

Unexpected patterns in the sexual reproduction of the Mediterranean scleractinian coral *Cladocora caespitosa*

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ABSTRACT: Knowledge of reproductive biology is essential to understanding population dynamics and ecological processes in corals. Sexual condition and the reproductive cycle of the Mediterranean endemic scleractinian *Cladocora caespitosa* was assessed through histological analyses. Our results showed that this species is gonochoric in the Western Mediterranean Sea. Oocytes and spermaries were detected annually from March to October, reaching their maximum size between July and August coincidentally with the highest seawater temperatures. A drastic decrease in gametes between August and October indicated that spawning occurred at the end of summer. These results differ from those obtained for the Adriatic Sea, where this species was described as hermaphroditic and spawning occurred at the beginning of summer. The unusual plasticity of this temperate coral and the endangered condition of *C. caespitosa* bioconstructions in the Mediterranean highlight the need for further research on this topic.

KEY WORDS: Coral reefs · *Cladocora caespitosa* · Reproduction · Mediterranean Sea

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INTRODUCTION

Understanding reproductive biology is essential to comprehending the population dynamics of marine organisms (Fadlallah 1983). Hence, knowledge of coral reproduction is necessary for the management and preservation of coral reefs. For example, successful reproduction can allow for the addition of new individuals to existing populations, the colonization of new areas, and the recovery of populations damaged by natural or human disturbances.

The majority of scleractinian species can be classified as either hermaphroditic or gonochoric; however, more complex sexual patterns have also been described (Harrison & Wallace 1990, Baird et al. 2009, Guest et al. 2012). Likewise, there are 2 types of larval development or reproductive modes. Fertilization is either internal, i.e. the embryo develops within the polyp and is released as a motile planula

larva (brooding), or external, with the embryo developing in the water column (broadcast spawning) (Harrison & Wallace 1990, Baird et al. 2009). However, information on the reproductive biology of temperate scleractinian species is relatively scarce in comparison to tropical scleractinian corals (see Harrison 2011 for a review), particularly for the Mediterranean Sea (Goffredo & Zaccanti 2004, Goffredo et al. 2006, Goffredo et al. 2010).

Hermaphroditic broadcast spawners are the dominant group among tropical scleractinian corals (Harrison & Wallace 1990, Harrison 2011, Kerr et al. 2011). In contrast, temperate scleractinians appear to display higher variability in their sexual condition and fertilization strategy, although the latter appears to be fairly consistent within the same family. Within the family Caryophyllidae, for example, the species *Caryophyllia inornata*, *C. smithi*, *Lophelia pertusa* and *Paracyathus stearnsii* are gonochoric, whereas *C. ambrosia*,

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C. cornuformis and *C. sequenzae* appear to be hermaphroditic (Fadlallah & Pearse 1982a, Waller et al. 2005, Waller & Tyler 2005, Goffredo et al. 2012). However, all these species, except for *C. inornata*, show the same fertilization mode (external; broadcast spawners) (Fadlallah & Pearse 1982b, Waller et al. 2005, Waller & Tyler 2005, Goffredo et al. 2012). Similarly, in the family Dendrophylliidae, *Balanophyllia elegans* and *Leptopsammia pruvoti* are gonochoric, whereas *B. europaea* is described as a hermaphroditic species (Fadlallah & Pearse 1982a, Goffredo & Zaccanti 2004, Goffredo et al. 2006). All species of the Dendrophylliidae are brooders and show internal fertilization of gametes (Fadlallah & Pearse 1982a, Goffredo & Zaccanti 2004, Goffredo et al. 2006).

The scleractinian *Cladocora caespitosa* (Linnaeus, 1767) is the only reef-forming Mediterranean endemic zooxanthellate coral (Morri et al. 1994, Aguirre & Jiménez 1998). This coral is physiologically and morphologically similar to the typical tropical reef-building scleractinians, being zooxanthellate, colonial and capable of forming extensive bioconstructions (Zibrowius 1982). *C. caespitosa* occurs from shallow waters to depths of approximately 40 m (where light still allows photosynthesis by the symbiotic zooxanthellae) and at sites characterized by calm waters or exposed to strong currents (Zibrowius 1982, Kružić & Benković 2008, Kersting & Linares 2012). Currently, living banks of the coral *C. caespitosa* appear to be restricted to a few Mediterranean locations and are threatened by the escalating impacts affecting coastal areas such as global warming and the spread of invasive species (Kružić & Požar-Domac 2007, Kružić et al. 2008b, Kersting & Linares 2012). Furthermore, *C. caespitosa* populations have been strongly affected during the past decade by mass-mortality events related to positive sea surface temperature (SST) anomalies (Perez et al. 2000, Rodolfo-Metalpa et al. 2005, Garrahou et al. 2009, Kersting & Linares 2009).

To date, only 2 studies based on *in situ* observations and preliminary histological analyses have provided insights into the reproduction of this emblematic species. The spawning of this coral species was first observed by Schiller (1993) in the Bay of Piran (Northern Adriatic Sea), where eggs and sperm bundles were released by a few colonies 4 d prior to the full moon in June. More recently, Kružić et al. (2008a) observed the timing and mode of spawning on banks of *C. caespitosa* in the saltwater lake Veliko jezero (Mljet National Park, Croatia) and described the species as colonial hermaphroditic but with colonies releasing either sperm or eggs during each spawning episode 2 nights before the full moon in June 2005.

The aim of this study was to increase our knowledge of the reproductive biology of *Cladocora caespitosa* in the Western Mediterranean. The bioconstructions of this emblematic species along the Mediterranean Sea are currently threatened by seawater temperature increases and other anthropogenic impacts, and a thorough understanding of the reproductive characteristics of the species is imperative. We used histological techniques to study the sexual condition, as well as the reproductive cycle of this species in order to assess the timing of spawning in the Columbretes Islands Marine Reserve (Western Mediterranean, Spain). This information was compared with results previously reported for the Adriatic Sea. In addition, we examined the sexual condition of *C. caespitosa* in 5 Western Mediterranean locations to determine the general patterns of reproduction in this area.

MATERIALS AND METHODS

To determine the sexual condition of *Cladocora caespitosa* (gonochoric vs. hermaphroditic) at both polyp and colony levels, colonies of *C. caespitosa* were sampled by SCUBA in 5 Western Mediterranean locations: Columbretes Islands Marine Reserve (Spain), Eivissa (Spain), Medas Island Marine Reserve (Spain), Cap de Creus Natural Park (Spain), and Natural Reserve of Scandola (Corsica) (Fig. 1). The number of sampled colonies per site was variable, depending on the abundance of the species at each sampling site (Table 1).

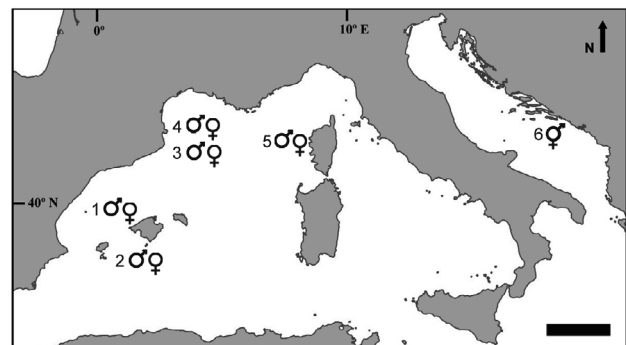


Fig. 1. Map of the study sites in the Western Mediterranean and Adriatic Sea (Sites 1–5 in this study and Site 6 in Kružić et al. 2008a). 1: Columbretes Islands Marine Reserve (W Mediterranean, Spain), 2: Eivissa (W Mediterranean, Spain), 3: Medas Island Marine Reserve (NW Mediterranean, Spain), 4: Natural Reserve of Scandola (NW Mediterranean, France), 5: Cap de Creus (NW Mediterranean, Spain) and 6: Mljet National Park (Adriatic Sea, Croatia). Scale bar = 200 km

To investigate the reproductive cycle of *Cladocora caespitosa*, 10 colonies were surveyed monthly from April 2008 to July 2009 in the Columbretes Islands Marine Reserve (Spain, NW Mediterranean, 39° 53.825' N, 0° 41.214' E) at a depth of 15 m. These colonies (20–50 cm in diameter) were individually marked in one of the areas with higher coral cover in Illa Grossa Bay (Kersting & Linares 2012). Particular efforts were made to select healthy colonies with no signs of recent or past mortality. Seawater temperature was measured daily during the study period with Stowaway Tidbits (ONSET, Cape Cod, MA, USA) autonomous sensors installed at the same depth and location as the studied colonies.

Initial histological analyses were conducted to assess the sexual condition of *Cladocora caespitosa* in all sampled sites, as well as to assess the sex of each of the 10 marked colonies in the Columbretes Islands; 3 polyps per colony were sampled for this purpose. According to these results, 3 male and 3 female colonies were selected and 3 polyps of each colony were further investigated. By the end of the study, 33 polyps per colony had been analyzed. The collected samples were fixed in 4% formaldehyde in seawater, decalcified in a solution of HCl (37%), formaldehyde and water (1.3:0.8:7.9) for 24 h, dehydrated through a graded alcohol series and finally embedded in paraffin. Cross sections of polyps (5–6 µm thick) were stained with haematoxylin-eosin and examined under a light microscope equipped with a micrometer. In female colonies, the total number of oocytes per polyp was counted and minimum and maximum diameters of oocytes (sectioned through the nucleolus) were measured. The number of oocytes per polyp was counted when less than 100; whenever more than 100 oocytes were observed, the polyp was classified in the class >100. Oocyte diameters were measured in a maximum of 30 oocytes per polyp. In male colonies, only the number of spermaries was recorded due to the impossibility of measuring their size accurately. Due to the low number of either oocytes or spermaries in some samples,

we were unable to establish specific stages of maturation; however, as maturation and oocyte size are correlated (Shlesinger et al. 1998) we used the latter to estimate oocyte development.

Pearson's product-moment correlation was computed to examine the relationship between oocyte size (diameter) and seawater temperature at 15 m depth using the software package STATISTICA 8.0.

RESULTS AND DISCUSSION

Colonies of the scleractinian coral *Cladocora caespitosa* from the Western Mediterranean were determined to be gonochoric, since all polyps examined within the same colony were of the same sex. This species was described as hermaphroditic in the Adriatic Sea by Kružić et al. (2008a), i.e. polyps within one colony had both male and female gonads. In fact, the preliminary histological analysis made by these authors showed that oocytes and spermaries developed on separate mesenteries within each polyp. Moreover, these authors found that a single colony of *C. caespitosa* in the field released either female or male gametes, but not both simultaneously. In contrast, we found either oocytes or spermaries in a single polyp and colony and no signs of sex reversal, which are both typical signs of a gonochoric sexual condition (Fig. 2). Even though spawning was not directly observed in this study, the simultaneous maturation of gametes and the drastic decrease in the number of oocytes and spermaries between August and October (Fig. 3) suggested that the release of sperm and eggs occurred at or around the same time in the Western Mediterranean *C. caespitosa*.

Although corals display great plasticity in their life-history characteristics (Richmond & Hunter 1990), sexuality is generally consistent within most coral species and genera and within certain families (Harrison 2011). However, some examples of changes in sexual condition among populations have been reported in the literature. The scleractinian reef building coral *Diploastrea heliophora* was first classified as gonochoric on the Great Barrier Reef (Harrison 1985) but in Singapore was recorded to have colonies with hermaphroditic polyps, showing concurrent male and female gametes (Guest et al. 2012). This species may exhibit alternate sexual function, with an overlap occurring when the end of one gametogenic cycle coincides with the beginning of the next cycle. In other species, unidirectional protandry has been related to colony size and age (e.g. *Stylophora pistillata*; Rinkevich & Loya 1979), and bidirectional sex

Table 1. Summary of the sexual condition of *Cladocora caespitosa* colonies sampled at 5 study sites in the Western Mediterranean. No colonies were hermaphroditic

Population	Males	Females	Immature
Columbretes Is.	4	5	1
Eivissa	0	2	0
Medas Islands	2	6	2
Scandola	2	0	0
Cap de Creus	4	0	0

change has also been described for corals from the family Fungiidae (Loya & Sakai 2008). Sexual mode variation has been also documented for *Protopalythoa* species in the Great Barrier Reef (Babcock & Ryland 1990) and for *Palythoa tuberculosa* in Japan

(Yamazato et al. 1973). In the latter study, colonies were reported to be hermaphroditic while polyps within these colonies were gonochoric (Hirose et al. 2011). The variability in sexual condition of *Cladocora caespitosa* appears to be one of the first records

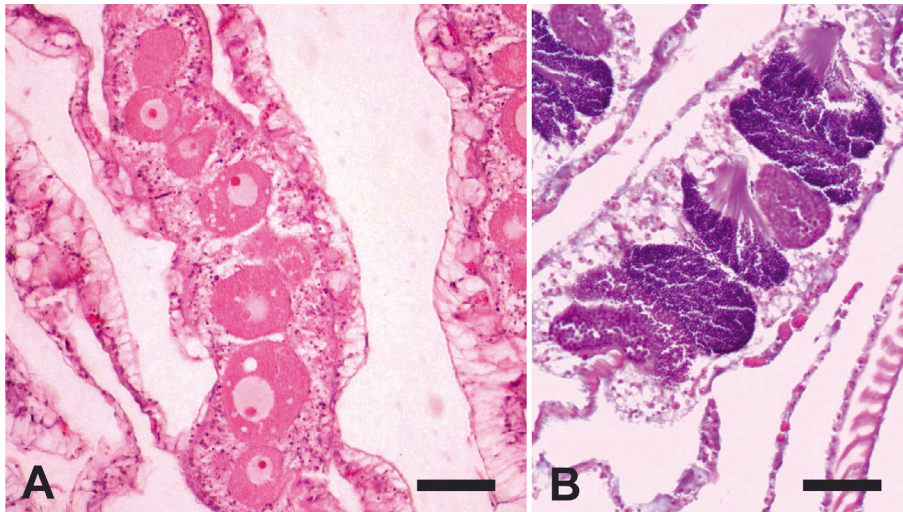


Fig. 2. Gonads of *Cladocora caespitosa*. (A) Female septum packed with mature oocytes (July 2008) containing an oval nucleus and a spherical nucleolus. (B) Male with spermaries filled with spermatozoa (August 2008). Scale bars = 50 µm

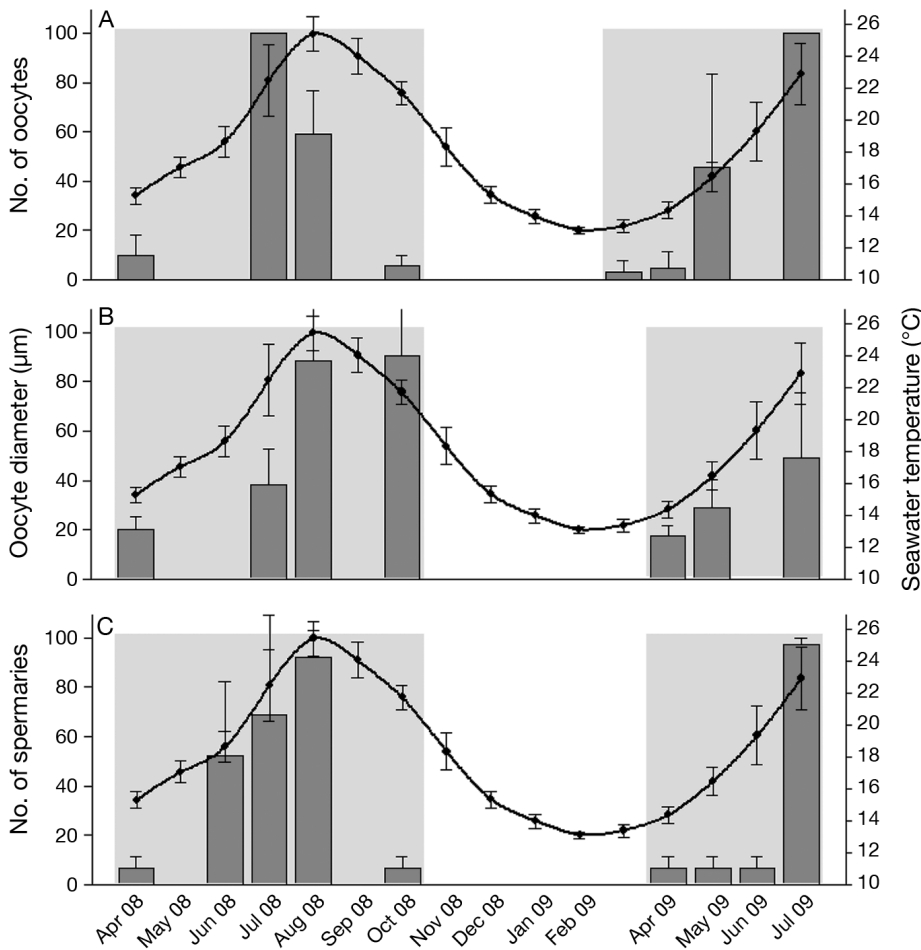


Fig. 3. *Cladocora caespitosa*. (A) Number of oocytes per polyp, (B) oocyte diameter, (C) number of spermaries per polyp and seawater temperature in the Columbetes Islands Marine Reserve. Oocyte and spermaries data are shown in bars (monthly average \pm SD), and SST is shown as points connected by a smoothed line (monthly average \pm SD). Grey background: reproductive season

of this unusual plasticity in a temperate coral, along with *Astroides calycularis*, which was described as hermaphroditic in Algeria (Lacaze-Duthiers 1873) and as gonochoric in the Southern Tyrrhenian Sea (Italy) (Goffredo et al. 2010).

During the first year of study in the Columbretes Islands, oocytes and spermaries were detected in the mesenteries from April to October 2008 (Fig. 3) and reached their maximum development in August 2008, when oocyte mean diameter was $88.43 \pm 22.53 \mu\text{m}$ (mean \pm SD) and the number of oocytes and spermaries reached approximately 100 per polyp (Fig. 3). Gamete abundance showed a monthly increase during both study years, with a peak in July and August 2008 and a remarkable decrease in October 2008. The number of oocytes per polyp increased from an average of 10 ± 8.64 in April 2008 to ~ 100 in July 2008. Similarly, the number of spermaries increased from 7 ± 4.71 in April 2008 to ~ 100 in July 2008. During the second year of the study (2009), oocytes and spermaries were first detected in March and April, respectively. Although the monthly number of oocytes was very comparable between the 2 study years, the number of spermaries showed higher variability, especially in June (52 ± 30.4 in 2008 vs. 7 ± 4.7 in 2009). The maximal oocyte size found in this study also contrasted with previous findings reported for *C. caespitosa* in the Adriatic Sea (Kružić et al. 2008a). The mean diameter of spawned eggs described by these authors was $416 \pm 73.12 \mu\text{m}$, over 4 times greater than our measurements. Even though Kružić et al. (2008a) estimated oocyte sizes after spawning, the difference in size is extraordinary. To date, only small changes in oocyte sizes of scleractinian corals have been reported during the last month before spawning (Shlesinger et al. 1998).

Oocyte development (in terms of size) were strongly correlated with seawater temperature ($r = 0.80$, $p < 0.05$, Fig. 3). The drastic decrease in number of gametes in October 2008 indicated that spawning occurred at the end of the summer in the Columbretes Islands, a pattern that differs from the spawning period described for the Adriatic Sea (early summer) (Schiller 1993, Kružić et al. 2008a). Several studies have demonstrated that reproductive traits, including the spawning period, vary with latitude and geographic location (Rinkevich & Loya 1979, Kojis 1986, Richmond & Hunter 1990, Fan & Dai 1995, Baird et al. 2009). Seasonal changes in seawater temperature are frequently cited as an important environmental factor controlling gametogenetic cycles or planulae release periods in scleractinian corals (see Richmond & Hunter 1990 and Harrison

2011 for reviews). Accordingly, we could hypothesize that differences in seawater temperature between the Western Mediterranean and the Adriatic Sea could result in a shift in the reproductive cycle of *Cladocora caespitosa*. However, populations in both regions are located at similar latitudes and subjected to similar seasonal seawater temperature regimes (Kružić & Benković 2008 and present study). However, gamete spawning appeared to be related to contrasting periods of seasonal SST regimes: increasing temperatures in the Adriatic versus decreasing temperatures in the Western Mediterranean. Thus, a temperature shift cannot explain the differences reported in gamete spawning, either in time (a >2 -mo lag occurs between spawning in the Adriatic and the Western Mediterranean Seas) or in the seasonal SST regime (decreasing versus increasing SST).

Alternatively, the differences in the reproductive traits (i.e. oocyte size) observed for *Cladocora caespitosa* from the Western Mediterranean and the Adriatic could be due to genetic divergences between these geographic regions. Further analyses using nuclear DNA markers are needed to investigate whether these regional populations correspond to different lineages. In fact, the taxonomy and systematics of the entire order Scleractinia are being reviewed using several genetic markers and results to date have revealed several discrepancies between morphological observations and phylogenetic analyses (Pinzón & LaJeunesse 2011, Budd et al. 2012).

In contrast to the reproductive differences found between *Cladocora caespitosa* populations in both Mediterranean regions investigated to date, our results revealed many reproductive similarities with the coral *Oculina patagonica* (cited as a Mediterranean alien species; Zibrowius 1974). *O. patagonica* has been described as gonochoric in both the Eastern and Western Mediterranean. In both regions, it reached its maximum gonadal development in August (oocyte mean diameter $100 \mu\text{m}$), coinciding with the highest water temperatures (Fine et al. 2001). As our results suggested for *C. caespitosa*, spawning in *O. patagonica* was observed in September, when the temperature began to decrease (Fine et al. 2001). Consequently, our results indicated that the driving factor for gonad development in *C. caespitosa* is directly related to increasing seawater temperatures in summer, although other factors, such as changes in photoperiod, were not investigated and cannot be excluded. As observed by Glynn et al. (2012), coral sexual traits in several taxa demonstrate strong phylogenetic relationships. The similarities

reported here between the reproductive cycles of *C. caespitosa* and *O. patagonica* support recent molecular phylogenies grouping both species within the same family (Oculinidae; Fukami et al. 2008).

Although *Cladocora caespitosa* reefs were abundant in the past history of the Mediterranean Sea (Aguirre & Jiménez 1998), bioconstructions of this coral are currently very rare and should be considered endangered (Kružić & Benković 2008, Kersting & Linares 2012). A thorough knowledge of the sexual reproduction of *C. caespitosa* will allow the design of efficient protection and conservation plans for this emblematic species in the Mediterranean Sea. Further research on this topic is needed to better understand the unusual reproductive plasticity of this temperate coral and how its reproductive biology might affect its ecology.

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