



Phenological and morphological variations in the Mediterranean orange coral *Astroides calycularis* between two distant localities

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ABSTRACT

Studies of intraspecific variation in the presence of different environmental features are essential to improving the knowledge of species population dynamics and structure. *Astroides calycularis* is an azooxanthellate scleractinian coral commonly found in shallow rocky habitats of the southwestern Mediterranean Sea. This study compares the fertilization period of two coral populations located in distantly separated localities; one in an upwelling area off the southern coast of the Iberian Peninsula, and the other on the southwestern coasts of Italy. Colony morphology varied between localities, the former having massive-shaped morphology with densely crowded polyps, the latter having bush-shaped morphology and separated polyps. These differences are possibly due to the different hydrodynamic conditions of their respective habitats. Gonochorism and planula brooding as sexual patterns and conditions of the coral coincide at both sites, but a delay in the timing of fertilization and planulation of the southern Iberian Peninsula population was observed, probably linked to a shift in the time at which seawater reaches its maximum temperature at each site.

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1. Introduction

The reproductive cycle of a species and the factors affecting it are important issues for understanding its population dynamics (Torrents and Garrabou, 2011). In the case of marine invertebrates, reproductive traits are related to environmental conditions, which may change in relation to geographical factors (Olive, 1995). Thus, studies of intraspecific variation in reproductive biology in the presence of different environmental features are essential for improving the knowledge of the geographic variation of life history traits (Giese, 1959; Olive, 1995). Comparisons of coral spawning patterns within a geographic-based framework may reflect regional variations in environmental cycles, and may be suitable for discerning species responses to those variations (Babcock et al., 1994). Some available studies on the sexual reproduction of anthozoans conclude that reproductive traits vary among geographical locations, along latitudinal gradients and between regions (Fan and Dai, 1995; Wilson and Harrison, 2003; Gori et al., 2007).

Sea surface temperature (SST) is one of the main parameters controlling the metabolic rates of marine organisms, which, in turn, affects numerous processes within species developmental rate and

survival (Allen et al., 2006). A slight increase in this parameter can have positive effects on individuals, for example by increasing rates of colony or population growth and larval development (O'Connor et al., 2007). Many marine invertebrates begin to reproduce when a certain temperature level is reached after a period of either increasing or decreasing temperature, or in response to sudden temperature changes (Kinne, 1970; Bates, 2005), often confining their reproductive period to relatively narrow thermal ranges (Riesgo and Maldonado, 2008). Traditionally, SST has been considered the most important seasonal environmental factor that affects reproductive timing of anthozoans; e.g., spawning time has been shown to correspond to the warming of seawater and the time when seawater reaches its annual maximum (Harrison and Wallace, 1990; Baird et al., 2009). SST may change across a species' distribution range, related to geographical factors such as latitudinal gradients (Kain, 1989), and the appearance of oceanographic phenomena such as upwelling (Sarhan et al., 2000). Other parameters such as nutrient availability and sediments, although less studied, have also been regarded as important features for coral fecundity (Séré et al., 2010). Up to now, few studies have compared intraspecific sexual reproductive traits between localities in anthozoans from the Mediterranean Sea (Fine et al., 2001; Gori et al., 2007; Torrents and Garrabou, 2011).

Astroides calycularis (Pallas, 1766) is a colonial scleractinian coral characterized by the bright orange color of its coenosarc and polyps (Zibrowius, 1995). It is an azooxanthellate coral that is found covering relatively large surfaces of vertical walls, cave entrances,

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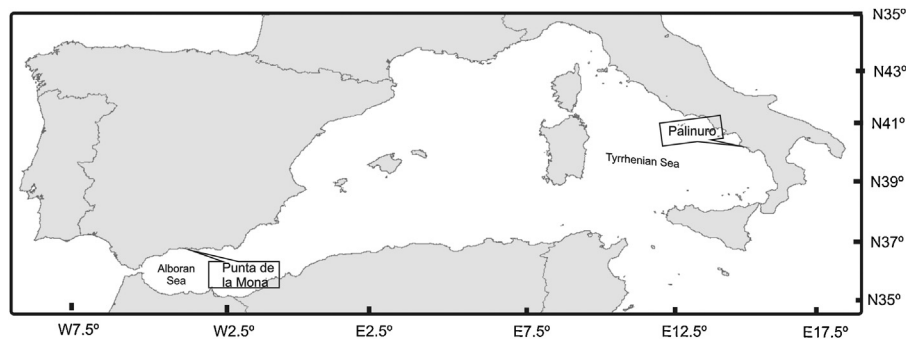


Fig. 1. Sampling sites of *Astroides calycularis*.

overhangs and slopes (Zibrowius, 1995). It is a typical shallow water coral that can be commonly found in abundance, from the intertidal fringe to a depth of 40 m, with lower abundances of the colonies below this level (Kruzic et al., 2002). It has been described as a species with a narrow temperature tolerance (Grubelic et al., 2004). While it was widely distributed in the western Mediterranean during the Pleistocene (Zibrowius, 1995), climatic fluctuations during that period led to a decline in its distribution range, restricting the species to the southwestern basin of the Mediterranean. Currently its presence has been observed on the Atlantic coast of the Iberian Peninsula (Moreno et al., 2008), and some spreading colonies have been observed in the northeastern part of the Adriatic Sea (Kruzic et al., 2002; Casellato et al., 2007). The recent records of this coral in the Adriatic Sea have been related to seawater warming and the prevailing sea current system and the rocky coastal configuration (Grubelic et al., 2004). The sexual reproductive cycle of *A. calycularis* has been previously studied by Goffredo et al. (2010, 2011), who described the different qualitative and quantitative aspects of its reproduction in the locality of Palinuro (Italy, Southern Tyrrhenian Sea).

The present study extends the current knowledge on the sexual reproduction of *A. calycularis* by studying its traits during the late spring–summer seasons of two consecutive years (2009 and 2010) in the locality of Punta de la Mona (South Iberian Peninsula, Alboran Sea) and comparing them with previous assessments from Palinuro (Italy, Southern Tyrrhenian Sea) (Goffredo et al., 2010, 2011). It focuses on the comparison of morphological and quantitative aspects of oogenesis and spermatogenesis between the two localities. The coasts of the newly studied locality are characterized by colder SST compared to Tyrrhenian waters due to the upwelling of deep Mediterranean waters (Sarhan et al., 2000). This difference in SST is expected to influence the reproduction of the study species (e.g., Wilson and Harrison, 2003; Guest et al., 2005; Gori et al., 2007).

2. Materials and methods

2.1. Sampling

A. calycularis samples were collected at Punta de la Mona (Granada, Spain, Alboran Sea, 36°43.13' N; 3°43.629' W) (Fig. 1) from the months of April to August during 2009 and 2010. Data from colonies in the Tyrrhenian Sea (Palinuro, Italy, Southern Tyrrhenian Sea; 40°01.81' N; 15°16.74' E) (Fig. 1) were based on samples collected during the same time period (from April to August) in 2004 and 2005 (Goffredo et al., 2010, 2011). During each sampling period, samples from 10 colonies of the coral were collected by scuba diving in a depth range of 7–10 m. Colonies were at least 2 m apart. Collected samples were fixed in saturated formalin solution (10% formaldehyde and 90% sea water; the solution was saturated with

calcium carbonate) and transferred to the laboratory for histological analysis.

2.2. Sea water temperature

Measurements of SST were taken from publicly available measurement networks of oceanographic parameters. Data for Punta de la Mona during 2009–2010 were available from the Spanish Port System (Ministry of Public Works of Spain; <http://www.puertosdelestado.es>). Data for the locality of Palinuro during 2004–2005 were obtained from the National Mareographic Network of the Agency for the Protection of the Environment and Technical Services (APAT, <http://www.apat.gov.it>). Moreover, available SST data for the years 2000–2010 were obtained from the same data sources and confirmed to behave similarly in both localities (see Section 3.1 for results of statistical analysis and data plotting).

2.3. Biometric analysis

For each colony, the major axis of the colony (colony length, L_c) and the minor axis of the colony (colony width, W_c) were measured, and colony area was calculated using the formula $A_c = \pi((L_c \times W_c)/4)$ (Goffredo et al., 2010). Also, a biometric analysis of each analyzed polyp was performed: major axis of the oral disc (polyp length, L_p), minor axis of the oral disc (polyp width, W_p) and height (oral–aboral axis, h). Body volume was calculated as $V_p = \pi((h \times L_p \times W_p)/4)$ (Goffredo et al., 2010).

2.4. Sexual pattern and gamete development

Histological protocol, polyps' post-fixation, decalcification and tissue staining followed the procedures in Goffredo et al. (2010, 2011). Histological observations were made under a light microscope. Gonadal measurements were made with a Leica 5001 W image analyzer (Leica Microsystems, Wetzlar, Germany). For each polyp, the maximum and minimum diameter of the spermaries and oocytes in nucleated sections were measured. Regarding samples from Punta de la Mona, only mature active polyps (>3–4 mm in length, according to Goffredo et al., 2011) that showed gonads were included in the analysis. Polyps within the above size range that did not show gonads were assumed to belong to male colonies, since female polyps have gonads during the entire year (Goffredo et al., 2010, 2011). The size of each reproductive element was determined as the mean of two diameters (maximum diameter, D and minimum diameter, d , for the nucleated section of oocytes and spermaries in the different developmental stages) and was classified into developmental stages following Goffredo et al. (2010, 2011).

Gamete index was expressed as the percentage of polyp body volume occupied by the gametes (Goffredo et al., 2005). Gamete volume was calculated using the formula $V_0 = (4/3)\pi(D/2) \times (d/2)^2$ (Goffredo et al., 2011), as oocytes and spermaries were ellipsoidal in shape, and total volume of gametes was calculated as the sum of the volumes of all oocytes and spermaries.

Fecundity (F) was expressed at the polyp level as the number of mature oocytes produced per female polyp, using the formula $F = ((A \times B)/C)$ (Goffredo et al., 2011), where A is the length of the “ovary”, based on the number of sections in which oocytes were found; B is the observed frequency of mature oocytes; and C is the size of mature oocytes. At the colony level, fecundity was calculated as the sum of the fecundity estimates for all polyps of the female colony.

2.5. Statistical analyses

Factorial ANOVAs and Spearman correlations were used for statistical comparisons among the quantitative aspects of the sexual reproduction of the coral. Wilcoxon matched paired tests were applied to SST comparisons between months per year and sampling locality, during the years in which samplings were performed. A Kruskal–Wallis test was used to compare SST among studied sites during the ten-year period 2000–2010. All statistical analyses were computed with Statistica 7.0 (StatSoft Inc., Tulsa, OK, USA).

3. Results

3.1. Sea water temperature

SST data for both localities are shown in Fig. 2, for the time series period 2000–2010 and for the sampling periods of the present study. The Wilcoxon matched paired test analysis revealed no significant differences in SST among years within sites (Punta de la Mona: $T=3$, $N=5$, $P=0.46$; Palinuro: $T=5$, $N=5$, $P=0.50$), but did show significant differences between the two localities ($T=6$, $N=10$, $P<0.05$). Mean average values within localities during the sampling period were 20.4 ± 1.8 °C in Punta de la Mona (ranging from 15.1 °C to 25.2 °C) and 21.5 ± 1.9 °C in Palinuro (ranging from 15.4 °C to 25.9 °C). The Kruskal–Wallis test also showed no significant differences within sites among years (Punta de la Mona, $df=8$, $P=0.9$; Palinuro, $df=8$, $P=0.9$), but did show differences among sites ($df=1$, $P=0.005$). Mean average values within localities were 18.5 ± 4.5 °C in Punta de la Mona (ranging from 13.9 °C to 21.7 °C) and 22.0 ± 4.3 °C in Palinuro (ranging from 16.1 °C to 26.3 °C).

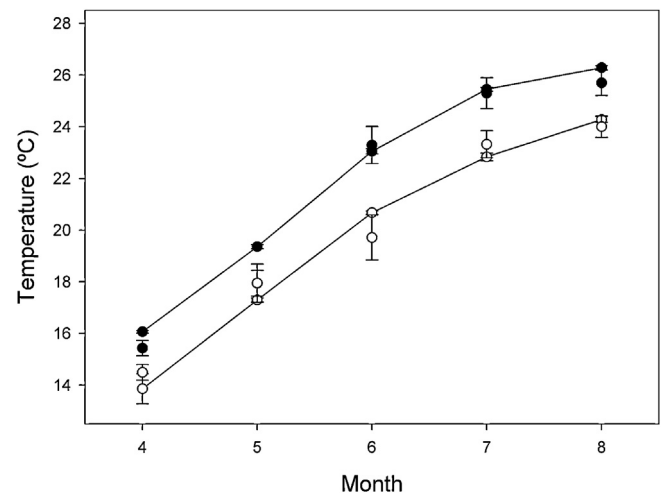


Fig. 2. Monthly average sea surface temperatures over a 10-year time series period. White circles = Punta de la Mona; black circles = Palinuro. Circles above and below the connecting lines represent average temperatures of the sampling periods for the present study.

3.2. Sexual pattern and biometry analysis

A total of 40 colonies and 88 polyps from Punta de la Mona, and 35 colonies and 97 polyps from Palinuro were used for the study (Goffredo et al., 2010, 2011). 20 polyps from Punta de la Mona and 31 polyps from Palinuro were inactive, and therefore assumed to be inactive males after fertilization.

All mature active polyps and colonies from Punta de la Mona were observed to have either female or male germ cells inside the mesenteries, as also seen in colonies from Palinuro. Therefore colonies from both sites were gonochoric, both at the polyp and the colony level.

Colonies in both localities were ellipsoidal in shape, but colony morphology differed between the two localities. Polyps in the colonies from Punta de la Mona were densely crowded, showing a massive-shaped morphology (Fig. 3); Palinuro polyps appeared separated, showing a bush-shaped morphology.

The biometric variables measured (L_c , W_c , A_c) did not differ significantly between female and male colonies either at Punta de la Mona or at Palinuro (factorial ANOVA, $P>0.20$, data not shown), or between localities (Table 1).

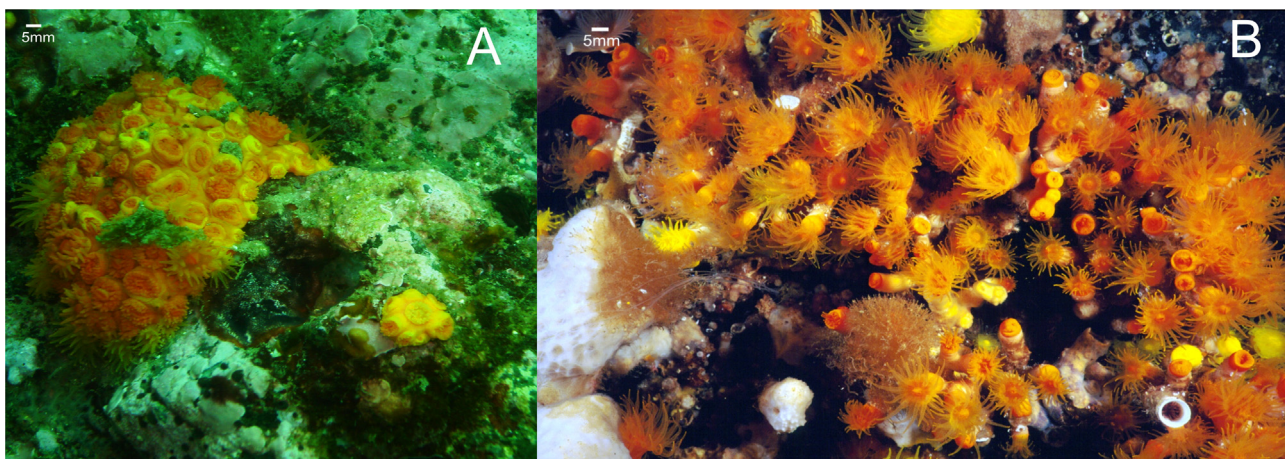


Fig. 3. (A) A colony of *Astroides calycularis* photographed at Punta de la Mona showing a massive-shaped morphology, in which polyps inside the colony are densely crowded and (B) colonies photographed at Palinuro showing a bush-shaped morphology, in which polyps are separated from each other.

Table 1
Biometric parameters (mean \pm SE) of *Astroides calycularis* colonies from Punta de la Mona (this study) and Palinuro (Goffredo et al., 2011). L_c = major axis of the colony; W_c = colony width; A_c = colony area.

	Punta de la Mona		Palinuro		Comparison between localities
	Females (N=20)	Males (N=20)	Females (N=16)	Males (N=19)	
L_c (cm)	5.47 \pm 1.84	5.55 \pm 1.43	5.37 \pm 2.04	6.08 \pm 1.88	$F_{(1,74)} = 0.01, P = 0.92$
W_c (cm)	4.12 \pm 0.98	4.31 \pm 1.09	4.14 \pm 1.50	4.44 \pm 1.62	$F_{(1,74)} = 0.05, P = 0.81$
A_c (cm ²)	18.91 \pm 10.40	19.26 \pm 8.70	19.41 \pm 14.55	23.36 \pm 14.63	$F_{(1,74)} = 0.18, P = 0.66$

Table 2
Biometric parameters (mean \pm SE) of *Astroides calycularis* polyps from Punta de la Mona (this study) and Palinuro (Goffredo et al., 2011). L_p = major axis of the polyp; W_c = minor axis of the polyp; h = height oral–aboral pole; V_p = polyp volume.

	Punta de la Mona		Palinuro		Comparison between localities
	Females (N=43)	Males (N=45)	Females (N=49)	Males (N=48)	
L_p (mm)	7.85 \pm 2.05	7.82 \pm 1.76	5.21 \pm 0.71	5.01 \pm 0.76	$F_{(1,184)} = 96.00, P < 0.01$
W_p (mm)	6.04 \pm 1.79	6.84 \pm 1.58	4.88 \pm 0.76	4.78 \pm 0.77	$F_{(1,184)} = 40.69, P < 0.01$
h_p (mm)	7.17 \pm 2.66	7.18 \pm 2.04	5.18 \pm 1.24	4.97 \pm 1.20	$F_{(1,184)} = 32.43, P < 0.01$
V_p (mm ³)	297.20 \pm 193.74	332.57 \pm 214.68	108.4 \pm 47.28	98.57 \pm 41.38	$F_{(1,184)} = 58.75, P < 0.01$

At the polyp level, the biometric variables (L_p , W_p , h_p , V_p) did not differ significantly between female and male polyps within localities (factorial ANOVA, $P > 0.09$, data not shown). However, significant differences were found between localities (Table 2), with polyps from Punta de la Mona being larger in size than those from Palinuro.

(Spearman rank correlation $r_{Ac} = 0.88, P < 0.05$). At this level, a mean of 472.33 ± 107.71 mature oocytes were found in mean-sized female colonies of $A_c = 13.46 \pm 3.74$ cm² ($L_c = 4.47 \pm 0.71$ cm; $W_c = 3.40 \pm 0.41$ cm; $N = 15$ colonies collected during the fertilization period from February to May).

3.3. Gamete development

Spermaries and oocytes from mature active polyps followed the characteristics described in Goffredo et al. (2010).

Spermatogenic indexes decreased in both localities as late spring–summer season advanced; in June, remaining spermaries were visible only at Punta de la Mona. The ovogenic index was higher in Punta de la Mona during the month of May (Fig. 4), and started decreasing in Palinuro during February–March (see Fig. 3 from Goffredo et al., 2011).

During the studied period, only spermaries in developmental stages III–V were found in both localities (Fig. 5), while developmental stage II was only found in Punta de la Mona in April. During June, no spermaries were found in Palinuro, but spermaries in stages IV and V were still found in Punta de la Mona (Fig. 5).

In Punta de la Mona, the number of mature oocytes ($>400 \mu\text{m}$) was found to increase from April to June (Fig. 6) and then decline again, indicating that the fertilization period ended in June. Mature oocytes ranged from 400 to 1960 μm . At the polyp level, 40 ± 10 mature oocytes (mean \pm SE, hereafter) were found in mean-sized female polyps of $V_p = 300.6 \pm 38.8$ mm³ ($L_p = 7.8 \pm 0.35$ mm; $W_p = 6.56 \pm 0.33$ mm; $h_p = 6.43 \pm 0.47$ mm; $N = 29$). At the colony level, fecundity also varied with colony area, with an average of 1135.93 ± 209.42 mature oocytes found in colonies of 18.24 ± 2.55 cm² in area ($L_c = 5.49 \pm 0.46$ cm; $W_c = 4.02 \pm 0.24$ cm; $N = 27$). There was a positive correlation between polyp length and fecundity (Spearman rank correlation $r_{Lp} = 0.42, N = 27, P = 0.03$), and a slight positive correlation was found between colony area and colony fecundity (Spearman rank correlation $r_{Ac} = 0.52, N = 14, P = 0.045$).

In the locality of Palinuro, fertilization occurred from February to May (Goffredo et al., 2011). During this period, mature oocytes ranged from 400 to 1590 μm . At the polyp level, a mean of 14 ± 2 mature oocytes were found in mean-sized female polyps of $V_p = 92.81 \pm 9.71$ mm³ ($L_p = 4.67 \pm 0.21$ mm; $W_p = 4.33 \pm 0.20$ mm; $h = 4.93 \pm 0.22$ mm; $N = 42$), with a positive correlation between polyp length and fecundity (Spearman rank correlation $r_{Lp} = 0.56, P < 0.05$). At the colony level, fecundity varied with colony area

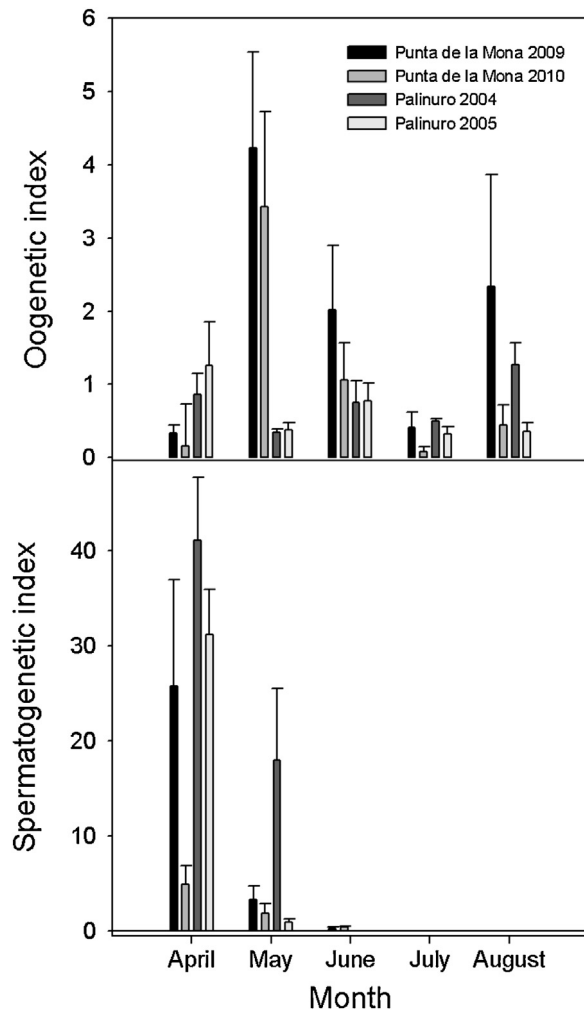


Fig. 4. Variation in gametic indexes of *Astroides calycularis* during the studied periods in both localities.

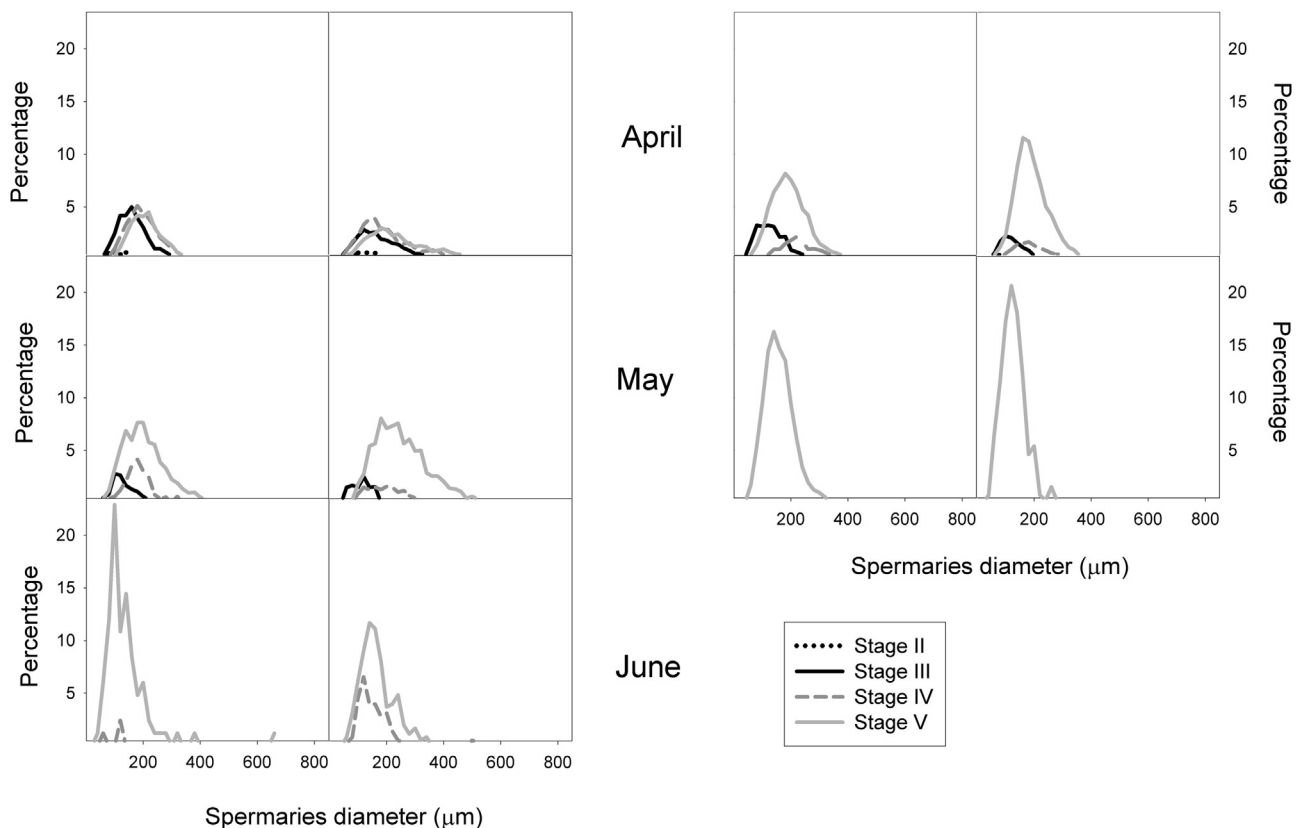


Fig. 5. Size–frequency distribution of the four stages of spermary maturation in *Astroides calycularis* samples collected during the months in which spermaries were present in both localities (April to June). Plots on the left side correspond to Punta de la Mona (this study), plots on the right side to Palinuro (Goffredo et al., 2011).

In both localities, embryos were found in the coelenteric cavity, and gastrulation was observed to take place by delamination. Moreover, in both localities, lipid vesicles were present inside the embryos, as well as inside the oocytes during the different stages of oogenesis. In Punta de la Mona, early stereoblastulae (solid and lacking a blastocoel; 481–802 μm in diameter) and intermediate stereogastrulae (a visible layer of cells surrounding the yolk mass; 653–917 μm) were observed during June 2009 (two female polyps) and July 2010 (three female polyps), when SST was 20–23 °C. In the locality of Palinuro, embryos were found in polyps collected during May. Stereoblastulae had diameters of 556–964 μm , and stereogastrulae had diameters of 991–1134 μm . In both localities planula larvae were observed in the field either in the female polyp tentacles or attached to the vertical wall and to other invertebrates. Planulation at Punta de la Mona was observed from the second week of June until the end of July, when SST was 20–23 °C; in contrast, planulation in Palinuro took place between May and July (both in 2004 and 2005), when SST was 17–23.0 °C.

4. Discussion

This study extends the current knowledge on the reproductive cycle and morphology of the Mediterranean coral *A. calycularis* by comparing the morphological and reproductive features of colonies in two distant localities, one in the northern Alboran Sea and the other in the southern Tyrrhenian basin.

The sexual pattern and condition observed in colonies of *A. calycularis* from the locality of Punta de la Mona (northern Alboran Sea) are in concordance with the morphologic analysis of sexual reproduction carried out by Goffredo et al. (2010), which characterizes *A. calycularis* as gonochoric at both the polyp and colony level in Palinuro (southern Tyrrhenian Sea). However, this contradicts

the observations made by Lacaze-Duthiers (1893) with a magnifying glass on dissected polyps from colonies sampled from Algerian coasts. The latter author described the colonies of the species to be hermaphroditic, formed mainly by sex-separated polyps, with some rare cases of simultaneous hermaphroditic polyps. Nevertheless, all the studies performed to date conclude that *A. calycularis* is a brooder species. Even though currently available data suggest that sexual patterns are generally consistent within most of the corals (Harrison, 2011), species changing sexual condition in different populations have been described in the literature. A case in point is the scleractinian reef builder coral *Diploastrea heliopora*, first classified as gonochoric on the Great Reef Barrier (Guest et al., 2005), but recorded to have colonies with hermaphroditic polyps, showing concurrent male and female gametes (Guest et al., 2012) in Singapore. As suggested by Guest et al. (2012), polyps within colonies of *D. heliopora* might be predominantly of a single sex but exhibit alternate sexual function with overlap occurring when the end of one gametogenic cycle coincides with the beginning of the next cycle. In other species, such as *Stylophora pistillata*, unidirectional protandry has been regarded as related to colony size and age (Rinkevich and Loya, 1979). Studies carried out with corals from the family Fungiidae also show bidirectional sex change in this family (Loya and Skai, 2008). Moreover, in octocorals, such as the alcyonarian *Sarcophyton glaucum*, changes in sexual traits have also been observed (Schleyer et al., 2004). Therefore, the possibility that *A. calycularis* might express a different sexuality in populations other than those of Palinuro and Punta de la Mona cannot be ruled out.

Colony morphology varied between localities, probably due to the differences in habitat at the sampling sites; samples from Punta de la Mona were collected on a vertical wall exposed to sea waves and high levels of hydrodynamism, while samples from Palinuro were collected near the entrance of a cave. These two morphologies

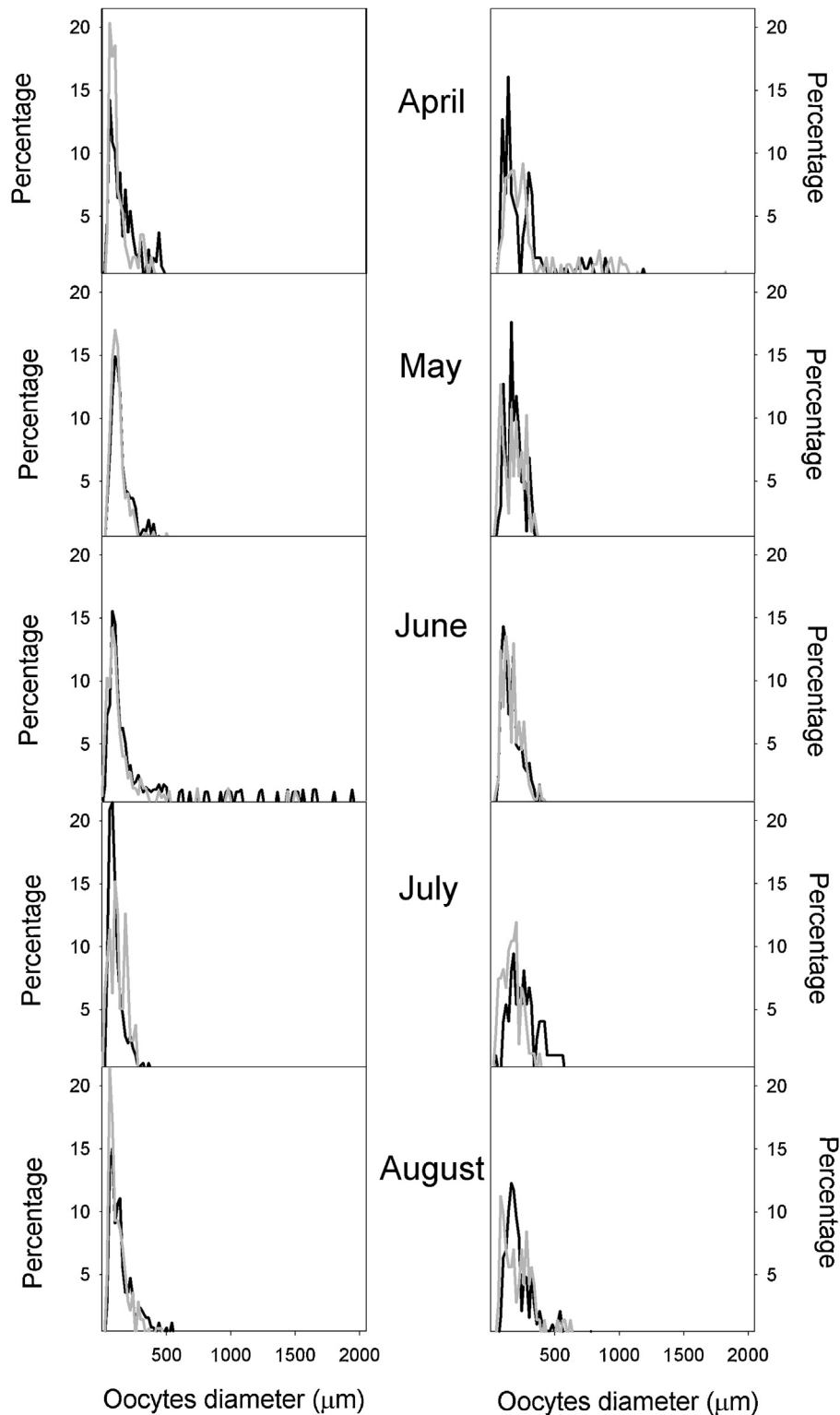


Fig. 6. Size–frequency distribution of oocytes of *Astroides calycularis*. Plots on the left side correspond to Punta de la Mona, plots on the right side to Palinuro. For both localities, black lines indicate first year samples, gray lines indicate second year samples.

have been previously described by Zibrowius (1980) and Kruzic et al. (2002). These authors mention that colonies near the surface (high hydrodynamism) have a massive-shaped morphology with densely crowded polyps and with corallites that have a circular or polygonal calix. In these colonies the new polyps bud both in the outskirts and between existing polyps. On the other hand, in deeper waters and sheltered areas such as caves, colonies appear

to have a bush-shaped morphology with separated polyps that bud at different heights of the calyx. Here, corallites show a circular calix.

It is understood in biology that phenotypic differences among individuals and species are related to differences in their ecology (Travis, 1994). In the case of *A. calycularis*, water movement is suggested to be the factor driving this morphological

plasticity. Todd (2008) provides a detailed review on the morphological plasticity of corals and the influence of environmental factors. This author found that the main environmental factors affecting morphological plasticity are light, seawater movement, sediment and nutrient availability. Similarly, Kaandorp (1999) noted that the degree of compactness in *Millepora alcicornis* and *Pocillopora damicornis* increased with increasing hydrodynamism. While this morphological feature could also be due to the strong genetic dissimilarities found among the species populations at the eastern and western limits of distribution (Casado-Amezúa et al., 2012), the most plausible factors are the differences in environmental conditions to which the colonies are exposed, since massive-shaped colonies have also been observed in the Aeolian Islands (156 km off Palinuro) (S. Goffredo, pers. obs.).

On the other hand, colonies from Punta de la Mona showed an average number of mature oocytes per colony area that was almost six times larger than that of colonies from Palinuro. The colony size of modular organisms affects the allocation of energy to reproduction (Hall and Hughes, 1996), suggesting that the relative investment in growth declines with colony size, allowing more energy for sexual reproduction (Goffredo and Lasker, 2006). In the case of coral reef builders, Hall and Hughes (1996) found a positive correlation between colony size and colony fecundity when comparing different corals from the Great Barrier Reef with different sizes and morphologies at the intraspecific level. As has been found in gorgonians, reproductive output is influenced by the density of polyps in the colony, with a positive relationship between colony size and fecundity (Beiring and Lasker, 2000; Tsounis et al., 2006). However, these differences in the average number of oocytes per colony area could also be due to differences in nutrient availability between the studied sites. The Mediterranean Basin is generally oligotrophic, but characterized by strong environmental gradients, following an eastern–western distribution (Coll et al., 2010). The locality of Punta de la Mona is influenced by the upwelling of deep waters associated with the geostrophic front generated by the Atlantic jet (Sarhan et al., 2000) in synergy with upwelling events induced by westerlies. These events lead to high productivity in the Western Alboran Sea, as reflected by the usually high annual chlorophyll-*a* concentrations found in this area, which are in the range of 0.05–4.3 µg/l, with chlorophyll levels being higher during the spring period (Mercado et al., 2005). This is in contrast to chlorophyll-*a* concentration values found in the area where Palinuro is located, which are in the range of 0.3–0.85 µg/l (Berline et al., 2012). Usually, higher levels of nutrients are detrimental to oocyte production (Ward and Harrison, 2000; Ferrier-Pagès et al., 2003), but some studies like that by Bongiorno et al. (2003) show a strong correlation between nutrient availability and the number of oocytes per polyp in two corals subjected to in situ fish-farm nutrient enrichment. Thus, even if the most plausible reason for the higher fecundity in massive-shaped colonies from Punta de la Mona might be the size and shape of the polyps, another possible factor might be nutrient availability in these colonies. *A. calycularis* is an azooxanthellate coral whose crucial means of survival is plankton feeding (Fenner et al., 2010). Even if the importance of planktonic food to corals remains controversial (Anthony and Fabricius, 2000) and little is known about the food-capturing abilities of polyps (Todd, 2008), most corals are heterotrophic and it seems possible that heterotrophy could drive skeletal change.

The results of the present study show a delay in the sexually reproductive period of *A. calycularis* in Punta de la Mona compared to Palinuro. In the former locality, mature oocytes, and even mature spermaries (stages IV and V), were seen mainly in June, while the fertilization period was described to be during February to May in Palinuro, as shown by the disappearance of mature oocytes and

the increase of mature spermaries in May (Fig. 3; see also Goffredo et al., 2011). In Punta de la Mona, embryos were found in the coelenteric cavity during June and July (SST 20–23 °C), while in Palinuro they were observed in May (SST 19 °C). In Punta de la Mona planula release was observed from the middle of June to the end of July, when SST was 20–23 °C (P. Casado-Amezúa, pers. obs.). Planulation during this period has been observed since 2008, coinciding with the period when SST reaches 18 °C (Terrón-Singler, 2011). In the locality of Palinuro planulation was observed to take place between May and July, when SST was 19–25 °C. Differences in timing among allopatric populations of a species, as in the case of *A. calycularis*, may represent adaptations to local environmental parameters (Richmond and Hunter, 1990). Annual mean sea surface temperature in the Mediterranean shows a high seasonality and a strong gradient from west to east and from north to south (Coll et al., 2010). Moreover, in Palinuro seawater reaches its maximum temperature earlier than in Punta de la Mona. SST in Punta de la Mona is influenced by the upwelling of deep waters, with this phenomenon being more evident in the summer when the thermal contrast is greater, as observed in infrared satellite images (La Violette, 1984), and more noticeable near the coast when another factor, namely the strong western winds, transports the water offshore where it sinks and meets less dense waters from the Atlantic (Sarhan et al., 2000). Thus, this phenomenon can cause marked SST declines during the spring/summer seasons. Therefore, these factors might be responsible for the delay observed in the fertilization of *A. calycularis* in Punta de la Mona.

The role of SST in controlling the reproductive cycle of coral species has been previously documented in Pacific stony corals with a broadcasting reproductive mode (e.g., Glynn et al., 2008; Putron and Rylan, 2009) showing that when other abiotic parameters appear to be stable, the timing of the reproductive season corresponds to species-specific temperature responses, with latitudinal variations across varying temperature profiles. Several scleractinian species from inshore and offshore reefs at the Great Barrier Reef have been observed to spawn within one month of each other, a feature that is suggested to be due to differences in increasing SST (Babcock et al., 1986). Other studies with scleractinian species from the central and lower Caribbean show relative homogeneity in spawning timing as similar oceanographical conditions mitigate the annual changes in seawater temperature (Soong, 1991; Steiner, 1995). In other anthozoans, such as the brooder gorgonians *Paramuricea clavata* and *Eunicella singularis*, the fertilization period has been observed to coincide with increases in SST in spring; however, a shift in SST increase was observed between localities, also affecting the fertilization timing of the gorgonians (Gori et al., 2007). Other factors that may contribute to differences in spawning time are lunar activity and daylight (Babcock et al., 1994; Glynn et al., 2008). All these factors ultimately act on reproductive features, i.e. physiological parameters, fertilization enhancement and predator avoidance (Oliver et al., 1988).

Thus, the present study contributes to the knowledge on the population dynamics and structure of Mediterranean scleractinian corals, important habitats for various marine species due to their bioconstruction, by showing their phenological and morphological responses to different environmental conditions. Studies such as this one are important for a better understanding of species responses in different geographical conditions. Moreover, it is suggested that mesocosm experiments could further clarify the dependence of the sexual reproductive cycle of these species on changing parameters (i.e., temperature and nutrients), and plasticity experiments (i.e., transplanting colonies from different habitats) could provide a more complete picture of their morphological plasticity.

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