

Exploitation of micro refuges and epibiosis: survival strategies of a calcareous sponge

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Sponges interact in various ways with a wide variety of organisms in benthic communities and ecological interactions may influence the distribution, abundance and diversity of these organisms in different sites. Although several studies have already been developed for Demospongiae, knowledge of ecological interactions in the class Calcarea is lacking. Some calcareous sponges are considered weak competitors for space and to have developed strategies to survive in highly dynamic environments, such as exploitation of micro refuges and epibiosis. We aimed to investigate the influence of intra- and interspecific interactions in the abundance, growth and lifespan of the calcareous sponge Clathrina aurea in south-eastern Brazil. Two peaks of abundance and area coverage were observed during the studied year, probably associated with reproductive effort. We found no evidence of intra- or interspecific competition between the sponge and the benthic community. Clathrina aurea was found using parts of other organisms as substrate (epibiosis), such as algae, demosponges and corals. It was seen that the interaction of the sponge with coral polyps positively affects the lifespan of sponge individuals and the interstices of corals probably promote a micro refuge for C. aurea against competitors for space and predators.

Keywords: *Clathrina aurea*, Porifera, ecological interactions, *Astrangia*, *Phyllangia*, competition, South-western Atlantic

INTRODUCTION

Sponges (phylum Porifera) are considered the oldest extant animals and are among the main components of marine benthic communities (Van Soest *et al.*, 2012). As sessile animals they interact in various ways with a wide variety of organisms (Bell, 2008), playing a key role in many ecological processes, such as competition, symbiosis and predation (e.g. Sarà & Vacelet, 1973; Ribeiro *et al.*, 2003; Wulff, 2006; López-Victoria *et al.*, 2006; Swain & Wulff, 2007; Batista *et al.*, 2012). Studies have shown that sponges' diversity patterns may result from their ecological interactions (e.g. Rützler, 1970; Wulff, 1997; Pawlik, 1998; Engel & Pawlik, 2005), which would affect their distribution, abundance and diversity in different sites (Wulff, 2006, 2012).

Space availability is often the most important limiting resource for the occurrence of sponges in marine hard substrata, leading to spatial competition with other sessile marine invertebrates and algae, or among individuals of the same species (Johnson, 1979; Engel & Pawlik, 2005). The exploitation of micro refuges can minimize the problems of spatial competition, mitigating the stresses of living in highly dynamic environments, such as rocky shores (Walters & Wethey, 1996). Besides physical refuges, sponges may also gain protection against predators or competitors by the association with other organisms because of their chemicals and/or body shape (e.g. Waddell & Pawlik, 2000; Loh & Pawlik, 2012;

Padua *et al.*, 2013a), making the local environment more favourable (Stachowicz, 2001).

Such dynamic interactions between organisms and substrate occupation can influence the structure of a community. To really understand the processes underlying these observed patterns, it is necessary to evaluate the relationship between community components (Dayton, 1971). However, to demonstrate how interactions constrain or enhance distribution and abundance, long-term field observations are necessary (Wulff, 2012). Although the importance of these ecological relationships for demosponges has already been shown (Wulff, 2012), this knowledge is lacking for calcareous sponges (class Calcarea), with very few works regarding topics such as associated fauna (Frith, 1976; Padua *et al.*, 2013a), symbiotic community (Santos *et al.*, 2010; Turque *et al.*, 2010; Fromont *et al.*, 2015) and competition (Rützler, 1970; Sarà, 1970; Johnson, 1979; Bell & Barnes, 2003; Longo *et al.*, 2012; Cavalcanti *et al.*, 2013).

Sponges belonging to the class Calcarea are, in general, small and inhabit cryptic habitats, together with some ascidians, echinoderms, bryozoans and other sponges (e.g. Sloan, 1979; Stoecker, 1980; Klautau & Borojevic, 2001; Grischenko *et al.*, 2007). These sponges are considered weak space competitors (Rützler, 1970) and may present alternative strategies to survive and increase chances of survival. For example, some calcareous sponges are commonly found as epibionts, avoiding the risk of being excluded by other competitors (Rützler, 1970; Sarà, 1970), and may exploit micro refuges, such as small crevices, ensuring competitive advantage on the substrate occupation (Maldonado & Uriz, 1998).

The calcareous sponge *Clathrina aurea* Solé-Cava *et al.*, 1991 (Clathrinidae, Calcinea) is very fragile, composed of

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thin-walled anastomosed asconoid tubes (Klautau & Borojevic, 2001). In Brazil this species is distributed in the south-eastern and north-eastern coasts and found especially in light protected environments such as ceilings and walls of small caves and burrows, where they are also protected from the action of waves (Klautau & Borojevic, 2001; Muricy *et al.*, 2011). Individuals of *C. aurea* are very often found in a patchy distribution (Monteiro & Muricy, 2004) and are commonly associated with other sponges, ascidians and algae but most frequently with coral polyps (authors' previous observations). The major association with coral polyps could, perhaps, represent a micro refuge for *C. aurea*, providing protection against substrate competition, which could influence its abundance, growth and survival.

In the present work, we aimed to investigate the influence of intra- and interspecific interactions in the abundance, growth and lifespan of the calcareous sponge *C. aurea* using a population from Cabo Frio (Rio de Janeiro State, Brazil) as a model.

MATERIALS AND METHODS

Study area

The present study was conducted in a small cave at Papagaio's Island in Cabo Frio, Rio de Janeiro State, South-eastern Brazil ($22^{\circ}53'50''S$ $41^{\circ}58'56''W$; Figure 1). The entrance of the cave is located at a depth of 4 m and is 1.2 m wide, becoming narrower towards the interior.

Quantitative and qualitative sampling

Sampling was undertaken monthly by scuba diving, from October 2012 to October 2013 (13 months). The benthic community of the cave was studied using permanent quadrats of 16×16 cm (total area of 256 cm^2) (three replicates – Q1, Q2 and Q3). The study area was chosen according to the highest abundance of *Clathrina aurea*. Photographs of the quadrats were taken *in situ* using a Canon G11 camera and small pieces of some organisms were collected at the end of the study in order to identify them to the lowest taxonomic level possible. The sponges and other taxa were identified by experts in each group.

Image processing

The area coverage of all organisms on the three photoquadrats was calculated using the digital image processing software AxioVision 4.6.3 (Carl Zeiss Imaging Solutions). In each photoquadrat, every organism was defined manually with an external outline, using a freehand drawing tool. All defined surfaces were assigned to the corresponding taxa based on the taxonomic identifications. All individuals of *C. aurea* inside the three photoquadrats were monitored for variations in area coverage and abundance.

Statistical analyses

ABUNDANCE AND AREA COVERAGE

To test if abundance and total area coverage each have a specific variation pattern in time, a spectral density analysis was



Fig. 1. Location of the study area. (A) Cabo Frio city (square) in South-eastern Brazil; (B) Papagaio's Island with the black arrow showing the sampling location; (C) *in vivo* photograph of *Clathrina aurea*.

performed in order to obtain the mean wave period (λ) for each month. Then we fitted a linear model (LM) to abundance and total area with sinusoidal waves (abundance $\sim \sin(\text{time} \times 2\pi/\lambda) + \cos(\text{time} \times 2\pi/\lambda)$). A similar technique was applied to individuals' area coverage (from five selected individuals with the longest lifespans) but using a repeated measure procedure.

In order to identify a possible dependence of area coverage of *Clathrina aurea* individuals upon their abundance, we performed a linear mixed-effects model (LME) fitted by restricted maximum likelihood (REML), using monthly abundance of individuals as fixed variable (independent) and quadrats as random effects.

INFLUENCES OF THE BENTHIC COMMUNITY

Some months were not included in the statistical analysis (Q1: Mar/2013; Q2: Nov, Dec/2012, Mar/2013; Q3: Apr, Jul, Sep, Oct/2013) because of inadequate photo quality caused by the sea conditions, hampering a precise analysis of the images. To detect possible effects of other benthic organisms on *Clathrina aurea*'s area coverage variations, a LME model was used with only the coverage of the most common sessile taxa in direct contact with *C. aurea* within quadrats as fixed variables (Table 1B), monthly samples as fixed effects and

Table 1. Area coverage and type of association between *Clathrina aurea* and the benthic community.

Taxa	(A) Average area coverage \pm SD (cm ²)			(B) Type of association with <i>Clathrina aurea</i>			
	Q1	Q2	Q3	Absent	Rare	Common	
Ann (1)	Serpulidae sp.*			X			
Bry (1)	Bryozoa sp.			X			
Cho (2)	Didemnidae sp.	1.62 \pm 1.33	0.80 \pm 0.81	0.37 \pm 0.28		X	
Cni (4)	Ascidacea sp.	–	0.45 \pm 0.20	–	X		
	<i>Astrangia rathbuni</i> Vaughan, 1906	21.76 \pm 2.80	6.72 \pm 1.68	7.21 \pm 1.08		X	
	<i>Phyllangia americana</i> Milne Edwards & Haime, 1849						
	<i>Tubastrea</i> sp.	0.37 \pm 0.15	–	–	X		
Mol (2)	<i>Carijoa riisei</i> (Duchassaing & Michelotti, 1860)	0.14 \pm 0.11	0.27 \pm 0.19	–		X	
	<i>Felimare lajensis</i> (Troncoso, Garcia & Urgan, 1998)**	3	–	2	X		
Por (17)	Gastropoda sp.**	6	3	4	X		
	<i>Clathrina aurea</i> Solé-Cava. <i>et al.</i> , 1991	7.79 \pm 4.78	0.96 \pm 0.47	1.49 \pm 1.02	–		X
	Clathrinidae sp.	0.24 \pm 0.08	–	–		X	
	<i>Scopalina ruetzleri</i> (Wiedenmayer, 1977)	46.51 \pm 6.37	9.51 \pm 2.58	2.70 \pm 2.01			X
	<i>Clathria (Microciona) campecheae</i> Hooper, 1996	4.12 \pm 1.28	–	27.77 \pm 5.98			X
	<i>Crella</i> sp.	–	0.3 \pm 0.13	12.96 \pm 4.29		X	
	<i>Dysidea etheria</i> de Laubenfels, 1936	36.34 \pm 7.21	3.83 \pm 1.77	8.30 \pm 4.07			X
	<i>Darwinella</i> sp.	–	–	1.38 \pm 0.79		X	
	<i>Darwinella</i> sp. 2	1.60 \pm 0.34	–	1.06 \pm 0.40		X	
	<i>Chondrosia</i> sp.	–	11.94 \pm 2.55	–	X		
	Demospongiae sp. 1	1.17 \pm 0.52	12.55 \pm 3.84	22.24 \pm 3.79		X	
	Demospongiae sp. 2	5.96 \pm 2.97	–	–	X		
	Demospongiae sp. 3	–	9.18 \pm 3.32	–	X		
	Demospongiae sp. 4	1.32 \pm 0.98	–	1.75 \pm 1.02	X		
	Demospongiae sp. 5	0.65 \pm 0.25	0.36 \pm 0.00	–		X	
	Demospongiae sp. 6	1.19 \pm 0.55	–	–	X		
	Calcinea spp.	0.24 \pm 0.08	0.31 \pm 0.20	–	X		
Calcaronea spp.	0.17 \pm 0.08	0.06 \pm 0.01	–	X			
Alg (1)	Algae sp.	122.52 \pm 13.01	194.56 \pm 14.94	159.50 \pm 8.12		X	

SD, Standard deviation; Ann, Annelida; Bry, Bryozoa; Cho, Chordata; Cni, Cnidaria; Mol, Mollusca; Por, Porifera; Alg, Algae.

Number of taxa of each group within the parentheses.

*Not quantified but present in all quadrats. **Quantified by the number of months they appeared. Absent – never in contact with *C. aurea*. Rare – once or twice associated with *C. aurea*. Common – three or more individuals associated with *C. aurea*.

quadrats as random effects. The taxa were selected as common when at least three different individuals were in direct contact with *C. aurea*. Model selection was performed to select the best variables that explain *C. aurea* variations, based on corrected Akaike's information criteria (AIC_c) using REML estimation. Models with AIC differences (Δ AIC_c) less than two were considered as indistinguishable and considered as best models.

SURVIVAL ANALYSIS

A survival analysis of *Clathrina aurea* individuals was performed using a survival fit approach in order to compare the lifespan in two conditions: associated and non-associated with coral polyps of the species *Astrangia rathbuni* Vaughan, 1906 and *Phyllangia americana* Milne Edwards & Haime, 1849. In general, individuals of *C. aurea* were more frequently associated with these coral polyps than with any other taxa, substantiating our choice of these organisms for the survival analysis. We defined as associated the direct contact of the sponge with the coral polyp and survival

time as the interval between the recruitment of the individual until its disappearance, interpreted as its death. It was not possible to determine the age for all individuals, because some individuals were already present at the beginning of the study and others did not die until after its end. Thus, these individuals were classified as censored data and owing to another study conducted 6 months before, we could obtain survival months before the beginning of the current study for some individuals (Padua *et al.*, 2016). Survival probabilities were estimated using the non-parametric Kaplan–Meier (KM) method (Kleinbaum & Klein, 2012), and differences between fitted models for the two conditions were statistically compared through a chi-square test of the log-rank.

Spectral density and linear model (LM) analysis, linear mixed-effects model analysis (LME), model selection (AIC) and survival analysis were performed using R version 3.2.3[®] software for Windows, using the packages *stats* (R documentation), *lme4* (Bates *et al.*, 2015), *MuMIn* (Kamil, 2016) and *survival* (Therneau, 2015), respectively.

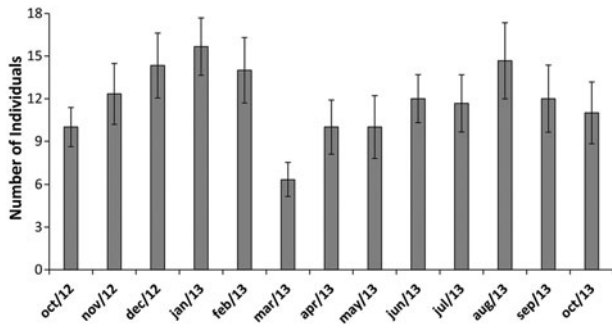


Fig. 2. Monthly abundance of *Clathrina aurea* in Cabo Frio. Mean density of the three analysed quadrats (bars: standard error). Significant dependence of abundance and months ($P = 0.0062$).

RESULTS

Abundance and area coverage

During the 13 months of the study, 138 individuals of *Clathrina aurea* were monitored and we observed a variation in the abundance (Figure 2) and area coverage (Figure 3) of this species along the year. Two peaks of abundance were observed, in January 2013 (16 ± 2 individuals) and August 2013 (15 ± 3 individuals), both followed by a slight decrease. The lowest number of individuals was observed in March 2013 (6 ± 1 individuals). The total area coverage increased during the first 5 months, achieving the first peak in February 2013 ($5.82 \pm 1.17 \text{ cm}^2$) followed by a steep decrease in March 2013, which represented the lowest area in the study ($0.42 \pm 0.07 \text{ cm}^2$). In April, the total area coverage started increasing again, accomplishing a second peak in July 2013 ($6.88 \pm 1.62 \text{ cm}^2$). The mean abundance of individuals presented a significant sinusoidal pattern over time (LM, $P = 0.0062$; Figure 4), while total area coverage did not present any significant pattern (LM, $P = 0.1368$; Figure 5). Nevertheless, there was significant correlation between total area coverage and abundance (LME, $P < 0.001$). Besides abundance variation, individuals of *C. aurea* varied greatly in their area coverage on the substrate (Figure 6), but with no dependence of area coverage with months (LM, $P = 0.347$). Nevertheless, there was significant correlation between total area coverage and abundance (LME, $P < 0.001$).

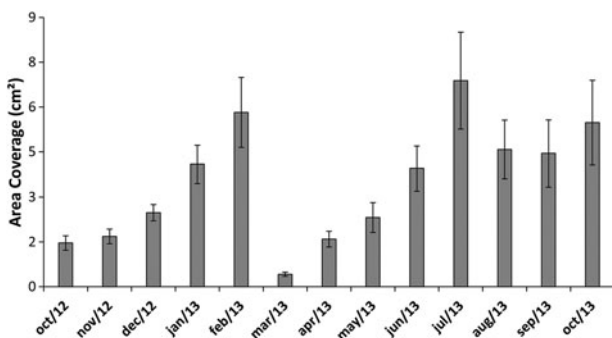


Fig. 3. Monthly area coverage of *Clathrina aurea* in Cabo Frio. Mean area coverage of the quadrats (bars: standard error). No significant dependence of area coverage and months ($P = 0.1368$).

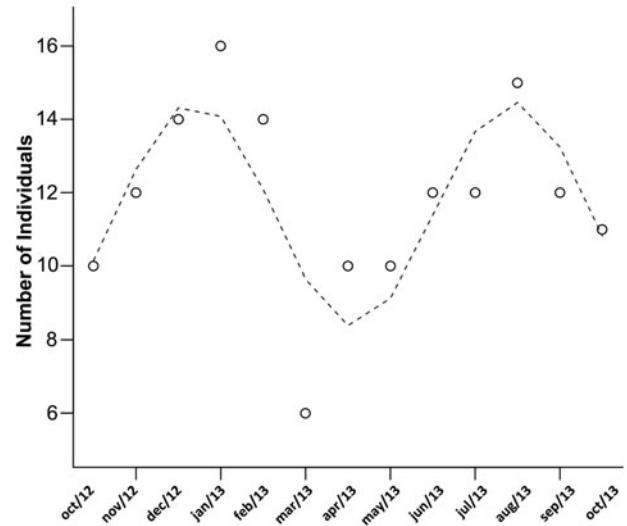


Fig. 4. Monthly abundance of *Clathrina aurea* in Cabo Frio (circles) with sinusoidal wave adjusted for the data (dashed line).

Influences of benthic community

A total of 28 taxa were identified in the quadrats, representing six animal phyla plus Algae neighbouring *Clathrina aurea* (Table 1A). The three quadrats presented different benthic fauna composition, so they will be treated separately. We observed a mean of 19 ± 4 (standard deviation) taxa per quadrat, eight of which were shared among them: Serpulidae sp., Didemnidae sp., *Astrangia rathbuni*, *Phyllangia americana*, Algae sp., *Scopalina ruetzleri* (Wiedenmayer, 1977), *Dysidea etheria* de Laubenfels, 1936 and Demospongiae sp. 1. The most representative taxa was Algae sp., which covered more than 50% of the quadrats, followed by the phylum Porifera, with 17 taxa. The highest mean area coverage (cm^2) was of *Scopalina ruetzleri* (46.51 ± 6.37) in Q1, Demospongiae sp. 1 (12.55 ± 3.84) in Q2, and *Clathria (Microcionia) campecheae* Hooper, 1996 (27.77 ± 5.98) in Q3. Although two species of coral polyps had been identified, *A. rathbuni* and *P. americana*, they will be treated

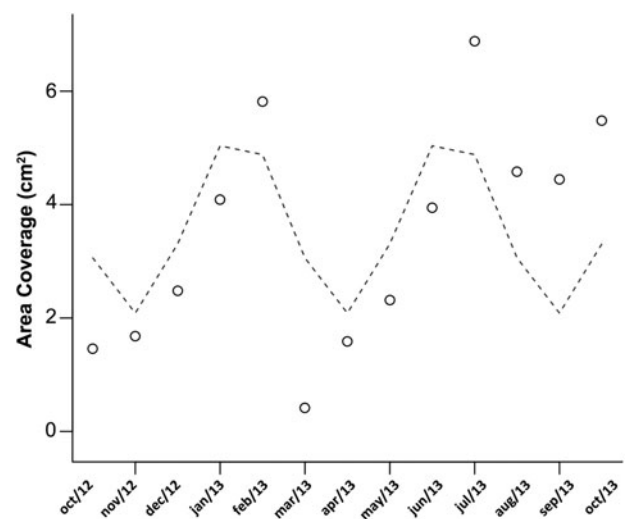


Fig. 5. Monthly area coverage of *Clathrina aurea* in Cabo Frio (circles) with sinusoidal wave adjusted for the data (dashed line).

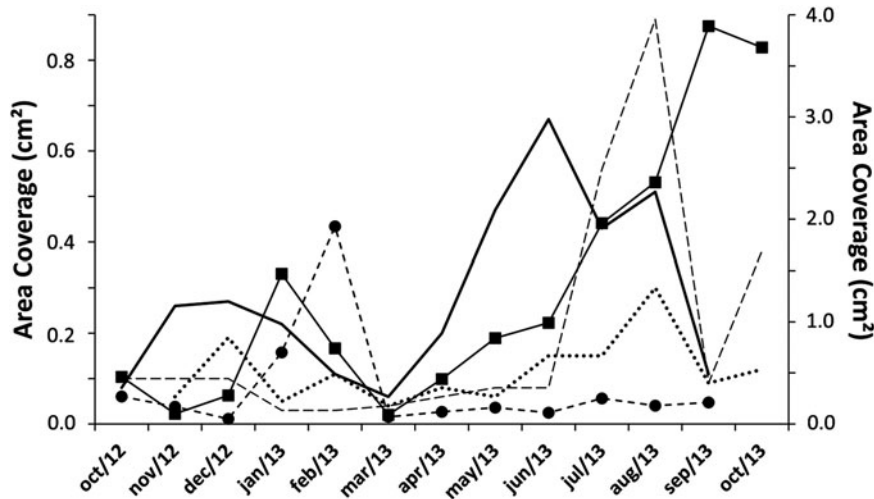


Fig. 6. Area coverage (cm²) per month of the five individuals of *Clathrina aurea* with the longest lifespan. Lines with markers (circles and squares) belong to the right axis scale, while the others belong to the left axis scale. No significant correlation of individuals' area coverage and months ($P = 0.347$).

together as 'Coral Polyps' due to the difficulty of specific recognition in the photoquadrats.

Of all taxa identified in the study, 13 were never found in direct contact with *C. aurea*. The most common associations in direct contact were with Didemnidae sp., coral polyps, *Scopalina ruetzleri*, *Clathria (Microciona) campecheae*, *Dysidea etheria* and Algae sp. (Table 1B).

The linear mixed effect model that best explained the variation in area coverage of *C. aurea* included only Didemnidae sp. (Model 1 - AIC_c weight = 0.34; Table 2). The other models that also received substantial support ($\Delta AIC_c < 2$) included *Scopalina ruetzleri* and coral polyps. The coefficient estimate showed a negative correlation with Didemnidae sp., being the most important variable as it was present in all models (Table 3).

Table 3. Coefficient estimate, standard error (SE) and the relative importance of the variables.

Variable	Coefficient estimate \pm SE	Relative importance
Didemnidae sp.	-1.94 \pm 0.49	1.00
<i>Scopalina ruetzleri</i>	-0.11 \pm 0.14	0.40
Coral polyps	-0.12 \pm 0.22	0.31
<i>C. campecheae</i>	-0.01 \pm 0.04	0.05

($\chi^2 = 4.8$, $df = 1$, $P = 0.0279$; Figure 7). Of the 138 individuals analysed, ~80% (110 individuals) were associated with coral polyps and the median survival time was 4 (Confidence Interval 95% 4-5) and 3 (CI 95% 2-5) months for associated and non-associated individuals, respectively (Table 4).

Survival analysis

Individuals of *Clathrina aurea* associated with coral polyps (*Astrangia rathbuni* and *Phyllangia americana*) lived longer than the non-associated individuals, the longest lifespan being 14 months for one associated individual and 7 months for a non-associated individual. The difference in survival between the two groups was statistically significant

Table 2. Analysis of linear mixed effect models fitted by REML evaluated using the Akaike's Information Criteria (AIC). All the models included Intercept values.

Model	df	Log Likelihood	ΔAIC_c	AIC _c weight
1 ^a	4	-73.03	0.00	0.34
2	5	-71.69	0.23	0.30
3	5	-72.06	0.97	0.21
4	6	-71.21	2.43	0.10
5	5	-73.49	3.83	0.05

^aAIC_c = 155.66.

(1) Didemnidae sp.; (2) Didemnidae sp. + *Scopalina ruetzleri*; (3) Didemnidae sp. + Coral Polyps; (4) Didemnidae sp. + Coral Polyps + *Scopalina ruetzleri*; (5) Didemnidae sp. + *Clathria (Microciona) campecheae*.

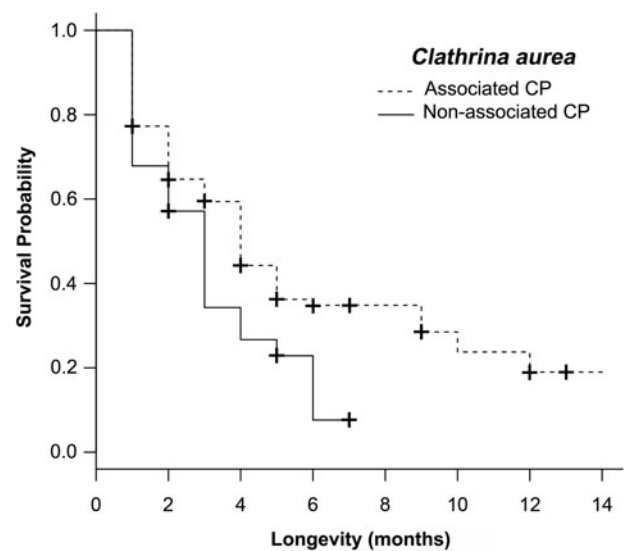


Fig. 7. Kaplan-Meier survival function for individuals of *Clathrina aurea* associated and non-associated with coral polyp (CP). The two groups differed ($P = 0.0279$) and the '+' in the step functions represents censored data.

Table 4. Comparison between individuals of *Clathrina aurea* associated and non-associated with coral polyp (CP). Median lifespan (month) with 95% confidence interval (CI).

<i>Clathrina aurea</i>	N (individuals)	Death observed	Death expected	Median lifespan (month 95% CI)
Associated CP	110	68	75	4 (4–5)
Non-associated CP	28	23	16	3 (2–5)

DISCUSSION

Abundance and area coverage

The calcareous sponge *Clathrina aurea* occurred throughout the year and was recruited continuously, as new individuals were seen arriving in the quadrats every month. Despite the continuous recruitment, two peaks of abundance and area coverage were observed, one in summer and another in winter (Figures 2 & 3). Continuous recruitment with peaks of abundance and area coverage has already been observed for other calcareous sponges. The congeners *C. coriacea* (Montagu, 1814) and *C. blanca* (Miklucho-Maclay, 1868) recruit during most of the year and reach their maximum abundance during winter, mainly due to asexual reproduction (Johnson, 1979), whereas the calcaronean *Paraleucilla magna* Klautau et al., 2004 reaches its maximum in summer, through sexual reproduction (Lanna et al., 2007; Padua et al., 2013b). Hence, although reproductive elements have never been seen in *C. aurea* (Lanna & Klautau, 2016), the occurrence of two abundance peaks during the year, as observed in the present study, and the low rate of clonality among individuals of the same study area (Padua et al., 2016), may suggest a double reproductive effort (one in summer and another in winter) with major participation of sexual reproduction. The most common cycle for calcareous sponges is only one reproductive season during the year (e.g. Johnson, 1978; Lanna et al., 2007; Padua et al., 2013b), but two breeding seasons have also been suggested for *Leucosolenia* sp. and *Sycon ciliatum* (Fabricius, 1780), one in summer and another in late autumn/winter (Orton, 1914).

After the abundance peak in summer, a significant decrease in the number of individuals was observed, followed by a gradual recovery of the population during the next 4/5 months reaching a second peak in winter followed by a new decrease (Figures 2 & 4). A similar pattern was observed for total area coverage but it was not significant (Figures 3 & 5). During the life cycle of *C. aurea*, there was a wide variation in individuals' area coverage, but without significant correlation with months (Figure 4). The dynamics of increase and reduction in area coverage of calcareous sponges has already been documented, and usually it was attributed to the species' reproductive period (Johnson, 1979; Gaino et al., 1996). A high reproductive effort could result in the reduction in area coverage of some asconoid species (Lanna et al., 2007), but we cannot state this for *C. aurea*, as the reproductive elements of this species remain unknown (Lanna & Klautau, 2016). The survival of some individuals of *C. aurea* between seasonal peaks contribute to the increase in population in the next season, as already suggested for *C. coriacea*, *C. blanca* and *Borojevia cerebrum* (Haeckel, 1872) (Johnson, 1979; Gaino et al., 1996).

We observed a positive significant correlation between abundance and area coverage in individuals of *C. aurea*. In a previous study with *C. blanca* by Johnson (1979) an increase

in total area coverage associated with a decrease in abundance was observed, that might imply intraspecific competition, since faster-growing individuals could be eliminating the slower ones. Based on that, we could not suggest intraspecific competition for individuals of *C. aurea* is not important in our study, since the area coverage increased with the abundance.

Influences of benthic community

The accurate determination of competition for space between calcareous sponges and other sessile marine invertebrates can be difficult due to the wide variation in abundance and area coverage of these sponges, especially the ones with an amorphous body shape, such as *C. clathrus* (Gaino et al., 1996). Even though, no evidence of spatial competition was observed between *C. aurea* and other benthic organisms. Only the area coverage of the colonial ascidian of the family Didemnidae presented a higher relative importance with *C. aurea* (Tables 2 and 3). However, we cannot assign conclusively this negative correlation as a direct consequence of the association between these two taxa, since this relationship could also be explained and influenced by other abiotic factors (temperature) and differences in life cycle (e.g. Hirose et al., 2006, 2007; McCarthy et al., 2007; Ritzmann et al., 2009), which were not assessed here. In fact, the interaction between *C. aurea* and the didemnid ascidian showed no clear outcome, with only one case of overgrowth of the sponge over colonies of the ascidian. Standoff interactions between the congener *C. coriacea* and didemnid ascidians have already been observed, with only one case of overgrowth of the sponge (Bell & Barnes, 2003). The low frequency of overgrowth between calcareous sponges and species of the family Didemnidae may be explained by the acidic tunic present in this family, making these ascidians usually free of epibionts (Stoecker, 1980).

It is common to find calcareous sponges living as epibionts (Rützler, 1970; Sarà, 1970; Johnson, 1980). In the present study, when not associated with coral polyps, *C. aurea* was observed in epibiosis with algae and the demosponges *Scopalina ruetzleri*, *Crella* sp., *Clathria (Microciona) campecheae*, *Dysidea etheria* and *Darwinella* sp. 2. Other calcareous sponges, like *Ascandra falcata* Haeckel, 1872, *C. clathrus* and *C. coriacea*, have already been observed growing upon other organisms, such as mollusc shells and algae (Johnson, 1980). They form a stratum of epibiotic species with a low degree of attachment on the basibionts and do not seem to cause any harm to the basibiont species (Rützler, 1970; Sarà, 1970). The clathrate body of *C. aurea* may favour the epibiosis on this species as it grows without suffocating the other organisms.

Survival analysis

The results of this study point to an increase of the lifespan of *Clathrina aurea* individuals when they are in direct contact with coral polyps (Figure 7). Eighty per cent (110) of all

sponge individuals analysed (138) were within the interstices of corals (Table 4), which probably promote a micro refuge for *C. aurea* against predators and competitors. Calcareous sponges are not considered good competitors for space (Rützler, 1970; Sarà, 1970). Hence, the exploitation of micro refuges in association with other organisms could enhance their survival. Although this interaction does not ensure avoidance of predation over time, because in a few cases the sponge occasionally becomes larger than the polyp, making predators able to reach it, it seems to be an efficient strategy for the sponge survival and apparently there are no negative results for the polyps.

The azooxanthellate scleractinian corals, *Astrangia rathbuni* and *Phyllangia americana*, are widely distributed in the Brazilian coast and can be found in shallow waters (Cairns, 2000). These corals usually inhabit the same habitat as *C. aurea*, such as caves and crevices, making contact between them possible (Cairns *et al.*, 2009; Correia, 2010). The sponge–coral association may be considered as a strategy to avoid risks of predation and competition, and indeed this strategy seems to enhance the lifespan of the sponge. The median lifespan of *C. aurea* was 3 months for non-associated individuals and 4 months for the associated ones (Table 4). The lifespan of calcareous sponges is usually short, ranging from weeks to one year (Orton, 1914, 1920; Johnson, 1979; Cavalcanti *et al.*, 2013; Padua *et al.*, 2016), while demosponges usually have a lifespan of months (Ereskovsky, 2000), decades (Mercado-Molina *et al.*, 2011) or even hundreds of years (Lehnert & Reitner, 1997; Wörheide *et al.*, 1997). Therefore, any strategy that increases even for one month the lifespan of a calcareous sponge may be important to maintain their populations.

Increase of the lifespan by interaction with other invertebrates or exploitation of protected areas has already been observed for demosponges and here we present the first example for the class Calcarea (e.g. Wilkinson & Vacelet, 1979; Fishelson, 1981; Wulff, 1997; Maldonado & Uriz, 1998, 1999; Turon *et al.*, 1998; Burns & Bingham, 2002). Ecological interactions may vary spatially and temporally (Palumbi, 1985), meaning that the contact between *C. aurea* and these coral polyps in other habitats may have different results. Changes in the environment by the removal or extinction of species may disrupt ecological interactions, causing replacements of local species and affecting the potential of survival, recovery and permanence of previously established species (Dulvy *et al.*, 2003).

In conclusion, our study suggests that *C. aurea* is a dynamic species that recruits continually over the year, changes its area coverage during its short lifespan and uses survival strategies that allow it to live in highly variable habitats. Their pattern of distribution can be explained by epibiosis and exploitation of micro refuges, mainly represented by a positive interaction with coral polyps, which enhances their survival, probably by avoiding space competition with other sessile marine invertebrates and predation. More studies on the ecological interactions of calcareous sponges with other organisms are needed for a better understanding of their ecological niches and which species could influence their life dynamics.

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