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Phenological and morphological responses of the Mediterranean coral *Astroides calycularis* to environmental conditions

Resumen

Estudios acerca de la variación intraespecífica en la presencia de diferentes características ambientales son esenciales para mejorar el conocimiento de la dinámica de las poblaciones. La temperatura superficial del agua (SST por sus siglas en inglés) juega un papel fundamental en el período de maduración gonadal de los corales escleractinios. *Astroides calycularis* es un coral escleractinio azooxanthelados que se encuentran comúnmente en hábitats rocosos poco profundos del suroeste del mar Mediterráneo. Este estudio compara el periodo de maduración gonadal del coral entre dos localidades distantes con diferentes SST, una en la costa sur de la Península Ibérica (promedio de SST 20,4 ± 1,8 º C), y la otra en la costa suroeste de Italia (promedio de SST 21,5 ± 1,9 º C). La colonias presentaban morfologías diferentes entre localidades, las colonias colectadas en la primera localidad presentaban una morfología “masiva” (i.e. colonias con gran densidad de pólipos), mientras que en la localidad de Italia las colonias mostraban una morfología “ramificada” (i.e. pólipos separados en el interior de las colonias), y los pólipos separados. Estas diferencias se deben posiblemente a las diferentes condiciones hidrodinámicas de sus respectivos hábitats. Gonocorismo e incubación de la plánula como condición y patrón sexual del coral coincidieron en ambas localidades, pero en relación a los aspectos cuantitativos de la gametogénesis, se observó un retraso en la maduración gonadal y planulación de la población del sur de la Península Ibérica con respecto a la del suroeste del mar Tirreno, ligado al periodo en el que el agua alcanza el máximo de temperatura anual en ambas áreas.

Abstract

Studies of intraspecific variation in the presence of different environmental features are essential in improving the knowledge of species population dynamics and structure. Sea surface temperature (SST) plays a fundamental role on the fertilization period of scleractinian corals. *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 the coral between two distant localities with different sea surface temperatures; one in the southern coast of the Iberian Peninsula (average SST 20.4±1.8ºC), and the other in the southwestern coasts of Italy (average SST 21.5±1.9ºC). Colony morphology varied between localities, the former having “massive” morphology with densely
crowded polyps, the latter having “branchy” 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 in both sites, but a delay in the timing of fertilization and planulation of the southern Iberian Peninsula population was observed, linked to a shift in the period that seawater reaches its maximum temperature in both sites.

**Introduction**

The reproductive cycle of a species and the factors affecting it are important issues to better understand its population dynamics (Torrents & Garrabou 2011). In the case of marine invertebrates, reproductive traits are related to environmental conditions, which may change in relation with geographical factors (Olive 1995). Thus, studies of intraspecific variation in reproductive biology in the presence of different environmental features are essential in 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 & Dai 1995; Wilson & 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 & Maldonado 2008). Traditionally SST has been considered as the most important seasonal environmental factor that affects reproductive timing of anthozoans, such that spawning time has been shown to correspond to the warming of seawater and the time when seawater reaches its annual maximum (Harrison & 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 (Sarahn et al. 2000). Up to now, few studies have been done comparing intraspecific sexual reproductive traits between localities in anthozoans from the Mediterranean Sea (Fine & Loya 2001; Gori et al. 2007; Torrents & 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, 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 (Kružić et al. 2002). It has been described as a species with a narrow temperature tolerance (Grubelíc et al. 2004). Despite it was widely distributed in the western Mediterranean during the Pleistocene (Zibrowius 1995), climatic fluctuations occurred during that period lead to a regression in its distribution range, restricting the species to the southwestern basin of the Mediterranean. Currently, its presence has been observed in the Atlantic coast of the Iberian Peninsula (Moreno et al. 2008), and some spread colonies have been cited in the northeastern part of the Adriatic Sea (Casellato et al. 2007; Kružić et al. 2002). The recent records of this coral into the Adriatic Sea have been related to the seawater warming together with the prevailing sea current system and the rocky coastal configuration (Grubelíc et al. 2004). A. calycularis sexual reproductive cycle has been previously documented 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).

This study extends the current knowledge on the sexual reproduction of A. calycularis, by studying its traits during the late spring-summer in the locality 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). We focus on the comparison of morphological and quantitative aspects of oogenesis and spermatogenesis between the two localities. The coasts of the new 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 & Harrison 2003; Guest et al. 2005; Gori et al. 2007).

**Material and Methods**

**Sampling**

A. calycularis samples were collected at Punta de la Mona (Granada, Spain, Alboran Sea, 36º43.13’N; 3º43.629’W) (Fig. 1) from the months of April to August during 2009-2010. Data from colonies from Palinuro (Italy, Southern Tyrrhenian Sea; 40º01.81’N; 15º16.74’E) (Fig. 1) was based on Goffredo et al. (2010, 2011).

In both localities, samples were collected by scuba diving in a depth range from 7-10 m. Colonies were at least 2 m apart. Collected samples were fixed in
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saturated Formalin solution (10% formaldehyde and 90% sea water; the solution was saturated with calcium carbonate) and transferred to the laboratories for histological analysis.

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 \( A_c = \pi \frac{L_c \times W_c}{4} \) (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 \( V_p = \pi \frac{h \times L_p \times W_p}{4} \) (Goffredo et al. 2010).

Sexuality pattern and gamete development

Histological protocol, polyps post-fixation, decalcification and tissue staining followed the conditions 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. At 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, according to the fact that only female polyps had gonads during all the year (Goffredo et al. 2010, 2011). The size of each reproductive element was determined as the mean of the 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. (2005, 2011).

Gamete index was expressed as the percentage of polyp body volume occupied by the gametes (Goffredo et al. 2005). Gamete volume was estimated using the formula \( V_p = \frac{4}{3} \pi \left( \frac{D}{2} \right) \left( \frac{d}{2} \right)^2 \) (Goffredo et al. 2011), as oocytes and spermaries were ellipsoidal.
in shape, and volume of gametes was calculated as the sum of the volume of each oocyte or spermary.

Fecundity was expressed at the polyp level as the number of mature oocytes produced per female polyp, using the formula $F = \frac{A \times B}{C}$ (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 each polyp of the female colony.

**Sea water temperature**

As in other studies on anthozoan reproduction (e.g. Fine et al. 2001; Neves & Pires 2002; Gori et al. 2007), measurements of SST were taken from publicly available measurement networks of oceanographic parameters. Data from locality of Punta de la Mona during years 2009-2010 was available from the Spanish Port System (Ministry of Public Works of Spain; http://www.puertosdelestado.es). Data from years 2003-2004 from the locality of Palinuro was obtained from the National Mareographic Network of the Agency for the Protection of the Environment and Technical Services (APAT, http://www.apat.gov.it).

**Statistical analyses**

Factorial ANOVA, and Spearman correlation, were used for statistical comparisons among the quantitative aspects of the sexual reproduction of the coral. Wilcoxon Matched Paired test were applied to SST comparisons between months per year and sampling locality. All statistical analyses were computed Statistica 7.0. (StatSoft, Inc) software.

**Results**

**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. Twenty 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 colony level.

Colonies in both localities were ellipsoidal in shape, but different colony morphology was observed between the localities. Polyps inside the colonies from Punta de la Mona were densely crowded, showing a “massive” morphology
Palinuro polyps appeared separated showing a “branchy” morphology.

No statistical significance was found in the biometric variables measured \( (L_c, W_c, A_c) \) between female and male colonies either at Punta de la Mona or Palinuro (Factorial ANOVA \( P>0.20 \), data not shown), even between localities (Table 1).

At the polyp level, no statistical significance was found in the biometric variables \( (L_p, W_p, h_p, V_p) \) between female and male polyps within localities (Factorial ANOVA \( P>0.09 \), data not shown). However, significant differences were found between localities among measured polyps (Table 2), with polyps from Punta de la Mona being larger in size than those from Palinuro.

Figure 2. A) colony photographed at Punta de la Mona showing the “massive” morphology, in which polyps inside the colony are densely crowded. B) colonies photographed at Palinuro showing “branchy” morphology, in which polyps are separated from each other.

Table 1. Biometric parameters (mean±SE) of colonies from Punta de la Mona (this study) and Palinuro (Goffredo et al. 2010, 2011). \( L_c \)=major axis of the colony; \( W_c \)=colony width; \( A_c \)=colony area

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<tr>
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<th>Punta de la Mona</th>
<th>Palinuro</th>
<th>Between localities</th>
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<tr>
<td></td>
<td>Females (N=20)</td>
<td>Males (N=20)</td>
<td>Females (N=16)</td>
</tr>
<tr>
<td>( L_c ) (cm)</td>
<td>5.47±1.84</td>
<td>5.55±1.43</td>
<td>5.37±2.04</td>
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<tr>
<td>( W_c ) (cm)</td>
<td>4.12±0.98</td>
<td>4.31±1.09</td>
<td>4.14±1.50</td>
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<tr>
<td>( A_c ) (cm²)</td>
<td>18.91±10.40</td>
<td>19.26±8.70</td>
<td>19.41±14.55</td>
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Gamete development

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

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

Table 2. Biometric parameters (mean±SE) of polyps from Punta de la Mona (this study) and Palinuro (Goffredo et al. 2010, 2011). Lp=major axis of the polyp; Wp=minor axis of the polyp; h=height oral-aboral pole; Vp=polyp volume.

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<th>Punta de la Mona</th>
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<tr>
<td></td>
<td>Females (N=43)</td>
<td>Males (N=45)</td>
<td>Females (N=49)</td>
</tr>
<tr>
<td>Lp (mm)</td>
<td>7.85±2.05</td>
<td>7.82±1.76</td>
<td>5.21±0.71</td>
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<tr>
<td>Wp (mm)</td>
<td>6.04±1.79</td>
<td>6.84±1.58</td>
<td>4.88±0.76</td>
</tr>
<tr>
<td>hp (mm)</td>
<td>7.17±2.66</td>
<td>7.18±2.04</td>
<td>5.18±1.24</td>
</tr>
<tr>
<td>Vp (mm3)</td>
<td>297.20±193.74</td>
<td>332.57±214.68</td>
<td>108.4±47.28</td>
</tr>
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During the studied period, only spermaries from development stages III to V were found in both localities (Fig. 4), 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 the IV and V stages were still found in Punta de la Mona (Fig. 4).

In Punta de la Mona, mature oocytes (>400µm) frequencies were found to increase from April to June (Fig. 5), indicating that the fertilization period finished in June. Mature oocytes ranged from 400 to 1960 µm. At the polyp level, 40 ± 10 mature oocytes (mean ± SE, hereafter) were found in mean-sized female polyps of $V_p = 300.6 \pm 38.8 \text{ mm}^3$ ($L_p = 7.8 \pm 0.35 \text{ mm}$; $W_p = 6.56 \pm 0.33 \text{ mm}$; $h_p = 6.43 \pm 0.47 \text{ mm}$; $N = 29$). 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 ($L_c = 5.49 \pm 0.46 \text{ cm}$; $W_c = 4.02 \pm 0.24 \text{ cm}$; $N = 27$). 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 $r_{Ac} = 0.52$, $N = 14$, $P = 0.045$). Meanwhile, in the locality of Palinuro, fertilization occurred from February to May (Goffredo et al. 2011). During this period, mature oocytes ranged from 400 to 1590µm. At the polyp level, a mean of 14 ± 2 mature oocytes were found in mean-sized female polyps of $V_p = 92.81 \pm 9.71 \text{ mm}^3$ ($L_p = 4.67 \pm 0.21 \text{ mm}$; $W_p = 4.33 \pm 0.20 \text{ mm}$; $h = 4.93 \pm 0.22 \text{ mm}$; $N = 42$), 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 (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 $A_c = 13.46 \pm 3.74 \text{ cm}^2$ ($L_c = 4.47\pm0.71 \text{ cm}$; $W_c = 3.40\pm0.41 \text{ cm}$; $N = 15$ colonies collected during the fertilization period from February to May). 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 stereoblastula (solid and lacking a blastocel; 481-802 µm in diameter) and intermediate stereogastrula (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. Planula larvae were seen in the field from the second week of June until the end of July. In the locality of Palinuro, embryos were found in polyps collected during May. Steroblastulae had diameters of 556-964 µm, and stereogastrulae had diameters of 991-1134 µm. Planulation in this locality took place between May and July (both in 2004 and 2005), when SST was 19-25.0°C.

**Sea water temperature**

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 significant differences between 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) (Fig. 6).

![Figure 3. Variation in gametic indexes during the studied period.](image_url)
This study is in concordance with the morphologic analysis on the sexual reproduction carried out by Goffredo et al. (2010), which characterizes *Astroides calycularis* as gonochoric at both the polyp and colony level in the Tyrrhenian Sea. Moreover, it contradicts the observations made by Lacaze-Duthiers (1873) 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 actual 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. Such is the case of 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* could be predominantly of a sin-

Figure 4. Size-frequency distribution of the four stages of spermaries maturation. Left plots represent Punta de la Mona years 2009-2010 (this study), right ones Palinuro years 2003-2004 (Goffredo et al. 2011), black lines year represents first year samples, grey lines second year samples.

**Discussion**

This study is in concordance with the morphologic analysis on the sexual reproduction carried out by Goffredo et al. (2010), which characterizes *Astroides calycularis* as gonochoric at both the polyp and colony level in the Tyrrhenian Sea. Moreover, it contradicts the observations made by Lacaze-Duthiers (1873) 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 actual 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. Such is the case of 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* could be predominantly of a sin-
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 related to colony size and age (Rinkevich & Loya 1979). Studies carried out with corals from the family Fungiidae, also show bidirectional sex change in this family (Loya & 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 Palinuro and Punta de la Mona cannot be ruled out.

Colony morphology varied between localities, probably due to the differences in habitat of the sampling sites; samples from Punta de la Mona were collected on a vertical wall exposed to sea waves and high levels of hydrodynamism and samples from Palinuro were collected near the entrance of a cave. These two morphologies have been previously described by Zibrowius (1980) and Kruzic et al. (2002). These authors mention that near the surface (high hydrodynamism) colonies have a massive morphology with densely crowded polyps and corallites 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 “branchy” morphology with separated polyps that are budded at different heights of the calyx. In the latter morphology 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 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, nutrients, sediment and nutrient availability.

![Figure 5. Size-frequency distribution of oocytes. Left plots correspond with Punta de la Mona and right ones with Palinuro. Black lines of both localities, indicate first year samples, grey lines indicates second year samples.](image)
Similarly, Kaandorp (1999) noted that the degree of compactness in *Millepora alcicornis* and *Pocillopora damicornis* increased with increasing hydrodynamism. On the other hand, colonies from Punta de la Mona showed an average number of mature oocytes per colony area, almost six times larger than colonies from Palinuro. Colony size of modular organisms affects the allocation of energy into reproduction (Hall & Hughes 1996), suggesting that the relative investment in growth declines with colony size, allowing more energy for sexual reproduction (Goffredo & Lasker 2006). As 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 size and morphology 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 relation between colony size and fecundity (Beiring & Lasker 2000; Tsounis et al. 2006).

The results show a delay in the sexually reproductive cycle of *A. calycularis* in Punta de la Mona compared to Palinuro. In the former locality, despite the lack of data during the previous months, mature oocytes were seen until June, and even mature spermarys were seen in the same month. The fertilization period was described to be during February to May in Palinuro, as shown by the disappearance of mature oocytes and the increase in spermarys in developmental stage V (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). Planula release was observed from the middle of June to the end of July in Punta de la Mona, when SST was 20-23°C (P. Casado-Amezúa Pers obs). Planulation during this period has also been seen since 2008, coinciding with the period when SST reaches 18°C (Terrón-Singler et al. 2011). Planulation in the locality of Palinuro was observed to take place between May and July, when SST was 19-25°C. There is a shift in the period that seawater reaches its maximum temperature from Punta de la Mona in comparison to Palinuro. 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 is more noticeable near the coast when another factor, namely the strong western winds, transport the water offshore where it sinks meeting less dense waters from the Atlantic (Sarhan et al.

![Figure 6. Monthly averages sea surface temperatures. White circles Punta de la Mona; black circles: Palinuro.](image-url)
2000). Thus, this phenomenon can cause marked SST declines during the spring-summer seasons. Therefore, these features could be responsible for the delay observed in the fertilization timing of *A. calycularis*.

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). Specifically, 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. 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 the spring; however, between localities a shift in SST increase was observed also affecting the fertilization timing of the gorgonians (Gori et al. 2007). Other factors that can contribute to differences in spawning timing are lunar activity and daylight (Babcock 1994; Glynn et al. 2008) or physiology to enhance fertilization, and predator avoidance (Oliver et al. 1988).

Thus, this study contributes to the knowledge on the population dynamics and structure of Mediterranean scleractinian corals, habitat to various marine species due to their bioconstrucntional features, by showing the phenological and morphological responses to different environmental conditions. Specifically, this survey shows different morphology patterns of *A. calycularis* depending on habitat hydrodynamism, as well as a delay on the fertilization timing of the coral linked with SST conditions.

**Acknowledgements**

We want to thank to L. Sánchez-Tocino (University of Granada), A.Terrón-Singler, D. León-Muez (Hombre y Territorio Association), Boichi, Charlie (Almuñécar, Granada), O. Hernández and A. Addamo (MNCN-CSIC), for their assistance in the field. We are very grateful to C. Pazzini, C. Marchini, M. Rocchi (Marine Sciences Group), M. Gallardo (MNCN-CSIC), S. Montalbán and O. Sánchez (CNB-CSIC) for their assistance with histological processing. M. Tourmente and E. Roldán (MNCN-CSIC) gave us support for the image analyses of part of the study. Photographed corals from Palinuro were provided by G. Neto. R. Barrientos (University of Castilla La Mancha) significantly improved this manuscript with suggestions. The Regional Government of Andalusia (Consejería
de Medio Ambiente), gave as the sampling permission for this study. S. Young improve significantly the English grammar and writing style. P. Casado-Amezua was funded by a grant from the Spanish Research Council (CSIC). S. Goffredo was funded by the European Research Council (CoralWarm, ERC grant agreement n° 249930). This study was supported by donations from Scuba Nitrox Safety International, Association of Italian Tour Operators, Ministry of Tourism of Egypt, Project Aware foundation and the Spanish Ministry of Science and Innovation (CTM2008-00496/MAR).

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