Sexual reproductive cycle of the epibiotic soft coral *Alcyonium coralloides* (Octocorallia, Alcyonacea)

Elena Quintanilla[1],*, Josep-Maria Gili[1], Pablo J. López-González[2], Georgios Tsounis[1,4], Teresa Madurell[1], Ida Fiorillo[1], Sergio Rossi[3]

[1]Institut de Ciències del Mar, ICM-CMIMA (CSIC), 08003 Barcelona, Spain
[2]Departamento de Zoología, Facultad de Biología, Universidad de Sevilla, 41012 Sevilla, Spain
[3]Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallés, Spain

[4]*Present address:* Department of Ecology, Leibniz Center for Tropical Marine Ecology, 28359 Bremen, Germany

ABSTRACT: *Alcyonium coralloides* is an epibiotic soft coral overgrowing living colonies of Mediterranean gorgonians. The main features of the sexual reproductive cycle of this soft coral species are described and quantified for the first time, in a population found at 18 to 22 m depth off the Medes Islands (NW Mediterranean). *A. coralloides* is a gonochoric internal brooder. The sexual cycle showed a single reproductive event per year. Gametogenesis took 5 to 6 mo, which is the shortest known gametogenesis in littoral octocorals (especially for oogenesis). The maximum mean ± SD diameter was 365 ± 86 µm for spermatic cysts and 632 ± 125 µm for mature oocytes. Sperm was released in spring (late May). Average male and female fecundity in this last phase of the cycle was 15 ± 9 spermatic cysts and 7 ± 4 oocytes per polyp, respectively. Larvae of about 1000 µm in length were observed in the gastrovascular cavities of female colonies in May, before they were released in June. We suggest that the remarkable short gametogenesis and timing shown by *A. coralloides* is an adaptation to optimize the colonization of its host (in this case the gorgonian octocoral *Paramuricea clavata*). We conclude that *A. coralloides* larvae could be ready to settle in early summer when the host *P. clavata* is probably more vulnerable as a result of its own reproductive cycle coming to an end.

KEY WORDS: *Alcyonium coralloides* · *Paramuricea clavata* · Epibiosis · Reproductive effort · Soft corals · Reproductive coupling · Gametogenesis

INTRODUCTION

Competition for substrate space is a key factor determining the survival of benthic species such as octocorals (Connell 1961, Pequegnat 1964, Paine 1974, Jackson 1977). Due to this dependence on the colonization of stable substrates (Gili & Coma 1998), octocorals have developed mechanisms and strategies allowing them to successfully compete for the available substrate (Jackson 1977). Epibiosis is a biological relationship consisting of a non-parasitic organism spending at least 1 phase of its life cycle growing on a larger organism (Wahl 1989). This strategy is adopted by many species in highly structured and diversified benthic communities where competition for space is vital, as in Mediterranean coralligenous formations (Ros et al. 1985, Witman & Dayton 2001).

Coralligenous formations are produced mainly by the accumulation of encrusting calcareous or coralline algae (Fredj & Laubier 1985, Ballesteros 2006). Octocoral species such as *Paramuricea clavata* (Risso, 1826), *Eunicella cavolinii* (Kock, 1887), *E. singularis* (Esper, 1791), *E. verrucosa* (Pallas, 1766) and *Corallium rubrum* (Linnaeus, 1758) and soft coral genera such as *Alcyonium* are important architectural com-

ponents of the coralligenous assemblages, increasing their biodiversity and complexity (Gili & Ros 1984, Wendt et al. 1985, Sebens 1991, Tsounis et al. 2006). These organisms are highly vulnerable to environmental perturbations because their slow growth rates, low recruitment, sessile life form and exposed structural colonial forms imply slow recovery rates (Coma et al. 2004). Disturbances of anthropogenic origin include injuries due to contact with fishing lines, anchors or SCUBA divers that may result in decreased fecundity and increase opportunities for colonization by epibionts (Bavestrello et al. 1997, Tsounis et al. 2012). Furthermore, partial mortalities due to persistent heat waves may be an advantage for new settlers in the denuded skeletons (Cerrano et al. 2000).

The octocoral (Cnidaria, Anthozoa) *Alcyonium coralloides* (Pallas, 1766) is an epibiont species that grows by fouling ('runner' type) the apical axis of (most likely injured) colonies of gorgonians such as *Paramuricea clavata, Eunicella singularis, E. cavolinii, E. verrucosa* and *Leptogorgia sarmentosa* (Esper, 1789) (McFadden 1999, McFadden et al. 2001). The 'runner' type morphology consists of building encrusting tissue networks that show low physical resistance and a large area of tissue to the organism that horizontally colonizes a surface (Jackson 1979). The soft coral indirectly adopts a 3-dimensional morphology by exploiting the arboreal morphology of the gorgonian host species. The water flow is greater with increasing distance from the substrate (Butman 1987). Thus, having a 3-dimensional morphology and a distal position on the branches of gorgonians can be a trophic advantage for the epibiont. Exposure to higher water flow enhances both passive suspension feeding and evacuation of metabolic waste of colonies (Boero 1987, Wahl 1989). Thus, an epibiotic habit provides this soft coral with a favourable hydrodynamic position that confers greater volumetric water flow and more efficient suspension feeding (Best 1988).

The reproductive pattern is the main feature describing the life strategy of a species. For the first time, we describe the main quantitative parameters of the sexual reproductive cycle of *Alcyonium coralloides* and compare them to those of other littoral octocoral species. The genus *Alcyonium* presents a wide diversity of patterns in the mode of reproduction and sexuality (McFadden et al. 2001, Kahng et al. 2011). However, little is known about the sexual reproduction of these anthozoans, which play an essential role in benthic communities (Gili & Coma 1998, Fautin 2002). We also investigated the implications of the epibiotic lifestyle of *A. coralloides* on its

reproductive pattern. We hypothesized that the relatively simple colonial structure and reproductive strategy shown by *A. coralloides* (and other encrusting organisms) might be evolutionarily favoured due to its lower energetic needs when growing on other erect substrata (in the case of *A. coralloides*, the branches of *Paramuricea clavata* and other gorgonians). We argue that the ecological advantage of epibiont species in highly structured and diversified benthic communities can also be expressed in their reproductive pathway.

MATERIALS AND METHODS

Alcyonium coralloides samples were cut from colonized branches of *Paramuricea clavata* off Cova de la Vaca, within the Marine Protected Area of the Medes Islands (NW Mediterranean, 42° 03′ N, 3° 15′ E) between 18 and 22 m depth. The sampling site is a large tunnel connecting 2 sides of one of the islets, and harbours a population of *P. clavata.* The abundance of *A. coralloides* is higher in this tunnel than usually found in other populations of *P. clavata*, due to the impact of SCUBA diving tourists that injure the corals, which thus favours colonization by *A. coralloides* (Tsounis et al. 2012). The tunnel is among the major SCUBA attractions along the Costa Brava and receives about 70 000 visitors per yr (Lloret 2003, Coma et al. 2004).

Nine sampling trips were carried out by SCUBA diving between March 2008 and March 2009, usually monthly when weather conditions allowed the fieldwork. Twenty colony fragments of *Alcyonium coralloides* growing on the same number of colonies of *Paramuricea clavata* were collected in each sampling trip, yielding a total of 180 samples in the whole sampling period of this study. All samples were immediately fixed in buffered formalin (4% in seawater). The collected colonies of *A. coralloides* were about 10 mm wide (coenenchyme covering the dead gorgonian axis) and ca. 50 mm long. We tried to sample the smallest fragments possible of *A. coralloides* , always from the apical part of the gorgonian branches, to minimize impact. Sampling was haphazard; however, because not many colonies were left to be sampled in the tunnel, we had to sample tissue from the same individuals repeatedly over time.

The colour pattern of *Alcyonium coralloides* colonies agrees with that described by Weinberg (1977) and morphotype M1 described by McFadden (1999): the sclerites of the coenenchyme were red, yellow in the tentacles and proximal part of the
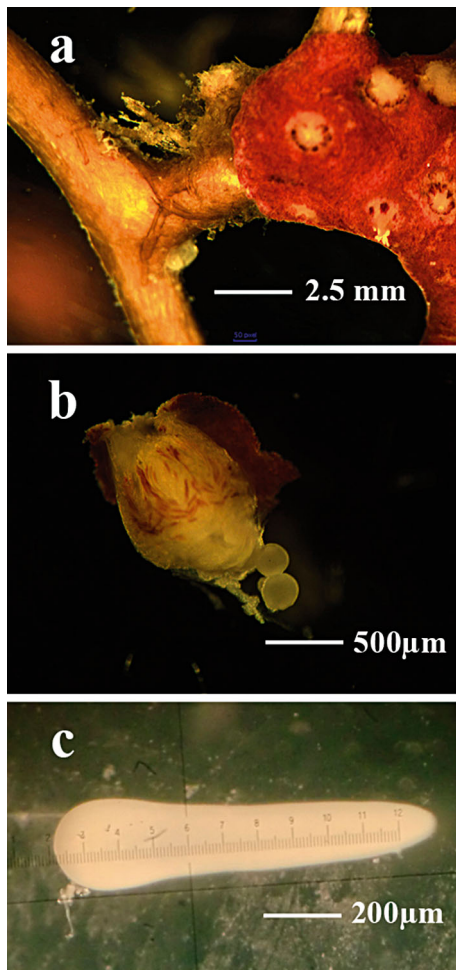
Fig. 1. (a) Colony of the epibiont *Alcyonium coralloides* on a branch of *Paramuricea clavata*. (b) Polyp from a male colony with spermatic cysts and (c) larvae of a female colony collected in May 2008

polyp, and red in the distal part of the polyp (Fig. 1a,b). Variability in colour patterns might exist, since white and pink colonies have been reported from deeper waters (Groot & Weinberg 1982). A total of 900 polyps (5 polyps per collected colony) were opened to count and measure reproductive products (oocytes and spermatic cysts). The sampling effort, representing the minimum significant sample size for the number of colonies and polyps in males and females that had to be removed, was the same as that used in other studies on reproduction in Mediterranean octocorals (e.g. Coma et al. 1995). Sex determination was carried out by direct observation of reproductive products and confirmed by subsequent histological sections. Oocytes were yellow and firm, whereas male spermatic cysts were white and relatively fragile to manipulation.

A binocular stereomicroscope (×20) was used for measuring the diameter of the oocytes and spermatic cysts. Polyps were dissected by removing the anthocodia to expose the gastrovascular cavity. The dissected polyps were chosen haphazardly. In each polyp, the diameter of the sexual products was counted and measured. The average diameter (minimum detection size 50 µm) and the average fecundity (number of oocytes or spermatic cysts per polyp) were obtained per sex and month. The size–frequency distributions of reproductive-product diameters and their average volume, measured as a sphere ($µm^3$ $polyp^{-1}$), were also analysed. Temperature data (20 m depth) were obtained from the meteorological station of l'Estartit every 3 to 4 d.

In order to detect and monitor gametogenic and embryonic development, selected samples from both sexes in all sampled months were prepared for histological observations. Fragments were decalcified in a solution of 10 % formic acid for a few minutes, rinsed in running water to remove excess acid in the tissues, dehydrated in a gradient of ethyl alcohols and then embedded in paraffin. Histological sections 6 to 8 µm thick were stained with Ramón y Cajal's Triple Stain (Gabe 1968).

RESULTS

Sexual cycle

Alcyonium coralloides is gonochoric, with all polyps of a colony of the same sex. Larvae were found inside polyps of female colonies in May 2008 (Fig. 1c). Although the reproductive cycle was annual, gametogenesis lasted only 5 to 6 mo. Based on presence and subsequent absence of larvae from May to June, larval release was inferred. However, spermatic cysts were present in May (Fig. 2a) in the gastrovascular cavities of male colonies. The maximum monthly (mean ± SD) spermatic cyst diameter observed was 365 ± 86 µm, and 632 ± 125 µm for mature oocytes in female colonies (Fig. 2). Both maximum values occurred in May, the last month of the gametogenic cycle. Also in this month fecundity (mean ± SD) was 15 ± 9 spermatic cysts $polyp^{-1}$ in male colonies, and 7 ± 4 oocytes $polyp^{-1}$ in females (Fig. 3).

Gametogenic cycle

Spermatic cysts and oocytes showed an annual cycle of development, with internal fertilization of
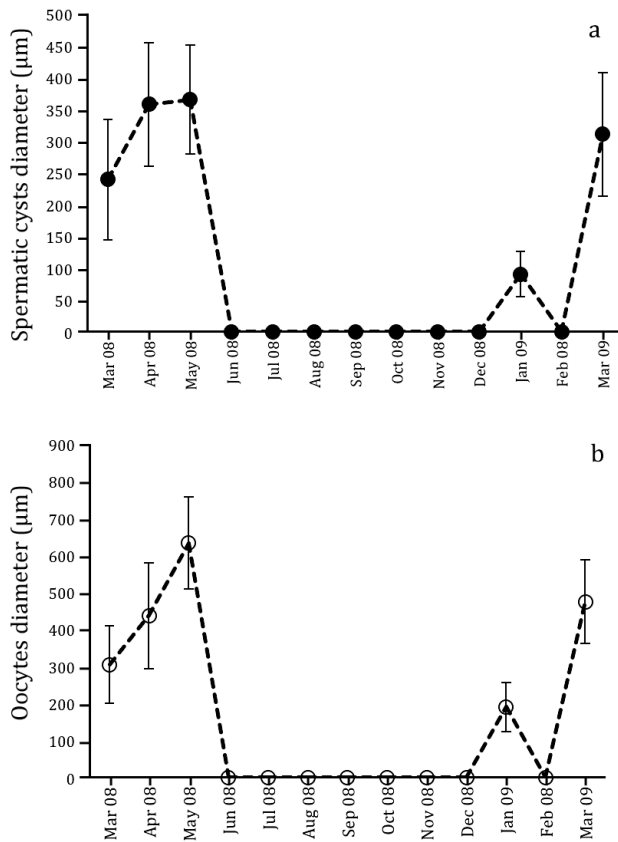
Fig. 2. *Alcyonium coralloides*. Diameter (mean ± SD) of (a) spermatic cysts and (b) oocytes in samples collected during 2008 and 2009

Fig. 3. *Alcyonium coralloides*. Fecundity (mean ± SD) of (a) male and (b) female colonies collected during 2008 and 2009

the oocytes and release of larvae in May. In both sexes, generation and development of reproductive products took 5 to 6 mo, probably beginning in December (no samples available) and ending with the release of sperm and larvae in May. In both males and females, the first evidence of small reproductive products (0–100 µm) was found in January, possibly marking the onset of oogenesis in the previous month (Figs. 4 & 5). Reproductive products of intermediate size classes (300–400 µm) were also present in fe-males, but smaller sizes were found in males (100–200 µm).

In male colonies, the diameter (mean ± SD) of sper-matic cysts increased by 34% between March 2008 (240 ± 95 µm) and May 2008 (365 ± 86 µm), just prior to the release of male sexual products (Fig. 2a). In January 2009, the first spermatic cysts were detected, with a diameter of 91 ± 36 µm; they achieved a final diameter of 311 ± 97 µm in March 2009 (Fig. 2a). No spermatic cysts were found in samples between June and November 2008. Polyp fecundity decreased from (mean ± SD) 34 ± 15 to 15 ± 9 spermatic cysts polyp^{-1}
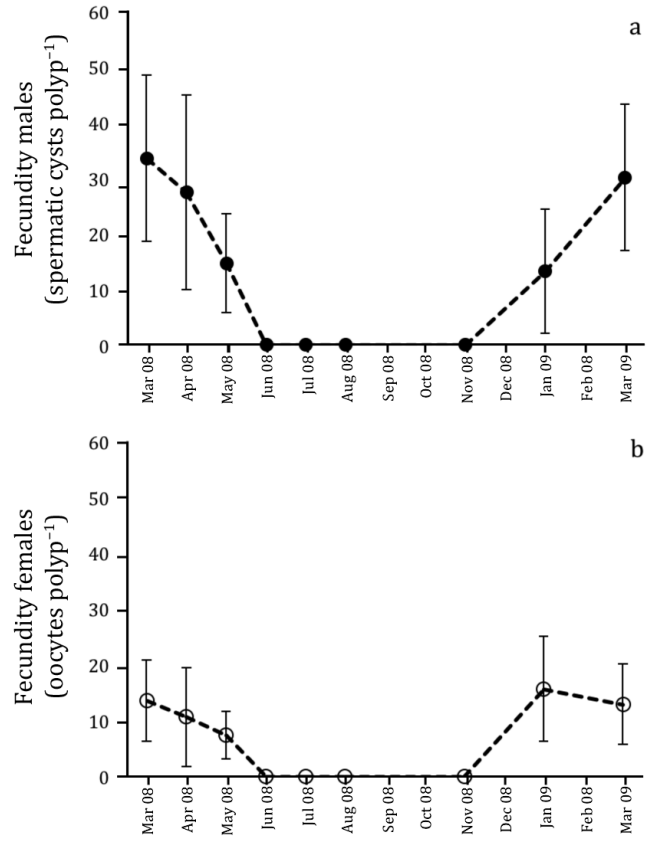
between March and May 2008, but increased 56% between January and March 2009 (13 ± 11 and 30 ± 13 spermatic cysts polyp^{-1}, respectively; Fig. 3a).

The average oocyte diameter in female colonies doubled in size over 2 mo, from 304 ± 105 µm in March 2008 to 632 ± 125 µm in May 2008 (Fig. 2b). During June, July, August and November of 2008, no oocytes were found in female colonies. In January 2009, the average size of oocytes was 191 ± 66 µm, increasing 60% up to 475 ±113 µm in March 2009 (Fig. 2b). The fecundity decreased by 46% in March and May 2008, whereas the highest fecundity was observed during January 2009 (16 ± 9 oocytes polyp^{-1}) and then decreased by 15% (13 ± 7 oocytes polyp^{-1} in March 2009; Fig. 3b).

The average volume (µm^3 polyp^{-1}) of spermatic cysts and oocytes (Fig. 6) increased with develop-ment; the average diameter of both sexes followed the same pattern. Temperature was registered be-tween March 2008 and March 2009 (Fig. 7).

The histological study showed that gametogenesis probably started in December: all male and female
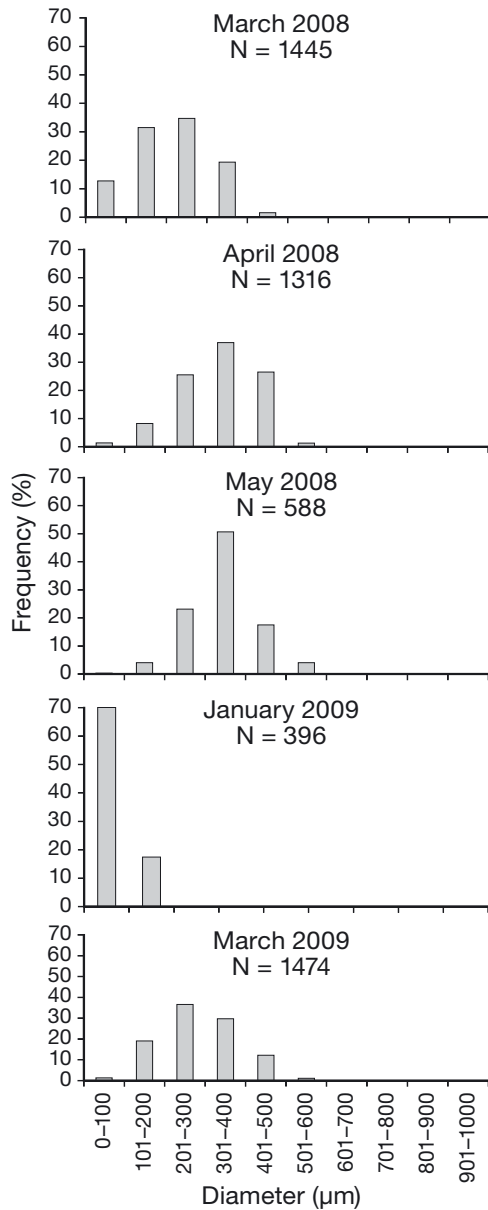
Fig. 4. *Alcyonium coralloides.* Distribution of spermatic cyst diameter (µm) frequencies in male colonies collected during 2008 and 2009. N: total number of spermatic cysts measured per month

Fig. 5. *Alcyonium coralloides.* Distribution of oocyte diameter (µm) frequencies in female colonies collected during 2008 and 2009. N: total number of oocytes measured per month

colonies sampled in November lacked reproductive products, whereas in the following sampled month (January), previtellogenic oocytes between 50 and 70 µm (Fig. 8b) and vitellogenic oocytes with increasing amount of lipid drops in the ooplasm (Fig. 8c,d) were present. Starting in January, male colonies showed spermatic cysts, which were present in all inspected male colonies in the following months. Spermatic cysts showed numerous heads of developing sperm and a thinner mesogleal envelope than oocytes (Fig. 9). Male colonies examined at the
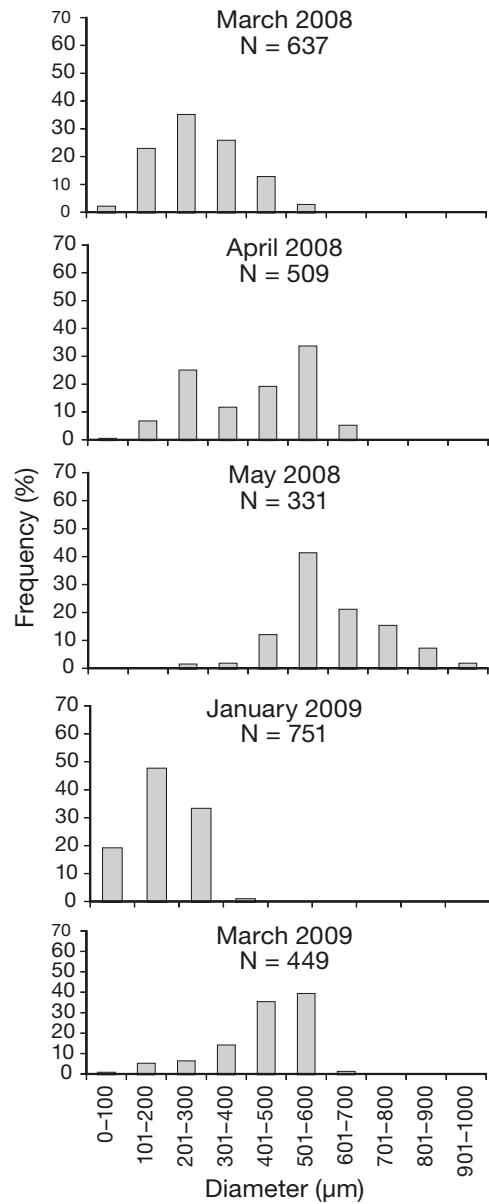
end of the cycle (May) were heterogeneous; the gastrovascular cavities of some colonies were completely empty (indicating the emission of spermatic cysts or sperm), whereas others still had some completely mature spermatic cysts full of sperm. Oocytes increased in size until May, when a few oocytes (some devoid of their mesogleal cover, and others still inside mesogleal capsules) but mainly larvae (showing epidermis with columnar cells and disaggregated internal yolk granular reserves) were observed in the gastrovascular cavities of polyps of female colonies.
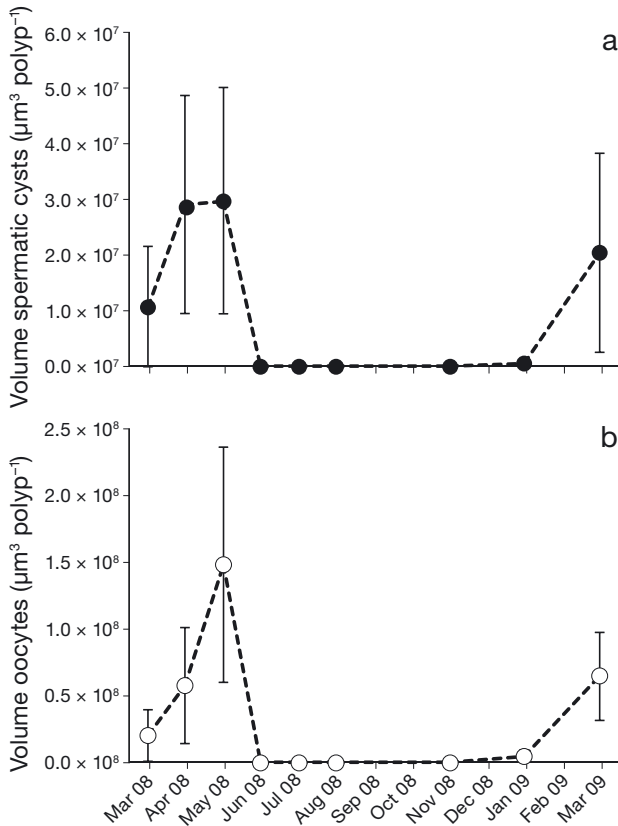
Fig. 6. *Alcyonium coralloides*. Volume for (a) total spermatic cyst content per polyp (male colonies) and (b) total oocyte content per polyp (female colonies) of samples collected during 2008 and 2009
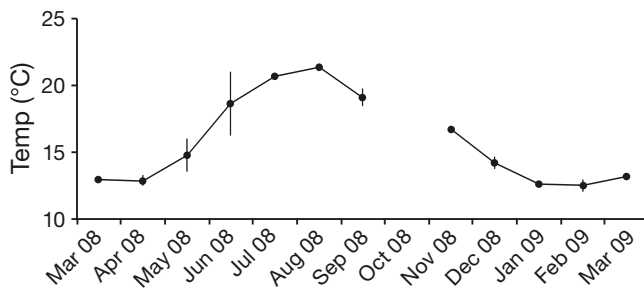

Fig. 7. Water temperature (°C) at 20 m depth between March 2008 and March 2009

DISCUSSION

Similar to several other *Alcyonium* species (6 out of 12, according to Kahng et al. 2011), *A. coralloides* is a gonochoric species (Groot & Weinberg 1982). Gono-chorism is the most common reproductive strategy in Octocorallia (70% according to Kahng et al. 2011), while hermaphroditism is the most common pattern among tropical scleractinian hexacorals (Harrison &

Wallace 1990, Kahng et al. 2011). *A. coralloides* is considered an internal brooder, and thus is charac-terized by internal fertilization and retention of lar-vae in the gastrovascular cavity of the polyps (Giese & Pearse 1974, McFadden et al. 2001). Internal brooding is the most common strategy among *Alcyo-nium* species (Kahng et al. 2011), whereas broadcast spawning is most common in tropical soft corals (Alino & Coll 1989, Cordes et al. 2001, Hwang & Song 2007, Kahng et al. 2011), and surface brooders are not common (Hwang & Song 2007, Kahng et al. 2011, Fiorillo et al. 2013).

Gametogenesis

Alcyonium coralloides showed an annual repro-ductive cycle, characterized by fast gametogenic de-velopment of similar duration for both sexes and an early release of larvae in spring (probably complet-ing it in late May since larvae were absent in the samples from June). Our data revealed a shorter cycle (by 2 mo) in *A. coralloides* than that observed in other *Alcyonium* species and Mediterranean littoral octocorals (Table 1, Kahng et al. 2011). However, because variability of the reproductive cycle may oc-cur due to local or regional environmental conditions (e.g. temperature, food availability, other biological variables), more than 1 yr of observations is needed to support these results. Weinberg (1977) observed small oocytes (as eggs in his study) in specimens of *A. coralloides* (as *Parerythropodium coralloides*) col-lected in November, whereas Lacaze-Duthiers (1900) (as *Sympodium coralloïdes*) mentioned May to July as the reproductive period, and Lo Bianco (1909, as cited by Weinberg 1977) obtained larvae in the aquarium in June.

Gametogenesis of male and female colonies had similar duration (5 to 6 mo), and oogenesis was shorter than that of other octocorals. In fact, the gen-eral tendency in octocorals is an oogenesis that lasts longer than spermatogenesis (Benayahu & Loya 1984, 1986, Benayahu et al. 1990). This is also the general tendency among scleractinian hexacorals (Harrison & Wallace 1990, Harrison 2011) and is explained by the fact that oogenesis requires more time and energy than spermatogenesis because these lecitotrophic species develop mature oocytes with a great amount of yolk. These reserves will be the source of energy for sustaining larval develop-ment (Vance 1973). For instance, oogenesis in Medi-terranean gorgonians such as *Eunicella singularis*, *Leptogorgia sarmentosa* and *Paramuricea clavata*
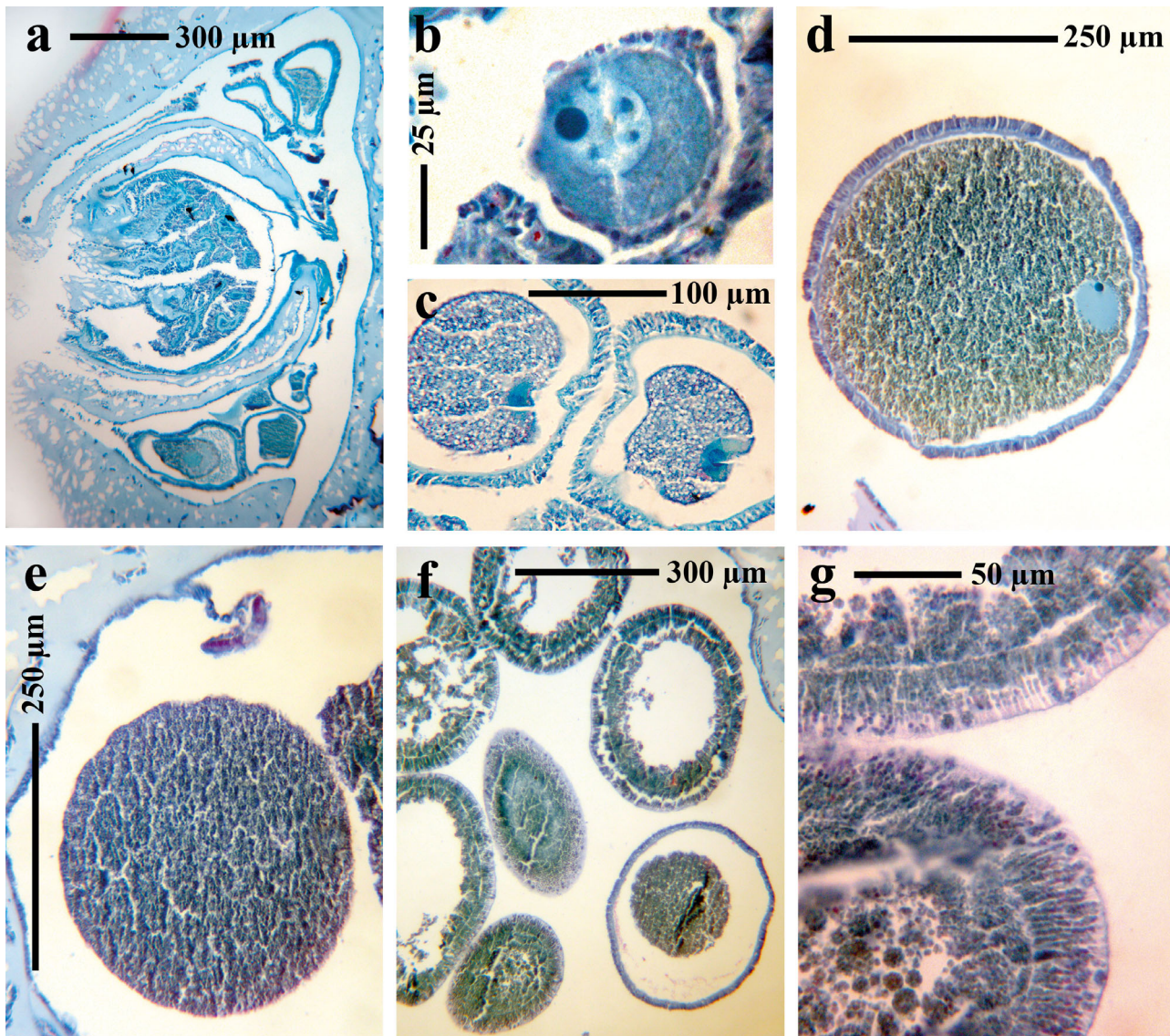
Fig. 8. *Alcyonium coralloides.* Histological sections of female colonies: (a) retracted polyp with oocytes in the gastrovascular cavity, (b) previtellogenic oocyte ca. 50 µm in diameter, (c) vitellogenic oocytes with the ooplasm increasing in drops of yolk, (d) oocyte (mature or close to maturity), still inside mesogleal capsule, (e) mature oocyte free in the gastrovascular cavity, without parental mesogleal capsule, (f) interior of a gastrovascular cavity showing a group of larvae with diverse amount of disaggregating reserves, and an oocyte still in its mesogleal capsule, (g) detail of the epithelia of adjacent larvae, showing typical columnar epidermis and a thin mesogleal layer separating it from their incipient gastrodermis

lasts 13 to 17, >12 and 13 to 18 mo, respectively, whereas spermatogenesis lasts 5 to 7 mo (Table 1). This trend is also characteristic in the soft coral *Alcyonium acaule* in the same area, with oogenesis and spermatogenesis lasting for 12 to 13 mo (Fiorillo et al. 2013; Table 1). In encrusting soft corals, this trend also appears in species such as *Rhytisma fulvum fulvum* (Forskål, 1775) (*Parerythropodium fulvum fulvum*; Benayahu & Loya 1983), in which oogenesis

lasts 10 to 11 mo, while spermatogenesis lasts 7 to 9 mo. Our results also showed an increase in average volume of spermatic cysts and oocytes with a concurrent decrease in average fecundity during gametogenic development. This could be partially explained by absorption of the smallest generated sexual products in favour of the development of other spermatic cysts and oocytes that subsequently end their gametogenic cycle (Fiorillo et al. 2013).
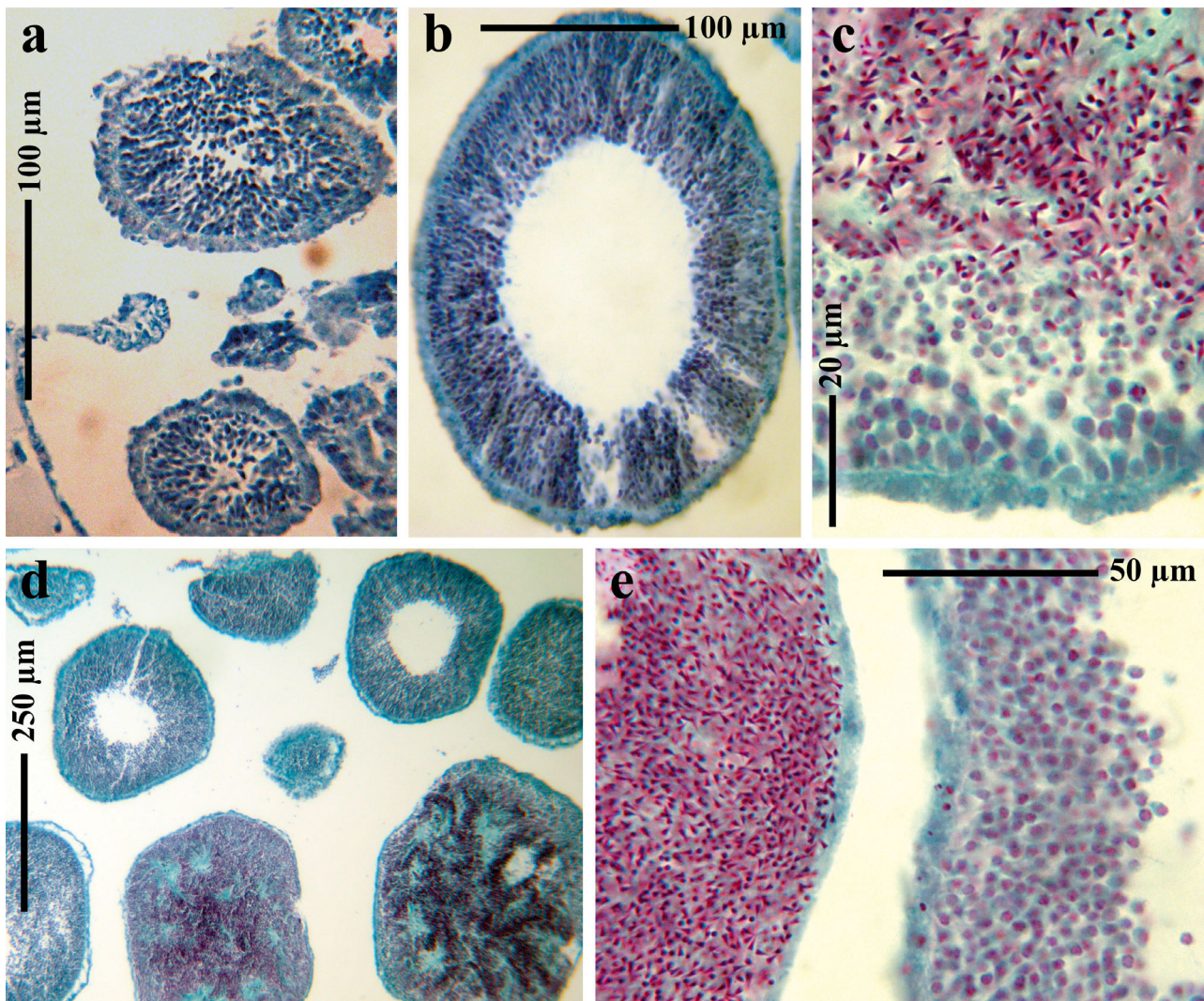
Fig. 9. *Alcyonium coralloides.* Histological sections of male colonies: (a) early spermatic cysts, without clear distinct lumen and disorganized spermaries, (b) developing spermatic cyst with typical lumen and future sperm flagellae and head of immature sperm still rounded and radially arranged, (c) developing spermatic cyst showing all maturation stages of the sperm heads, from rounded bodies (on the periphery of the cyst; bottom of the image), more concentrated (centre of the image) and fully defined and mature sperm heads, distinctly triangular and strongly stained (in the most internal parts of the cyst; upper part of the image), (d) interior of a gastrovascular cavity of a colony collected in April, showing spermatic cysts in different stages of development (sperm heads at the bottom of the image are strongly stained, denoting an advanced stage of maturation), (e) two adjacent spermatic cysts from a colony collected in April, showing the asynchrony in the development of cysts (the one on the left is fully developed, with disorganized sperm heads reaching the parental mesogloeal capsular layer, while the one on the right still contains rounded immature sperm heads)

Release of male sexual products

The synchronization of both sexes in the release of sexual products is a common trend among broadcast-spawning octocorals that allows maximizing the fertilization success (Alino & Coll 1989). This synchronization is promoted by external factors such as temperature (Grigg 1977) and lunar cycle (Brazeau & Lasker 1989, 1990). In subtropical alcyonaceans, the release of male gametes coincides with increased water temperature in late spring (e.g. *Eunicella singularis, Paramuricea clavata, Sarcophyton glaucum* (Quoy & Gaimard, 1833), *Alcyonium acaule* Linnaeus, 1758; see Coma et al. 1995, Benayahu & Loya 1986, Ribes et al. 2007, Fiorillo et al. 2013). In the case of *E. singularis*, male gametes are released in May to June, fertilization is internal, and release of larvae occurs in June to July (Ribes et al. 2007). The release

Table 1. Sexuality and mode of reproduction, length of reproductive cycle, season of the onset and duration of gamete proliferation, maturation and spawning or breeding, and cohorts for selected soft corals and gorgonian species from different geographic areas. F: female, M: male, blank cells: no data. Sources: Coma et al. (1995), Ribes et al. (2007), Rossi & Gili (2009), Kahng et al. (2011), Betti et al. (2012), Fiorillo et al. (2013)

Species	Study site	Sexuality	Reproductive mode	Cycle (mo)	Spawning or breeding	Cohorts
Alcyoniidae						
Alcyonium acaule	NE Mediterranean Sea	Gonochoric	Surface brooder	12–13 (M and F)	July	2 F
Alcyonium coralloides[a]	NW Mediterranean Sea	Gonochoric	Internal brooder	6–7 (M and F)	Mid-May–June	
Alcyonium digitatum	Man Island (N Atlantic)	Gonochoric	Broadcast spawner	12–13 (F)	December–January	
Alcyonium glomeratum	Atlantic and Mediterranean Sea	Gonochoric	Broadcast spawner			
Alcyonium hibernicum	Man Island (N Atlantic)	Parthenogenic	Internal brooder	12 (F)	Late summer (1–2 mo)	
Alcyonium pacificum	Aleutian Islands	Gonochoric	Internal brooder		July–August	
Alcyonium palmatum	Mediterranean Sea	Gonochoric	Broadcast spawner		August–October	
Alcyonium sidereum	NW Atlantic Sea	Hermaphroditic	Internal brooder		August	
Alcyonium sp. A	Irish Sea	Hermaphroditic	Internal brooder			
Alcyonium sp. A3	Portugal	Unknown	Internal brooder			
Alcyonium sp. C	San Juan Islands	Unknown	Internal brooder			
Alcyonium sp. M2	Mediterranean Sea	Unknown	Unknown			
Coralliidae						
Corallium rubrum	NE Mediterranean Sea	Gonochoric	Internal brooder	24 (F), 12 (M)	July–August	2 F
Cornulariidae						
Cornularia cornucopiae	NE Mediterranean Sea	Parthenogenic	Unknown	5 (F)	August	
Gorgoniidae						
Eunicella singularis	NE Mediterranean Sea	Gonochoric	Internal brooder	13–17 (F), 5–6 (M)	May–July	2 F
Leptogorgia sarmentosa	NE Mediterranean Sea	Gonochoric	Broadcast spawner	>12 (F)	Late August–early September	
Plexauridae						
Paramuricea clavata	NE Mediterranean Sea	Gonochoric	Surface brooder	13–18 (F), 6–7 (M)	June–July	2 F

[a]Data from present study

of sperm in *A. coralloides* occurs from mid-May on, while the oocytes are retained in the female polyp for internal ripening and fertilization. This release of sperm coincides with a 2° increase in water temperature (from 14.8 to 16.7°C between 14 and 21 May 2008, Fig. 7), but it appears to precede spawning in other *Alcyonium* species and Mediterranean octocorals (see Table 1).

Release of larvae

In octocorals, less than 1 wk is enough for the transition from zygote to planula (Alino & Coll 1989, Babcock 1990, Gutierrez-Rodríguez & Lasker 2004). Internal fertilization and planulae development might occur in a short period, as is the case of *Paramuricea clavata*, in which blastulae developed in 24 h and planulae appeared after 48 to 72 h (Linares et al. 2008). As mentioned above, the release of *Alcyonium coralloides* larvae probably occurs in May to early June (larvae were completely absent in samples collected in June (see Figs. 2b, 3b, 5, & 6b). Although unknown for the majority of octocoral species, some anthozoan larvae are already competent 2 h after release, whereas other larvae require several days (Atoda 1947, Harii & Kayanne 2003). Thus, it is plausible that larvae of *A. coralloides* are ready to settle on naked segments of *P. clavata* axes if these are available. Denudation can occur through biological (depredation by gastropod molluscs, e.g. *Simnia* and *Coralliophilia* species; Crocetta & Spanu 2008) or environmental causes (mortality events and diseases linked to climate warming; see Cerrano et al. 2000, Linares et al. 2008, Coma et al. 2009, Garrabou et al. 2009) or due to physical damage (e.g. excessive SCUBA diving activities in particular areas, fishing nets and lines; see Harmelin & Marino-poulos 1994, Tsounis et al. 2012), as occurred at our study site.

Epibiotic strategy of *Alcyonium coralloides*

There are similarities between the reproductive patterns of *A. coralloides* and some zoanthids. Most zoanthid species also grow in fouling form as encrusting colonies on hard substrates or as epibionts on other organisms (e.g. sponges, hydrozoans, gorgonians, antipatharians; Ryland & Westphalen 2004, Previati et al. 2010, Sinniger et al. 2010). These species rarely reproduce sexually or do so in a short period, as asexual reproduction is the fastest way of covering substrate (Ryland & Babcock 1991, Garrabou 1999). A short gametogenesis (oogenesis) is shared among zoanthids: 4 to 5 mo in the genus *Protopalythoa*, 5 to 6 mo in *P. parasiticus* (Duchassaing & Michelotti, 1860) and 8 mo in *P. axinellae* (Schmidt, 1862) (Ryland & Babcock 1991, Ryland et al. 2000, Ryland & Westphalen 2004, Previati et al. 2010). A recent study in the Adriatic Sea (Betti et al. 2012) showed that in the octocoral *Cornularia cornucopiae* (Pallas, 1766), an epibiont growing over ascidians and sponges, oogenesis occurs from March to August. This pattern coincides with the remarkably short oogenesis of *A. coralloides*, suggesting that a short gametogenesis could be a common feature of epibiont fouling species. Epibiont species (defined by Wahl 1989) show fast growth, sexual reproduction limited to short and seasonal periods (Coma et al. 1992, 1998) and asexual reproduction (Faucci & Boero 2000). These are features of opportunistic species ('r strategy'; Jackson 1977) and are consistent with the epibiosis strategy, for which the main priority is to persist under high levels of spatial competition.

The lack of reproductive products during 6 mo in *Alcyonium coralloides* suggests that energy is invested into processes other than sexual reproduction (such as growth and maintenance), or environmental conditions do not permit investments in reproductive tasks for this epibiotic species. In zoanthids, it seems that the short gametogenesis means a higher energetic investment towards asexual reproduction, leading to faster growth of the colony, and thus to higher height over the substrate (Rossi et al. 2012). In any case, shortening the reproductive cycle implies a significant advantage in substrate colonization.

The release of larvae by *Alcyonium coralloides* occurred before the gamete output of *Paramuricea clavata* (Coma et al. 1995). In the Mediterranean, many suspension feeders show aestivation (Coma et al. 2000). The summer trophic crisis leads to relative inactivity of anthozoans (Coma et al. 1998, Garrabou 1999). Minimum levels of protein, carbohydrates and lipid concentration, as well as a notable expression of stress proteins (HSP 70 and 90) related with trophic constraints in summer (beginning in June), support this seasonal variation of the ecophysiological parameters for the basibiont *P. clavata* (Rossi et al. 2006, Gori et al. 2007). Due to the minimum levels of food intake in *P. clavata* in summer, energy investment into reproduction is concentrated in spring (March and June) when conditions of food availability are more favourable (Coma et al. 1998). The breeding period takes place between June and July, afterwards leaving colonies exhausted and more vulnerable to potential colonization aggressions like that caused by the larval settlement of *A. coralloides*. Furthermore, *P. clavata* is a surface brooder; females secrete a mucus that bounds the eggs together and keeps them adhered to the surface of the mother colony (Coma et al. 1995). Thus the timing of reproduction in *A. coralloides* can also be regarded as an adaptive strategy that allows successful colonization of the gorgonian axes, avoiding *P. clavata* secretions, which would impede its own larval settlement. The related species *Rhytisma fulvum fulvum*, also a soft coral encrusting species although not an epibiont, has comparatively longer oogenesis (Benayahu & Loya 1983).

The reproductive cycle of the epibiont *Alcyonium coralloides* seems to be evolutionarily coupled to that of its gorgonian basibiont, allowing the presence of both species in Mediterranean ecosystems. A shorter reproductive cycle in *A. coralloides* implies a significant advantage in substrate colonization during a period of the year when the basibiont decreases activity as a result of the high cost of its own reproduction and less favourable trophic environmental conditions.

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