Marine Biology Research

Colony and polyp biometry and size structure in the orange coral *Astroides calycularis* (Scleractinia: Dendrophylliidae)

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First published on: 18 March 2011

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ORIGINAL ARTICLE

Colony and polyp biometry and size structure in the orange coral *Astroides calycularis* (Scleractinia: Dendrophylliidae)

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Abstract

Coral polyps inside a colony may differ in reproductive activity and ecological function even while sharing the same genetic identity. Although polyps are the basic units of coral colonies, their size, biometry and size structure have rarely been studied. This study investigated, for the first time, colony and polyp biometric relationships and intra-colony polyp population size structure in the Mediterranean endemic *Astroides calycularis* (Pallas, 1766). Biometric parameters for 160 colonies and 4162 polyps were measured with consideration of polyp position inside the colony (central or peripheral). The positive allometric relationship between polyp width and length, resulting in a progressively circular oral disc as polyp size increases, may relate to the low-sedimentation characteristics of the habitat of this species. The smaller size of peripheral polyps compared to central ones suggests that polyp budding occurs preferentially at the outskirts of the colonies, possibly increasing the competitive advantage for space utilization. Larger colonies had polyps with smaller size than small and medium colonies, due to an over-representation of the size class containing polyp size at sexual maturity. It is proposed that large colonies may invest energy in increasing polyp size up to the size at sexual maturity, rather than increasing the size of already mature polyps.

Key words: *Dendrophylliidae, Mediterranean coral, morphometry, Scleractinia, size frequency*

Introduction

A scleractinian coral colony is derived from a single polyp by budding, so that the polyps of the colony are usually genetically identical (Jackson & Coates 1986), and likely to have the same structure and potential for any physiological function (Meesters & Bak 1995). However, it has been demonstrated that scleractinian coral polyps inside a colony may differ in reproductive activity (Harriott 1983; Chornesky & Peters 1987; Harrison & Wallace 1990; Szmant 1991; Soong & Lang 1992; Van Veghel & Kahmann 1994; Hall & Hughes 1996; Sakai 1998) and ecological function (e.g. sweeping polyps; den Hartog 1977; Hidaka & Yamazato 1984; Sebens &

Miles 1988; Goldberg et al. 1990; Williams 1991; Peach & Guldberg 1999; Lapid et al. 2004) even if they share the same genetic identity. Although the polyp is the basic unit of scleractinian coral colonies, its biometry and functional activity has not often been studied, with exception of the studies on the different reproductive output of polyps with different size and position inside the colony (Harriott 1983; Van Veghel & Kahmann 1994; Sakai 1998, 2005; Leuzinger et al. 2003; Kai & Sakai 2008). To date, no study that we are aware of has investigated the biometric relationships of scleractinian polyps inside the colonies and their size structure, except for a polyp volume–frequency

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population structure in the colonies of the subtropical *Goniastrea aspera* Verril, 1905, showing an exponential decrease of the frequencies as volume increases (Sakai 1998).

Astroides calycularis (Pallas, 1766) is distributed in the south-central part of the Western Mediterranean Sea (Zibrowius 1980, 1983, 1995; Bianchi & Morri 1994; Ocaña et al. 2000; Kruzic et al. 2002, 2005; Cebrián & Ballesteros 2004; Grubelic et al. 2004; Álvarez-Pérez et al. 2005; Bianchi 2007; Casellato et al. 2007), with some recent records in the northeastern part of the Adriatic Sea, along the coasts of Croatia (Kruzic et al. 2002, 2005; Grubelic et al. 2004; Bianchi 2007) up to the Gulf of Venice (Casellato et al. 2007). The recent range expansion into the Adriatic Sea is thought to be due to seawater warming and to the Ionian cyclonic stream (Bianchi 2007), with the ascending (northward) circulation that seems to have favoured the flow of larvae along the Croatian coasts (Grubelic et al. 2004). Although *A. calycularis* is a Mediterranean species, it has been found along the Atlantic coasts of Morocco and Spain (Zibrowius 1983, 1995; Bianchi 2007), probably due to the currents dispersing larvae out of the Gibraltar Strait (Ocaña et al. 2000).

Astroides calycularis is found at depths of 0–50 m (Rossi 1971), but is typically found in the shallow infralittoral (0–15 m depth), on vertical walls or inside caves (Rossi 1971; Cinelli et al. 1977; Zibrowius 1978; Kruzic et al. 2002). It is an azooxanthellate species (Zibrowius 1983; Cairns 1999), gonochoric at the colony level, and brooding (Goffredo et al. 2010), living in both light and dark and seems to prefer elevated hydrodynamism (Cinelli et al. 1977; Zibrowius 1978, 1995; Kruzic et al. 2002). The population density can be high, with colonies covering up to 90% of the bottom (Goffredo et al., unpublished data).

The aim of this study is to investigate colony and polyp biometric relationships and intra-colony polyp population size structure in the Mediterranean endemic temperate–subtropical Dendrophylliid coral *A. calycularis* from a permanent experimental field site on the coast of Italy. This is expected to provide a solid basis for the future non-destructive investigations on the abundance and reproductive output of the population. The study addresses the following questions: (1) What are the biometric relationships between colony and polyp size parameters and how do they relate to ecological factors? (2) Which parameter is the best representative of colony size? (3) Is there any difference in the biometric relationships between polyps from different regions of the colony, and may this relate to ecological factors? (4) What is the size structure of polyps inside colonies, and is it conserved in colonies of different size?

Materials and methods

From April 2004 to September 2005, colonies of *Astroides calycularis* (Figure 1) were collected at Palinuro (Italy, Southern Tyrrhenian Sea, 40°01.81′N; 15°16.74′E). Scuba divers collected colonies at 7–10 m depth along a single random transect line, parallel to the coast line; the distance between two consecutive sampled colonies was 2 m. A total of 160 random colonies were collected, and care was taken to ensure an overall sampling which is representative of the entire cave (Grotta Azzurra) where they were collected. Colonies had an approximately elliptical shape. Of each collected colony, colony length (L_C, major axis of the colony) and colony width (W_C, minor axis of the colony) were measured, and colony area (A_C) was calculated using the formula for the ellipse $A_C = \pi(L_C \star W_C)/4$. Colony area was selected as the main biometric parameter for colonies, since it is a more accurate and representative measure of colony size than colony length (Bak & Meesters 1998; Meesters et al. 2001; Vermeij & Bak 2002; Nozawa et al. 2008).

A subsample of 65 colonies was randomly chosen for polyp-based analyses. Colonies were dried at 50°C for 4 days and the number of corallites (=polyps) in each colony was counted. For each of these 65 colonies, an imaginary elliptical region having the maximum and minimum axes corresponding to half of the axes of the colony was determined for each colony. Polyps inside this region were termed as 'central' while polyps outside this region were termed as 'peripheral'. Each corallite was then separated from the others using scalpels, performing the cut along the junction between the two polyps, which was clearly visible. For each polyp, the length (L_P, maximum axis of the oral disc), width (W_P, minimum axis of the oral disc) and height (h_P, oral–aboral axis) were measured using a caliper, and polyp dry skeletal mass (M_P) was measured with a precision balance. Polyp volume (V_P) was determined by applying the formula for the elliptic cylinder:

$$V_P = \frac{L_P}{2} \times \frac{W_P}{2} \times h_P \times \pi$$

Figure 1. *Astroides calycularis*. One colony from the sampling site at Palinuro.

(Goffredo et al. 2002, 2006, 2007, 2009, 2010). Polyp length was selected as the main biometric parameter for polyps, since it is a good indicator of skeletal mass and has been used as the primary measure of size in other biometric, reproductive biology and population dynamics studies of this species (Goffredo et al. 2010) and other corals (Lasker 1981; Foster et al. 1988; Goffredo et al. 2002, 2004, 2007, 2008, Goffredo & Chadwick-Furman 2003; Vermeij 2006).

Pearson correlation coefficients were calculated for the relationships among biometric parameters. Student's *t*-test was used to compare mean L_P, W_P, h_P, V_P and M_P between central and peripheral polyps. The corrected Student's *t*-test value for non-homogenous variances was used in case of data heteroscedasticity (e.g. for h_P, V_P and M_P). The non-parametric Kruskal–Wallis test (for heteroscedastic data) was used to compare mean V_P, M_P and percentage of peripheral polyps among colony size classes, and Tamhane post-hoc test was used to identify significantly different subsets of colony size classes. The non-parametric Kolmogorov–Smirnov test was used to compare the polyp size frequency distributions among colony size classes. All analyses were computed using SPSS 12.0 (Apache Computer Software Foundation).

Results

Colony length, width, mass and number of polyps all correlated positively with colony area, whose variation explained 74.7–91.6% of their variance (Figure 2). Colony length, width, mass and area all correlated positively with number of polyps, whose variation explained 68.7–90.9% of their variance (Figure 2).

Polyp width, height, volume and mass all correlated positively with polyp length, whose variation explained 60.5–95.9% of their variance (Figure 3). The increase of polyp width in comparison with polyp length was allometric, with polyp width increasing more quickly than polyp length did (the confidence interval of the regression exponent > 1, 95% CI $= 1.042$–1.046), thus resulting in a circular oral disc as polyp size increased.

The regression coefficients of the biometric relationships of central polyps were not significantly different from those of peripheral polyps (the 95% CI of the exponents and coefficients were always overlapped; Figure 4). This was also confirmed by analysing the residuals of the regression of biometric relationships between central and peripheral polyps (ANOVA, $P > 0.05$). Central polyps were significantly larger, wider, higher, more voluminous and heavier than peripheral polyps (Student's *t*-test, $P < 0.001$, $N = 4162$; Table I).

Colonies were divided in three area-based subsets: small colonies (0.0–20.0 cm^2), medium colonies (20.1–40.0 cm^2) and large colonies (> 40.1 cm^2). Small and medium colonies had polyps significantly more voluminous and heavier than large colonies (Kruskal–Wallis test, $P < 0.001$;
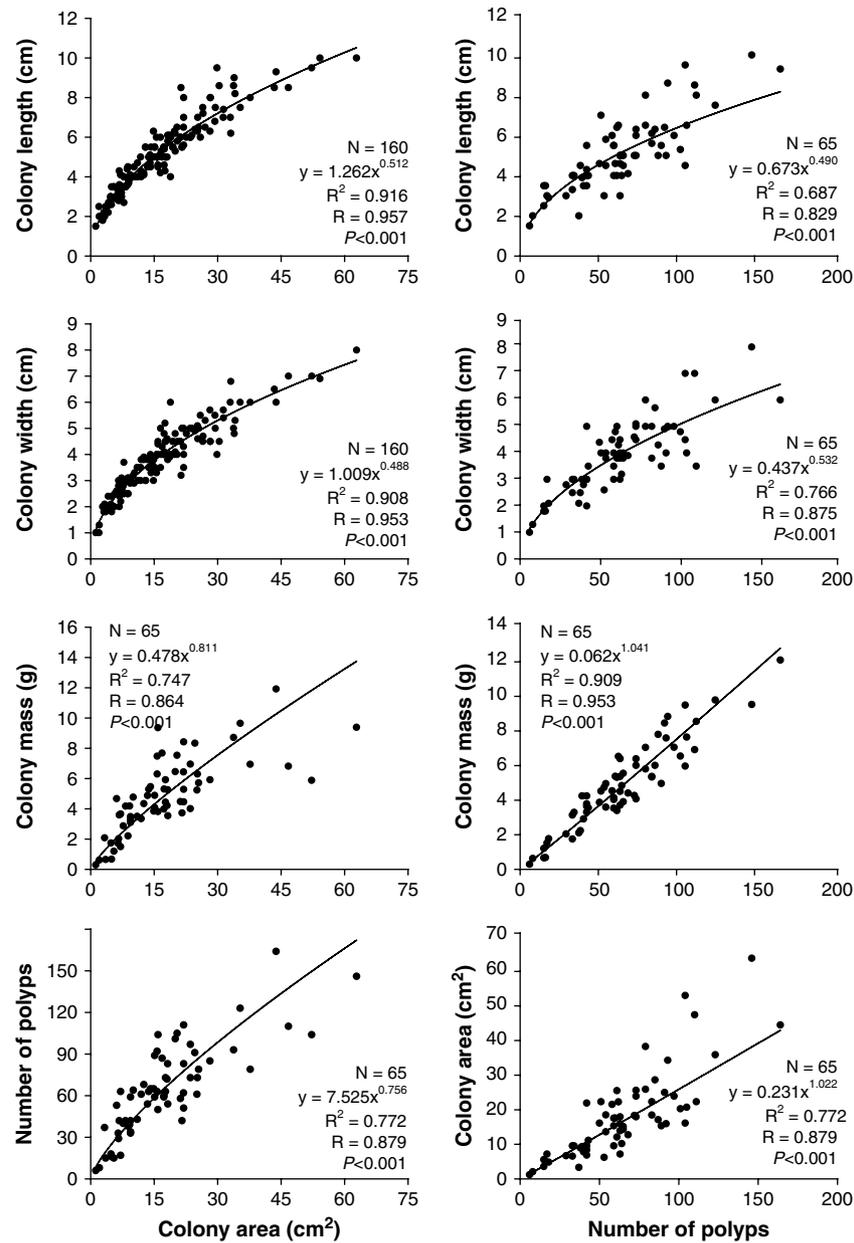
Figure 2. *Astroides calycularis*. Dependence of colony biometric parameters on colony area and colony number of polyps.

Tamhane post-hoc test identified the homogeneous subsets of small and medium colonies, which were significantly different from the large colonies subset, $P < 0.001$; Table II). The percentage of peripheral polyps in small, medium and large colonies was not significantly different (Kruskal–Wallis test, $P > 0.050$).

Polyp population size structures for the all colonies dataset and for the subsets of small, medium and large colonies were determined (Figure 5). Polyp population size structure of small colonies

was not significantly different from the one of medium colonies (Kolmogorov–Smirnov test, $P > 0.050$). Polyp population size structure of large colonies was significantly different from the one of small colonies (Kolmogorov–Smirnov test, $P < 0.050$) and from the one of medium colonies (Kolmogorov–Smirnov test, $P < 0.001$). When polyp size class 4 was excluded from the analysis, all of the three colony subsets had homogeneous polyp population size structures (Kolmogorov–Smirnov test, $P > 0.050$).
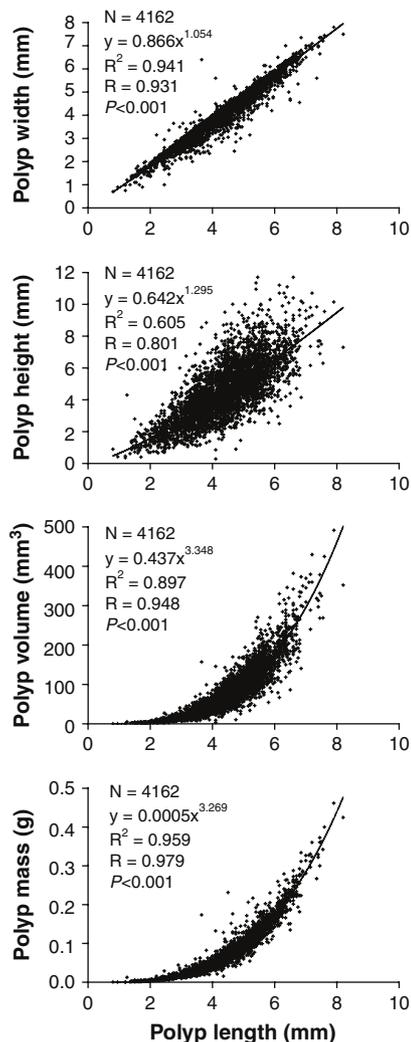
Figure 3. *Astroides calycularis*. Dependence of polyp biometric parameters on polyp length.

Discussion

The biometric relationships of *Astroides calycularis* colonies and polyps were described here for the first time. Colony length, width, mass and number of polyps all showed marked relationships with colony area (Figure 2), confirming that this parameter is a powerful representative of colony size, as reported in previous studies (Bak & Meesters 1998; Meesters et al. 2001; Vermeij & Bak 2002; Nozawa et al. 2008). Only colony mass showed a better relationship with

number of polyps than with colony area (Figure 2), but while the latter can be easily derived by linear parameters measured during underwater surveys, the former can be accurately assessed only by an invasive sampling which implies removal of the colony from the environment. The relationships between biometric parameters and colony area determined in this study will be used for the characterization of the population reproductive output of this species at this location, based on abundance estimates by means of non-invasive photographic transects, which is currently underway.

Polyp width, height, volume and mass all showed marked relationships with polyp length (Figure 3). This parameter was chosen as the main measure of size for different Mediterranean and subtropical solitary and colonial corals (Lasker 1981; Foster et al. 1988; Goffredo et al. 2002, 2004, 2007, 2008, Goffredo & Chadwick-Furman 2003; Vermeij 2006) and proved to be a good representative of polyp size also for the colonial coral object of this work.

The positive allometric relationship between polyp width and length, resulting in a more circular oral disc as polyp size increases may be related to sedimentation. Sedimentation has many negative effects on corals, including prevention of growth and calcification, interference with respiration, nourishment and photosynthesis, increase in energy dissipation, damaging polyp tissues, lowering the fecundity, and interfering with substratum colonization process (Rosenfeld et al. 1999, and references therein). Corals can adopt different strategies to prevent these negative effects, i.e. sediment rejection behaviour or resistant growth forms (Stafford-Smith & Ormond 1992; Bell & Turner 2000). In the solitary coral *Balanophyllia europaea* (Risso, 1826), as polyp size increases the oral disc becomes more oval, and this is believed to represent a resistant growth form against sedimentation (it decreases the area exposed to sediments and favours its removal from the polyp surface; Hoeksema 1991; Goffredo et al. 2004, 2007). On the contrary, the polyps of the solitary coral *Leptopsammia pruvoti* Lacaze-Duthiers, 1897, which lives on the vaults of overhangs, have polyps either with isometric growth of a circular oral disc or polyps with progressively circular oral discs as their size increases, depending

Table I. *Astroides calycularis*. Mean (standard deviation) values of biometric parameters of central and peripheral polyps. N, number of polyps.

	L_P (mm)	W_P (mm)	h_P (mm)	V_P (mm^3)	M_P (g)
Central polyps $N = 558$	4.62(1.05)	4.37(1.07)	5.02(1.88)	93.99(67.18)	0.090(0.062)
Peripheral polyps $N = 3604$	4.33(1.05)	4.07(1.06)	4.45(1.73)	74.30(57.82)	0.072(0.055)
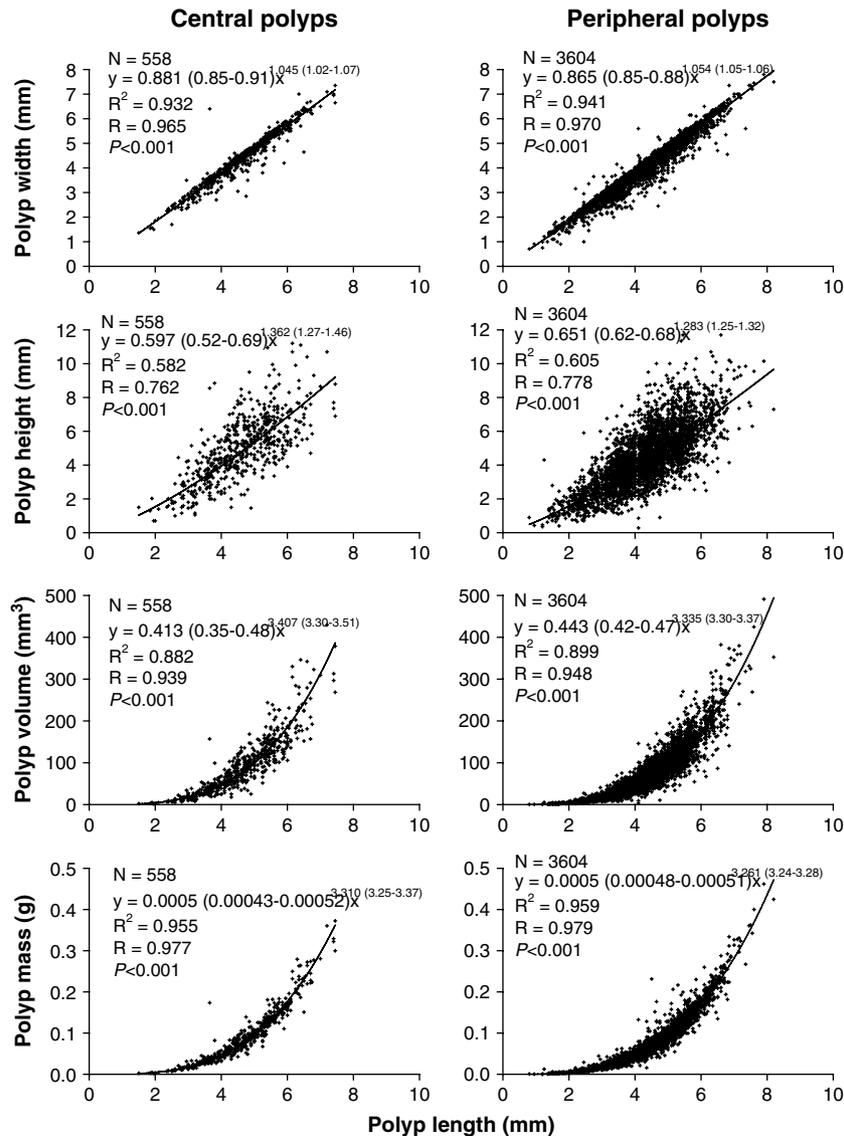
Figure 4. *Astroides calycularis.* Dependence of polyp biometric parameters on polyp length in central and peripheral polyps. Values in the parentheses indicate the 95% CI of the regression coefficients.

on the population (Goffredo et al. 2007). In corals living on the vertical walls, the removal of sediment is carried out by gravity, rather than by active mechanisms (Stafford-Smith & Ormond 1992). The polyps of *A. calycularis*, living in a similar habitat as the one of *L. pruvoti*, may need no particularly resistant growth form against sedimentation, and this would result in a more circular rather than oval oral disc. Studies on polyp biometry in colonies from populations subjected to different sedimentation rates are needed to verify this hypothesis.

The smaller size of peripheral polyps, compared to central ones, was not due to a difference in biometric relationships, which were homogeneous between peripheral and central polyps. A polyp budding pattern localized mostly in the outskirts of the colony may be responsible for this difference, as previously reported for the subtropical colonial coral *Goniastrea aspera* in Japan (Sakai 1998). Colonies of *A. calycularis* living near the surface (high hydrodynamism) are reported to be massive and to have polyps which bud both in the outskirts of the colony, and between the existing polyps. In deeper waters (low hydrodynamism) colonies are reported to be bush-like and to have polyps that produce buds at different heights of their calyx (Rossi 1971; Kruzic et al. 2002). The colonies analysed in the present study were sampled at 7–10 m, which is quite shallow relative to the depth limit of the species

Table II. *Astroides calycularis*. Mean (standard deviation) values of polyp volume and mass in the three area-based colony subsets (small colonies: 0.0–20.0 cm^2; medium colonies: 20.1–40.0 cm^2; large colonies >40.1 cm^2). N_C number of colonies, N_P number of polyps.

	V_P (mm^3)	M_P (g)
Small colonies		
$N_C = 44$		
$N_P = 2272$	77.9(58.9)	0.074(0.055)
Medium colonies		
$N_C = 17$		
$N_P = 1366$	80.0(63.4)	0.079(0.060)
Large colonies		
$N_C = 4$		
$N_P = 524$	65.1(49.9)	0.065(0.049)
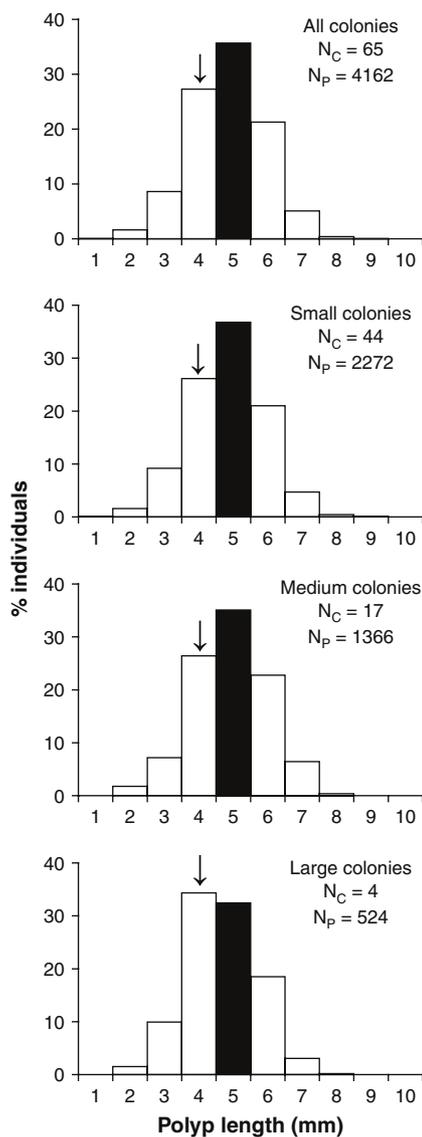
Figure 5. *Astroides calycularis*. Polyp size-class structures. The black column represents the size class containing the observed mean length of the polyps. The arrow indicates polyp size at sexual maturity. N_C number of colonies, N_P number of polyps.

(0–50 m; Rossi 1971), and then the expected budding pattern would be the former. Particular local conditions, such as a strong competition for space could be responsible for the preferential budding scheme found in this work (i.e. less intra-polyp budding and more colony outskirts budding), which would result in a better competitive performance for the colonies (Sakai 1998). The role of competition in influencing the distribution of cave benthic assemblages is largely unknown (Bussotti et al. 2006), notwithstanding its recognized importance in affecting natural communities at small spatial scales (Jackson 1977; Buss & Jackson 1979; Sebens 1982). Moreover, in the narrow depth range of colony collection used in this work (7–10 m), both massive and bush-like colonies were found, indicating that the previously reported relationship between growth form, budding pattern and hydrodynamism may not be so strict, or that local conditions may strongly influence it. Studies on the growth form and budding pattern in colonies from populations subjected to different hydrodynamic regimes are needed to verify the influence of this environmental parameter on colony architecture.

The fact that small and medium-sized colonies had more voluminous and heavier polyps than large colonies is in contrast with previous reports for the subtropical *Goniastrea aspera* (Sakai 1998). Our result would suggest a higher percentage of peripheral (smaller) polyps in the latter size class. However, this was not the case since the percentage of peripheral polyps was homogeneous among all size classes, in contrast with previous reports for the subtropical *G. aspera* and *Favites chinensis* (Verril, 1866), where larger colonies have more marginal polyps than smaller ones (Kai & Sakai 2008). An explanation to this may arise from the polyp population size structure analysis. When analysing the structures of the three colony subsets (Figure 5), an over-representation of polyp size class 4 in the large colonies subset was responsible for the significant difference of the structure of this subset from the small and medium colonies subsets. In fact, when excluding size class 4, all size classes had homogenous structures (see results). Since polyp size class 4 is smaller than the size class containing the average polyp size (Figure 5), the lower size of polyps in large colonies is clearly due to an over-representation of this size class. Since size class 4 contained the polyp size at sexual maturity (Goffredo et al., unpublished data), then large colonies may invest energetic resources to increasing the size of young polyps up to the size at sexual maturity, rather than increasing the size of already mature polyps (>4 mm). Large colonies may direct towards reproduction the energy they initially

invested towards colony growth to escape the high risk of mortality experienced by small individuals (Hall & Hughes 1996). This would enhance colony sexual reproductive output, increasing the probability of successful reproductive events involving the genotype of the colony, and would be consistent with the previous findings of higher average fecundity in large colonies, compared to smaller ones (Van Veghel & Kahmann 1994; Hall & Hughes 1996; Sakai 1998). Analyses of the reproductive output of this species at this location are currently underway and may clarify if large colonies have higher reproductive outputs than small and medium ones.

Acknowledgements

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