the conservation of habitats and species associated with seamounts, underwater caves and canyons, aphotic hard beds and chemo-synthetic phenomena in the Mediterranean Sea, UNEP-MAP-RAC/SPA 2015).

At European level, for Member States (European Union), the biotope formed by CWCs (facies, banks and communicates) could be considered[4] as "habitat type 1170 Reefs" under Annex I of the EC Habitats Directive 92/43/EEC. Pursuant to this Directive, measures shall be taken by Member States to maintain or restore the favourable conservation status for those habitats listed, as CWCs provide important habitat for deep-sea commercial species (fish and crustaceans) (Nouar and Maurin 2001; D'Onghia et al. 2010, 2011, 2012; Baillon et al. 2012; Mastrototaro et al. 2017; D'Onghia, this volume), spatial closures to protect CWCs may also be a useful tool for the management of those species or the habitat they create (Milligan et al. 2016).

Compared with coastal systems, the capacity for recovery from human disturbance of deep-sea ecosystems is much less understood and recovery rates are thought to be longer (Van Dover et al. 2014). Thus, prioritisation of conservation policies with a more holistic approach that ensures those species and community assemblages identified most at-risk of global or regional extinction or those that play important ecological roles should be part of the guiding principles for marine management. Populations of CWCs are especially vulnerable because their slow growth rates (Orejas et al. 2008; 2011a, b; Lartaud et al. 2013, 2014, 2017, this volume) and frequent patchy distribution (Orejas et al. 2009; Vertino et al. 2010; Gori et al. 2013; Savini et al. 2014; Chimienti et al., this volume). These considerations have led to enhanced efforts worldwide for the protection of CWC species and their habitats at international and regional level through their inclusion within biodiversity conservation and fisheries policies.

Given the existing policy context, increasing numbers of MPAs have been designated, with few also involving offshore areas (MedPAN & UNEP-MAP RAC/SPA, in prep). Therefore, the establishment of MPAs in deep waters is however very limited. The presence of the framework-forming species *L. pertusa* and *M. oculata* with, among others, soft corals, sponges, bryozoans and black corals occurs in only a few designated MPAs from the western Mediterranean Sea such as the National Park of Calanques in France or the Chella bank (Seco de los Olivos) in Spain, this last one declared in 2014 as Site of Community Importance (SCI). In addition, it is also worth highlighting that important hard-bottom communities dominated by millenial colonies of *L. glaberrima* as well as soft-bottom communities dominated by the now rare bamboo coral *I. elongata*, occur in areas which remain unprotected (Bo et al. 2015; Mastrototaro et al. 2017).

These few examples provide an idea that overall, the current Mediterranean MPA network offers very limited protection to CWC habitats, and in turn, to its associated

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[3] See Annex II to Draft Decision IG.23/8 (UNEP(DEPI)/MED IG.23/11): Updated Action Plan for the Conservation of Marine and Coastal Bird Species listed in annex II to the Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean. Updated Reference List of Marine and Coastal Habitat Types in the Mediterranean. 20th Ordinary Meeting of the Contracting Parties to the Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean and its Protocols. Tirana, Albania, 17–20 December 2017.

[4] According to the Interpretation Manual of European Union Habitats (European Commission 2013).

biodiversity. Despite recommendations made following the 2012 MPA status report (Gabrié et al. 2012) about the lack of protection for deep-sea areas, no substantial changes have been made to address this gap in recent years. While MPAs and Other Effective area-based Conservation Measures (OECMs) coverage increased from 4.56% (2012) to 7.14% (2016) in the Mediterranean basin, more than 55% of this increment just covers depth ranges between 0–200 meters leaving highly biodiverse deep-sea areas unprotected.[5] To counter these deficiencies in spatial coverage, legislative protection for representative populations of these species is urgently needed given the current threats and pressures.

From a fisheries perspective, the conservation of CWCs is linked to the protection of vulnerable marine ecosystems (VMEs) which has been a legal mandate for Regional Fisheries Management Organisations (RFMO) and States since 2008. Specific requirements for that are laid out under UNGA Resolutions 59/25, 61/105 and 64/72 which FAO used to develop the International Guidelines for the Management of Deep-sea Fisheries (Armstrong et al. 2014). These are the basic guidelines to develop and implement further measures (e.g. encounter protocols with associate thresholds, closure areas, etc.) in order to ensure protection of certain groups of species and habitats from significant adverse fisheries impacts at regional and national level. CWCs (stony corals (Scleractinia), alcyonaceans (Octocorallia), and black corals (Antipatharia) are included among the group of species considered sensitive and potentially vulnerable to deep-sea fisheries and could be initially considered as habitat-building species which may contribute to forming VMEs (FAO 2009). According to the FAO Guidelines (paragraph 66), "*in areas where VMEs have been designated, or are known or likely to occur, based on seabed surveys and mapping or other best available information, States and RFMO/As should close such areas to DSFs until appropriate conservation and management measures have been established to prevent significant adverse impacts on VMEs and ensure long-term conservation and sustainable use of deep-sea fish stocks*". Following this recommendation, current spatial closures aiming to provide protection for VMEs are further on need of implementation in certain regions (Gianni et al. 2016) including the Mediterranean Sea.

More in detail, while general criteria have been produced through the Guidelines (Armstrong et al. 2014) there are no protocols that elaborate the procedure, from initial identification to the protection of VMEs (Ardron et al. 2014). Consequently, implementation of such resolutions varies in terms of approach and performance of management measures in place along the different RFMOs (Gianni et al. 2016; see Table 46.3). Criteria for identifying VMEs have not been applied consistently across regions and different approaches have been used when selecting fauna as indicators, from order or family level to species (FAO 2016a). Considering that threshold limits need to be appropriated for the specific biogeographic region – or sub-region – and the taxa concerned, the approach to define bycatch thresholds in most of the RFMOs cases seems to be particularly inadequate to ensure conservation of these ecosystems. Thus could be the case given the nature of certain deep-sea corals (e.g. *Funiculina quadrangularis*, *I. elongata*) with low weights and elongated or arborescent shape where standard encounter protocols generally set the bycatch limits in weight and at such high levels that rules becomes meaningless (Weaver et al. 2011) and are likely to have little or no conservation value. Thereafter, the designation of closures also varies depending on the region (see Table 46.4) and may be based on known occurrence of VMEs, predictive modelling, or just based on a precautionary approach because of certain geomorphological features (e.g. seamounts) where VMEs occurs or is likely to occur (FAO 2016a).

In addition, with respect to performance, very few encounters are usually reported to RFMOs Secretariats, which may indicate: (1) a lack of compliance with the protocols; (2) the fact that thresholds have been set too high; or (3) as result of the protocols or management measures in place, fishing vessels actively avoid areas where VMEs might be encountered. This highlights the further need to refine the different approaches, standardise them when suitable, assess their effectiveness and make improvements where needed. Given the uncertainties about the location of many Mediterranean VMEs and their resilience, additional measures such as the employment of onboard scientific observers, the identification of VMEs and decision criteria for encounters while fishing, the avoidance of bottom-contact fishing (trawlnets and longlines) in some areas and the delineation of boundaries for VMEs are still on need to be defined for the Mediterranean.

In the Mediterranean context, the General Fisheries Commission for the Mediterranean (GFCM) is the RFMO in charge of implementing such measures. While VME protocols and measures have been already developed and implemented in other regions globally, the only Mediterranean-wide measure established by GFCM to date with regards to protection of these VMEs is the prohibition of trawling below 1000 m. Such a measure leaves many CWC habitats entirely unprotected knowing the depth-range for most of these species is 100–600 m. Only three spatial closures for fisheries (Fisheries Restricted Areas, FRA) have been established in order to safeguard deep-sea sensitive habitats and from these, a single site, "*Lophelia* reef off Capo Santa Maria di Leuca" has been reported with CWCs occurrence (see Table 46.4). Furthermore, weakness in the management and effectiveness

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[5] GIS calculation based on MapaMED database, http://www.mapamed.org/.

Table 46.3 Implementation approaches for VME protection developed by Regional Fisheries Management Organisations

RFMO Biogeographic region	VME INDICATOR TAXA		Threshold
	Taxa level	CWCs considered (species/group or species/habitat)	
NAFO[a] Northwest Atlantic	Family	Stony Corals Gorgonian corals Sea pens	60 kg of live coral
NEAFC[a] North East Atlantic	Family or species	CWC reefs Coral garden (hard and soft bottoms)	>30 kg of live coral
SEAFO[a] South East Atlantic	Order or Family	Gorgonacea (Order): Gorgonian corals Anthoathecatae (Family): Hydrocorals Scleractinia (Order): Stony corals Antipatharia (Order): Black corals Zoantharia (Order): Zoanthids Alcyonacea (Order): Soft corals Pennatulacea (Order): Sea pens	Bottom trawling: 60 kg of live coral Longline: at least 10 VME-indicator units (1 unit = 1 kg or 1 L of live coral) in one 1200 m section of line or 1000 hooks Pot set – at least 10 VME-indicator units (1 unit = 1 kg or 1 L of live coral and/or live sponge) in one 1200 m section of line in both existing and new fishing areas
CCAMLR[a] Antartic	Order or Family	Gorgonacea (Order) Anthoathecatae (Order) Stylasteridae (Family) Scleractinia (Order) Antipatharia (Order) Zoantharia (Order)	Reporting thresholds >5 units on one line segment
SPRFMO[a] South Pacific	Order	Actinaria Scleractinia Antipatharia Alcyonacea Gorgonacea Pennatulacea	NO
GFCM[b] Mediterranean*	Order	Hexacorallia (Antipatharia, Scleractinia) Octocorallia (Alcyonacea, Pennatulacea)	Not defined yet

Based on Weaver et al. (2011), Gianni et al. (2016) and RFMOs
*As adopted at the 42nd session of the GFCM Commission (2018)
[a]Move-on rule in place
[b]No move-on rule in place

Table 46.4 Closure areas in place by RFMO

RFMO Biogeographic region	Closure areas for VME protection
NAFO Northwest Atlantic	6 Seamounts: Fogo Seamounts 1; Fogo Seamounts 2; Orphan Knoll; Corner Seamounts; Newfoundland Seamounts; New England Seamounts 1 Coral Area Closure 9 High Sponge and Coral Concentration Area Closures: Tail of the Bank; Flemish Pass/Eastern Canyon; Beothuk Knoll; Eastern Flemish Cap; Northeast Flemish Cap; Sackville Spur; Northern Flemish Cap; Northwest Flemish Cap; Beothuk Knoll
NEAFC North East Atlantic	13 Seamounts: Northern, Middle (Charlie-Gibbs Fracture Zone and sub-Polar Region) and Southern Mid-Atlantic-ridge (MAR); Altair Seamount; Antialtair Seamount; Hatton Bank 1 and 2; Rockall Bank; Logachev Mounds; West Rockall Mounds; Edora's bank; Southwest Rockall Bank; Hatton-Rockall Basin
SEAFO South East Atlantic	12 Seamounts: Unnamed seamount; Kreps seamount; Malachit Guyot Seamount; Wüst seamount; Africana seamount; Schmidt-Ott Seamount; Unnamed; Vema Seamount; Herdman Seamounts; Unnamed Seamounts; Unnamed Seamounts; Valdivia Bank South (pots and longlines allowed)
CCAMLR Antartic	46 identified VME areas (of these, 42 VMEs are in areas where bottom fishing is currently prohibited; in the remaining 4, toothfish fisheries are permitted and are afforded specific protection)
SPRFMO South Pacific	20 areas in New Zealand No one in Australia
GFCM Mediterranean	Eratosthenes seamount; Santa Maria di Leuca (CWC reefs); Nile delta (cold seeps. Jabuka/Pomo Pit (mud volcanoes, pockmarks, sea pen fields, oyster beds)

Based on Weaver et al. (2011), Gianni et al. (2016), FAO (2016a), and RFMOs of these fisheries restricted areas (FRA) has also been reported (GFCM 2014).

Discussions at the Mediterranean level for the implementation of management measures to enhance conservation of VMEs (including CWCs) are now ongoing under the newly established GFCM Working Group of Vulnerable Marine Ecosystems (WGVME April 2017). Future works should continue on this line, defining appropriate encounter protocols with associated move-on rules, impact assessments and developing management measures in areas where a VME encounter has been reported or VMEs are likely to exist according to FAO Deep-sea Guidelines (FAO 2016b).

46.4 Future Perspectives for Conservation Planning and Good Governance

With the realisation of the economic value of the coastal and open seas, the concept of sustainable development linked to the "Blue Growth" EU strategy is becoming of increased importance in the development of policies and instruments in the Mediterranean Sea. The Blue Growth (BG) agenda promulgated by the European Commission (2012) is seen as an ambitious framework for ocean management within EU waters, seeking to foster a more coherent approach to maritime issues and the growth of marine economic sectors (blue energy, aquaculture, maritime, coastal and cruise tourism, marine mineral resources, and blue biotechnology). This further requires appropriate management measures to ensure environmental sustainability and good environmental status (GES) in line with the Marine Strategy Framework Directive[6] (MSFD). At the broader regional scale, within the Barcelona Convention, the Mediterranean Strategy for Sustainable Development (MSSD) has also formulated a similar agenda for the period 2016–2025. This framework embeds the need for BG and the increase in the exploration for, and exploitation of, non-living open sea resources. This effort would be directed to establishing and enforcing regulatory mechanisms, including Maritime Spatial Planning (MSP), to prevent and control unsustainable open ocean resource exploitation as well as support sustainable development. From fisheries perspective, the GFCM has developed and adopted the Mid-Term Strategy 2017–2020 towards the sustainability of Mediterranean and Black Sea fisheries. This strategy is based on five targets, one of them (Target 4) aiming to "*minimize and mitigate unwanted interactions between fisheries and marine ecosystems and environment*".

Within these aforementioned overarching policies and strategies, significant challenges remain as how to achieve and properly regulate the economic outcomes from the "Blue economy" while mitigating the negative impact of certain economic activities in the open seas of the Mediterranean basin. CWCs are likely to be significantly impacted by these policies and their resulting anthropogenic activities.

Climate change including OA will further put at risk deep-sea communities in the near future (see chapters by Maier et al., this volume; Movilla, this volume). Incorporating climate change projections into conservation planning for CWCs are essential components for future efforts in the Mediterranean Sea. This could be used for example to identify locations for MPAs or FRAs where CWCs are less likely to be affected by climatic disturbances while facilitating, at the same time, connectivity among populations to enhance their resilience. A possible example could be made by exploring the protection through a network of deep-sea MPAs or FRAs covering the know distribution of the important sites for living white corals frameworks (dominated by *Madrepora oculata*). These sites located in the South-western Adriatic Sea, northern Ionian Sea, Strait of Sicily, the Gulf of Lion, the westwards to Alborán Sea and off Sardinia, seem to correspond to the core water flux of the Levantine Intermediate Water (LIW) which possibly acts as a vector for larval dispersal thus connecting disjoint CWC areas in the Mediterranean Sea (Taviani et al. 2017; Chimienti et al., this volume). Similar approaches could be explored with pristine and unique black coral gardens, the now rare bamboo coral *Isidella elongata*, and other longevous and rare coral species (e.g. Bo et al. 2015; Mastrototaro et al. 2017; Bo and Bavestrello, this volume; Chimienti et al., this volume).

Configure an MPA network that enhances connectivity of these key habitats while furthermore estimating and assessing the timescale and distances over which climate change impacts will be expected, will mitigate these effects and assist to establish ecological linkages and pathways for a wide range of species.

Moreover, good governance is still underdeveloped for managing Mediterranean Sea affairs. The involvement of stakeholders with an interest in the deep-sea (governments, members of industry, academic world, intergovernmental panels, NGOs) will likely evolve and expand as human activities increase. Mechanisms that promote this participation and multi-stakeholder engagement, e.g., national and international governance frameworks, corporate responsibility or voluntary code of conduct, could be effective means to share tools and to make collective decisions that ensures conservation as well as adequate, viable, and long-term management measures.

Additional scientific studies are also essential to have a more comprehensive census and understand the distribution of CWCs and their assemblages. This information represents

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[6] Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive).

a tool to legislate and manage the marine environment in a sustainable manner. Collectively these measures could have a considerable impact on conservation and management efforts ensuring a more dynamic approach to safeguard Mediterranean deep-sea biodiversity, including CWCs.

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References

Ardron JA, Clark MR, Penney AJ, et al (2014) A systematic approach towards the identification and protection of vulnerable marine ecosystems. Mar Policy 49:146–154

Armstrong CW, Foley NS, Kahui V, et al (2014) Cold water coral reef management from an ecosystem service perspective. Mar Policy 50:126–134

Baillon S, Hamel JF, Wareham VE, et al (2012) Deep cold-water corals as nurseries for fish larvae. Front Ecol Environ 10:351–356. https://doi.org/10.1890/120022

Blasiak R, Yagi N (2016) Shaping an international agreement on marine biodiversity beyond areas of national jurisdiction: lessons from high seas fisheries. Mar Policy 71:210–216

Bo M, Bava S, Canese S, et al (2014) Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. Biol Conserv 171:167–176. https://doi.org/10.1016/j.biocon.2014.01.011

Bo M, Bavestrello G, Angiolillo M, et al (2015) Persistence of pristine Deep-Sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS One 10:e0119393. https://doi.org/10.1371/journal.pone.0119393

Calcinai B, Moratti V, Martinelli M, et al (2013) Uncommon sponges associated with deep coral bank and maerl habitats in the Strait of Sicily (Mediterranean Sea). Ital J Zool 80:412–423. https://doi.org/10.1080/11250003.2013.786763

Cairns SD (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. Bull Mar Sci 81:311–322

CBD (2014) Report of the Mediterranean regional workshop to facilitate the description of ecologically or biologically significant marine areas. UNEP/CBD/EBSA/WS/2014/3/4. http://www.cbd.int/doc/meetings/mar/ebsaws-2014-03/official/ebsaws-2014-03-04-en.pdf

Crisci C, Bensoussan N, Romano JC, et al (2011) Temperature anomalies and mortality events in marine communities: insights on factors behind differential mortality impacts in the NW Mediterranean. PLoS One 6:e23814. https://doi.org/10.1371/journal.pone.0023814

D'Onghia G, Maiorano P, Sion L, et al (2010) Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. Deep-Sea Res Part 2 Top Stud Oceanogr 57:397–411. https://doi.org/10.1016/j.dsr2.2009.08.022

D'Onghia G, Indennidate A, Giove A, et al (2011) Distribution and behaviour of deep-sea benthopelagic fauna observed using towed cameras in the Santa Maria di Leuca cold-water coral province. Mar Ecol Prog Ser 443:95–110

D'Onghia G, Maiorano P, Carlucci R, et al (2012) Comparing Deep-Sea fish Fauna between coral and non-coral "Megahabitats" in the Santa Maria di Leuca cold-water Coral Province (Mediterranean Sea). PLoS One 7:e44509. https://doi.org/10.1371/journal.pone.0044509

D'Onghia C, Calculli C, Capezzuto F, et al (2016) Anthropogenic impact in the Santa Maria di Leuca cold-water coral province (Mediterranean Sea): observations and conservation straits. Deep-Sea Res Part 2 Top Stud Oceanogr 145:87–101. https://doi.org/10.1016/j.dsr2.2016.02.012

Danovaro R, Dell'Anno A, Pusceddu A (2004) Biodiversity response to climate change in a warm deep sea. Ecol Lett 7:821–828

Davies J, Guillaumont B, Tempera F, et al (2017) A new classification scheme of European cold-water coral habitats: implications for ecosystem-based management of the deep sea. Deep-Sea Res Part 2 Top Stud Oceanogr 145:102–109. https://doi.org/10.1016/j.dsr2.2017.04.014

DeLeo DM, Ruiz-Ramos DV, Baums IB, et al (2016) Response of deep-water corals to oil and chemical dispersant exposure. Deep-Sea Res Part 2 Top Stud Oceanogr 129:137–147

Druel E, Gjerde KM (2014) Sustaining marine life beyond boundaries: options for an implementing agreement for marine biodiversity beyond national jurisdiction under the United Nations convention on the law of the sea. Mar Policy 49:90–97

European Commission (2012) Blue Growth Opportunities for marine and maritime sustainable growth. Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. Directorate-General for Maritime Affairs and Fisheries, Luxembourg, Publications Office of the European Union, COM (2012) 494 final. Available via http://eur-lex.europa.eu/

European Commission (2013) Interpretation manual of European habitats. DG Environment. Nature ENV B 3 http://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/Int_Manual_EU28.pdf

Fabri MC, Pedel L, Beuck L, et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Part 2 Top Stud Oceanogr 104:184–207. https://doi.org/10.1016/j.dsr2.2013.06.016

FAO (2009) International guidelines for the management of deep-sea fisheries in the high seas. FAO, Rome, Italy, 73 pp

FAO (2016a) Vulnerable marine ecosystems: processes and practices in the high seas, by Anthony Thompson, Jessica Sanders, Merete Tandstad, Fabio Carocci and Jessica Fuller (eds). FAO fisheries and aquaculture technical paper no. 595. Rome, Italy

FAO (2016b) Report of the FAO workshop on deep-sea fisheries and vulnerable marine ecosystems of the Mediterranean, Rome, Italy, 18–20 July 2016. FAO fisheries and aquaculture report no. 1183, Rome, Italy

Freiwald A, Beuck L, Rueggeberg A, et al (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–74. https://doi.org/10.5670/oceanog.2009.06

Gabrié C, Lagabrielle E, Bissery C, et al (2012) The status of marine protected areas in the Mediterranean Sea. MedPAN & CAR/ASP. Ed: MedPAN collection, 254 pp

GFCM (2014) Final report of working group on marine protected areas. Subcommittee on marine environment and ecosystems-scientific advisory committee GFCM. Bar, Montenegro, 3 February 2014

Gianni M, Fuller S, Currie DEJ, et al (2016) How much longer will it take?: a ten-year review of the implementation of United Nations general assembly resolutions 61/105, 64/72 and 66/68 on the management of bottom fisheries in areas beyond national jurisdiction. Deep Sea conservation coalition, July 2016

Giorgi F (2006) Climate change hot-spots. Geophys Res Lett 33:L08707. https://doi.org/10.1029/2006GL025734

Gori A, Orejas C, Madurell T, et al (2013) Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10:2049–2060

Gori A, Ferrier-Pagès C, Hennige SJ, et al (2016) Physiological response of the cold-water coral *Desmophyllum dianthus* to thermal stress and ocean acidification. PeerJ 4:e1606. https://doi.org/10.7717/peerj.1606

Harris PT, Whiteway T (2011) Global distribution of large submarine canyons: geomorphic differences between active and passive continental margin. Mar Geol 285:69–86

Heestand Saucier E (2016) Phylogenetic studies of the Deep-Sea Bamboo Corals (Octocorallia: Isididae: Keratoisidinae). Chapter 3 Systematics of the deep-sea bamboo coral genus Acanella. PhD thesis dissertation, University of Louisiana at Lafayette, 221 pp

Huvenne VAI, Bett B, Masson DG, et al (2016) Effectiveness of a deep-sea cold-water coral Marine Protected Area, following eight years of fisheries closure. Biol Conserv 200:60–69

IPCC (2007) Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, 1523 p

IPCC (2013) Climate change 2013: the physical science basis. Working Group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, 1538 p

Lacoue-Labarthe T, Nunes PALD, Ziveri P, et al (2016) Impacts of ocean acidification in a warming Mediterranean Sea: an overview. Reg Stud Mar Sci 5:1–11

Larsson AI, Purser A (2011) Sedimentation on the cold-water coral *Lophelia pertusa*: cleaning efficiency from natural sediments and drill cuttings. Mar Poll Bull 62:1159–1168

Lartaud F, Pareige S, de Rafelis M, et al (2013) A new approach for assessing cold-water coral growth in situ using fluorescent calcein staining. Aquat Living Resour 26:187–196

Lartaud F, Pareige S, de Rafelis M, et al (2014) Temporal changes in the growth of two Mediterranean cold-water coral species, in situ and in aquaria. Deep-Sea Res Part 2 Top Stud Oceanogr 99:64–70

Lartaud F, Meistertzheim AL, Peru E, et al (2017) In situ growth experiments of reef-building cold-water corals: The good, the bad and the ugly. Deep-Sea Res Part 1 Oceanogr Res Pap 121:70–78

Lastras G, Canals M, Ballesteros E, et al (2016) Cold-water corals and anthropogenic impacts in La Fonera Submarine Canyon Head, Northwestern Mediterranean Sea. PLoS One 11:e0155729. https://doi.org/10.1371/journal.pone.0155729

Lazzari P, Mattia G, Solidoro C, et al (2014) The impacts of climate change and environmental management policies on the trophic regimes in the Mediterranean Sea: Scenario analyses. J Mar Syst 135:137–149. https://doi.org/10.1016/j.jmarsys.2013.06.005

Lejeusne C, Chevaldonné P, Pergent-Martini C, et al (2010) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends Ecol Evol 25:250–260

López-González PJ, Grinyó J, Gili JM (2015) *Chironephthya mediterranea* n. sp. (Octocorallia, Alcyonacea, Nidaliidae), the first species of the genus discovered in the Mediterranean Sea. Mar Biodivers 45:1–22

Maier C, Watremez P, Taviani M, et al (2012) Calcification rates and the effect of ocean acidification on Mediterranean cold-water corals. Proc R Soc B 279:1716–1723

Martín J, Puig P, Palanques A, et al (2014) Trawling-induced daily sediment resuspension in the flank of a Mediterranean submarine canyon. Deep-Sea Res Part 2 Top Stud Oceanogr 104:174–183. https://doi.org/10.1016/j.dsr2.2013.05.036

Mastrototaro F, Chimienti G, Acosta J, et al (2017) *Isidella elongata* (Cnidaria: Alcyonacea) facies in the western Mediterranean Sea: visual surveys and descriptions of its ecological role. Eur Zool J 84:209–225

Maynou F, Cartes JE (2011) Effects of trawling on fish and invertebrates from deep-sea coral facies of *Isidella elongata* in the western Mediterranean. J Mar Biol Assoc UK 92:1501–1507. https://doi.org/10.1017/S0025315411001603

MedPAN & UNEP-MAP-SPA/RAC (in prep) The 2016 status of marine protected areas in the Mediterranean

Milligan R, Spence G, Roberts JM (2016) Bailey DM (2016) Fish communities associated with cold-water corals vary with depth and substratum type. Deep-Sea Res Part 1 Oceanogr Res Pap 114:43–54. https://doi.org/10.1016/j.dsr.2016.04.011

Movilla J, Gori A, Calvo E, et al (2014a) Resistance of two Mediterranean cold-water coral species to low-pH conditions. Water 6:59–67. https://doi.org/10.3390/w6010059

Movilla J, Orejas C, Calvo E, et al (2014b) Differential response of two Mediterranean cold-water coral species to ocean acidification. Coral Reefs 33:675–686

Mytilineou Ch, Smith CJ, Anastasopoulou A, et al (2014) New cold-water coral occurrences in the Eastern Ionian Sea: Results from experimental long line fishing. Deep-Sea Res Part 2 Top Stud Oceanogr 99:146–157

Nouar A, Maurin C (2001) Nature of and typical populations on the characteristic facies of substratum of *Parapenaeus longirostris* (Lucas, 1846) along the Algerian coast. Crustaceana 74:129–135

Orejas C, Gori A, Gili JM (2008) Growth rates of live *Lophelia pertusa* and *Madrepora oculata* from the Mediterranean Sea maintained in aquaria. Coral Reefs 27:255–255

Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Mar Ecol Prog Ser 397:37–51. https://doi.org/10.3354/meps08314

Orejas C, Ferrier-Pagès C, Reynaud S, et al (2011a) Long-term growth rates of four Mediterranean cold-water coral species maintained in aquaria. Mar Ecol Prog Ser 429:57–65

Orejas C, Ferrier-Pagès C, Reynaud S, et al (2011b) Experimental comparison of skeletal growth rates in the cold-water coral *Madrepora oculata* Linnaeus, 1758 and three tropical scleractinian corals. J Exp Mar Biol Ecol 405:1–5

Orejas C, Gori A, Jiménez C, et al (2017) First in situ documentation of a live population of the deep-water coral *Dendrophyllia ramea* off Cyprus (Levantine Basin, Mediterranean Sea) and evidence of human impacts. Galaxea, J Coral Reef Stud 19:15–16

Otero M, Garrabou J, Vargas M (2013) Mediterranean marine protected areas and climate change: a guide to regional monitoring and adaptation opportunities. IUCN, Malaga, 52 p

Otero MM, Numa C, Bo M, et al (2016) Overview of the conservation status of Mediterranean anthozoans. IUCN, Malaga, Spain. x + 73 p

Palanques A, Martín J, Puig P, et al (2006) Evidence of sediment gravity flows induced by trawling in the Palamós (Fonera) submarine canyon (northwestern Mediterranean). Deep-Sea Res Part 1 Oceanogr Res Pap 53:201–214. https://doi.org/10.1016/j.dsr.2005.10.003

Paradis S, Puig P, Masqué P, et al (2017) Bottom-trawling along submarine canyons impacts deep sedimentary regimes. Sci Rep 7:43332. https://doi.org/10.1038/srep43332

Parravicini V, Mangialajo L, Mousseau L, et al (2015) Climate change and warm-water species at the north-western boundary of the Mediterranean Sea. Mar Ecol 36:897–909. https://doi.org/10.1111/maec.12277

Pianté C, Ody D (2015) Blue growth in the Mediterranean Sea: the challenge of good environmental status. MedTrends Project. WWF-France, 192 p

Puig P, Canals M, Martín J, et al (2012) Ploughing the deep sea floor. Nature 489:286–289

Reed JK, Koenig CC, Shepard AN (2007) Impacts of bottom trawling on a deep-water *Oculina* coral ecosystem off Florida. Bull Mar Sci 81:481–496

Rees SE, Foster NL, Langmead O, et al (2018) Defining the qualitative elements of Aichi Biodiversity Target 11 with regard to the marine and coastal environment in order to strengthen global efforts for marine biodiversity conservation outlined in the United Nations sustainable development goal 14. Marine Policy 93:241–250

Reichelt-Bruschett A (2012) Risk assessment and ecotoxicology: limitations and recommendations for ocean disposal of mine waste in the coral triangle. Oceanography 25:40–51

Roberts JM, Wheeler AJ, Freiwald A, et al (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, Cambridge, 334 p

Sanfilippo R, Vertino A, Rosso A, et al (2013) *Serpula* aggregates and their role in deep-sea coral communities in the southern Adriatic Sea. Facies 59:663–677. https://doi.org/10.1007/s10347-012-0356-7

Sartoretto S (2012) New records of *Dendrobrachia bonsai* (Octocorallia: Gorgonacea: Dendrobrachiidae) in the western Mediterranean Sea. Mar Biodivers Records 5:1–4. https://doi.org/10.1017/S175526721100114X

Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral habitats at different scales within the Northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108. https://doi.org/10.1371/journal.pone.0087108

Secretariat of the Convention on Biological Diversity (2014) Global Biodiversity Outlook 4. Montréal 155

Taviani M, Vertino A, López Correa M, et al (2011) Pleistocene to recent scleractinian deep-water corals and coral facies in the Eastern Mediterranean. Facies 57:579–603

Taviani M, Angeletti L, Canese S, et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep Sea Research Part II: Topical Studies in Oceanography https://dx.doi.org/10.1016/j.dsr2.2015.12.008

Tittensor DP, Baco AR, Hall-Spencer JM, et al (2010) Seamounts as refugia from ocean acidification for cold-water stony corals. Mar Ecol 31:212–225

UNEP-MAP-RAC/SPA (2015) Action Plan for the conservation of habitats and species associated with seamounts, underwater caves and canyons, aphotic hard beds and chemo-synthetic phenomena in the Mediterranean Sea. Dark Habitats Action Plan. Ed. RAC/SPA, Tunis, 17p

Van Dover C, Aronson J, Pendleton L, et al (2014) Ecological restoration in the deep sea: Desiderata. Mar Policy 44:98–106

Vertino A, Savini A, Rosso A, et al (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Province (Mediterranean). Deep-Sea Res Part 2 Top Stud Oceanogr 57:380–396

Weaver PPE, Benn A, Arana PM, et al (2011) The impact of deep-sea fisheries and implementation of the UNGA Resolutions 61/105 and 64/72. Report of an international scientific workshop, National Oceanography Centre, Southampton, 45 p. http://hdl.handle.net/10013/epic.37995

Yang LH, Rudolf VH (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. Ecol Lett 13:1–10. https://doi.org/10.1111/j.1461-0248.2009.01402.x

Cross References

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Species Index

C. Orejas, C. Jiménez (eds.), *Mediterranean Cold-Water Corals: Past, Present and Future*, Coral Reefs of the World 9,
https://doi.org/10.1007/978-3-319-91608-8

Subject Index

*When a keyword has more than 400 instances in the book, first instance page number from each chapter and page number where the term is explained in detail are referred in the index.

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