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Short communication

Modeled day–night biases in decapod assessment by bottom trawling survey

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ABSTRACT

The activity rhythms of marine species may consistently bias demographic evaluation by bottom trawl survey, depending on the time of day. In this study, we examine occurrence data of selected commercial and non-commercial decapod species at different depths (0–800 m) of the western Mediterranean as produced by the Mediterranean international trawl survey (MEDITS) UE Program by sampling during daytime. In order to show how the activity rhythms and types of displacement (pelagic, nektobenthic and endobenthic) of different species can alter the occurrences determined by bottom trawling, and to quantify relative bias, we modeled potential outcomes of a putative nocturnal MEDITS sampling. MEDITS and published data for studies with 24-h hauls were compared in order to obtain a folding correction factor. We found that the temporal bias of sampling is moderate when trawling is performed on the continental slope and more important when it occurs on the continental shelf. The configuration of daytime and nighttime occurrence data by depth was performed using non-metric multidimensional scaling (nMDS). For the daytime configuration, association with irradiance (PAR) was evaluated by fitting occurrence data with a generalized additive model (GAM). Symmetry in species assemblages was found according to depth (inflection point at 200 m depth) as a significant irradiance-dependence distribution pattern of occurrences that took place on the shelf, above 200 m depth. For the night configuration, the inflection point relaxed due to the active displacements of some species, mixing the assemblages reported in daytime data. Results of the present study indicated that a deep knowledge of the autoecology of decapod species as it relates to activity rhythms (including a precise assessment of displacement typology) is of importance in population distribution and biomass evaluation and also influences locally perceived biodiversity. Accordingly, bottom trawl surveys for population assessment should take into account the timing of sampling as a factor potentially biasing obtained abundances.

1. Introduction

Light intensity influences how animals perceive their environment, modulating their inter- and intra-specific interactions (reviewed by Pulcini et al., 2008; Aguzzi et al., 2009b). Accordingly, species show a temporal component in their ecological niche related to the level of light intensity experienced by individuals during different phases of behavioral activity (Kronfeld-Schor and Dayan, 2003). Therefore, all marine communities exposed to light intensity variations are expected to react to them, producing changes in species compositions at sampling sites in relation to the time of day (reviewed by Naylor, 2005; Aguzzi and Company, in press). Thus, a complex scenario of species presence–absence can be reported in continental margins depending on timing, method, and depth location of sampling (Naylor, 2005).

The management of commercially important fishery resources in continental margins is based on reliable assessments of population size, demographics, and areas of distribution (reviewed by Bertrand et al., 2002). Bottom trawl surveying is one of the most reliable methods of population sampling in areas where depth makes more direct observations technically and economically unfeasible (Raffaelli et al., 2003). Collected animals are those readily present in the sampling area at the time of the tow. However, when the pelagic-seabed space is considered, one can assume that animals' presence at the bottom only occurs during a limited time according to precise behavioral rhythms, expressed across these compartments (Aguzzi and Company, in press).

To date, three major types of displacement are recognized in relation to behavioral rhythms (reviewed by Aguzzi et al., 2009b): vertical, in the water column as pelagic or benthopelagic (when animals touch the bottom); nektobenthic, across a depth gradient along the seabed; and finally, endobenthic, a metric for burrowers and buriers, with phases of emergence from the substrate and retraction in it. These behavioral displacements produce a bias in trawl survey data according to the time of day, based on

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sampling depth, with effects on population assessment that are poorly understood at present (Bahamon et al., in press).

The activity rhythm of commercially exploited resources may consistently bias demographic assessments of their populations (reviewed by Aguzzi and Sardà, 2008). Within a certain sampling area, the assumption of a behaviourally based bias for one population of a species should be assumed also for all populations of different species within the local community. Therefore, a bias in locally perceived biodiversity, as determined by demographic assessments, should be also assumed. The aim of our study is to report how diel behavioral rhythms and typologies of displacement can consistently alter our perception of the occurrences of crustacean decapods at different depths of deep water continental margins, depending on the time of sampling. We used published occurrence data by the MEDITS-UE Program (International Bottom Trawls Survey) from different depths of the western Mediterranean (Abelló et al., 2002) for selected species with known behavioral rhythms and typologies of disablement. MEDITS campaigns, begun in 1994, organize periodic large-scale bottom trawl surveys and are a key program in the monitoring of fishery demersal resources (Bertrand et al., 1997). Sampling is always carried out during the day (Cau et al., 2002). By using notions on behavioral rhythms from other studies with temporally distributed bottom trawl samplings, we modeled a potential scenario for species occurrence by depth as if MEDITS samplings were repeated at night.

2. Materials and methods

MEDITS data with percentages of occurrence for different species of decapods at different depths (Abelló et al., 2002) were used in our study. Selected species (see Table 1) were those for which combined information on activity rhythms (i.e., diurnal or nocturnal) and typology of displacement (i.e., pelagic, nektobenthic, and endobenthic) were both known (Aguzzi et al., 2009b). The species sample size is necessarily reduced from the total surveyed by MEDITS since behavioral information is generally unavailable for the majority of continental margin species (Aguzzi and Company, in press).

Following Abelló et al. (2002), we set our analysis of occurrence data for the following depth ranges: 1–50 m, 51–100 m, 101–200 m, 201–300 m, 301–400 m, 401–500 m, 501–600 m, 601–700 m, and 701–800 m. Species occurrences were transformed into a percentage of the maximum (subsequently referred to as occurrence data) to make the relative sample size of different species comparable despite their differences in true biomass.

We modeled species' bathymetric distributions at night by correcting MEDITS bathymetric daytime occurrence data (Abelló et al., 2002) for a folding factor. We estimated a folding factor bias for each species, which is a factor indicating how many times the daytime catch occurrences should be folded to approach to a maximum occurrence within a 24-h cycle. That factor was therefore inferred by comparing maxima and minima in catches as reported by other studies where trawling occurred both at day and night (Table 1). For species listed in Sardà et al. (2003), the day–night bottom trawling occurred at different depths. The depth of maximum species abundance was chosen as a reference for estimating the folding factor of day *versus* night catches. For all other studies (i.e., those by Aguzzi et al., 2009c), species folding factor was computed at two depths of reference, 100–110 m (shelf) and 400–430 m (slope).

Table 1
Biological information for selected species divided by typology of displacement (benthopelagic, nektobenthic, and endobenthic burrowers and buriers): common names and codes, maxima catchability timings (nocturnal-N, diurnal-D, and crepuscular-Cr or arrhythmic-Ar), and estimated biases in MEDITS occurrences based on folding factors derived from published studies with temporally scheduled trawling (Sources). Numbers in the Sources column refer to studies on the behavioral rhythms of species (the ordinal number corresponds to the alphabetic order in the reference section).

Common names	Species	Codes	Maxima		Folding factor		Sources
			Shelf	Slope	Shelf	Slope	
Benthopelagic							
Deep-sea shrimp	*Acanthephyra eximia*	*Acaexi*	–	D	–	1.1	9
Deep-sea shrimp	*Acanthephyra pelagica*	*Acapel*	–	N	–	0.1	9
Benthesicymid shrimp	*Gennadas elegans*	*Genele*	–	N	–	0.1	9
Pink glass shrimp	*Pasiphaea multidentata*	*Pasmul*	–	N	–	0.1	3
White glass shrimp	*Pasiphaea sivado*	*Passiv*	–	N	–	0.1	3
Sergestid shrimp	*Sergestes arcticus*	*Serarc*	–	N	–	0.1	2
Nektobenthic							
Pandalid shrimp	*Plesionika acanthonotus*	*Pleaca*	–	D	–	0.1	9
Pandalid shrimp	*Plesionika gigliolii*	*Plegig*	–	D	–	0.1	5
Pandalid shrimp	*Plesionika martia*	*Plemar*	–	D	–	0.1	5
Deep-water red shrimp	*Parapenaeus longirostris*	*Parlon*	N	–	10	–	2
Deep-water red shrimp	*Aristeus antennatus*	*Arisant*	–	N	–	2.0	9
Endobenthic burrowers							
Norway lobster	*Nephrops norvegicus*	*Nepnor*	Cr	D	10	0.1	8
Polychelid lobster	*Polycheles typhlops*	*Poltyp*	–	N	–	2.0	9
Humpback prawn	*Pontophilus norvegicus*	*Ponnor*	–	N	–	3.0	9
Alpheid shrimp	*Alpheus glaber*	*Alpgla*	N	Ar	10	1.0	1
Angular crab	*Goneplax rhomboides*	*Gonrho*	N	Ar	10	2.0	1
Endobenthic buriers							
Galatheid squat lobster	*Munida intermedia*	*Munint*	–	D	–	0.5	7
Galatheid squat lobster	*Munida tenuimana*	*Munten*	–	N	–	2.0	7
Green prawn	*Chlorotocus crassicornis*	*Chlcra*	N	–	100	–	5
Geryonid crab	*Geryon longipes*	*Gerlon*	–	N	–	2.0	9
Portunid crab	*Liocarcinus depurator*	*Liodep*	N	Cr	5	2.5	7
Mediterranean prawn	*Processa canaliculata*	*Procan*	N	D	100	–	6
Mediterranean prawn	*Processa nouveli*	*Pronou*	N	D	100	–	6
Mud shrimp	*Solenocera membranacea*	*Solmem*	N	D	100	0.3	4

[1]Aguzzi et al. (2009a); [2]Aguzzi and Company (in press); [3]Aguzzi et al. (2006a); [4]Aguzzi et al. (2006b); [5]Aguzzi et al. (2007a); [6]Aguzzi et al. (2008); [7]Aguzzi et al. (2009a); [8]Aguzzi et al. (2003); [9]Sardà et al. (2003).

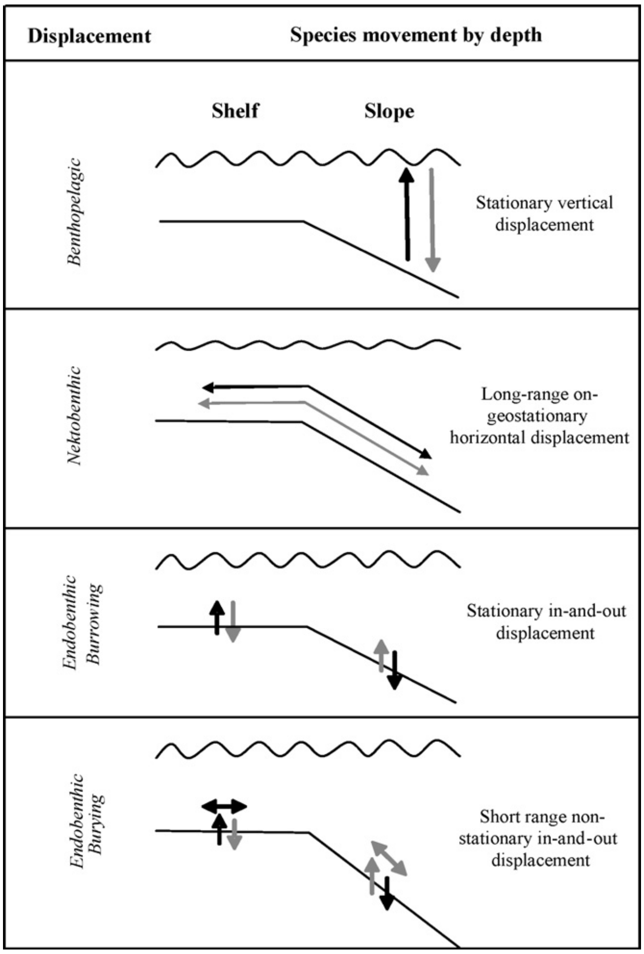

Fig. 1. Schematic description of the different typologies of rhythmic displacement (as indicated by arrows) in relation to the water column-seabed compartments of the shelf and slope (adapted from Aguzzi and Company, in press). Displacements of nocturnal (black arrow) and diurnal (grey arrow) character are distinguished for all species with the exception of nektobenthic species. Some of these species present nocturnal, diurnal and/or other rhythms of continental margin ascent. Benthopelagic species are absent on the shelf.

In order to efficiently forecast nocturnal species occurrence by depth in our model, we grouped selected species according to their different typologies of displacement (i.e., benthopelagic, nektobenthic, and endobenthic; the last was for burrowers and buriers) (see Table 1). In Fig. 1, the different types of diel movements are schematized according to Aguzzi and Company (in press). Species occurrences at night were estimated as follows. For benthopelagic species, we assumed a Boolean pattern of occurrence at any depth stratum considered, as their diel displacement is completely vertical within the water column (reviewed by Aguzzi et al., 2009b). Nektobenthic species gradually displace back and forth along the different depth strata of continental margins. We assumed that species with incrementally increasing abundance during daytime in deeper depth strata of the MEDITS survey, which are absent in shallower areas, are coming from bathymetries below the sampled range (Cartes et al., 1993; Sardà et al., 2003). Conversely, species showing variations in their occurrence by depth during day and night samplings were assumed to perform long-range displacements encompassing both the shelf and the slope. Finally, for endobenthic species, we assumed a similar Boolean dynamic of occurrence at the seabed: animals are captured by bottom trawling when walking or swimming within the benthic boundary later during phases of active emergence from the substrate.

To picture the pattern of bathymetric species distribution reported by MEDITS for the daytime, we used non-metric multidimensional scaling (nMDS) on occurrence data, reflecting as closely as possible the dissimilarities among sampled assemblages at different depths. Such an analysis is commonly used in community ecology as it allows the identification of changes in species assemblages according to selected environmental gradients (reviewed by Aguzzi et al., 2009a). The rank of distances between species occurrences by depth was estimated using the Bray–Curtis dissimilarity index. These distances were used to generate two-dimensional plots where species from different sampling stations but with similar occurrences were plotted in a proximal fashion (Oksanen et al., 2007). To compute a solution minimizing the lack of fit between pairs of species distances, the function metaMDS was used in the Vegan package (Oksanen et al., 2007) in R (R-Development Core Team, 2008).

Light was considered as potentially determinant for the bathymetric distribution of species, since it regulates the expression of their behavioral rhythms (Aguzzi and Company, in press). In order to estimate the amount of light reaching the different sampling depths, we assumed an averaged PAR at water surface of 125 W/m^2 in the study area, based on MODIS Aqua PAR imagery for May 1997 (http://oceancolor.gsfc.nasa.gov/). That light value is within the range of those reported for the area in modeling studies (Bahamon and Cruzado, 2003). Then we applied the exponential function $I_z = I_o\, e^{-kz}$, where I_o represents the photosynthetically available radiation (PAR) at surface; k is the extinction coefficient equal to 0.55 (Bahamon and Cruzado, 2003); and finally, z is the sampling depth. The irradiance values at the sampling depths of 101–200 m and 401–500 m were approximately those measured in other trawl cruises (Aguzzi et al., 2003).

In the nMDS plot for daytime occurrences, a generalized additive model (GAM; Hastie and Tibshirani, 1990) was fitted onto the data by depth in order to establish possible significant pattern variations (i.e., associations) in relation to PAR. A back-fitting algorithm was used to iteratively adjust the GAM vector to occurrence data by cycling through the light variable until the highest significance was reached (Wood, 2006).

3. Results

Comparisons of MEDITS data with published studies revealing diel variations in captures at comparable depths (Table 1) showed differences in species occurrences in a putative nighttime sampling across the depth range considered. The temporal bias in sampling was moderate when trawl catches were performed on fishing grounds of the continental slope (i.e., a folding factor between 0.1 and 3). That bias became substantially important for catches performed in the shallower depth zones of the continental shelf (0–200 m). The folding factor to be applied to daily catches performed in these depth strata, in order to approach more realistic nocturnal occurrences, spanned from 2 to 100, depending on the considered species.

The bias in daytime occurrence data was related to the typology of species displacement (Table 1). From MEDITS data, benthopelagic species were scarce on the shelf. These species did not present sampling errors at any depth since their capture occurs in bottom trawling at around 100% during the day. Nektobenthic species were also scarce on the shelf. On the slope, these presented a smaller error in estimated abundances in daytime than at night. Endobenthic species also presented a depth-dependent sampling error. For burrowers on the shelf, this error was elevated in a daytime sampling: species occurrences at nighttime were 10-fold higher than during daytime. On the slope, that error was comparatively reduced, with species occurrences only 2–3 times higher

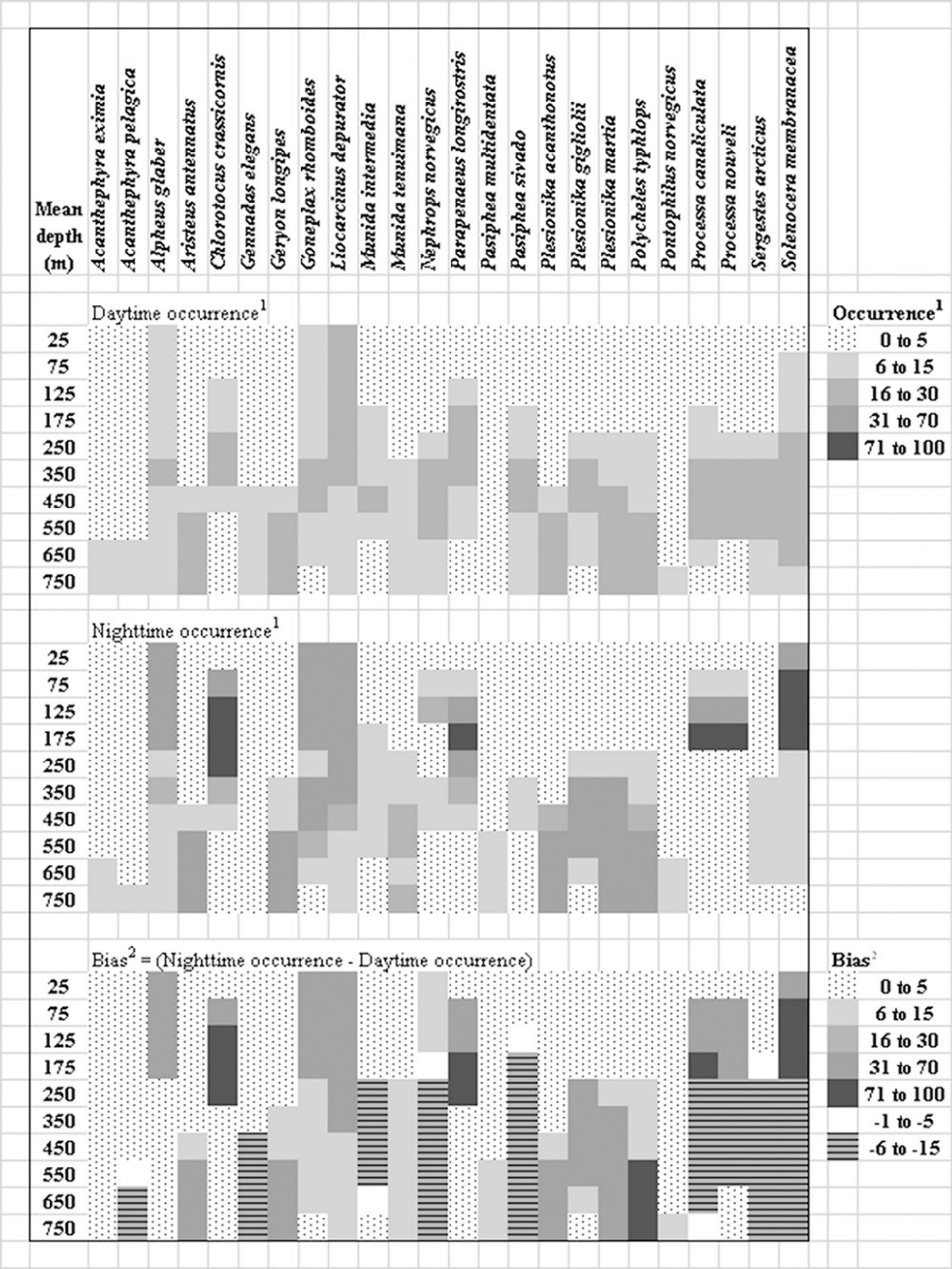

Fig. 2. MEDITS daytime, modeled nocturnal and day–night estimated differences in species occurrences (as percentage of the maximum) at different depths of the shelf and the slope. Daytime ordination was constructed from reported occurrences by Abelló et al. (2002). Nighttime ordinations were estimated from 24-h temporally repeated trawl samplings, by comparing day *vs.* night data. Occurrences (1) were scaled to 100; biases (2) were calculated on the base of non-scaled occurrences. Positive bias values indicate higher occurrence of individuals at nighttime than at daytime. Negative bias values indicate the reverse.

during the day than the night. Buriers presented a more elevated daytime error of sampling on shelf and slope. Their occurrence increased at night up to 100 times on the shelf, with a smaller sampling error on the slope (up to 4 times more elevated during day than night).

The plot of species occurrences during the day and night modeled sampling (Fig. 2) indicates a global nocturnal increase in species occurrences both on the shelf and the slope. During the daytime, *Chlorotocus crassicornis*, *Parapenaeus longirostris*, *Processa canaliculata*, *Processa nouveli*, and *Solenocera membranacea* show moderate occurrences on the edge of the shelf and slope. At night, these species show a dramatic increase in occurrence on the shelf (above 200 m depth) and a decrease in occurrence on the slope. Other species, like *Gennadas elegans*, were relatively abundant on the slope during daytime and scarce at night. Conversely, *Pasiphaea multidentata* was chiefly found during the day and was scarce at night. Day night-differences are also indicated as marker of biomass differences according to the timing of sampling.

The nMDS analysis of daytime species occurrence data from MEDITS published data (Fig. 3A) presented symmetry according to the depth gradient. Species assemblages within depth strata of the shelf (0–200 m) were similar to those between 201 m and 800 m depth. This occurred for species associations with certain depth strata: some species present with higher occurrences in shallow water areas are replaced by others with equivalently high occurrences in deeper water strata. For example, *Liocarcinus depurator*,

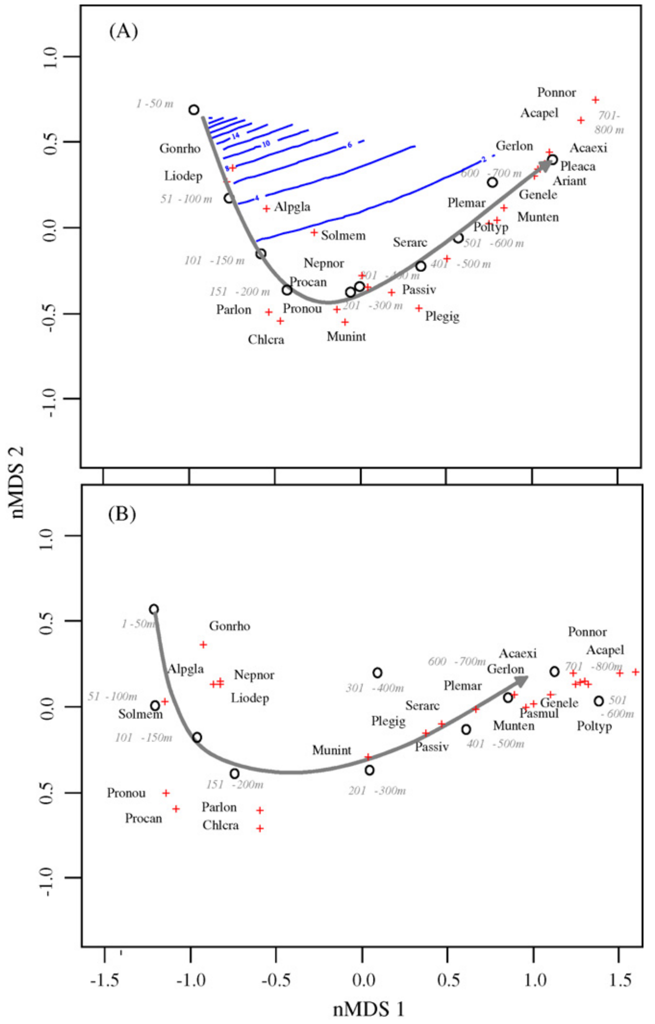

Fig. 3. Species ordination in nMDS analysis according to depth during MEDITS daytime (A) and modeled nighttime (B) samplings (see Table 1 for species codes). Ranges of sampling depths are indicated by small circles located along an arrow depicting the depth-increasing direction. The ecological distance among species during the daytime follows a light-dependent distribution. Light gradients (PAR; W/m^2), are represented by thin lines as modeled by GAM. At night ecological distance among sampling depths is reduced.

Goneplax rhomboides, and *Alpheus glaber* show similar and associated occurrence from 51 to 100 m depth and are replaced by *Geryon longipes*, *Pontophilus norvegicus*, *Acanthephyra eximia*, *Aristeus antennatus*, and *Plesionika acanthonotus* at greater depths of 701–800 m.

In the nMDS plot of Fig. 3A, the inflection point at the bottom of the continental shelf (i.e., around 200 m depth) indicates that PAR significantly explains the bathymetric distribution of species within the selected depths of the continental margin as confirmed by GAM analysis (deviance explained = 98.5%; $p < 0.001$). Below 200 m depth, the species distribution is comparatively less vinculated to the trend of PAR reduction.

At night, modeled occurrences of selected species by depth were more similar (Fig. 3B), and ecological distances in the nMDS plot generally shortened. The inflection point at 151–200 m depth (see Fig. 3A) almost disappeared since the difference in abundances for the species reported on the shelf and slope was reduced. For example, on the shelf, the distance between *G. rhomboides* and *C. crassicornis* is much smaller at night than during the day. On the slope, the distance between *Munida intermedia* and *P. norvegicus* is also smaller at night. Several species are more associated with the edge of the slope (200 m depth) during the day than at night, including *Nephrops norvegicus*, *P. canaliculata*, *P. nouveli*, *P. longirostris*, *C. crassicornis*, *Plesionika gigliolii*, *Pasiphaea sivado*, *Sergestes arcticus*, and *M. intermedia*. At night, the species associated with 151–200 m depth show similar daytime ecological distances to *M. intermedia* and *P. sivado*.

4. Discussion

In this study, we estimated the bias in reported occurrences of decapod species at different depths of the western Mediterranean based on the diurnal MEDITS trawl sampling. In order to obtain reliable estimations of decapod distributions in an equivalent nighttime sampling, MEDITS data by Abelló et al. (2002) were adjusted with estimated abundances from other bottom trawling studies carried out during both day and night in the same area (see Table 1 for reference). We find that the diurnal *versus* nocturnal bias in sampling is moderate when the trawl catches are performed on fishing grounds of the continental slope. The bias becomes substantially more important for catches performed in the shallower depth zones of the continental shelf. The comparison of these results with light intensity measures stresses how this environmental variable significantly contributes to the observed bias, as studied depths include the photic zone (i.e., 0–150 m depth) and the twilight zone (i.e., 151–800 m depth) of the continental margin (Margalef, 1986).

The western Mediterranean commercial trawl fishing is restricted to operating during the day and is not allowed at night (Martin, 1991). As consequence, nighttime abundance data are generally scarce for several continental margin species. Therefore, one major criticism of our modeling is its limitation to a reduced number of decapod species for which rhythmic activity and typology of displacement are known. In the past few years, we have made an effort to clarify how a time series of bottom trawling data can account for behavioral rhythms in decapods (reviewed by Aguzzi and Company, in press). In fact, trawling provides only indirect indications of animals' behavior based on their presence–absence in sampling windows (Al-Adhub and Naylor, 1977). Reported variations in captures were often weighted for the different means that species have for traveling between different water column-seabed compartments (i.e., pelagic, nektobenthic, and endobenthic; reviewed by Aguzzi et al., 2009b). To our knowledge, such an analytic effort is still limited to few species in continental margin areas, and information for other taxonomic groups – for example, fishes and cephalopods – is still fragmented into several independent autoecological observations. Also, MEDITS occurrence data by depth are to our knowledge only available for decapods.

The redistribution in species occurrences by depth according to the modeled diurnal *versus* nocturnal sampling was estimated by considering the different typologies of species' displacement. Benthopelagic species did not present sampling errors in the MEDITS survey at any depth as their maximum rate of capture occurred during diurnal bottom trawling. For these species, we assumed a Boolean pattern of occurrence at any sampling depth considered, as their diel displacement is fully vertical (reviewed by Aguzzi et al., 2009b). Animals rest on the seabed when light increases and swim higher into the upper layer of the water column to feed at darkness (i.e., reviewed by Aguzzi and Company, in press). Accordingly, their presence in trawl tow catches increases during the daytime, irrespective of sampling depth. The only major observation on their distribution in the western Mediterranean area (e.g., *Pasiphaea* spp. and *S. arcticus*) is their absence from shelf zones. Aguzzi and Company (in press) hypothesized that these species require a certain vertical distance for their diel upward movement. That distance is determined by light intensity values at the extremes of their diel migration, especially during the daytime, when animals hiding on the seabed may became too visible to benthic predators on the shelf in comparison to the deeper slope realm.

Nektobenthic species presented time-related sampling errors that varied based on the different nocturnal or diurnal phases of continental margin ascent. MEDITS data for nektobenthic diurnal movers as obtained by daytime sampling correctly represent the size of these populations. Nektobenthic diurnal species (e.g., Pandalid shrimps of *Plesionika* ssp.) appeared during daytime within selected depth ranges as they move from deeper aphotic areas of the slope (Sardà et al., 2003; Aguzzi et al., 2007a).

Conversely, for nocturnally migrating species the opposite conclusions can be drawn. Diurnal MEDITS data for these species are reliable, but reported depth distributions are bathymetrically shifted downward in comparison to what would be reported by an equivalent nocturnal sampling. For example, the abundance of the red shrimp *A. antennatus* is increased at night both on the shelf and the slope. On the slope, this increment occurs as animals of deeper depth strata not considered in our analysis move into the targeted sampling areas. Similarly, other animals already present in the targeted sampling areas move up, reaching shallower shelf zones (in a reduced quantity; Cartes et al., 1993). This species may follow a staggered pattern of migration (Tobar and Sardà, 1992; Sardà et al., 2003) similarly to what is proposed for fully pelagic species (reviewed by Frank and Widder, 1997; Naylor, 2006).

The diurnal population assessment of endobenthic species by MEDITS increases in reliability with sampling depth. That is, on the shelf, the estimated error was elevated for daytime sampling, while on the slope, daytime sampling error was minor. Animals are collectable only when moving within the benthic boundary layer during phases of active substrate emergence (reviewed by Aguzzi et al., 2009a). Species shift the timing of emergence from night to day as depth increases (Aguzzi et al., 2009a), according to the known "*Nephrops* model" (reviewed by Bell et al., 2006; Aguzzi and Sardà, 2008). Therefore, these species present maxima in captures with timing dependent upon depth.

On the shelf, burrowing species show increased occurrence in trawl sampling at night, a 10-fold increase *versus* daytime. Buriers present a similar time-related bias in trawl sampling but with a stronger intensity. Their occurrence in night trawl catches increases to up to 100 times in comparison to the day. This is due to their different behavioral habits (Bellwood, 2002). Burier emergence occurs in a synchronous fashion, provoking the schooling of animals within the benthic boundary layer (Aguzzi et al., 2006b). The whole population is hence more exposed to bottom trawling at once. Conversely burrowers can retract within their tunnels when nets approach, using the door-keeping behavior (i.e., periods of waiting at burrow entrances; Aguzzi et al., 2007b).

These results have deep implications in the management of the commercially important species of deep water continental margins (e.g. *N. norvegicus*, *A. antennatus*, and *Plesionika* spp.), as there is a temporal bias in population assessments. Also, present data indicate that such a bias can influence the reported distributions of both commercially and ecologically important species to varying extents, depending on behavior. Data on global diel changes in the western Mediterranean shelf and slope community in relation to diurnal and nocturnal bottom trawl surveys are not yet available (Bahamon et al., in press). In this context, we propose that a deep knowledge of the autoecology of species activity rhythms is of importance in population distribution and biomass evaluations. Stock assessment should then be performed at different depths of shelf and slope at times of species maximum abundance, as determined based on their nocturnal and diurnal behavior, in relation to their benthopelagic, nektobenthic, and endobenthic burrowing or burying habit.

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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, J.B. Chronobiology of deep water continental margin decapods. Adv. Mar. Biol., Ann. Rev., in press.

Aguzzi, J., Sardà, F., 2008. A history of recent advancements on *Nephrops norvegicus* behavioural and physiological rhythms. Rev. Fish Biol. Fish. 18, 235–248.

Aguzzi, J., Sardà, F., Abelló, P., Company, J.B., Rotllant, G., 2003. Diel patterns of *Nephrops norvegicus* catchability (Decapoda: Nephropidae) in the north-western Mediterranean: a perspective through depth and season. Mar. Ecol. Prog. Ser. 258, 201–211.

Aguzzi, J., Company, J.B., Abelló, P., García, J.A., 2006a. Ontogenetic changes in the vertical migratory rhythms of benthopelagic shrimps *Pasiphaea multidentata* and *P. sivado* (Crustacea: Caridea). Mar. Ecol. Prog. Ser. 335, 167–174.

Aguzzi, J., Company, J.B., Abelló, P., García, J.A., 2006b. Rhythmic behavior of the burying prawn *Solenocera membranacea* (Decapoda: Penaeoidea: Solenoceridae) in the western Mediterranean: a perspective through depth and season. Bull. Mar. Sci. 7, 353–364.

Aguzzi, J., Company, J.B., Abelló, P., García, J.A., 2007a. Rhythmic diel movements of some pandalid shrimps (Decapoda: Caridea) in the western Mediterranean continental shelf and upper slope. J. Zool. 273, 340–349.

Aguzzi, J., Company, J.B., Sardà, F., 2007b. The activity rhythm of berried and unberried females of *Nephrops norvegicus* (Crustacea, Decapoda). Crustaceana 80, 1121–1134.

Aguzzi, J., Company, J.B., García, J.A., 2008. The activity rhythm of the western Mediterranean prawn *Processa canaliculata* Leach, 1815 (Decapoda: Processidae) trough its day–night catchability patterns. Crustaceana 81, 1301–1316.

Aguzzi, J., Company, J.B., García, J.A., 2009a. Ontogenetic and gender modulated behavioural rhythms in the deep water decapods *Liocarcinus depurator* (Brachyura: Portunidae), *Munida tenuimana* and *M. intermedia* (Anomura: Galatheidae). Mar. Ecol. 30, 93–105.

Aguzzi, J., Costa, C., Antonucci, F., Company, J.B., Menesatti, P., Sardà, F., 2009b. Influence of rhythmic behaviour in the morphology of Decapod Natantia. Biol. J. Linn. Soc. 96, 517–532.

Aguzzi, J., Bahamon, N., Marotta, L., 2009c. The influence of light availability and predatory behavior of *Nephrops norvegicus* on the activity rhythms in continental margin decapods. Mar. Ecol. 30, 366–375.

Al-Adhub, A.H.Y., Naylor, E., 1977. Daily variation in *Dichelopandalus bonnieri* (Caullery) as a component of the epibenthos. In: Keegan, B.F., O'Ceidigh, P., Boaden, P.J.S. (Eds.), Biology of Benthic Organisms. Pergamon Press, New York, pp. 1–6.

Bahamon, N., Cruzado, A., 2003. Modeling nitrogen fluxes in oligotrophic marine environments: NW Mediterranean Sea and NE Atlantic. Ecol. Mod. 163, 223–244.

Bahamon, N., Sardà, F., Aguzzi, J. Fuzzy diel patterns in commercial catchability of deep-water continental margin species. ICES J. Mar. Sci., in press.

Bell, M.C., Redant, F., Tuck, I., 2006. *Nephrops* species. In: Phillips, B.F. (Ed.), Lobsters: Biology, Management, Aquaculture and Fisheries. Blackwell Publishing, Oxford, pp. 412–461.

Bellwood, O., 2002. The occurrence, mechanics and significance of burying behaviour in crabs (Crustacea: Brachyura). J. Nat. Hist. 36, 1223–1238.

Bertrand, J., Gil de Sola, L., Papacostantinou, P., Relini, G., Souplet, A., 1997. An international bottom trawl survey in the Mediterranean: the MEDITS programme. In: ICES Am. Sci. Conf., Baltimore, MD, Y/03.

Bertrand, J., Gil de Sola, L., Papacostantinou, P., Relini, G., Souplet, A., 2002. The general specifications of the MEDITS survey. Sci. Mar. 66 (Suppl. 2), 9–17.

Cartes, J.E., Sardà, F., Company, J.B., Lleonart, J., 1993. Day–night migrations by deep-sea decapod crustaceans in experimental samplings in the western Mediterranean sea. J. Exp. Mar. Biol. Ecol. 171, 63–73.

Cau, A., Carbonell, A., Follesa, M.C., Mannini, A., Norrito, G., Orsi-Relini, L., Chrissi-Yianna, P., Ragonese, S., Rinelli, P., 2002. MEDITS-based information on the deep-water red shrimp *Aristaeomorpha foliacea* and *Aristeus antennatus* (Crustacea: Decapoda: Aristeidae). Sci. Mar. 66 (Suppl. 2), 103–124.

Frank, T.M., Widder, E.A., 1997. The correlation of downwelling irradiance and stagged vertical migration patterns of zooplankton in Wilkinson basin, Gulf of Maine. J. Plank. Res. 19, 1975–1991.

Hastie, T.J., Tibshirani, R.J., 1990. Generalized Additive Models. Chapman & Hall, London.

Kronfeld-Schor, N., Dayan, T., 2003. Partitioning of time as an ecological resource. Ann. Rev. Ecol. Syst. 34, 153–181.

Margalef, R., 1986. Ecología. Ediciones Omega, Barcelona.

Martin, P., 1991. La pesca en Cataluña y Valencia (NW Mediterráneo): análisis de las series hist6ricas de captura y esfuerzo. Inf. Tec. Sci. Mar. 162, 1–43.

Naylor, E., 2005. Chronobiology: implications for marine resources exploitation and management. Sci. Mar. 69, 157–167.

Naylor, E., 2006. Orientation and navigation in coastal and estuarine zooplankton. Mar. Fresh. Behav. Physiol. 39, 13–24.

Oksanen, J., Kindt, R., Legendre, R., O'Hara, B., Henry, M., Stevens, H., 2007. Vegan: Community Ecology Package. R-package Version 1.8-8. http://cran.r-project.org/, http://r-forge.r-project.org/projects/vegan/.

Pulcini, D., Costa, C., Aguzzi, J., Cataudella, S., 2008. Light and shape: a contribution to demonstrate morphological differences in diurnal and nocturnal teleosts. J. Morphol. 269, 375–385.

Raffaelli, D., Bell, E., Weithoff, G., Matsumoto, A., Cruz-Motta, J.J., Kershaw, P., Parker, R., Parry, D., Jones, M., 2003. The ups and downs of benthic ecology: considerations of scale, heterogeneity and surveillance for benthic-pelagic coupling. J. Exp. Mar. Biol. Ecol. 285–286, 191–203.

Sardà, F., Company, J.B., Castellón, A., 2003. Intraspecific aggregation structure of a shoal of western Mediterranean (Catalan coast) deep-sea shrimp, *Aristeus antennatus* (Risso, 1816), during the reproductive period. J. Shellfish Res. 22, 569–579.

Tobar, R., Sardà, F., 1992. Annual and diel light intensity cycle as a predictive factor in deep-water fisheries for the prawn *Aristeus antennatus* Risso, 1816. Fish. Res. 15, 179–196.

Wood, S., 2006. Generalized Additive Models: An Introduction with R. CRC/Chapman & Hall, Boca Raton, Florida.