REVIEW / SYNTHÈSE

The ecology of the sponge larva[1]

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Abstract: The present work summarizes the progress attained in the study of sponge larval ecology since the state-of-the-art reviews performed in the 1970s and stresses the major weaknesses in our current understanding. Most available information on this subject comes from laboratory studies, with just occasional field observations or experiments. The data are also strongly biased because they are mostly derived from just one larval type out the eight types known in the phylum Porifera. Descriptive studies on larval histology are relatively abundant, but investigations directed at unravelling the cytological basis of the main larval behaviors are scarce. Most aspects of basic larval metabolism and sensing processes remain largely not investigated. Modelling of larval ecology is virtually lacking, with no serious attempt to investigate how the major features of larval ecology affect the structure and dynamics of sponge populations. In summary, the ecology of the sponge larva needs further research attention if we are to achieve a global understanding of the biology of the phylum Porifera.

Résumé : Le présent travail fait le point sur les progrès accomplis dans l'étude de l'écologie des larves d'éponges depuis les excellentes rétrospectives des années 1970 et il souligne les principales faiblesses de notre compréhension actuelle du domaine. La majorité de l'information sur le sujet provient d'études de laboratoire et de quelques observations ou expériences occasionnelles sur le terrain. Les données sont aussi fortement inégales, car elles ont principalement été obtenues sur un seul des huit types de larves connues dans le phylum des porifères. Les études descriptives de l'histologie des larves sont relativement nombreuses, mais il y a peu de recherches sur la base cytologique des principaux comportements larvaires. La plupart des aspects du métabolisme de base des larves et des processus sensoriels restent à éclaircir. Il n'y a à peu près pas de modélisation de l'écologie larvaire, ni aucune tentative sérieuse pour déterminer comment les composantes principales de l'écologie des larves affectent la structure et la dynamique des populations d'éponges. En somme, il faudra concentrer plus de recherches scientifiques sur l'écologie des larves d'éponges afin d'obtenir une compréhension globale de la biologie du phylum des porifères.

[Traduit par la Rédaction]

The biphasic life cycle of the Porifera: ecological need or phylogenetic imposition?

Animals use two primary life-history modes, direct and indirect development. In the former, the embryo directly develops into a post-embryonic stage built according to the same body plan as the adult. In contrast, the embryo of indirect developers becomes a larval form ("primary larva"), which may strongly differ from the adult stage in body architecture. In this case, a startling reorganization of the larval body, the metamorphosis, occurs to transform the larva into a post-embryonic stage with a body plan similar to that of the adult.

Indirect development is the life-history mode of most marine invertebrates (about 80% of known species), being particularly common in organisms that are sessile as adults. It is thought that most sponges belonging to the classes Calcarea and Demospongiae develop through a larval stage (Tables 1, 2; Fig. 1). It may be the same for the class Hexactinellida, but information on this group is still very scarce in this regard (Table 2). Indeed, in all three poriferan classes there are groups in which it is unclear whether those sponges really lack the larval stage or have a larval stage that remains elusive to spongiologists. So far direct development with absence of a dispersing larval stage has only been documented in very few spirophorid and hadromerid demosponges (Table 1).

From a theoretical point of view, the biphasic life cycle with a larval stage may have been favored by a complex combination of ecological and phylogenetic factors. For most invertebrate phyla, there is intense debate about whether the ancestral organism was a direct developer or an indirect developer. Because most invertebrate animals use a biphasic cycle, some authors have suggested that this was the primary condition in the ancestral metazoan (e.g., Jägersten 1972; Strathmann 1978; Rieger 1994); others have

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[1]This review is one of a series dealing with aspects of the biology of the phylum Porifera. This series is one of several virtual symposia on the biology of neglected groups that will be published in the Journal from time to time.

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Table 1. Summary of available information about development mode and larval type for members of the class Demospongiae.

Order	Family	Development type	Larval type*
Homosclerophorida	Plakinidae	Indirect and internal	Cinctoblastula
Spirophorida	Tetillidae	Direct and either external or internal in *Tetilla* Schmidt, 1686; indirect and external in other genera	Absent; ?
	Samidae	Unknown	?
	Spirasigmidae	Unknown	?
Astrophorida	Ancorinidae	Unknown in most genera; external in *Stelletta* Schmidt, 1862 and *Ancorina* Schmidt, 1862	?
	Calthropellidae	Unknown	?
	Geodiidae	Unknown in most genera; indirect and external in *Geodia* Lamarck, 1815 and *Erylus* Gray, 1867	?
	Pachastrellidae	Unknown in most genera; external in *Thenea* Gray, 1867	?
	Thrombidae	Unknown	?
	Alectonidae	Indirect and internal, when known	Hoplitomella
Hadromerida	Clionidae	Indirect and external; *Cliona lobata* Hancock, 1849 broods	Clavablastula
	Hemiasterellidae	Unknown in most genera; indirect and external in *Adreus* Gray, 1867	?
	Placospongiidae	Unknown	?
	Polymastiidae	Indirect and external, when known	Clavablastula
	Spirastrellidae	Unknown	?
	Stylocordylidae	Direct and internal, when known	Absent
	Suberitidae	Indirect and external; *Protosuberites* Swartschewsky, 1905 broods	?
	Tethyidae	Indirect and external, when known	Clavablastula
	Timeidae	Unknown	?
	Trachycladidae	Unknown	?
	Acanthochaetetidae	Unknown	?
	Sollasellidae	Unknown	?
Chondrosida	Chondrillidae	Indirect and external	Clavablastula
"Lithistid demospongiae"	13 families; 41 genera	Unknown in most genera; external in *Theonella* Gray, 1868	?
Poecilosclerida	Acamidae	Indirect and external in some studied genera; but *Iophon* Gray, 1867 broods	?; non-tufted parenchymella
	Microcionidae	Indirect and internal	Non-tufted parenchymella
	Raspailiidae	In most species indirect and external, but *Eurypon* Gray, 1867 and *Echinodictyum* Ridley, 1881 brood	Non-tufted parenchymella (to be revised)
	Rhabderemiidae	Unknown	?
	Chondropsidae	Unknown in most genera; internal in *Batzella* Topsent, 1891	?
	Coelosphaeridae	Indirect and internal, when known	?
	Crambeidae	Indirect and internal, when known	Non-tufted parenchymella
	Crellidae	Indirect and internal, when known	Non-tufted parenchymella
	Dendoricellidae	Unknown	?
	Desmacididae	Indirect and internal, when known	Non-tufted parenchymella
	Hymedesmiidae	Indirect and internal, when known	Non-tufted parenchymella
	Iotrochotidae	Unknown	?
	Myxillidae	Indirect and internal, when known	Non-tufted parenchymella
	Phellodermidae	Unknown	?
	Tedaniidae	Indirect and internal, when known	Non-tufted parenchymella
	Cladorhizidae	Indirect and internal, when known	?
	Desmacellidae	Indirect and internal, when known	?

Table 1 (*concluded*).

Order	Family	Development type	Larval type*
	Guitarridae	Unknown	?
	Esperiosidae	Indirect and internal, when known	Non-tufted parenchymella
	Hamacanthidae	Unknown	?
	Mycalidae	Indirect and internal, when known	Non-tufted parenchymella
	Merliidae	Unknown	?
	Podospongiidae	Indirect and internal, when known	To-be-studied parenchymella
	Isodictyidae	Indirect and internal, when known	?
	Latrunculiidae	Indirect and internal, when known	To-be-studied parenchymella
Halichondrida	Axinellidae	Indirect and external, when known	? (report on larva of *Axinella cristagalli* Maas, 1893 = *Crambe crambe* (Schmidt, 1862))
	Bubaride	Unknown	?
	Desmoxyidae	Unknown	?
	Dictyonellidae	Indirect and internal, when known	Non-tufted parenchymella
	Halichondriidae	Indirect and internal, when known	Tufted and non-tufted parenchymella
Agelasida	Agelasiidae	Indirect and external	Non-tufted parenchymella (to be revised)
	Astroscleridae	Indirect and internal, when known	To-be-studied parenchymella
Haplosclerida	Callyspongiidae	Indirect and internal, when known	Tufted parenchymella
	Chalinidae	Indirect and internal, when known	Tufted parenchymella
	Niphatidae	Indirect and internal, when known	Tufted parenchymella
	Phloeodictyidae	Indirect and external, when known	?
	Petrosiidae	Indirect and external, when known	To-be-studied parenchymella
	Calcifibrospongiidae	Unknown	?
	Spongillidae	Indirect and internal	Non-tufted parenchymella
Dictyoceratida	Irciniidae	Indirect and internal	Tufted parenchymella
	Thorectidae	Indirect and internal, when known	Tufted parenchymella
	Spongiidae	Indirect and internal	Tufted parenchymella
	Dysideidae	Indirect and internal, when known	Tufted parenchymella
Dendroceratida	Darwinellidae	Indirect and internal, when known	Tufted parenchymella
	Dictyodendrillidae	Indirect and internal, when known	?
Halisarcida	Halisarcidae	Indirect and internal	Dispherula
Verongida	Aplysinidae	Indirect and external	?
	Pseudoceratinidae	Indirect and external, when known	?
	Ianthellidae	Indirect and external, when known	?
	Aplysinellidae	Indirect and external, when known	?
Verticillitida	Verticillitidae	Indirect and internal, when known	To-be-studied parenchymella

*Question mark indicates that larvae were never seen in the taxon.

postulated that a planktonic direct-developer organism was the ancestral stage (e.g., Haeckel 1874; Salvini-Plawen 1978; Nielsen 1995). Nevertheless, both hypotheses were proposed and further expounded under unsuitable circumstances, since many crucial data on sponge embryogenesis and larval biology were not available until recently (see reviews by Maldonado and Bergquist 2002; Maldonado 2004; Leys and Eerkes-Medrano 2005; Leys et al. 2006). The substantial progress attained for the past 10 years in the study of many relevant processes of sponge embryogenesis, such as gastrulation, larval diversity, and metamorphosis, is revealing crucial detail for not only a more comprehensive understanding of the biological, ecological, and evolutionary meaning of sponge embryos and larvae, but also for reformulation of our hypotheses on the origin and early diversification of the Metazoa and their life cycle. The most traditional, widespread view on the biphasic cycle of sponges postulates that an ancestral sessile stage developed a motile larval stage. Nevertheless, the alternative idea that the primitive sponge, from which the remaining metazoan evolved, could have been a planktonic, larva-like organism has been postulated from a recent review on poriferan embryogenesis and larval histology (Maldonado 2004). Such a perspective is consistent with recent suggestions that the body plans of bilateralians have emerged as derived conditions from primary larva-like organisms, triggered by changes in developmental genes (Davidson et al. 1995).

Irrespective of the evolutionary origin of the biphasic cycle, there is little doubt that the occurrence of a dispersing larval stage may provide some relevant advantages for animals that are sessile during the adult phase, such as sponges. It provides a means to colonize new suitable habitats in either local or geographically distant areas, hence enlarging the biogeographical distributions and minimizing the chances of species

Table 2. Summary of available information about development mode and larval type for members of the classes Calcarea and Hexactinellida.

Class and order	No. of families and genera	Development type	Larval type*
Calcarea			
Clathrinida	6 families, 16 genera	Indirect and internal, when known	Calciblastula
Murrayonidae	3 families, 3 genera	Indirect and internal, when known	Calciblastula (predicted from embryos)
Leucosolenida	9 families, 42 genera	Indirect and internal, when known	Calciblastula (e.g., *Leucosolenia* Bowerbank, 1864) or Amphiblastula (e.g., *Grantia* Fleming, 1828, *Sycon* Risso, 1826), depending on family
Lithonida	2 families, 6 genera	Indirect and internal in *Petrobiona* Vacelet and Lévi, 1958	Amphiblastula, when known
Baerida	3 families, 8 genera	Unknown for most genera; indirect and internal in *Lepidoleucon* Vacelet, 1967	Amphiblastula, when known
Hexactinellida			
Amphidiscosida	3 families, 12 genera	Unknown	?
Hexactinosida	7 families, 36 genera	Unknown for most genera, but indirect and internal in *Farrea* Bowerbank, 1862	Trichimella (predicted from embryos)
Aulocalycoida	2 families, 7 genera	Unknown	?
Lychniscosida	2 families, 3 genera	Unknown	?
Lyssacinosida	3 families, 53 genera	Unknown for most genera; indirect and internal in *Leucopsacus* Ijima, 1898, *Vitrollula* Ijima, 1898, and *Oopsacas* Topsent, 1927	Trichimella (in *Oopsacas*)

*Question mark indicates that larvae were never seen in the taxon.

extinction if drastic shifts in local environmental and ecological conditions occur. The dispersal capability provided by a larval stage may also enhance population health by favoring gene flux between subpopulations, decreasing population consanguinity, and increasing recruitment success. Despite these theoretical implications, little research has been conducted to test the real ecological and genetic impacts of the dispersal ability of larvae on the structure and dynamics of sponge populations. During the past 30 years, most advances have concerned the histological investigation of larvae, fuelled by the advent of electron microscopy. Unfortunately, our understanding of sponge larval ecology has not paralleled the histological advances. Only moderated progress has been attained since the state-of-the-art, excellent reviews by Sarà and Vacelet (1973), Fell (1974), and Bergquist (1978).

Larval diversity vs. sponge diversity

From an anatomical point of view, the Porifera are a coherent, distinctive group, with body plan organization of adult sponges being relatively homogeneous across major taxa. However, the relative uniformity in adult body organization does not appear to apply so strictly to the larval stage. According to embryological origin and histological features, at least eight larval types are recognizable in the phylum Porifera (reviewed by Maldonado and Bergquist 2002; Maldonado 2004), namely the amphiblastula, calciblastula, trichimella, cinctoblastula, clavablastula, parenchymella, dispherula, and hoplitomella (Fig. 1). Because the externally developed larva of many oviparous sponges remains unknown (Tables 1, 2), it cannot be ruled out that new larval types will be described in the future. The diversity of larvae known so far grossly corresponds with the major taxonomic divisions in the Porifera. This matching is partially due to Lévi (1957, 1973), who first implemented embryogenesis as a major structuring criterion for the taxonomic classification of the Porifera. Recent works (Boury-Esnault et al. 1999; Leys et al. 2006) have corroborated the fact that larval histology also reflects basic differences between the syncytial subphylum Symplasma (class Hexactinellida) and the cellular subphylum Cellularia (classes Calcarea and Demospongiae).

According to the available information, it can be summarized that sponge larvae are lecithotrophic, ciliated to some extent, and with a relatively short planktonic life. Major exceptions to these generalizations are (*i*) the unciliated hoplitomella of some tetractinellid demosponges (see Vacelet 1999; Maldonado and Bergquist 2002; Borchiellini et al. 2004) that consists of a sub-spherical body provided with several long, radial projections (Fig. 1) and (*ii*) the benthic larva of some hadromerid and halichondriid demosponges that, despite being ciliated, crawls on the substrates rather than swims in the water column (e.g., Borojevic 1967; Bergquist et al. 1970; Ayling 1980). The fact that all sponge larvae known so far are lecithotrophic is intriguing (Maldonado 2004), since in most marine invertebrate phyla lecithotrophy is regarded to be a derived condition attained from a planktotrophic stage (e.g., Strathmann 1978; Pernet 2003).

Regarding body size, sponge larvae fall within the categories of both microplankton (50–500 μm) and mesoplankton (0.5–5 mm). Some amphiblastulae of *Sycon* Risso, 1826 and the dispherulae of *Halisarca* Johnston, 1842 are only about 50 μm at their largest diameter, while the parenchymella of the genera *Fasciospongia* Burton, 1934 and *Svenzea* Alvarez, van Soest and Rützler, 2002 may reach up to 5–6 mm. Larval

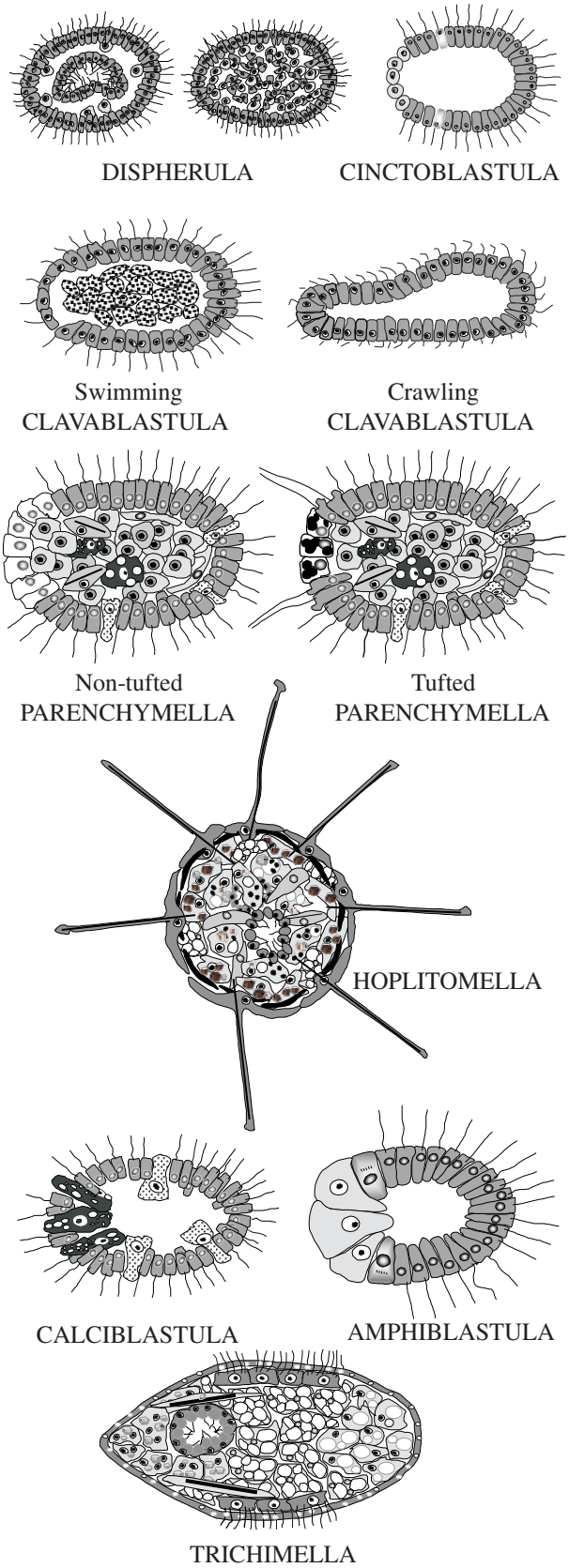


Fig. 1. Schematic representation of larval types known in Porifera (modified from Maldonado 2004, reproduced with permission of Invertebr. Biol., vol. 123, p. 5, © 2004 Blackwell Publishing). Further information on their anatomy and embryological development can be found in Maldonado and Bergquist (2002) and Maldonado (2004).

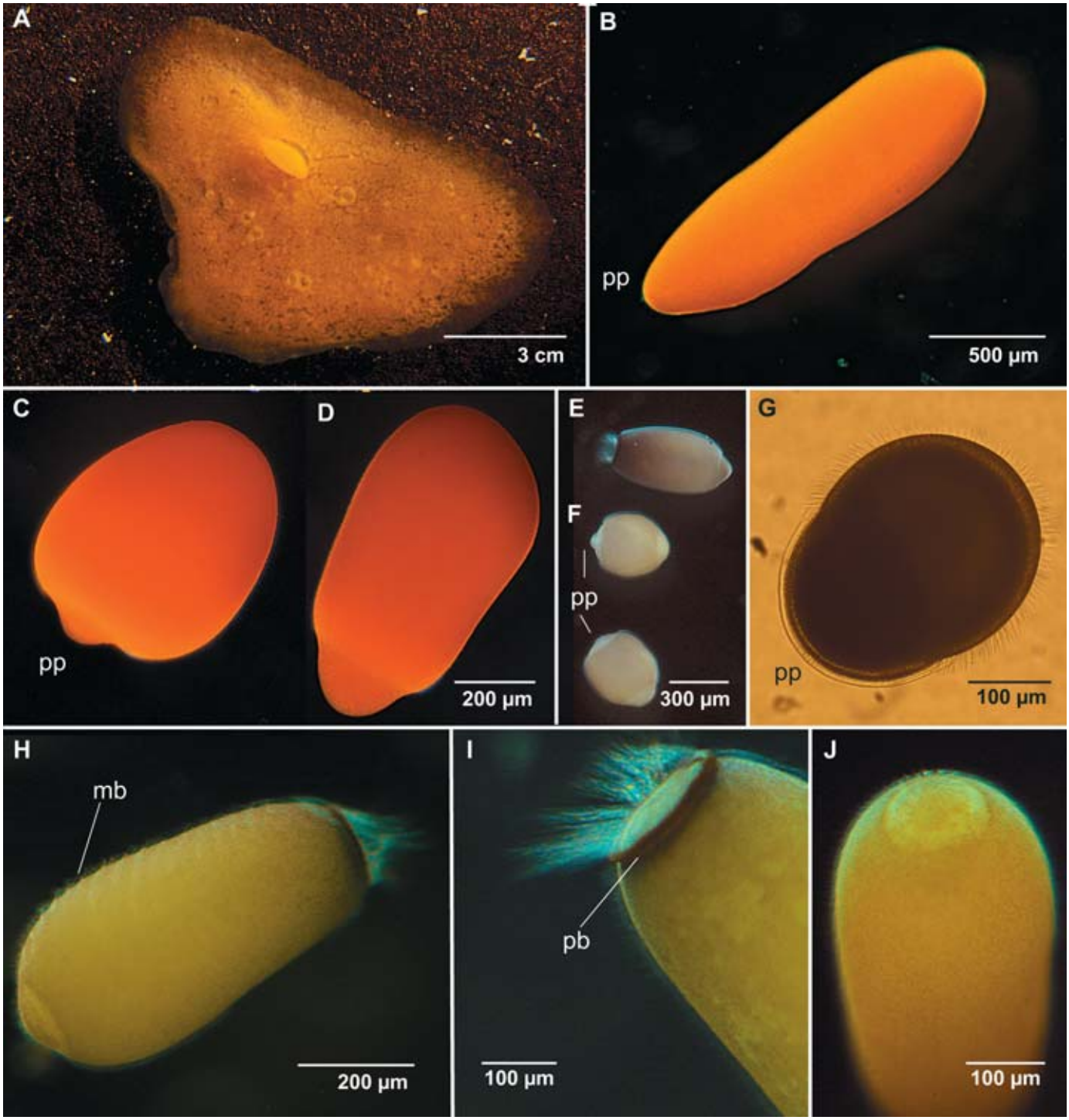
size also varies intraspecifically. Differences of about 25% in mean length have been detected between parenchymellae released by different conspecifics of a same local population (Maldonado et al. 1997).

Reproductive timing and larval release

In many sponges, the embryo develops into a larva within the maternal body and, once larvae are ready to be released, they may start swimming within the aquiferous canals of the mother (Bergquist and Sinclair 1968; Fell 1989; Maldonado and Young 1996; Maldonado and Uriz 1999). Most brooded larvae leave the mother sponge in the excurrent flow, throughout the oscules (Fig. 2*a*). Nevertheless, larvae have been observed leaving the maternal body by squeezing themselves through tiny secondary oscules and ostioles in demosponges such as *Callyspongia diffusa* Ridley, 1884 (Sivaramakrishnan 1951) and *Tedania ignis* (Duchassaing and Michelotti, 1864) (Maldonado and Young 1996). When the tissue of ripe, brooding sponges is experimentally disorganized and aquiferous canals disassembled, larvae are able to find their way out of the maternal body by crawling throughout the adult tissues (Maldonado and Uriz 1999). Such observations suggest that larval release is a process controlled by not only the mother sponge but also the brooded larvae themselves.

In sponges with external development, embryogenesis occurs either in the water column or, more often, at the bottom, because eggs or early embryos are usually expelled within negatively buoyant envelops and (or) mucous strands. While larval development in brooding sponges usually takes several weeks to months, external developers may complete this process in only 2–3 days after fertilization (e.g., Lévi and Lévi 1976; Fromont and Bergquist 1994; Mariani et al. 2001). Likewise, the hatching of externally developing embryos from their mucous strands and sticky envelopes appears to be a highly synchronous event, extending usually for <2 days at the population level (e.g., Lévi and Lévi 1976; Mariani et al. 2001). Such a synchronization is partially the consequence of rapid embryonic development following a highly synchronous gametogenesis that is putatively controlled at the population level by diverse exogenous and endogenous signals, including temperature, photoperiod, lunar cycles, and even putative pheromones (e.g., Reiswig 1970, 1983; Watanabe 1978; Fell 1983; Hoppe and Reichert 1987; Fromont 1994). This situation contrasts with hatching dynamics of brooded larvae, the release of which concentrates in one or two annual peaks, each extending at the population levels for weeks to months, usually during the warm season (e.g., Lévi 1956; Wapstra and Soest 1987; Maldonado and Young 1996; Lindquist et al. 1997; Maldonado and Uriz 1998; Mariani et al. 2005). It has also been reported that some sublittoral and intertidal brooding demosponges may release small quantities of larvae throughout the year, though

Fig. 2. (A) Parenchymella of the halichondrid *Scopalina lophyropoda* being released through the oscule of a small sponge individual. (B) Parenchymella of *S. lophyropoda* showing the posterior pole (pp) with cilia. (C, D) Parenchymellae of the poecilosclerid *Crambe crambe* showing the posterior pole (pp) lacking cilia. Figs. 2C and 2D show the same swimming larva pictured a few seconds apart to illustrate the remarkable change in body shape and in the degree of extrusion of the posterior pole. (E) Tufted parenchymella of the dendroceratid *Ircinia oros*. (F) Parenchymellae of the poecilosclerid *Mycale* sp. showing a bare area at both the posterior pole (pp) and the anterior pole. (G) Cinctoblastula of the plakinid *Corticium candelabrum* showing a posterior pole (pp) with shorter cilia. (H) Tufted parenchymellae of the dendroceratid *Cacospongia* sp. showing metachronal waves of ciliary beating (mb). (I, J) Details of the posterior and anterior poles of larva in Fig. 2H showing the ring of posterior cilia (I), the 2-band pigment ring (pb), and the protruding anterior pole (J) where the cilia are less dense than in the surrounding regions.



massive peaks of release occurs only once or twice a year (e.g., Bergquist and Sinclair 1973; Koolwijk 1982; Zea 1993). The maximum asynchrony at larval release is found in some tropical and subtropical sponges, which may incubate variable amounts of embryos at any time during the year (e.g., Storr 1964; Bergquist 1978; Kaye and Reiswig 1991; Ilan and Loya 1990; Meroz and Ilan 1995).

The duration of the reproductive period may be determined by not only species-specific genetic factors, but also by environmental factors such seawater temperature. Storr (1964) noticed that a low number of individuals of the Caribbean demosponge *Hippospongia lachne* (de Laubenfels, 1936) is reproductive throughout the year in populations from British Honduras to the Bahamas, while no reproduction occurs during winter in populations from the Florida keys (Storr 1964; Kaye and Reiswig 1991), where seawater temperature declines rapidly after autumn. Likewise, remarkable interpopulation differences in reproductive timing have also been reported for the demosponges *Halichondria bowerbankii* Burton, 1830 and *Halichondria panicea* (Pallas, 1766) by Wapstra and Soest (1987).

There are few field observations about the rate at which larvae are released by brooding sponges, but many laboratory observations suggest that it varies largely both between and within species. For instance, members of a New Zealand population of the intertidal demosponge *Ophlitaspongia seriata* (Grant, 1826) expelled larvae in the laboratory during several days at rates of 4–5 larvae·individual^{-1}·min^{-1} (Bergquist and Sinclair 1968), whereas North Atlantic individuals released the entire brood, which comprised 1–15 larvae·individual^{-1}, in about 2 h (Fry 1971). Meroz and Ilan (1995) monitored an individual of the encrusting demosponge *Mycale fistulifera* (Row, 1911) under laboratory conditions and reported larval release rates of 500 larvae·individual^{-1}·day^{-1} for 5 consecutive days, mostly between 0800 and 1400. By counting embryos in adult tissue samples of four subtidal Caribbean demosponges, i.e., *Halichondria melanodocia* de Laubenfels, 1936, *Haliclona* (*Gellius*) *caerulea* (Hechtel, 1965) — described as *Sigmadocia caerulea* —, *Haliclona tubifera* George and Wilson, 1919, and *T. ignis*, it was estimated that larval release at the population level lasted 3–4 months (Maldonado and Young 1996). Laboratory observations revealed that each individual from the first three species above required at least three massive releases, usually on successive days, to expel its entire brood. However, in the fourth species, *T. ignis*, massive releases in consecutive days were never observed. Rather, small numbers (15–50) of larvae were released by ripe individuals several days before and after each massive release, until the entire brood was expelled.

Wide interspecies variability in larval output has also been revealed by field observations. While a local North Atlantic population of *O. seriata* was estimated to release just 18 larvae·m^{-2}·day^{-1} during the release season (Fry 1971), higher larval numbers have been detected in several demosponges of the Spanish Mediterranean sublittoral. For instance, a large (about 2 L in volume) individual of the abundant dictyoceratid *Ircinia oros* (Schmidt, 1864) was observed expelling larvae through 1–3 oscules for 2 weeks (M. Maldonado, unpublished data). During the daytime, larvae were expelled continuously at rates of 1–10 larvae·min^{-1}, whenever the sponge was pumping, which occurred for about two-thirds of the observation time. By assuming that larval release is maintained at similar rates during the entire daytime period (nighttime release was not monitored), it can be deduced that this individual released, on average, 2350 larvae·day^{-1} and about 3.3×10^4 larvae throughout the entire release period. In the same Mediterranean sublittoral habitat, the population of the encrusting poecilosclerid demosponge *Crambe crambe* (Schmidt, 1862), which covers about 12.5% ± 13.3% of rocky substratum at the 5–20 m deep cliff (Maldonado et al. 2005), is estimated to release, on average, about 9375 larvae·m^{-2} of rocky bottom and up to 140.6×10^6 larvae·(linear km)$^{-1}$ of the sublittoral cliff throughout July and early August (A. Riesgo and M. Maldonado, unpublished data). These figures derive from a very conservative approach based on serial histological sections of samples taken immediately prior to the onset of larval release at the population level, which revealed that only about 50% of the individuals brood embryos each year and that those brooding (N = 25) contain, on average, about 15 developing embryos·cm^{-2} of sponge cover (2–5 mm thick). This embryo density is about 3 times lower than that estimated by us in a previous study based on observations of brooding individuals under a compound microscope (Uriz et al. 1998).

Little is known about larval production by externally developing sponges; however, it is assumed to be substantial according to the scarcely available information. Fromont and Bergquist (1994) estimated that a female of the demosponge *Xestospongia bergquistia* Fromont, 1991 spawned 1.4 million eggs with a fertilization success of about 71.4%, which totals about 1 million larvae derived from this sponge alone.

The high larval outputs estimated for brooding and nonbrooding sponges by direct counts on tissue samples or at hatching contrast with the relatively modest outputs inferred from the use of larval traps. Traps settled around 15 individuals belonging to the tropical demosponges *Callyspongia vaginalis* (Lamarck, 1814) and *Niphates digitalis* (Lamarck, 1814) collected 2–191 and 0 to >200 larvae·individual^{-1}·day^{-1}, averaging 54.2 and 42.7 larvae·individual^{-1}·day^{-1}, respectively (Lindquist et al. 1997). It seems difficult to account for the great abundance of *C. vaginalis* and *N. digitalis* in Caribbean reefs from these modest larval outputs; about 200 000 larvae may be required to produce 1 adult according to estimates for a commercial demosponge by Storr (1964). Therefore, it may be that these sponges rely heavily on asexual reproduction. Alternatively, abnormally low larval output may have resulted from traps disturbing the normal pumping activity of the sponges, since the upper portion of their body was enclosed within a fine-mesh net stretched around it and kept vertical by a buoyant container. It is known from laboratory observations that, while the absence of water movement induces larval release, any extraneous changes in the water flow around the sponges induce oscule retraction, leading to either slackening or interruption of larval release (Bergquist et al. 1970; Fry 1971; Sarà and Vacelet 1973). Similar effects have been noticed on wild populations of *I. oros* and *C. crambe*, whereby larval release ceases under stormy conditions and resumes once calm conditions return (M. Maldonado, unpublished data). Likewise, larval emission also ceases temporarily after finger pressing

the sponges, which causes retraction of both oscules and peripheral aquiferous canals.

Another external factor affecting rates of larval release is the illumination regime, which appears to influence mostly brooding sponges. In the laboratory, many ripe sponges release their larvae upon exposure to intense illumination (light shock) after a period of complete darkness (e.g., Fry 1971; Amano 1986; Maldonado and Young 1996). Such a response is thought to be an adaptation that favors larval release shortly after sunrise (Lévi 1951, 1956). Manipulation of light cycles revealed an unexpected complexity in the action mechanism of this stimulus. While morning larval release for some demosponges (e.g., *H. panicea*; Amano 1986) is a direct consequence of the onset of darkness the day before, it is the consequence of illumination onset the day before for others (e.g., *Callyspongia ramosa* (Gray, 1843); Amano 1988). The question that remains is how do adult sponges detect light cues, given that photoreceptors have only been identified in some larvae to date?

Larval release may also be stimulated in some demosponges by exposing ripe adults to air for a few seconds, such as in *H.* (*G.*) *caerulea* (Maldonado and Young 1996). Moon phases and tidal rhythms appear to be cues more related to gamete release than to larval release. Nevertheless, tidal rhythm can be relevant for intertidal sponges, which have been observed expelling their larvae during the peak of high tide (Fry 1971). For some deep-sea sponges, the timing of reproductive activity may be regulated by patterns of primary production in the photic zone of the ocean and subsequent sinking of the generated production (Witte 1996).

Larval motion

The small size of sponge larvae have profound effects on the way in which they relate to their environment. At a microscopic scale, it can be said that the molecules of seawater stick to and come into friction with each other, also with any solid object that they contact; a fluid property known as viscosity. The relative importance of viscous and inertial forces in animal locomotion within a fluid is given by the Reynolds number (*Re*), which depends on the animal size (*L*), the animal swimming speed or fluid velocity with respect to the animal (*U*), and the kinematic viscosity of the fluid (ν) according to the following equation:

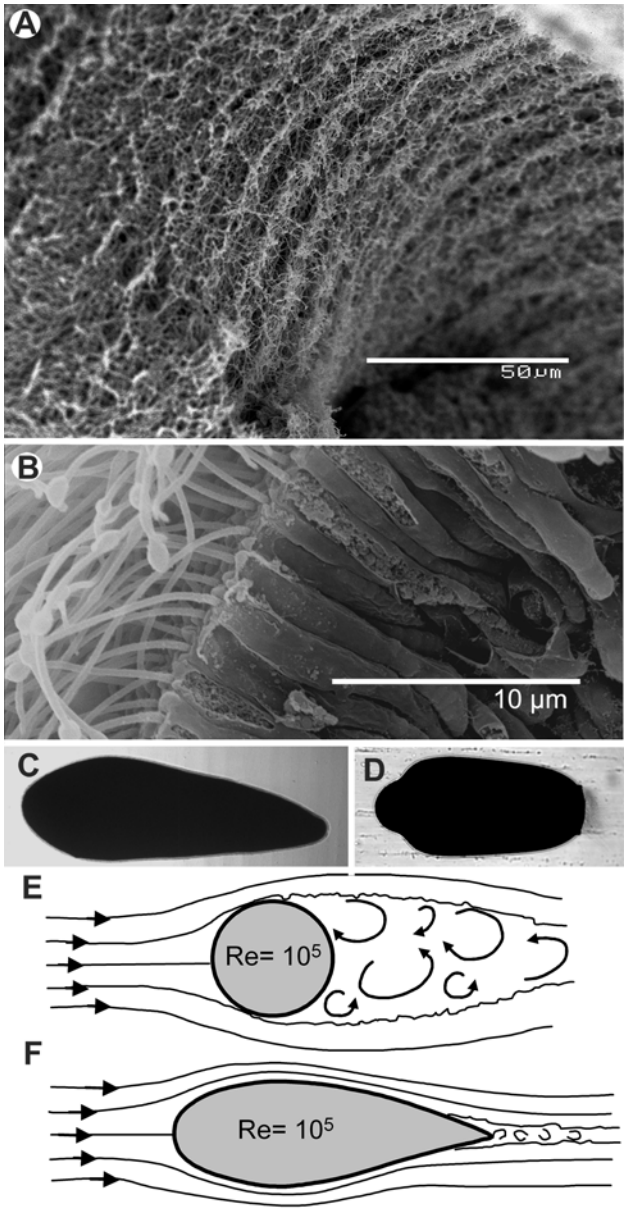
$$Re = UL/\nu$$

Re values for fish and other relatively large, fast-moving marine animals fall well above 1000 (e.g., Vogel 1994), while sponge larvae, which usually measure from 0.05 to 6 mm and swim at speeds of 0.1–1 $cm \cdot s^{-1}$ (e.g., Bergquist et al. 1970; Maldonado and Young 1996; Maldonado et al. 1997), exhibit *Re* values below 1. At these low *Re* values, the viscous forces rather than the inertial forces dominate the interaction of the larva with the surrounding seawater. A major consequence is that as soon as the thrust exerted by a swimming larva ceases, the larva stops instantaneously and is entrapped by the viscous forces, resulting in no gliding by inertia. Such a situation is similar to the one that a fish swimming in a pool of honey would experience. In the viscous world of low *Re* values, propulsion by helical and undulating cilia, which generate thrust by viscous shearing, appears to be particularly favored. Because viscous flow is reversible, the flexible nature of cilia allows them to maximize drag by moving almost broadside on their power stroke and to minimize drag by moving almost lengthwise during their recovery stroke (see Purcell 1977; Vogel 1994). This drag difference overcomes the problem of symmetric flow at low *Re* values and generates net thrust for motion. Therefore, it is not surprising that all but one of the known larval types in Porifera are ciliated to some extent (Fig. 1).

The ciliated areas of the larval body are produced by monociliated cells (Fig. 3*a*), except in the trichimella larva, which is characterized by multiciliated cells. The cilia may entirely cover the external surface of the larval body, such as in the clavablastula and the dispherula larval types (Figs. 2*b*, 2*g*). Alternatively, the posterior and (or) the anterior poles may exhibit unciliated areas of variable extension, such as in the trichimella, amphiblastula, and some parenchymellae (Figs. 2*c*, 2*d*, 2*f*), cinctoblastulae (Fig. 2*g*), and calciblastulae. In most larval types, the length of cilia is similar across body regions, except for the cinctoblastula (Fig. 2*g*), in which cilium length may decrease from the anterior pole to the posterior pole, and the "tufted" parenchymellae (Figs. 2*e*, 2*h*–2*j*, 3), in which the unciliated posterior pole is encircled by a ring of cilia that is 4–6 times longer than those covering the remaining portions of the body.

The motion of larval cilia has only been investigated in detail in the parenchymella (Maldonado and Young 1996; Maldonado et al. 1997, 2003; Leys and Degnan 2001). Larval cilia exhibit planar beating, are arranged in rows parallel to the anterior–posterior larval axis (Fig. 3*a*), and beat with a planar effective stroke that is parallel to that longitudinal axis. The coordinated movement of these cilia generates waves with diaplectic metachronism (Fig. 3*a*) that propagate from the anterior pole to the posterior pole of the larva along the ciliary fields (Fig. 2*h*). Therefore, diaplectic metachronism generates the thrust for forward motion. In addition, metachronal waves travel across the longitudinal ciliary fields, moving either to the right (dexioplectic waves) or to the left (leioplectic waves) of the effective stroke (Fig. 2*h*). Dexioplectic or leioplectic ciliary waves make the larva rotate around its longitudinal axis. Literature records, as well as unpublished observations by this author, support the fact that most parenchymella and cinctoblastula larvae produce dexioplectic waves so that they rotate clockwise when viewed from the anterior pole. Alternatively, some parenchymellae and amphiblastulae have been reported to rotate counterclockwise. Nevertheless, not all types of sponge larvae rotate when moving forward. The trichimella larva of hexactinellids, the motion of which relies on a wide equatorial band of multiciliated rather than monociliated cells, does not rotate along the longitudinal axis. Rather, it moves forward without rotating while describing a trajectory in counterclockwise translating circles (Boury-Esnault and Vacelet 1994). Interestingly, some parenchymellae also describe wise translating circles rather than straight trajectories while rotating, as reported for larvae of the demosponge *Mycale* (Wapstra and Soest 1987; Maldonado and Young 1996). Such a trajectory, also used by predatory dinoflagellates as a strategy to maximize encounter rates with potential prey (Bartumeus et al. 2003), could enhance the larval chances of contacting suitable substrates for settlement or minimize the

Fig. 3. (A) Detail of metachronal waves in cilia of the non-tufted parenchymella of *Mycale* sp. (B) Detail of the monociliated columnar cells in the larval epithelium of the parenchymella of *S. lophyropoda*. (C, D) Body contour of the non-tufted parenchymella of *S. lophyropoda* and the tufted parenchymella of *I. oros* as seen through a compound microscope. (E, F) Approximate lines of flow around a solid ball and a streamlined object at high Reynolds number (*Re*). Note that while flow separates from the lee side of the ball dissipating much energy as turbulence, flow lines remain close to most of the lee region of the streamlined object with minimum energy dissipation.



probability of being located by planktonic grazers that systematically search the plankton for prey, or both.

The shape of larvae appears to have some relevant implications on motion, although the importance of body shape on movement is less important at low than at high *Re* values. The body of most sponge larvae can be approximated to a prolate spheroid, typically with a blunt front (anterior pole) and a tapering rear (Figs. 3*c*, 3*d*). Such a shape is highly advantageous for organisms moving at high *Re* values, since the energy invested in accelerating seawater to get it around this streamlined body is not dissipated in the wake, but returned to the body in decelerating fluid near its rear (Figs. 3*e*, 3*f*). At high *Re* values, a streamlined organism is literally pushed forward by the wedge-like closure of the seawater behind it (Fig. 3*f*). However, at low *Re* values, streamlining becomes inefficient, because viscous forces dominate motion and streamlined body forms expose more surface than other shapes relative to either exposed area or volume contained. This means an increment of drag and "skin friction" (as defined by Vogel 1994) that may outweigh any advantage obtained by the closure of the fluid behind. According to Vogel (1994), "this is one of the reasons why very small swimming creatures do not look obviously streamlined". Nevertheless, it is obvious that most sponge larvae have converged toward such theoretically inefficient body shape (Figs. 3*c*, 3*d*), apparently contradicting the biomechanical predictions. However, there is no contradiction, because sponge larvae are not primarily designed for active displacement in seawater. Observations of larvae in the field have revealed that, unlike in the laboratory, they rarely exhibit active swimming to attain horizontal displacement (Maldonado et al. 2003). Rather, larvae maintain a vertical position most of the time, with the anterior blunt pole oriented upward. In this "resting orientation", larvae drift along with the local water masses, virtually entrapped among the seawater molecules by viscous forces. Therefore, it appears that the body shape of sponge larvae has become "streamlined" because maximizing the effects of viscosity may be, in the end, advantageous for their long-range dispersal. From this perspective, sponge larvae, which have often been described as bullet-shaped forms (e.g., Maldonado and Bergquist 2002), should instead be considered to be "hydrostatic balloons" that are efficiently designed to facilitate permanence in the water column at minimum energy investment. Larvae rarely perform horizontal displacement by ciliary beating during their dispersal in open waters. Instead, the cilia are only used to keep larvae rotating along their longitudinal axis, which apparently allows for the re-adjusting of the depth range while drifting (Maldonado et al. 2003). Therefore, the ability of sponge larvae for long-range dispersal may be little related to the forward motion generated by their cilia. Indeed, the only sponge larva assumed to experience a long planktonic life is unciliated, i.e., the hoplitomella. This spherical larva exploits the viscous forces of seawater and avoids sinking by forming 6–10 long, radiating protrusions that increase surface area without adding significant mass, a strategy similar to that developed by radiolarians and other microscopic unciliated organisms of the plankton.

Given that cilia do not appear to be strictly necessary for achieving long-distance dispersal, at first sight, it may be surprising that nearly all sponge larvae known so far have developed cilia. A reasonable explanation is that the cilia, although of little help in active long-range dispersal, may be extremely useful for selective settlement at specific sites. Field observations have revealed that the parenchymella of several species ceases its "drifting attitude" whether encountering strong turbulence, entering the boundary layer of a

solid object, or experiencing drastic changes in irradiance (Maldonado et al. 2003). Under these circumstances, the drifting larva re-gains its "horizontal position", placing the longitudinal axis parallel to the direction of movement and starts swimming forward propelled by the thrust of its cilia. As previously discussed, the larval body is particularly unsuitable for forward displacement through the water, as its shape maximizes drag and "skin friction". I postulate that most streamlined sponge larvae have developed rotation along their longitudinal axis to facilitate forward motion so that they virtually drill the viscous medium in which their unfavorable body needs to progress.

Apart from the short, uniform ciliation that covers the larval body entirely or mostly, some parenchymellae show a ring of long cilia, known as the tuft, at the posterior pole (Figs. 2*e*, 2*h*, 2*j*, 3, 4; Table 1). Although it has been shown that tufted parenchymellae can swim faster than non-tufted parenchymellae, the locomotory function of the posterior tuft appears to be more related to providing maneuverability than forward thrust (Maldonado and Young 1996). While non-tufted larvae are unable to swimming backwards, tufted parenchymellae of *Cacospongia* Schmidt, 1862 and *Ircinia* Nardo, 1833 have been observed swimming backwards when tangling with debris in petri dishes (M. Maldonado, unpublished data). The backward displacement is far slower than the forward motion and is attained by spasmodic contractions of the tuft. Such behavior suggests that these larvae have a sophisticated control for the movement of the cilia in the tuft, a process which is currently beyond our understanding. Because the cilia of both the tuft and the remaining body of some parenchymellae and dispherulae keep beating for some time after larval attachment for metamorphosis (Maldonado and Young 1996, 1999; Gonobobleva and Ereskovsky 2004), it cannot be ruled out that ciliary beating may have secondary functions in addition to motion. Putative advantages of post-attachment beating would involve renovation of the boundary layer around the metamorphosing body to facilitate dispersal of cell excretion products, oxygen diffusion, and pinocytic/phagocytic activity by ciliated cells.

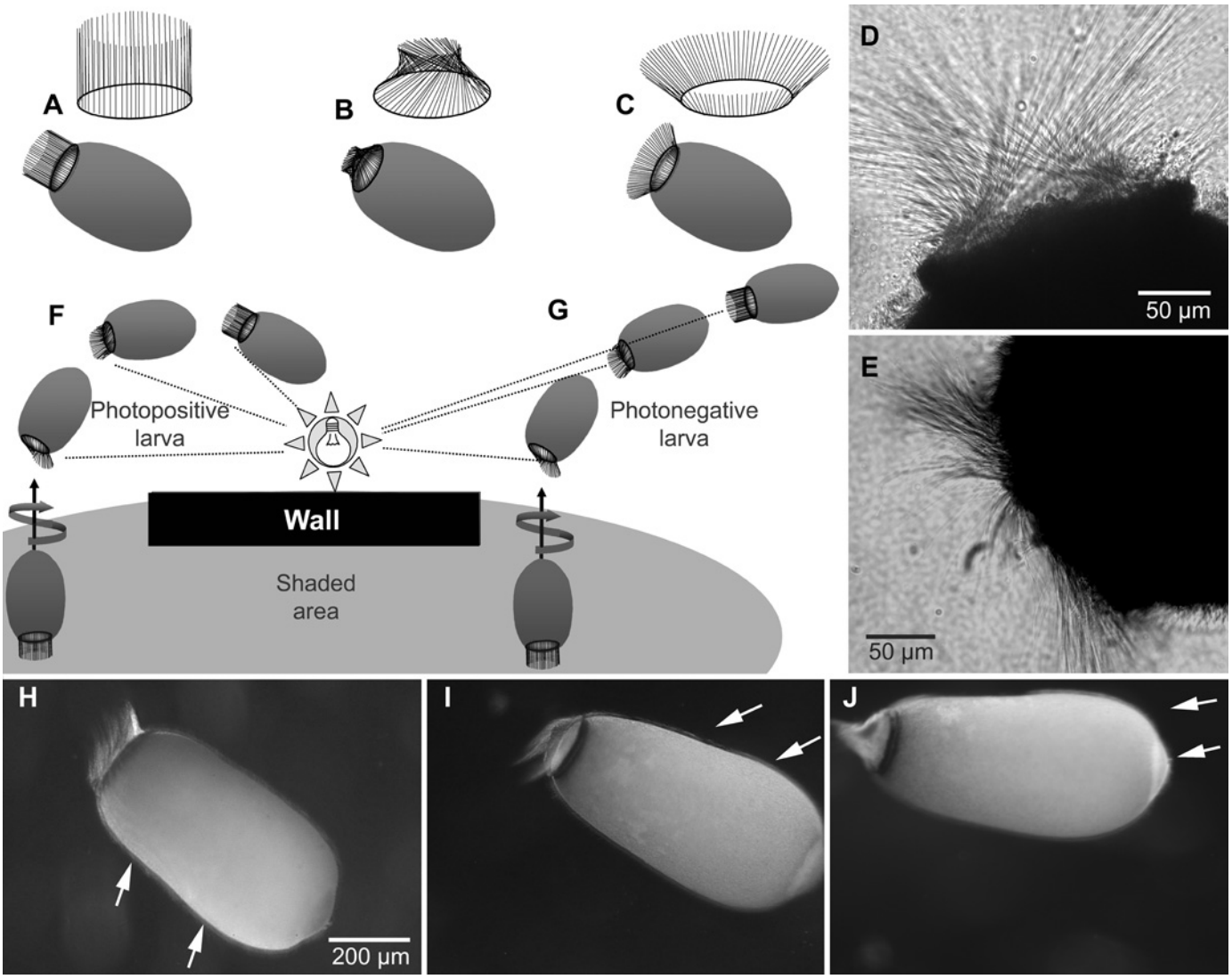
Observations through compound microscopy of swimming parenchymellae reveal that larvae are able to make remarkable, sudden changes in speed (i.e., acceleration). Speed of ciliary beating is known to be increased by high irradiance (Maldonado et al. 1997) and decreased by decreasing temperature (Maldonado and Young 1996). However, sudden changes in speed of larvae may be more related to transient changes in the shape of the larval body than to changes in beating speed. In some parenchymellae with large, unciliated posterior regions, such as those of *Crambe* Vosmaer, 1880 (Figs. 2*c*, 2*d*), *Tedania* Gray, 1867, *Rhaphidophlus* Ehlers, 1870, and *Phorbas* Duchassaing and Michelotti, 1864, sudden changes occur in body shape owing to protraction and retraction of the posterior pole and (or) the anterior pole (Wapstra and Soest 1987; Woollacott 1990; Maldonado and Young 1996; Mariani et al. 2005). These changes in shape are likely to cause abrupt shifts in larval drag and skin friction, which may be partially responsible for larval accelerations and decelerations. Mariani et al. (2005) have described rhythmic (every 2 min) retractions and extrusions of the posterior pole of the parenchymella of *Phorbas tenacior* (Topsent, 1925), with larvae crawling without rotation at the bottom of the dishes when the posterior pole is completely retracted into the body. Hence, ciliary beating and changes in body shape must somehow be coordinated by the larvae. Dramatic changes in body shape and swimming ability also occur if larvae encounter abnormally low temperatures. The body of the larva of *Halichondria magniconulosa* Hechtel, 1965 lengthened to between 50% and 100% when larvae acclimated to swimming in 25 °C seawater were exposed to 10 and 15 °C for a few hours (Maldonado and Young 1996). At these low temperatures, most larvae rested at the bottom of the laboratory dishes, showing some ciliary beating but no swimming capability. Body lengthening may be related to the increase in seawater viscosity caused by low temperatures, while immobility may be explained by the temperatures below the physiological optimum causing partial disruption of ciliary beating.

Dispersal and larval mortality

After hatching, sponge larvae become part of the merozooplankton, drifting in the water column for a limited time period before settling on the seafloor to become sessile juvenile sponges. Theoretically, the longer a larva remains in the plankton, the greater its opportunities for dispersal and for encountering appropriate settlement cues and optimal sites for settlement. However, a longer planktonic life also increases the risk of mortality during dispersal by either augmenting the chances of coming across predators or being washed to unsuitable environments. Mortality during larval dispersal is assumed to be high for most marine invertebrates (Rumril 1990), most losses being caused by predation and advection away from suitable settlement habitats (Young and Chia 1987; Lindquist and Hay 1996; Roughgarden et al. 1988). Unlike planktothrophic larvae, lecithotrophic larvae have limited provision of energy in the form of yolk and may soon run out of energy to maintain their vital processes if the dispersal period is by any reason overextended. Therefore, from a physiological point of view, the duration of the dispersal period is determined by a combination of three major factors: (1) the level of energy reserves in the larva, (2) the species-specific tempo of the developmental program, and (3) the availability of settlement cues in the environment. It is likely that a combination of ecological and physiological pressures have selected for each species a duration that allows for acceptable levels of dispersal under tolerable risk of mortality before and after settlement.

Most detailed observations on the duration of the planktonic larval life come from laboratory approaches (e.g., Ilan and Loya 1990; Woollacott 1993; Meroz and Ilan 1995; Maldonado et al. 1997; Maldonado and Young 1999) in which sponge larvae are suspected of delaying settlement relative to field conditions (Lindquist et al. 1997). The available data indicate that most sponge larvae are anchiplanic, that is remaining in the water column for minutes to a few days (usually <2 weeks). It is well known that sponge larvae rarely appear in off-shore plankton samples (Trégouboff and Rose 1957), while they are abundant during the reproductive period in the near-shore water mass close to the substrates where parental populations occur (e.g., Mariani et al. 2005). Paradoxically, the unciliated hoplitomella is the only sponge larva consistently reported from off-shore plankton samples

Fig. 4. Schematic drawing illustrating the larval tuft of a parenchymella in a relaxed (A), contracted (B), and expanded (C) conformation. (D, E) Details of the contracted (D) and expanded (E) arrangements of the posterior tuft of the parenchymella of *I. oros*. (F, G) Diagram illustrating changes in swimming trajectory and tuft conformation in a photopositive and a photonegative tufted parenchymella when entering an illuminated area from a shaded area. (Modified from Maldonado et al. 2003, reproduced with permission of Mar. Biol. (Berl.), vol. 143, p. 431, © 2003 Springer-Verlag.) (H–J) Changes in the orientation of the cilia in the posterior tuft of the photonegative larva of *I. oros* in response to changes in light direction (white arrows).



(Trégouboff 1939, 1942). Its off-shore occurrence, along with the complex skeletal changes described within its planktonic period (Trégouboff 1939, 1942), suggests that the hoplitomella may remain in the plankton for a long time (Vacelet 1999), perhaps months.

The duration of the dispersal phase has been shown to shorten drastically for some parenchymellae when exposed to either temperatures of 10–15 °C below the optimum (Maldonado and Young 1996) or excess Cs^+ and K^+ ions (Woollacott and Hadfield 1996). In both experiments, rapid attachment and metamorphosis were induced, although low temperatures caused high mortality among settlers. Some sponges have benthic larvae rather than planktonic larvae, as illustrated by the parenchymella of *Halichondria moorei* Bergquist, 1961 and the flattened clavablastula of *Polymastia robusta* (Bowerbank, 1861). The former settles in about 2–3 days (Bergquist et al. 1970), while the latter can creep on the substrate for up to 20 days before settlement (Borojevic 1967).

It is surprising that very little experimental and observational information are available on mortality during dispersal of sponge larvae. Sponge larvae are very conspicuous organisms, since they usually match the bright colors of the adult internal tissues. Such colorful larvae, which are also charged with yolk, should be appealing prey for zooplankton consumers. However, relatively few cases of predation on larvae have been documented. Instead, small fish, copepods, and other potential predators appear to ignore these larvae. A study involving 11 Caribbean sponges concluded that the larvae were consistently unpalatable to fish, with larvae that were occasionally mouthed by fish being rapidly rejected with no further negative effects on larval survivorship and success at metamorphosis (Lindquist and Hay 1996). Interestingly, larvae proved unpalatable even in the case of

sponges with a palatable adult. Such a "Caribbean pattern" contrasts with laboratory observations that larvae and early settlers of the Mediterranean demosponge *C. crambe* are ingested by starved juveniles of the small benthic fish *Tripterygion tripteronotus* (Risso, 1810) and *Parablennius incognitus* (Bath, 1968) under laboratory conditions (Uriz et al. 1996). At first sight, predation on larvae by fish seemed unlikely, since adult tissues of this sponge are chemically defended by a wide variety of powerful cytotoxic compounds. Nevertheless, it was later suggested that larvae of *C. crambe* are chemically undefended, as they lack the spherulous cells in which adults store the putative cytotoxic compounds (Uriz et al. 2001). Therefore, although larvae of *C. crambe* are rarely predated by pelagic fish while drifting in open water far from substrates (M. Maldonado, personal observations), larvae may experience substantial predation by small benthic fish once they start swimming close to the substrates searching for settlement sites. Likewise, Vivien (1973) reported that larvae of keratose sponges are often found in the stomach of pomatrocentrid fish in reefs of Tuléar. Nevertheless, high predation pressure by fish and other visual predators may not be the rule for sponge larvae, since most observed sponges release their larvae early in the morning or during daytime hours. Such a pattern contrasts with the nighttime release strategy preferred by other marine invertebrate groups, the larvae of which are known to be attractive to visual predators (Morgan 1995).

Field observations on the parenchymella of several Mediterranean sponges indicated that larvae swimming close to the substrata during the exploratory phase can occasionally be captured by unselective predators, such as the large ascidian *Halocynthia papillosa* (L., 1767), the terebellid deposit-feeding polychaete *Eupolymnia nebulosa* (Montagu, 1818), and several sea anemones (M. Maldonado, unpublished data). There are earlier similar observations confirming such larval predation. Lévi (1956) reported eggs and embryos within the branchial sac of ascidians. Bergquist and Sinclair (1968) reported how newly released larvae of the intertidal sponges *Clathria* (*Microciona*) *coccinea* (Bergquist, 1961) and *O. seriata* were massively ingested by spionid polychaetes: "The long tentacles of the worm can range over the entire sponge surface and larvae are captured and conveyed between the two arms to the mouth. The long red fecal strands produced by the worms indicated that sponge larvae, at least temporarily, formed the bulk of their diet." A study by Lindquist and Hay (1996) revealed that even corals and sea anemones are not unselective, but choosy predators, since larvae of 6 out of 9 offered Caribbean demosponges were frequently rejected with little effects on subsequent larval survivorship and settlement success.

Some larval mortality may also occur by "physiological stress", resulting from an overextended planktonic phase. Under laboratory conditions, most parenchymellae of *H.* (*G.*) *caerulea* settle after swimming 25–28 h. However, some larvae may swim for only 8 h before settlement, while others do it for 70 h. When the post-settlement survival of these outliers was examined, it was found that larvae settling after a brief swimming period (<12 h) gave rise to juveniles that experienced only about 10% average mortality after 17 days in the laboratory. In contrast, larvae that settled more than 72 h after release produced juveniles of reduced vigor, which grew comparatively slow and experienced about 60% average mortality during the same period (Maldonado and Young 1999). Such increased laboratory mortality is suggested to be a direct consequence of overconsumption of yolk during the dispersal phase. Measurements of total protein and total lipid contents in newly released (6 h old) larvae of this sponge revealed mean values of 0.75 and 1.1 $\mu g \cdot larva^{-1}$, respectively; in late-stage (36 h old) larvae, these figures had slightly decreased to 0.55 and 0.95 $\mu g \cdot larva^{-1}$, respectively (Maldonado et al. 1997). Although low replication caused these between-time differences not to be statistically significant, those data suggest that nearly half of the proteins and one-third of the lipids could be consumed by a larva after 72 h of planktonic dispersal. By taking into account that the non-usable structural proteins and lipids are to be detracted from these figures, the yolk remaining after an overextended dispersal may be energetically insufficient to successfully complete the crucial, energy-demanding processes of settlement and metamorphosis.

Yet an additional process is to be considered when balancing energy consumption by sponge larva during dispersal. Sponge larvae are often assumed to be strictly lecithotrophic organisms that rely just on their maternally supplied yolk reserves, but the real situation is somewhat more complex. By studying the ultrastructure of the epithelium of some larvae, Bergquist and Green (1977) suggested that the monociliated cells could incorporate dissolved compounds by pinocytotic activity. Such ability was experimentally demonstrated 20 years later in the parenchymella of *T. ignis*, the ciliated cells of which are able to assimilate dissolved organic materials from seawater, such as the amino acid alanine and the fatty acid palmitic acid (Jaeckle 1995). Interestingly, while the incorporation of alanine was energetically insignificant, palmitic acid transport was estimated to account for 21%–55% of larval metabolism. To my knowledge, there is no further study on the mobilization of yolk during the sponge larval life, although it would be desirable to clarify the role of yolk consumption on settlement success and juvenile survival. This matter becomes even more complex after a recent report indicating that the ciliated cells of the *Halichondria* parenchymella are able to phagocytose and digest bacteria and small (<4 μm) unicellular organisms (Ivanova 1999). The degree at which this ability is widespread among poriferan larvae remains unaddressed.

Depth regulation and substrate exploration

Dispersal is followed by a period in which larvae become demersal and start swimming close to available substrates for settlement. It is generally agreed that dispersal (i.e., passive transport and random deposition) of most marine invertebrate larvae operates at a different spatial scale than active substratum selection. As expressed by Pawlik (1992), larvae passively accumulate and are deposited under the influence of hydrodynamic processes that operate at large spatial scales (tens of metres to kilometres), while active substratum exploration and selection occur only at much smaller scales (centimetres to metres). For some sponge larvae, the exploration phase must extend for several days, which is even lon-

ger than the planktonic phase, at least under laboratory conditions.

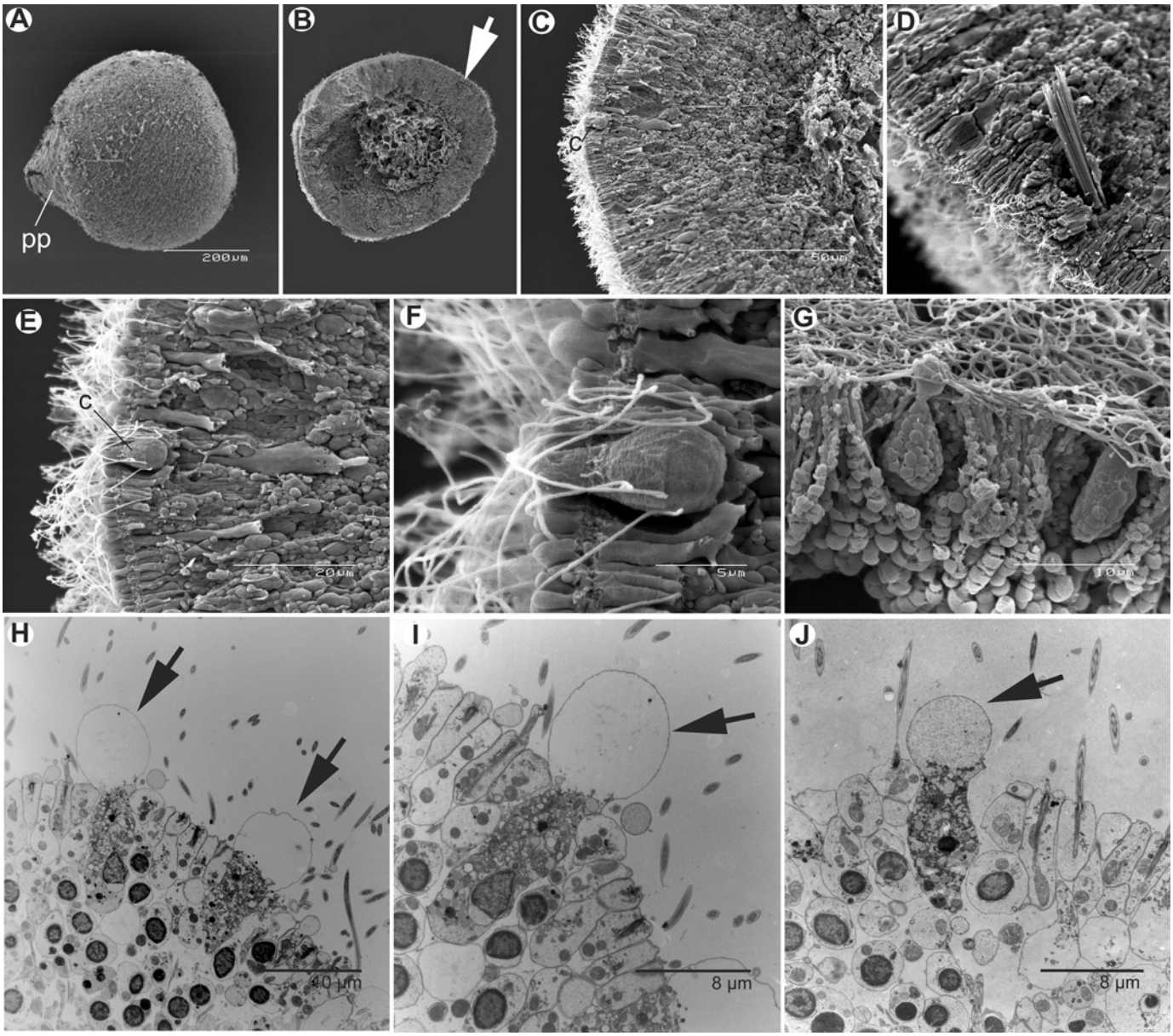
To reach the seafloor or the appropriate depth range along rocky walls for exploration, sponge larvae either swim downward or sink passively by changing their buoyancy. It is well known that downward swimming in many species is the result of either activation or intensification of a negative phototaxis. There is also the long-standing belief that newly released larvae disperse in the water column because of the activation of a negative geotactic behavior and that they return to the bottom for settlement because their geotactic response shifts to negative (e.g., Warburton 1966; Fry 1971; Sarà and Vacelet 1973; Fell 1989). However, claims that sponge larvae are able to express a geotactic response remain unconvincing, since these larvae have neither recognizable statocysts nor other putative sensors for detecting the direction of gravitational pull. On the other side, a geotaxis-like effect could be achieved by larvae having a low center of gravity and using the entire, rotating body as an orientation mechanism (see Young 1995). In many parenchymellae, such an unequal distribution of mass would result from spicule production being localized at the posterior pole of the larva (e.g., Bergquist and Sinclair 1973; Woollacott 1993; Maldonado and Bergquist 2002; Leys 2003). Interestingly, spicules do not always occur exclusively at the posterior pole of the parenchymella (Figs. 5*a*–5*d*).

Based on experimental and observational evidence, Maldonado et al. (1997) have shown that alternative mechanisms to a geotactic response may operate in some larvae to lead them towards the bottom for exploration and eventual settlement. Investigations on the tufted parenchymella of *H.* (*G.*) *caerulea* revealed that this larva leaves the plankton and starts swimming close to the bottom by combining a negative phototactic behavior with a decrease in buoyancy and motion power. In experimental conditions, newly released photonegative larvae swam directly away from a light source at higher speed than older larvae. However, they stopped swimming after only a relatively short distance from the light source, whereas older larvae swam until they attained a distance from the light source about 4 times that of newly released larvae. At such a distance, light intensity was estimated to be about two orders of magnitude lower than that required for cessation of swimming by newly released larvae. The fact that larvae stopped swimming after a certain distance away from the light source suggests that a minimal light intensity is required to trigger the photonegative behavior, indicating that the photoresponse is a complex combination of phototactic and photokinetic behaviors. Because the photokinetic response slows motion when the larva enters a zone with low light intensity, it is likely that it facilitates larval retention in dark microhabitats for settlement (Maldonado et al. 1997). Besides, these larvae increased their mass by secreting internal spicules near their posterior pole during their planktonic dispersal, which in turn involves the loss of power motion. Indeed, newly released larvae were measured to swim about twice as fast as older larvae. Towards the end of the planktonic periods, the increase in skeletal mass and the reduction of power motion are so important that the photonegative larvae will sink in the water column even if strong light is shone from below. Thus, depth regulation in the terminal stages appears to be largely a function of larval density rather than behavior (Maldonado et al. 1997). Production of larval spicules, most of which are extruded soon after larval attachment and not transferred to the juveniles (Maldonado and Young 1999), appears to play a relevant role in this task. Such a mechanism for depth regulation may be common in parenchymellae of many other demosponges. Larval spicules are not only relevant in regulating buoyancy because their production/dissolution modifies larval density, but also because they may be responsible for maintaining a particular larval shape. This is the case for the unciliated, radiolarian-like hoplitomella larva known from some tetractinellid sponges (Table 1). It bears a heavy skeleton of siliceous plate-like spicules in the periphery of its spherical body, which also serve as support for several long, protruding needle-like spicules (Fig. 1). These radiating spicules in turn provide internal skeletal support to several long and thin body protrusions emerging from the larval body. These projections increase larval drag, retarding the sinking of the larva. When settlement approaches, the hoplitomella, unlike the parenchymellae, starts allegedly dissolving and disassembling its siliceous skeleton. By doing this, the larva decreases its body mass, but also disorganizes the skeletal system that keeps the radiating protrusions in place. The loss of mass must be of little importance relative to the decreases in drag, since after loosing their plate-like and needle-like protruding spicules the larvae sink in the water column (Trégouboff 1942). Likewise, the adults of various sponge species of Demospongiae and Calcarea are known to reproduce asexually by releasing small pieces of somatic tissue, which by bearing long, thin protruding spicules are able to stay suspended in the water column for a long time, occasionally reaching off-shore locations (e.g., Trégouboff 1942).

Mechanisms of depth regulation in larvae lacking spicules remain unclear. These larvae may potentially combine tactic responses that stimulate downward swimming and negative kinetic responses that decelerate ciliary beating. Additionally, there are diverse processes for passive sinking, such as depletion of buoyant yolk (lipids), production of heavier storage materials (proteins), and decreasing of drag by changing body shape and disorganization of floatation structures. The parenchymella of freshwater demosponges may yet use another mechanism, since it possesses an internal cavity that is lined by pinacocytes. In the absence of detailed studies, the cavity is assumed to serve as an osmoregulatory organ, a floatation device, or both.

From some laboratory observations, it could be inferred that agitation of the seawater at the ocean surface induces larval sinking. Fry (1971) reported that larvae of *O. seriata*, which usually "rest" at the seawater–air interface in experimental containers, leave the interface when the water is agitated by a gentle jet of air. Furthermore, when a strong jet of air was applied for sometime, all larvae were soon found swimming close to the bottom of the containers. Nevertheless, the shift in larval depth distribution can also be explained by a passive mechanism rather than by a behavioral response. By applying a strong jet of air to the water surface for sometime, evaporation increases, resulting in a dramatically rapid increase in water salinity and density that causes the surface water to sink, which drags the sponge larvae to the bottom. Therefore, it remains unclear from Fry's

Fig. 5. (A) Scanning electron micrograph showing the parenchymella of *Mycale* sp., which is characterized by a large bare posterior pole (pp). (B) Longitudinal cryofracture of a *Mycale* larva. The white arrow indicates the region of interest in the anterior pole that is magnified in subsequent micrographs. (C, D, E) Detail of the anterior pole showing a complex epithelium that is reinforced by spicule bundles (D) and containing some flask-like, unciliated cells ("c" in C and E) that are interspersed among the columnar monociliated cells. (F) Details of an unciliated, flask-like cell in the anterior pole of the *Mycale* parenchyemella (from Maldonado 2004, reproduced with permission of Invertebr. Biol., vol. 123, p. 10, © 2004 Blackwell Publishing). (G) Detail of 2 flask-like, unciliated cells at the anterior pole of the parenchymella of *C. crambe*. Note that the distal region of these cells protrudes from the epithelium. (H–J) Transmission electron micrographs illustrating unciliated, flask-like cells interspersed among the monociliated cells of the anterior pole of the tufted parenchymella of *Haliclona* (*Gellius*) *caerulea*. The black arrows indicate the distal globe-like protrusion of these cells. Note that their cytoplasm, charged with abundant small vacuoles, is clearly distinguishable from that of the monociliated cells.



observations which are the relative contributions of behavior and of water density to the shift in the depth distribution of larvae.

Once larvae contact the seafloor, they initiate the exploratory phase. Water viscosity plays an important role in facilitating the behavioral exploration of the substratum. It is well-known that water movement attenuates around solid substrates, with flow speed becoming progressively slower with decreasing distance to the solid surfaces. This region of slower flow around immersed solids is known as the benthic boundary layer. In the innermost portion of this layer, termed the viscous sublayer, both flow speed and turbulence are at a minimum. The thickness of the viscous sublayer is strongly dependent on the water velocity in mid-water and substratum roughness. Sponge larvae entering the deepest regions of the boundary layer should have some chance to

maneuver, explore the substratum for settlement cues, and perform selective attachment at the microhabitat scale. Although there is no accurate observation on this critical step for sponge larvae, there are some studies for larvae of other marine benthic invertebrates. In a series of laboratory experiments, Butman (1986) predicted that polychaete larvae attempting to settle on a soft bottom dominated by tidal currents would be unable to explore the sea floor, requiring the ability to maneuver within a 100 μm thick viscous sublayer, during about 40% of the tidal cycle. This situation should not be very different from that experienced by sponge larvae during their exploratory phase. When parenchymellae of the four demosponge species were placed in small circular flumes and exposed to average current speeds (3 $cm \cdot s^{-1}$) that were much higher than their larval swimming speeds (0.1–0.35 $cm \cdot s^{-1}$), larvae initially demonstrated a positive rheotaxis by facing into the current. Nevertheless, they were unable to swim upstream and soon were dragged by the turbulent current, sometimes rolling on the bottom of the flumes. However, the boundary shear stress at this flow rate did not prevent larvae from attaching, since after 8 days under these conditions most larvae had successfully settled on the bottom and walls of the flumes (Maldonado and Young 1996). More importantly, most larvae had selectively settled in the shaded portion of the flumes, making effective use of their photonegative behavior despite the strong turbulent current.

Once larvae initiate the phase of substratum exploration prior to settlement, they may enter, leave, and re-enter the viscous sublayer repeatedly until they locate a site for settlement. The exploratory phase can be quite complex, depending on the species, and apparently comprises systematic and random displacements. During settlement of the barnacle *Semibalanus balanoides* (L., 1767), three subphases have been described, which may also apply to the exploratory behavior of many sponge larvae. Each subphase involves substrate exploration at a different spatial scale: (*i*) "broad exploration", at an estimated spatial scale of about 1 m; (*ii*) "close exploration", at a scale of about 1 mm; and (*iii*) "inspection", at a scale below 300 μm. When appropriate cues are present, larvae may shorten or even skip some of these phases.

There have been occasional reports that some parenchymellae swim or crawl temporarily without rotating when exploring the substrate prior to settlement (e.g., Bergquist et al. 1970; Mariani et al. 2005). Nevertheless, many published data, as well as a few unpublished observations by this author, indicate that parenchymellae rotate at any time during their exploratory phase and until the very last minute prior to attachment. During the inspection phase, the tufted parenchymella of many sponges is known to alternate short horizontal displacement with "inspection stops", during which the larva spins slowly with the anterior pole in contact with substrate, some times for hours. Such a behavior is strongly reminiscent of the spiral trajectories (Archimedes' spiral) described for desert isopods when searching for their protecting burrow (Hoffmann 1983), and it may be indicative of a systematic larval strategy for finding the most suitable spot for successful attachment at nearly microscopic scale. If so, the development of such a specialized behavior in organisms as primitive as sponge larvae would constitute a remarkable achievement.

Settlement and metamorphosis

Dispersal is followed by settlement, but this can theoretically occur only after larvae have attained a threshold of physiological and morphological maturities that render them "competent" for settlement. Attainment of competence has been observed to occur within minutes under field conditions (Lindquist et al. 1997); however, according to most laboratory observations, competence in most species is only attained after hours or days of dispersal. In most marine invertebrates, larvae remain competent for variable, but limited, periods of time during which some can delay settlement until an appropriate substratum is found. Larvae that remain unsettled after the competence period is over usually die. This may not be the case for many sponge larvae, since the high totipotent nature of their cells makes it possible for small fragments of the larval body and even cells that have experimentally disaggregated to attach unselectively to the bottom of the dishes to produce small juvenile sponges (e.g., Borojevic and Lévi 1965).

Much has been speculated about selective settlement of sponge larvae, but very little evidence is available. It has been long believed that a wide variety of environmental stimuli (light, gravity, chemical substances, substratum texture, etc.) may affect larval behavior and guide competent sponge larvae for selective settlement (see reviews by Fry 1971; Sarà and Vacelet 1973; Fell 1974). The role of light as a settlement cue is probably the most investigated. It is widely known that the amphiblastula of some calcareous sponges and the parenchymella of many demosponges react to light. It is believed that negative phototaxis guides the late-stage parenchymella of many species towards the bottom for settlement (e.g., Wilson 1935; Ali 1956; Bergquist and Sinclair 1968; Bergquist et al. 1970; Sarà and Vacelet 1973; Fell 1989; Woollacott 1990, 1993; Maldonado and Young 1996; Maldonado et al. 1997). The cytological mechanism by which larvae respond to light has partially been elucidated for tufted parenchymellae, which are extremely reactive to changes in light intensity and quality (Maldonado and Young 1996; Leys and Degnan 2001; Leys et al. 2002; Maldonado et al. 2003). Drastic changes in light intensity cause a predictable, instantaneous movement of cilia in the posterior tuft (Figs. 2*h*, 2*i*, 3), but do not affect the beating direction of the short cilia that cover the rest of the larval body. Therefore, the ability to detect light and to elicit a photoresponse appears to reside exclusively in the pigmented monociliated cells that form the posterior tuft. The cilium of these cells, which has an atypical 9 × 2 + 3 microtubule structure at their transition zone, a peculiar modular basal body, and a large branched ciliary rootlet (Maldonado et al. 2003), does not beat metachronally, but moves instantaneously in response to changes in light intensity. In larvae observed under a compound microscope and exposed to moderate levels of irradiance (100–180 $\mu mol \cdot L^{-1}$ of photons$\cdot m^{-2} \cdot s^{-1}$), the cilia of the tuft lay parallel to the longitudinal axis of the larva (Fig 4*a*). However, when light intensity is increased, the cilia of the tuft of photonegative larvae suddenly move approximately 45° clockwise (as viewed from the anterior pole), inclining themselves centripetally and causing the tuft to close in the form of a cone (Figs. 4*b*, 4*d*). If light intensity is experimentally decreased, the cilia move instantaneously

counterclockwise and incline themselves centrifugally to open and expand the tuft (Figs. 4*c*, 4*e*). Similar movement, but with an opposite sign, is seen in the photopositive larvae (Leys and Degnan 2001; Maldonado et al. 2003). The combination of individual cell responses, as well as the shading effect that pigmented cells exert on each other and, in turn, on their photoresponse, make the whole posterior tuft not only a photoreceptor organ but also the effecter exerting the change to the swimming trajectory by working as a light-sensitive rudder. Figure 4 illustrates how the individual, independent photoresponse of each pigmented cell in the tuft translates into a deviation of the larval trajectory with respect to light.

The mechanism by which some photonegative larvae that expand their tuft when exposed to high light intensity can turn away from the light remains unclear (Maldonado et al. 2003). It has been proposed that cilia in the illuminated side of the tuft would beat more rapidly, which would cause the larva to turn away from light (Leys and Degnan 2001). Nevertheless, it remains intriguing why two different reaction mechanisms should have been developed by photonegative larvae of close taxonomic groups. Observations on the tufted larva of *H. magniconulosa* revealed that cilia in the tuft of this sponge do not show planar beating, but instead show undulating beating (Maldonado and Young 1996). Therefore, it cannot be discarded that the above described mechanisms explaining the photoresponse of tufted parenchymellae in the orders Haplosclerida, Dictyoceratida, and Dendroceratida may not apply to tufted parenchymellae in the order Halichondrida (Table 1). Non-tufted larvae are usually less reactive to light than tufted larvae, but some of the former ones, such as the parenchyemella of *Mycale macilenta* (Bowerbank, 1866) (Bergquist et al. 1970) or the amphiblastula of *Scypha* Gray, 1821 (Elliott et al. 2004), also exhibit intense photonegative swimming reactions. Amphiblastula larvae posses four cross cells located by the larval equator, which have been suggested as participating in the photoresponse (see Maldonado and Bergquist 2002). Nevertheless, the cytological mechanisms involved in light sensing by non-tufted larvae remain little understood and largely not investigated.

To date, there has been a single attempt to investigate the spectral sensitivity of photoresponse in sponge larvae (Leys et al. 2002). The results indicate that the tufted parenchymella of *Reniera* Schmidt, 1862 responds most to blue light and orange–red light, suggesting that the photoreceptive pigment might be a flavin or a carotenoid, respectively. However, further investigations are required to corroborate such a suggestion, since the action spectrum detected could also be explained by either a combination of pigments or short-wavelength rhodopsins (Leys et al. 2002; Maldonado et al. 2003).

Irrespective of the mechanisms by which the phototactic response is effected, there is general agreement that light cues are used by some sponge larvae to identify suitable sites for settlement. Maldonado and Uriz (1998) have demonstrated that some parenchymellae that show weak phototactic responses in the laboratory settle preferentially in shaded microhabitats in the field. Such behavior allows them to find and settle in grooves and crevices, where the survival of the juveniles is enhanced because these microhabitats provide protection against unspecific grazers such as sea urchins and starfishes. Additionally, selective settlement in shaded microhabitats, such as grooves, crevices, pits, and downward facing surfaces, may provide additional protection for juvenile sponges against other major mortality factors such as visual predators, silt, UV radiation, and photoautotrophic spatial competitors.

Chemical compounds either dissolved in seawater or absorbed on surfaces are other cues commonly alleged to affect the behavior of sponge larvae at settlement. It is theoretically postulated that compounds produced by conspecifics, competitors, predators, bacterial films on substrates, etc., may somehow determine the spatial distribution of new sponge settlers relative to the sources of chemicals by either stimulating or inhibiting larval settlement, as is known for other invertebrate larva (e.g., Pawlik 1992; Maldonado and Young 2004). However, evidence for such a chemical regulation of settlement is scarce in the Porifera, and it remains unclear at which degree the spatial pattern of the sponge recruits results from selective settlement or from selective post-settlement mortality at unsuitable microhabitats. One of the few available examples indicating active selection at settlement is provided by the larva of *Pleraplysilla* Topsent, 1905, which apparently discriminates between biofilmed egg membranes, biofilmed valves of a bivalve, biofilmed glass, and clean polystyrene, with larvae attaching and metamorphosing preferentially on the former substrate (Woollacott and Hadfield 1996). Likewise, parenchymellae of the demosponge *Reniera* sp. are induced to settle in the presence of coral rubble and non-geniculate coralline algal substrata (Jackson et al. 2002), but again the point at which this substrate selection is chemically or texturally mediated remains unclear.

In contrast to the above reports, some authors have suggested that most sponge larvae are little specific regarding substrate preferences at settlement, as they are able to settle on a wide variety of natural and experimental surfaces (e.g., Bergquist and Sinclair 1968; Bergquist 1978). A remarkable case of non-specificity at settlement is provided by *Cliona celata* Grant, 1826, an obligate borer of calcareous substrates. When larvae of *C. celata* were experimentally offered clean glass and calcite crystal for settlement, surprisingly larvae settled on the glass as often as on the calcite (Warburton 1966). Nevertheless, a previous report by Hartman (1958) showed preferred settlement on oyster valves. These contradicting results basically reflect the difficulty in performing reliable experiments under laboratory conditions.

Regarding chemically mediated settlement induction, negative experimental reports appear to be more abundant than positive findings. Experiments investigating phylopatric settlement for larvae of the demosponge *Scopalina lophyropoda* Schmidt, 1862, in which groups of 10 larvae were placed in petri dishes, each containing either a small inert solid (control), a sponge explant clonal to their mother, an explant of other conspecifics from the local population, or an explant of a direct spatial competitor (the demosponge *C. crambe*), revealed no detectable effect on settlement in terms of time and spatial patterns (M. Maldonado, unpublished data). Similarly, no effect in preventing or stimulating settlement relative to controls was observed when larvae were placed in petri dishes filled with seawater conditioned for 24 h by tissue from their mother, other conspecifics, or

the spatial competitor, which theoretically might have released waterborne compounds eliciting some behavioral response in the larvae (M. Maldonado, unpublished data).

The role of waterborne compounds on sponge settlement is even less understood than that of surface-bounded compounds. From a theoretical point of view, sponge larvae are unlikely to follow large plumes of dissolved chemicals in open waters, where compound concentration experiences non-linear, eddy diffusion. To follow such "odor" plumes, a chemically oriented organism should exhibit rapid sampling rates of chemical gradients by specialized sensory organs, as well as enhanced swimming abilities. The current knowledge of larval histology (e.g., Maldonado and Bergquist 2002) suggests that sponge larvae do not meet such requirements. Nevertheless, waterborne chemical cues are more likely to be exploited by these larvae if encountered within the deepest region of the boundary layers. In the viscous sublayer, turbulent energy is low and chemical compounds experience molecular diffusion rather than eddy diffusion. As a consequence, dissolved cues remain at high concentrations longer than when advected to the water column, providing higher chances of being tracked by organisms that sample chemical gradients at low rates and move at low *Re* values.

Larvae of *Pleraplysilla* have been demonstrated to respond to dissolved chemical cues (Woollacott and Hadfield 1996). Elevated concentrations of CsCl and KCl in seawater promoted attachment and metamorphosis of these larvae in the laboratory, but the former inducer was effective only when applied simultaneously with biofilmed egg membranes as substratum. A variety of hypotheses have been proposed to explain the induction effect, including the action of K^+ and Cs^+ on putative sensory receptor cells. A major problem in really understanding the control mechanisms behind the induction process is that no chemical receptors have been identified in sponge larvae at the cellular or the molecular level to date. Nevertheless, there are a few reports that parenchymellae appear to examine the substrates to be settled for chemical and (or) textural features by extruding their anterior end (Figs. 2*h*, 2*j*) and by repeatedly contacting the surfaces during the exploration phase (e.g., Wapstra and Soest 1987; Woollacott 1990; Maldonado and Young 1996). To date, there is no compelling evidence to support a sensory structure at the anterior pole of the larvae, although distinct cells of unclear function have been found. In the parenchymella of *Reniera* sp., the monociliated cells protrude at the anterior pole and have been suggested to be receptors for an undetermined environmental cue, because these cells have their distal portion charged with electron-clear vesicles and their cilium inserted in a very deep invagination (Jackson et al. 2002). Nevertheless, because the suggested link between anatomy and function is weak, further investigations are desirable to corroborate such a proposal. A neuroactive substance, such as serotonin, has been detected in the parenchymella of *T. ignis*, but the immunoassays demonstrated that the compound is located in the internal archeocyte-like cells rather than in the ciliated epithelial cells (Weyrer et al. 1999). Globular monociliated cells abundantly charged with small vesicles also occur interspersed among the columnar monociliated cells in several parenchymellae, reaching greater density at the anterior larval pole (e.g., Woollacott 1993). Likewise, similar globular cells charged with vesicles but lacking the cilium have been reported scattered among the larval ciliated cells of the putative clavablastula of *Axinella* Schmidt, 1862 (Maas, 1893), the cinctoblastula of *Oscarella* Vosmaer, 1884 (Lévi and Porte 1962), and several tufted and non-tufted parenchymellae (Meewis 1939, 1941; Boury-Esnault 1976). Interestingly, the late-stage parenchymella of many demosponges has been reported to loose all or part of their cilia at the anterior pole (see Wapstra and Soest 1987), which may become slightly depressed in some cases, such as in the larva of *Aplysilla rosea* (Barrois, 1876) (Bergquist 1978). During the free-swimming phase of the parenchymellae of *Mycale contarenii* (Martens, 1824), unciliated globose cells charged with abundant vesicles appear to migrate from subepithelial regions and enter the ciliated epithelium (Lévi 1964). Such cell migration may explain why ciliation becomes less dense or is entirely lost at the anterior pole prior to settlement. Herewithin, I report on a variety of unciliated, globular, and flask-like cells interspersed among the typical columnar monociliated cells of the anterior larval pole in the non-tufted parenchymellae of *Mycale* sp. and *C. crambe*, as well as in the tufted parenchymellae of *H.* (*G.*) *caerulea* (Fig. 5). These cells, usually charged with abundant mid-sized electron-dense inclusions, may protrude substantially from the epithelium (Figs. 5*h*–5*j*). Nevertheless, it remains unclear whether such cellular differentiation at the anterior pole of late-stage larvae is related to the formation of either a sensory system for selective settlement or a secretion system for larval attachment. Immediately before attachment, many parenchymellae secrete some putative adhering compounds (presumably collagen and (or) basal spongin) at the anterior pole, which is in contact with the substrate while the larvae spin slowly. Alternatively, larvae of some species, mostly demosponges in the order Halichondriida, are known to rest on the anterior–lateral region immediately prior to attachment, which may explain why these vesicular globular cells are also found in lateral regions in some larvae.

Sibling and non-sibling sexually derived sponge larvae of many species are known to fuse at settlement and, occasionally, while swimming at high densities under laboratory conditions (e.g., Wilson 1907; Warburton 1958; Ilan and Loya 1990; Maldonado 1998). There is no evidence that larval encounters are mediated by chemical cues, and preliminary tests with larvae of *Scopalina* Schmidt, 1862 and *Crambe* have been negative in this regard (M. Maldonado, unpublished data). Indeed, spontaneous aggregation of larvae that form chimerae in the laboratory has only been reported for an undescribed species of *Chalinula* Schmidt, 1868 from the Red Sea (Ilan and Loya 1990), and it is not expected to be a widespread process among sponges under field conditions. Disregarding a speculative report by Burton (1929), the available data suggest that fusion of swimming larvae in natural conditions may occur only in exceptional circumstances, such as at hatching in *C. celata* (Warburton 1958). In this species, larval fusion occurs when hatched larvae cannot leave the strand of mucus and debris that surrounds the externally developing embryos so that swimming larvae are retained at high density within small spaces between the egg capsules.

Irrespective of the mechanisms that make larval fusion possible, it is remarkable that juvenile sponges derived from

fused larvae are chimeric (i.e., contain cells of different genotypes) and are also initially larger than one-larva-derived juveniles. A large initial size favors rapid post-metamorphic growth and may also enhance survival of new recruits, because the young sponges may soon reach a size that makes them less vulnerable to grazing and other physical disturbances (Reiswig 1973; Ayling 1980; Fell 1993). In addition, chimeric juveniles have greater genetic variability than genetically homogeneous individuals, which should theoretically translate into higher adaptive potential and wider ranges of physiological resistance. However, in the only sponge (i.e., demosponge *T. ignis*) in which the ecological performance of chimeric individuals resulting from fused larvae has been investigated, chimeric sponges did not show increased survival under field conditions, despite the fact that they were about twice as large as non-chimeric individuals (Maldonado 1998). Therefore, the ecological and evolutionary significances of the ability of sponge larvae to fuse remain little understood.

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References

Ali, M.A. 1956. Development of the monaxonid sponge *Lissodendoryx similis* (Thiele). J. Madras Univ. **26**: 553–581.

Amano, S. 1986. Larval release in response to a light signal by the intertidal sponge *Halichondria panicea*. Biol. Bull. (Woods Hole), **171**: 371–378.

Amano, S. 1988. Morning release of larvae controlled by the light in a intertidal sponge, *Callyspongia ramosa*. Biol. Bull. (Woods Hole), **175**: 181–184.

Ayling, A.L. 1980. Patterns of sexuality, asexual reproduction and recruitment in some subtidal marine Demospongiae. Biol. Bull. (Woods Hole), **158**: 271–282.

Bartumeus, F., Peters, F., Pueyo, S., Marrasé, C., and Catalan, J. 2003. Helical Lévy walks: adjusting searching statistics to resource availability in microzooplankton. Proc. Natl. Acad. Sci. U.S.A. **100**(22): 12771–12775.

Bergquist, P.R. 1978. Sponges. University of California Press, Berkeley.

Bergquist, P.R., and Green, C.R. 1977. An ultrastructural study of settlement and metamorphosis in sponge larvae. Cah. Biol. Mar. **18**: 289–302.

Bergquist, P.R., and Sinclair, M.E. 1968. The morphology and behaviour of larvae of some intertidal sponges. N.Z. J. Mar. Freshw. Res. **2**: 426–437.

Bergquist, P.R., and Sinclair, M.E. 1973. Seasonal variation in settlement and spiculation of sponge larvae. Mar. Biol. (Berl.), **20**(1): 35–44.

Bergquist, P.R., Sinclair, M.E., and Hogg, J.J. 1970. Adaptation to intertidal existence: reproductive cycles and larval behaviour in Demospongiae. Symp. Zool. Soc. Lond. **25**: 247–271.

Borchiellini, C., Alivon, E., and Vacelet, J. 2004. The systematic position of *Alectona* (Porifera, Demospongiae): a tetractinellid sponge. Boll. Mus. Ist. Biol. Univ. Genova, **68**: 209–217.

Borojevic, R. 1967. La ponte et le développement de *Polymastia robusta*. Cah. Biol. Mar. **14**: 130–151.

Borojevic, R., and Lévi, C. 1965. Morphogenèse expérimentale d'une Eponge à partir de cellules de la larve nageante dissociée. Z. Zellforsch. **68**: 57–69.

Boury-Esnault, N. 1976. Ultrastructure de la larve parenchymella d'*Hamigera hamigera* (Schmidt) (Démosponge, Poecilosclerida). Origine des cellules grises. Cah. Biol. Mar. **17**: 9–20.

Boury-Esnault, N., and Vacelet, J. 1994. Preliminary studies on the organization and development of hexactinellid sponge from a Mediterranean cave, *Oopsacas minuta*. *In* Sponges in time and space. *Edited by* R.W.M. van Soest, T.M.G. van Kempen, and J.C. Braekman. A.A. Balkema, Rotterdam, the Netherlands. pp. 407–415.

Boury-Esnault, N., Efremova, S., Bézac, C., and Vacelet, J. 1999. Reproduction of a hexactinellid sponge: first description of gastrulation by cellular delamination in the Porifera. Invertebr. Reprod. Dev. **35**: 187–201.

Burton, M. 1929. Observations on post-larval development in the sponge *Iophon hyndmani* (Bowerbank). Ann. Mag. Nat. Hist. (3) **10**: 196–201.

Butman, C.A. 1986. Larval settlement of soft-sediments invertebrates: some predictions based on an analysis of near-bottom velocity profiles. *In* Marine interfaces ecohydrodynamics. *Edited by* J.C.J. Nihoul. Elsevier, New York. pp. 487–513.

Davidson, E.H., Peterson, K.J., and Cameron, R.A. 1995. Origin of bilaterian body plans: evolution of developmental regulatory mechanisms. Science (Washington, D.C.), **270**: 1319–1325.

Elliott, G.R.D., Macdonald, T.A., and Leys, S.P. 2004. Sponge larval phototaxis: a comparative study. Boll. Mus. Ist. Biol. Univ. Genova, **68**: 291–300.

Fell, P.E. 1974. Porifera. *In* Acoelomate and pseudocoelomate metazoans. *Edited by* A.C. Giese and J.S. Pearse. Academic Press, New York and London. pp. 51–132.

Fell, P.E. 1983. Porifera. *In* Reproductive biology of invertebrates. *Edited by* K.G. Adiyodi and R.G. Adiyodi. John Wiley and Sons Ltd., Chichester, UK. pp. 1–29.

Fell, P.E. 1989. Porifera. *In* Reproductive biology of invertebrates. Vol. IV. Part A. Fertilization, development and parental care. *Edited by* K.G. Adiyodi and R.G. Adiyodi. John Wiley and Sons, New York. pp. 1–41.

Fell, P.E. 1993. Porifera. *In* Reproductive biology of invertebrates. Vol. VI. Asexual propagation and reproductive strategies. *Edited by* K.G. Adiyodi and R.G. Adiyodi. Oxford and IBH Publ. Co., New Delhi. pp. 1–44.

Fromont, J. 1994. The reproductive biology of tropical species of Haplosclerida and Petrosiida on the Great Barrier Reef. *In* Sponges in time and space. *Edited by* R.W.M. van Soest, T.M.G. van Kempen, and J.C. Braekman. A.A. Balkema, Rotterdam, the Netherlands. pp. 307–311.

Fromont, J., and Bergquist, P.R. 1994. Reproductive biology of three sponge species of the genus *Xetospongia* (Porifera: Demospongiae: Petrosiida) from the Great Barrier Reef. Coral Reefs, **13**: 119–126.

Fry, W.G. 1971. The biology of larvae of *Ophlitaspongia seriata* from two Nord Wales populations. *In* Proceedings of 4th European Marine Biology Symposium, Bangor, North Wales, UK, 14–20 September 1969. *Edited by* D.J. Crisp. Cambridge University Press, Cambridge. pp. 155–178.

Gonobobleva, E.L., and Ereskovsky, A.V. 2004. Polymorphism in free-swimming larvae of *Halisarca dujardini* (Demospongiae, Halisarcida). Boll. Mus. Ist. Biol. Univ. Genova, **68**: 349–356.

Haeckel, E. 1874. Die Gastraea-Theorie, die phylogenetische Classification des Thierreichs nud die Homologie der Keimblätter. Z. Natwiss. **8**: 1–55.

Hartman, W.D. 1958. Natural history of the marine sponges of southern New England. Peabody Mus. Nat. Hist. Bull. **12**: 1–155.

Hoffmann, G. 1983. The search behavior of the desert isopod *Hemilepistus reaumuri* as compared with a systematic search. Behav. Ecol. Sociobiol. **13**: 93–106.

Hoppe, W.F., and Reichert, M.J.M. 1987. Predictable annual mass release of gametes by the coral reef sponge *Neofibularia nolitangere* (Porifera: Demospongiae). Mar. Biol. (Berl.), **94**: 277–285.

Ilan, M., and Loya, Y. 1990. Sexual reproduction and settlement of the coral reef sponge *Chalinula* sp. from the Red Sea. Mar. Biol. (Berl.), **105**: 25–31.

Ivanova, L.V. 1999. New data about morphology and feeding patterns of Barentz Sea *Halichondria panicea* Pallas. Mem. Queensl. Mus. **44**: 262.

Jackson, D., Leys, S.P., Hinman, V.F., Woods, R., LAvin, M.F., and Degnan, B.M. 2002. Ecological regulation of development: induction of marine invertebrate metamorphosis. Int. J. Dev. Biol. **46**: 679–686.

Jaeckle, W.B. 1995. Transport and metabolism of alanine and palmitic acid by field-collected larvae of *Tedania ignis* (Porifera, Demospongiae): estimated consequences of limited label translocation. Biol. Bull. (Woods Hole), **189**: 159–167.

Jägersten, G. 1972. Evolution of the metazoan life cycle: a comprehensive theory. Academic Press, London.

Kaye, H.R., and Reiswig, H.M. 1991. Sexual reproduction in four Caribbean commercial sponges. III. Larval behaviour, settlement and metamorphosis. Invertebr. Reprod. Dev. **19**: 25–35.

Koolwijk, T., van. 1982. Calcareous sponges of the Netherlands (Porifera, Calcarea). Bull. Zool. Mus. Univ. Amst. **8**(12): 89–98.

Lévi, C. 1951. L'Oviparité chez les Spongiaires. C. R. Acad. Sci. Paris, **233**: 272–275.

Lévi, C. 1956. Étude des *Halisarca* de Roscoff. Embryologie et systématique des Demosponges. Arch. Zool. Exp. Gen. **93**: 1–181.

Lévi, C. 1957. Ontogeny and systematics in sponges. Syst. Zool. **6**(4): 174–183.

Lévi, C. 1964. Ultrastructure de la larve parenchymella de Démosponge. I. *Mycale contarenii* (Martens). Cah. Biol. Mar. **5**: 97–104.

Lévi, C. 1973. Systématique de la classe des *Demospongiaria* (Démosponges). *In* Spongiaires. Anatomie, physiologie, systématique, ecologie. *Edited by* P.P. Grassé. Masson et C^{ie}, Paris. pp. 577–631.

Lévi, C., and Lévi, P. 1976. Embryogénese de *Chondrosia reniformis* (Nardo), démosponge ovipare, et transmission des bactéries symbiotiques. Ann. Sci. Nat. Zool. **18**: 367–380.

Lévi, C., and Porte, A. 1962. Étude au microscope électronique de l'éponge *Oscarella lobularis* Schmidt et de sa larve amphiblastula. Cah. Biol. Mar. **3**: 307–315.

Leys, S.P. 2003. Comparative study of spiculogensis in demosponge and hexactinellid larvae. Microsc. Res. Tech. **63**: 300–311.

Leys, S.P., and Degnan, B.M. 2001. Cytological basis of photoresponsive behavior in a sponge larva. Biol. Bull. (Woods Hole), **201**: 323–338.

Leys, S.P., and Eerkes-Medrano, D.I. 2005. Gastrulation in calcareous sponges: In search of Haeckel's Gastraea. Integr. Comp. Biol. **45**: 342–351.

Leys, S.P., Cronin, T.W., Degnan, B.M., and Marshall, J.N. 2002. Spectral sensitivity in a sponge larva. J. Comp. Physiol. A, **188**: 199–202.

Leys, S.P., Cheung, E., and Boury-Esnault, N. 2006. Embryogenesis in the glass sponge *Oopsacas minuta*: formation of syncytia by fusion of blastomeres. Integr. Comp. Biol. **46**(1). In press.

Lindquist, N., and Hay, M.E. 1996. Palatability and chemical defense of marine invertebrate larvae. Ecol. Monogr. **66**(4): 431–450.

Lindquist, N., Bolser, R., and Laing, K. 1997. Timing of larval release by two Caribbean demosponges. Mar. Ecol. Prog. Ser. **155**: 309–313.

Maas, O. 1893. Die Embryonal-Entwicklung und metamorphose der Cornacuspongien. Zool. Jahrb. **7**(2): 331–448.

Maldonado, M. 1998. Do chimeric sponges have improved chances of survival? Mar. Ecol. Prog. Ser. **164**: 301–306.

Maldonado, M. 2004. Choanoflagellates, choanocytes, and animal multicellularity. Invertebr. Biol. **123**: 1–22.

Maldonado, M., and Bergquist, P.R. 2002. Phylum Porifera. *In* Atlas of marine invertebrate larvae. *Edited by* C.M. Young, M.A. Sewell, and M.E. Rice. Academic Press, San Diego. pp. 21–50.

Maldonado, M., and Uriz, M.-J. 1998. Microrefuge exploitation by subtidal encrusting sponges: patterns of settlement and post-settlement survival. Mar. Ecol. Prog. Ser. **174**: 141–150.

Maldonado, M., and Uriz, M.-J. 1999. Sexual propagation by sponge fragments. Nature (London), **398**: 476.

Maldonado, M., and Young, C.M. 1996. Effects of physical factors on larval behavior, settlement and recruitment of four tropical demosponges. Mar. Ecol. Prog. Ser. **138**: 169–180.

Maldonado, M., and Young, C.M. 1999. Effects of the duration of the larval life on post-larval stages of the demosponge *Sigmadocia caerulea*. J. Exp. Mar. Biol. Ecol. **232**(1): 9–21.

Maldonado, M., and Young, C.M. 2004. Induction of settlement in merozooplankton. *In* Marine ecology. *Edited by* C.M. Duarte. UNESCO/EOLSS Publishers, Oxford. Available from http://www.eolss.net.

Maldonado, M., George, S.B., Young, C.M., and Vaquerizo, I. 1997. Depth regulation in parenchymella larvae of a demosponge: relative roles of skeletogenesis, biochemical changes and behavior. Mar. Ecol. Prog. Ser. **148**: 115–124.

Maldonado, M., Durfort, M., McCarthy, D., and Young, C.M. 2003. The cellular basis of photobehavior in the tufted parenchymella larva of demosponges. Mar. Biol. (Berl.), **143**: 427–441.

Maldonado, M., Carmona, M.C., Velásquez, Z., Puig, M.A., Cruzado, A., López, A., and Young, C.M. 2005. Siliceous sponges as a silicon sink: an overlooked aspect of benthopelagic coupling in the marine silicon cycle. Limnol. Oceanogr. **50**(3): 799–809.

Mariani, S., Piscitelli, M.P., and Uriz, M.-J. 2001. Temporal and spatial co-occurrence in spawning and larval release of *Cliona viridis* (Porifera: Hadromerida). J. Mar. Biol. Assoc. U.K. **81**: 565–567.

Mariani, S., Uriz, M.-J., and Turon, X. 2005. The dynamics of sponge larvae assemblages from northwestern Mediterranean nearshore bottoms. J. Plankton Res. **27**: 249–262.

Meewis, H. 1939. Contribution à l'étude de l'embryogenèse des Chalinidae: *Haliclona limbata* (Mont.). Ann. Soc. R. Zool. Belg. **70**: 201–244.

Meewis, H. 1941. Contribution à l'étude de l'embryogenèse des eponges siliceuses. Dévelopement de l'oeuf chez *Adocia cinerea* (Grant) et *Halichondria coalita* (Bowerbank). Ann. Soc. R. Zool. Belg. **72**(2): 126–149.

Meroz, E., and Ilan, M. 1995. Life history characteristics of a coral reef sponge. Mar. Biol. (Berl.), **124**: 443–451.

Morgan, S.G. 1995. The timing of larval release. *In* Ecology of marine invertebrate larvae. *Edited by* L. McEdward. CRC Press, Boca Raton, Fla. pp. 157–192.

Nielsen, C. 1995. Animal evolution. Interrelationships of the living phyla. Oxford University Press, Oxford.

Pawlik, J.R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr. Mar. Biol. Annu. Rev. **30**: 273–335.

Pernet, B. 2003. Persistent ancestral feeding structures in non-feeding annelid larvae. Biol. Bull. (Woods Hole), **205**: 295–307.

Purcell, E.M. 1977. Life at low Reynolds number. Am. J. Phys. **45**: 3–11.

Reiswig, H.M. 1970. Porifera: sudden sperm release by tropical Demospongiae. Science (Washington, D.C.), **170**: 538–539.

Reiswig, H.M. 1973. Population dynamics of three Jamaican Demospongiae. Bull. Mar. Sci. **23**: 191–226.

Reiswig, H.M. 1983. Porifera. *In* Reproductive biology of invertebrates. Spermatogenesis and sperm function. *Edited by* K.G. Adiyodi and R.G. Adiyodi. John Wiley, Chichester, UK. pp. 1–21.

Rieger, R.M. 1994. The biphasic life cycle. A central theme of metazoan evolution. Am. Zool. **34**: 484–491.

Roughgarden, J., Gaines, S., and Possingham, H. 1988. Recruitment dynamics in complex life cycles. Science (Washington, D.C), **241**: 1460–1466.

Rumrill, S.S. 1990. Natural mortality of marine invertebrate larvae. Ophelia, **32**(1–2): 163–198.

Salvini-Plawen, L. 1978. On the origin and evolution of the lower Metazoa. Z. Zool. Syst. Evolutionsforsch. **16**: 40–88.

Sarà, M., and Vacelet, J. 1973. Ecologie des Démosponges. *In* Spongiaires. Anatomie, physiologie, systématique, ecologie. *Edited by* P.P. Grassé. Masson et C^{ie}, Paris. pp. 462–576.

Sivaramakrishnan, V.R. 1951. Studies on early development and regeneration in some Indian sponges. Proc. Indian Acad. Sci. Sect. B, **34**: 213–310.

Storr, J.F. 1964. Ecology of the Gulf of Mexico commercial sponges and its relation to the fishery. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. **466**: 1–73.

Strathmann, R.R. 1978. The evolution and loss of larval feeding stages of marine invertebrates. Evolution, **32**: 894–906.

Trégouboff, G. 1939. Sur les larves planctoniques d'éponges. C. R. Acad. Sci. Paris, **208**: 1245–1246.

Trégouboff, G. 1942. Contribution à la connaissance des larves planctoniques d'éponges. Arch. Zool. Exp. Gen. **82**: 357–399.

Trégouboff, G., and Rose, M. 1957. Manuel de planctonologie méditerranéenne. C.N.R.S., Paris.

Uriz, M.-J., Turón, X., Becerro, M.A., and Galera, J. 1996. Feeding deterrence in sponges. The role of toxicity, physical defenes, energetic contents, and life-history stage. J. Exp. Mar. Biol. Ecol. **205**: 187–204.

Uriz, M.-J., Maldonado, M., Turon, X., and Martí, R. 1998. How do reproductive output, larval behaviour, and recruitment contribute to adult spatial patterns in Mediterranean encrusting sponges? Mar. Ecol. Prog. Ser. **167**: 137–148.

Uriz, M.-J., Turon, X., and Becerro, M.A. 2001. Morphology and ultrastructure of the swimming larvae of *Crambe crambe* (Demospongiae, Poecilosclerida). Invertebr. Biol. **120**: 295–307.

Vacelet, J. 1999. Planktonic armoured propagules of the excavating sponge *Alectona* (Porifera: Demospongiae) are larvae: evidence from *Alectona wallichii* and *A. mesatlantica* sp. nov. Mem. Queensl. Mus. **44**: 627–642.

Vivien, M.L. 1973. Contribution à la connaissance de l'éthologie alimentaire de l'ichthyofaune du platier interne des récifs coralliens de Tuléar (Madagascar). Tethys, Suppl. **5**: 221–308.

Vogel, S. 1994. Life in moving fluids. The physical biology of flow. Princeton University Press, Princeton, N.J.

Wapstra, M., and Soest, R.W.M., van. 1987. Sexual reproduction, larval morphology and behaviour in demosponges from the southwest of the Netherlands. *In* Taxonomy of Porifera. *Edited by* J. Vacelet and N. Boury-Esnault. Springer-Verlag, Berlin. pp. 281–307.

Warburton, F.E. 1958. Reproduction of fused larvae in the boring sponges *Cliona celata*. Nature (London), **181**: 493–494.

Warburton, F.E. 1966. The behavior of sponge larvae. Ecology, **47**(4): 672–674.

Watanabe, Y. 1978. The development of two species of *Tetilla* (Demosponge). Nat. Sci. Rep. Ochanomizu Univ. **29**(1): 71–106.

Weyrer, S., Rützler, K., and Rieger, R. 1999. Serotonin in Porifera? Evidence from developing *Tedania ignis*, the Caribbean fire sponge (Demospongiae). Mem. Queensl. Mus. **44**: 659–665.

Wilson, H. van P. 1907. On some phenomena of coalescence and regeneration in sponges. J. Exp. Zool. **5**(2): 245–258.

Wilson, H.V. 1935. Some critical points in the metamorphosis of the halichondrine sponge larva. J. Morphol. **58**(2): 285–353.

Witte, U. 1996. Seasonal reproduction in the deep-sea sponges triggered by vertical particle flux? Mar. Biol. (Berl.), **124**(2): 571–581.

Woollacott, R. 1990. Structure and swimming behavior of the larva of *Halichondria melanodocia* (Porifera: Demospongiae). J. Morphol. **205**: 135–145.

Woollacott, R.M. 1993. Structure and swimming behavior of the larva of *Haliclona tubifera* (Porifera: Demospongiae). J. Morphol. **218**: 301–321.

Woollacott, R.M., and Hadfield, M.G. 1996. Induction of metamorphosis in larvae of a sponge. Invertebr. Biol. **115**: 257–262.

Young, C.M. 1995. Behavior and locomotion during the dispersal phase of larval life. *In* Ecology of marine invertebrate larvae. *Edited by* L. McEdward. CRC Press, Boca Raton, Fla. pp. 249–277.

Young, C.M., and Chia, F.-S. 1987. Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrographic factors. *In* Reproduction of marine invertebrates. *Edited by* C. Giese, J.S. Pearse, and V.B. Pearse. Blackwell Scientific, Palo Alto, Calif. pp. 385–463.

Zea, S. 1993. Recruitment of demosponges (Porifera, Demospongiae) in rocky and coral-reef habitats of Santa Marta, Colombian Caribbean. Mar. Ecol. **14**: 1–21.