

## Original Article

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# Temporal variation in the recruitment of calcareous sponges (Porifera, Calcarea) in Todos os Santos Bay, tropical Brazilian coast

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## Abstract

Recruitment is related to the occupation of the substrate by fouling organisms. It plays an important role in the maintenance and distribution of benthic populations, being under the influence of biotic and abiotic factors. In the present work, the recruitment of calcareous sponges was monitored over two years in a marina at Todos os Santos Bay, a large bay in the tropical portion of the Brazilian coast. Artificial plates were immersed, being replaced bimonthly and the potential influence of the seawater temperature, photoperiod and precipitation on the number of sponge recruits was tested. The results showed that the number of calcareous sponge recruits had significant temporal variation. Nevertheless, different species showed different patterns over time. Significant differences were observed for *Sycon avus*, *Sycon* sp. and *Leucandra serrata*, and the periods with the highest number of recruits were different amongst them. *Sycon bellum*, *Paraleucilla incomposita*, *Leucilla* sp. and *Heteropia glomerosa* did not show significant variation in the number of recruits over time. None of the three tested environmental factors were correlated with the number of recruits, but results indicated *S. avus* recruitment might be driven by seawater temperature. Our results contribute to improve the current knowledge on the dynamics of each species found on the plates and reinforce the general view that the pattern of recruitment varies greatly in Calcarea, even amongst sympatric species.

## Introduction

In benthic communities, recruitment corresponds to the arrival, establishment and survival of new individuals to the substrate. It typically involves several pre- and post-settlement processes (Pineda *et al.*, 2009; Émond *et al.*, 2015), being fundamental to the continuous replacement of organisms and playing an important role in the maintenance of community structure (Underwood & Fairweather, 1989; Pineda *et al.*, 2009; Adjeroud *et al.*, 2016). In general, recruitment is under the influence of environmental and/or biological factors, such as predation, spatial competition, fecundity rates, larvae availability and competence, substrate type, temperature, light, sedimentation, depth and precipitation (Anderson & Underwood, 1994; Pineda *et al.*, 2009; Rico *et al.*, 2009; Cavalcanti *et al.*, 2013; Émond *et al.*, 2015; Chase *et al.*, 2016; Fuentes-Santos *et al.*, 2016; Sotelo-Casas *et al.*, 2016). The importance of each factor varies greatly among species and in space and time (Pineda *et al.*, 2009).

Sponges are one of the main components of benthic communities and are widely recognized for their importance in providing environmental services (Bell, 2008). Despite the relevance of recruitment as a fundamental process for the maintenance of populations, the number of studies on the recruitment of marine sponges is relatively small (e.g. Pronzato, 1972; Zea, 1993; Cavalcanti *et al.*, 2013; Padua *et al.*, 2013; Wulff, 2013; Dayton *et al.*, 2016, 2019; Stubler *et al.*, 2017). Regarding calcareous sponges (class Calcarea), recruitment knowledge is particularly scarce. They are commonly recognized as pioneers in the colonization of hard substrates, being subsequently overgrown by late colonizers such as demosponges (class Demospongiae), tunicates and bryozoans (Johnson, 1979; Vacelet, 1980, 1981; Pansini & Pronzato, 1981; Pierri *et al.*, 2010; Cavalcanti *et al.*, 2013; Ribeiro *et al.*, 2016). Concise observations were reported on their recruitment over time (discussed in Vacelet, 1980), and it was only during the 1970s and 1980s that the first accurate results became available (Pansini *et al.*, 1974; Vacelet, 1980, 1981; Pansini & Pronzato, 1981). These former works showed that, among other reasons, the number of recruits may vary according to depth, composition and immersion time of the substrates (Pansini & Pronzato, 1981; Vacelet, 1981). More recently, habitat selection and the influence of other factors were evaluated (Cavalcanti *et al.*, 2013; Padua *et al.*, 2013; Ribeiro *et al.*, 2016).

Most of the data on the recruitment of calcareous sponges came from studies developed in temperate regions, most specifically in the Mediterranean Sea (Pronzato, 1972; Pansini *et al.*, 1974; Vacelet, 1980, 1981; Pansini & Pronzato, 1981; Pierri *et al.*, 2010) and the



Pacific coast of California, USA (Johnson, 1979). It was only in the past few years that this topic was addressed in the tropics, in studies performed along the coast of Rio de Janeiro state, Brazil (Cavalcanti *et al.*, 2013; Padua *et al.*, 2013; Ribeiro *et al.*, 2016). Three species were used as models, the exotics *Paraleucilla magna* Klautau, Monteiro & Borojevic, 2004 and *Sycettusa hastifera* (Row, 1909), and the native sponge *Clathrina aurea* Solé-Cava, Klautau, Boury-Esnault, Borojevic & Thorpe, 1991. In the case of the former species, the influence of substrate orientation and exposure to light and hydrodynamics were revealed. For *P. magna*, data about the mortality of juveniles was also provided (Cavalcanti *et al.*, 2013; Padua *et al.*, 2013), while for *C. aurea*, the authors focused on the influence of benthic community in the abundance (recruits and adults) and lifespan (Ribeiro *et al.*, 2016). These works provided the first contributions for understanding the recruitment of tropical sponges belonging to Calcarea and further studies on this subject are needed.

The role of environmental parameters on the dynamics of recruits of calcareous sponges had never been tested. Johnson (1978) suggested that the seasonal recruitment of *Clathrina blanca* and *C. coriacea* from Santa Catalina island may be regulated by fluctuations in seawater temperature. This factor was identified as important for demosponges in the Caribbean, where increases in seawater temperature were correlated with a higher number of recruits (Zea, 1993). Therefore, based on the observations raised by Johnson (1978) and the results obtained by Zea (1993), we hypothesized that the same may occur for calcareous sponges from other tropical regions. An argument to support this hypothesis is that variations in seawater temperature may trigger the reproduction of calcareous sponges (Lanna *et al.*, 2015; Calazans & Lanna, 2019). Then, it is expected that some effects may extend to their recruits. Depending on the target species, tides, photoperiod and abundance of bacterioplankton may also predict the reproduction, while the production of larvae may be related to the local precipitation (Lanna *et al.*, 2015; Calazans & Lanna, 2019). As for seawater temperature, their influence on recruitment needs to be evaluated.

Beyond the influence of the environment, the description of temporal patterns of recruitment is an essential step to understand benthic population dynamics and structure. Therefore, in the present work, the recruitment of calcareous sponges was monitored over two years, and the putative influence of three environmental parameters on the number of recruits over time was tested: seawater temperature and photoperiod were chosen due to their previously observed effects in the reproduction of some species (Lanna *et al.*, 2015; Calazans & Lanna, 2019), while precipitation was chosen because it can be related to larval production (Calazans & Lanna, 2019) and due to the occurrence in the study area of marked dry (September–March) and rainy (April–August) seasons (Lessa *et al.*, 2009). Our study provides new insights on the recruitment dynamics of calcareous sponges from tropical areas, highlighting particularities of different species under the same environmental conditions.

## Materials and methods

### Study area

The study was performed in a recreational marina (Marina of the Nautical Tourist Terminal of Bahia; 12°58'19.9"S 38°30'55.8"W) in Salvador, Bahia state, north-eastern Brazilian coast (Figure 1). It is in the entrance of Todos os Santos Bay (TSB), one of the largest bays in Brazil, which is an important nautical route and contains several large harbours (Hatje & Andrade, 2009).

### Recruitment plates

The local assemblage of calcareous sponges was sampled using artificial recruitment plates. Artificial plates are widely used mainly due to their relative ease of handling and to their non-destructive characteristics (Menge *et al.*, 2011; Ronowicz *et al.*, 2014; South, 2016; Sokołowski *et al.*, 2017). Based on the fact that the authors observed high abundances of calcareous sponges attached to marine cables in TSB (Figure 2A–C), the plates were prepared by attaching fragments of polyester nautical cables with cable ties to form plates of 15 × 10 cm (Figure 2D, E, G).

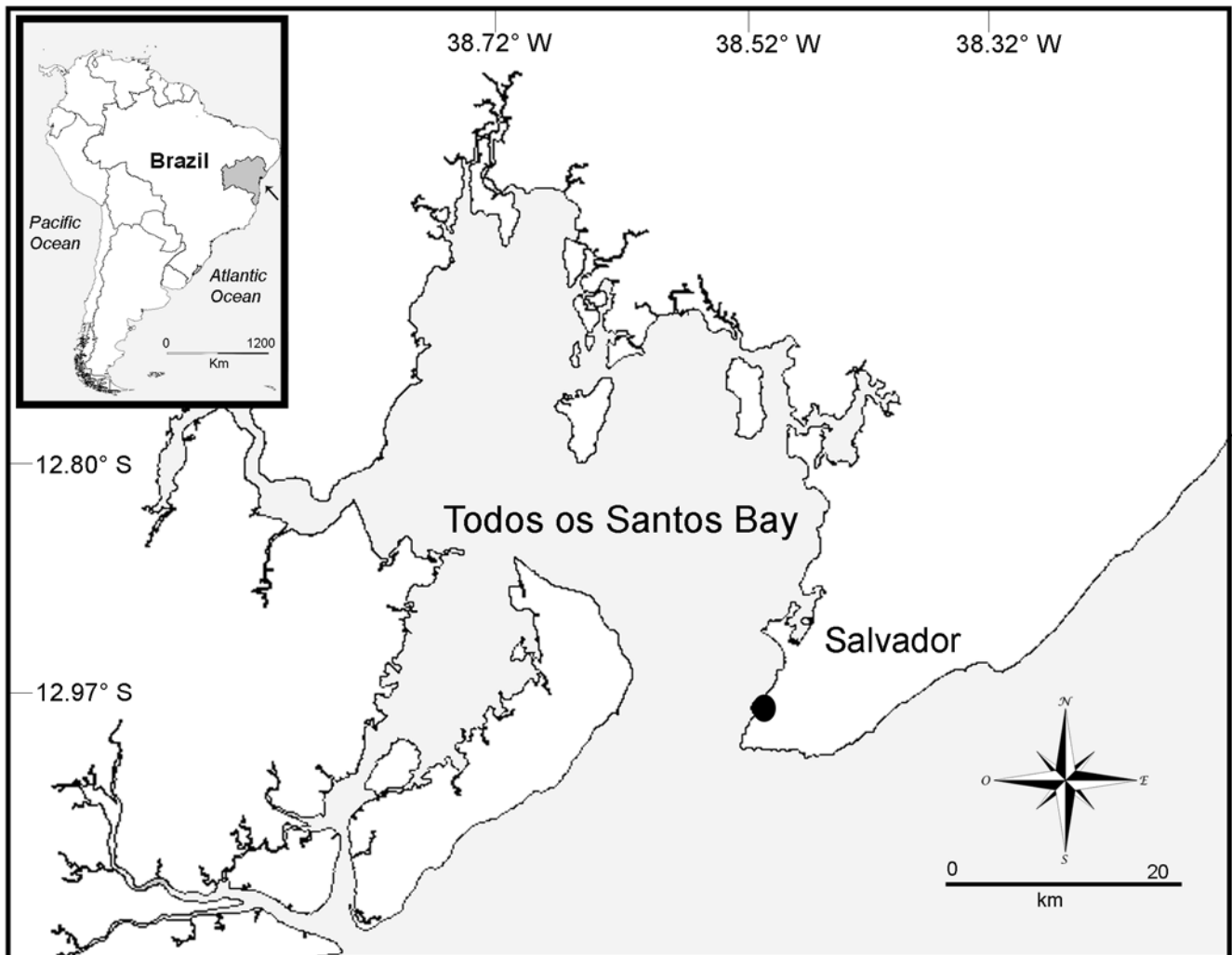
The study was performed from August 2015 to August 2017. The recruitment plates (10 replicates per month) were vertically submerged at 1 m depth, ~1.5 metres distant from each other, being attached to a floating pier (Figure 2D–F). A cable was used to hold the plates, being in touch with them. Therefore, only the side of the plates opposed to this cable was analysed (Figure 2E, H). All the plates were replaced bimonthly by new plates and the emerged plates were fixed in 80% ethanol. In the laboratory, they were analysed under a stereomicroscope. The calcareous sponges were removed from the plates, identified and counted. Recruits that could not be easily identified by their gross morphology and that were too small (<5 mm) for the preparation of microscope slides were grouped in a category named as 'others' and only considered in the analysis of the temporal variation of the total abundance.

### Environmental factors

Seawater temperature (°C) was automatically recorded every hour over the entire period of the experiment using a datalogger DS1922E (+15°/+140°C), attached to one of the cables that held the recruitment plates (Figure 2E). Along the period of study, data on the photoperiod and precipitation in the TSB were also obtained. The daily values of the photoperiod were obtained from TuTiempo (<http://www.tutiempo.net/brasil/salvador.html?datos=calendario>, last accessed on September 2017). Precipitation data (accumulated values) was obtained from the database of the Brazilian Center for Weather Forecasting and Climate Studies/National Institute of Space Research (CPTEC-INPE; <http://bancodedados.cptec.inpe.br/>, last accessed on September 2017). Bimonthly averages were calculated for temperature and photoperiod, while for precipitation values are expressed as the accumulated rain, as previously used in Lanna *et al.* (2015, 2018).

### Data analyses

Potential differences among bimesters in the number of recruits (total per plate and each of the seven identified species separately) and in the photoperiod and temperature data were investigated using one-way analysis of variance (ANOVA). When significant differences were found, it was followed by a Tukey *post hoc* test. Data were tested for normality and homoscedasticity. Total number of recruits of calcareous sponges, number of recruits of the most abundant species (*Sycon avus* Chagas & Cavalcanti, 2017), and the environmental parameters were under normal distribution. Data on recruits of the other six identified species were not normally distributed (Shapiro–Wilk,  $\alpha = 0.05$ ,  $P < 0.05$ ). Thus, Kruskal–Wallis tests were performed and where significant differences were observed, the Holm–Sidak *post hoc* test was applied. The statistical analyses were carried out using the software GraphPad Prism 6. Variations in precipitation were not tested as it was expressed as accumulated millimetres of rain in the two months of immersion of the plates. We applied Bonferroni correction for biological variables ( $\alpha = 0.006$ ) and for environmental variables ( $\alpha = 0.025$ ).



**Fig. 1.** South America and Brazil (in detail) showing the Bahia state (dark grey) and the location of the Todos os Santos Bay (arrow). The black dot in the large map indicates the study area, in Salvador city.

Multiple regression analyses were used to evaluate whether the number of recruits was related to variations in the seawater temperature, photoperiod and/or precipitation. These analyses were performed with each of the seven identified species separately and for the total number of recruits in each bimester, using the software PAST 3.25, and Bonferroni correction was also applied ( $\alpha = 0.006$ ). The results were graphically represented by GraphPad Prism 6.

## Results

### Recruitment of calcareous sponges

A total of 708 specimens were quantified on the plates. Most of them could be identified and only 111 specimens (16%) were classified as 'others'. The identified specimens belong to the following calcareous species (class Calcarea, subclass Calcareonea): *Sycon avus*, *S. bellum* Chagas & Cavalcanti, 2017, *Sycon* sp., *Paraleucilla incomposita* Cavalcanti, Menegola & Lanna, 2014, *Leucandra serrata* Azevedo & Klautau, 2007, *Leucilla* sp. and *Heteropia glomerosa* (Poléjaeff, 1883) (Figure 3). The most abundant species was *S. avus*, corresponding to 331 specimens (46.6%), which was the only species that recruited continuously over the two years (Figure 3A) and showed significant differences over time ( $F_{11,108} = 4.764$ ,  $P < 0.0001$ ; Table 1). Significantly higher numbers of *S. avus* recruits were found from December 2015/

February 2016 ( $6.5 \pm 4.1$  specimens per plate) to April/June 2016 ( $5.6 \pm 2.6$  recruits per plate) (Figure 3A).

The Kruskal–Wallis tests showed that differences were detected in the temporal recruitment of *Leucandra serrata* and *Sycon* sp. (Figure 3B, E; Table 1). *Paraleucilla incomposita* was not recorded from August/October 2016 to February/April 2017 (Figure 3D), while *Sycon* sp. recruited during almost the entire period of the experiment (Figure 3B). No clear patterns were observed for *Leucandra serrata*, *Leucilla* sp., *Heteropia glomerosa* and *S. bellum* (Figure 3C, E–G).

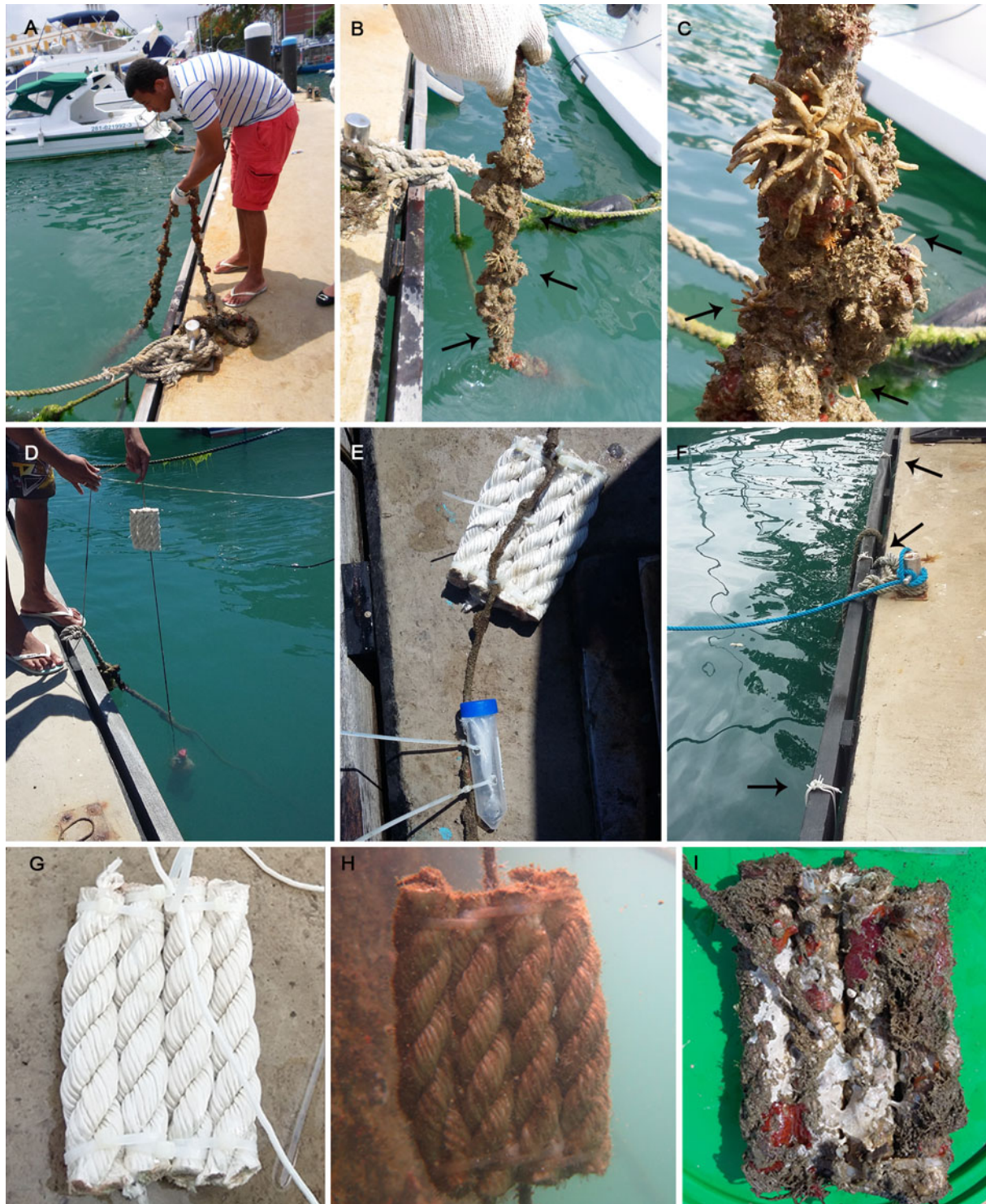
The total number of recruits varied significantly among bimesters (Figure 3H;  $F_{11,108} = 6.662$ ,  $P < 0.0001$ ; Table 1), even after reanalysing the data with the exclusion of *S. avus* ( $F_{11,108} = 5.222$ ,  $P = 0.002$ ). Peaks in the mean number of recruits occurred from December 2015/February 2016 ( $12.5 \pm 6.3$  specimens/plate) to April/June 2016 ( $9.6 \pm 5.4$  specimens/plate) (Figure 3H).

In addition to calcareous sponges, colonial ascidians, demosponges and algal turfs (to which hydroids were possibly added) were commonly found. Solitary ascidians, barnacles and serpulids also colonized the plates, but were observed less often.

### Environmental parameters

The seawater temperature varied significantly along the two years of experiment (Figure 4A; Table 1). Differences were

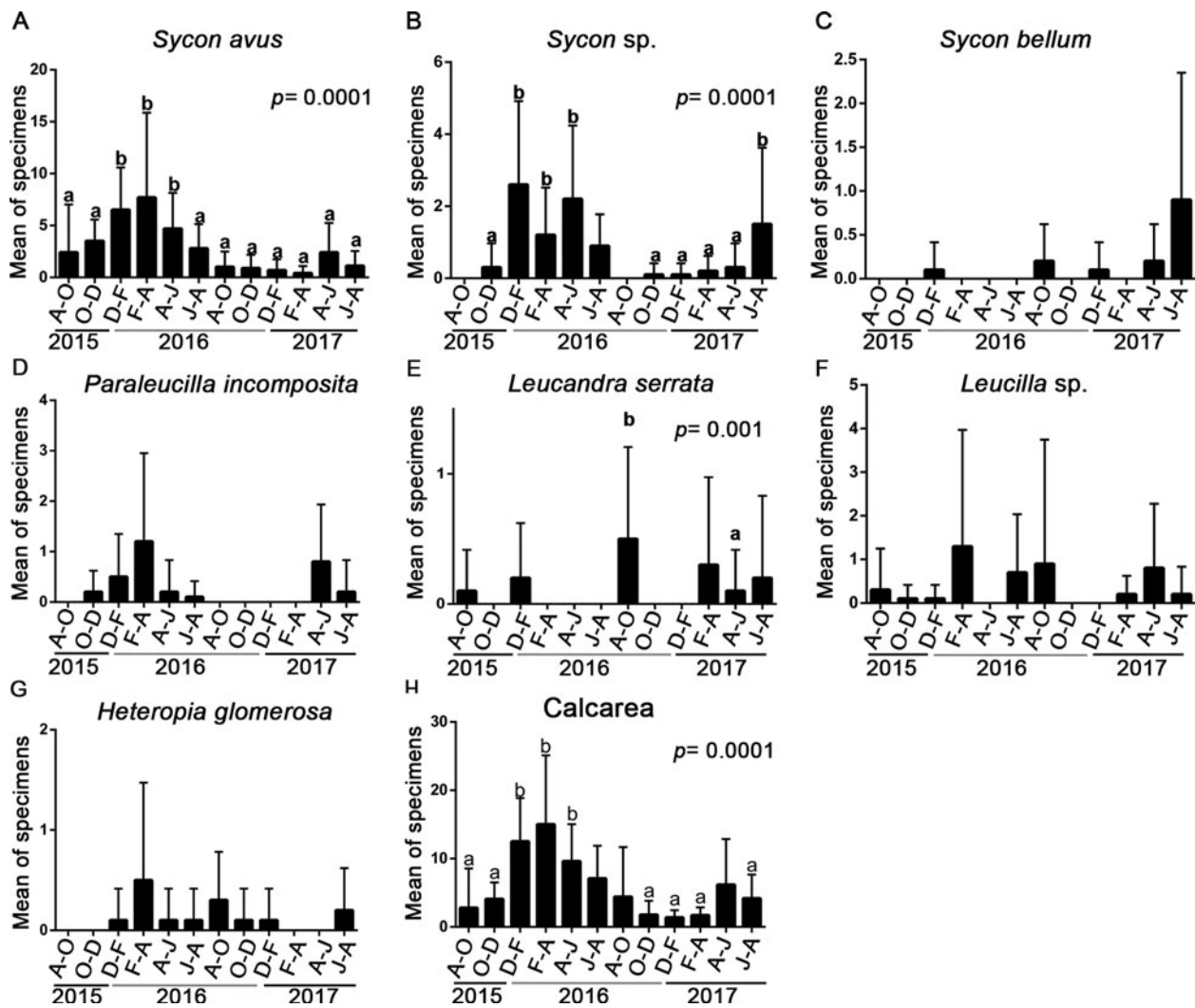




**Fig. 2.** General view of the study area and the experiment in the field. (A) Cable originally used by the marina to dock the vessels being taken out of the water. (B) Calcareous sponges (arrows) and other fouling organisms on the cable. (C) A large specimen of *Heteropia glomerosa* and (arrows) smaller calcareous sponges. (D) One of the recruitment plates attached to the floating pier at the moment in which it was immersed. A PET bottle filled with sand was used to maintain the cable stretched. (E) Tube containing the datalogger used to record the seawater temperature attached close to one of the recruitment plates. (F) Cables (arrows) that held the recruitment plates tied to the floating pier. (G) Experimental plate formed after attaching the fragments of nautical cables using cable ties. (H) A plate after few days of immersion. (I) A plate after two months of immersion.

observed among most of the bimesters, except between June/August 2016 and August/October 2016, and between February/April 2017 and April/June 2017. The minimum bimonthly average temperature was recorded in June/August 2017 ( $24.8^{\circ}\text{C} \pm 0.01$ ), while the maximum occurred in February/April 2016 ( $29.4^{\circ}\text{C} \pm 0.01$ ) (Figure 4A). Photoperiod varied significantly over time (Table 1) and the highest values

occurred in December/February of both years of study ( $753 \pm 2.52$  and  $760 \pm 2.52$  min of radiation, respectively), while in April/June 2016 and in June/August 2017 photoperiod was lower ( $684 \pm 1.90$  min of radiation; Figure 4B). Precipitation was mainly around 100 mm, but it increased at the end of the second year and reached the peak in April/June 2017 (510 mm; Figure 4C).



**Fig. 3.** Recruitment (mean and SE) over the experiment. (A) *Sycon avus*, (B) *Sycon sp.*, (C) *Sycon bellum*, (D) *Paraleucilla incomposita*, (E) *Leucandra serrata*, (F) *Leucilla sp.*, (G) *Heteropia glomerosa*, and (H) the whole assemblage of calcareous sponges. Letters a and b indicate significant differences. A-O = August – October; O-D = October – December; D-F = December – February; F-A = February – April; A-J = April – June; J-A = June – August. P-values reflect the results of ANOVA.

**Table 1.** Results of ANOVAs for testing the effect of time on the number of recruits of each species separately (a), the whole assemblage (b) and on environmental parameters (c)

	df	F	P
(a)			
<i>Sycon avus</i>	11	4.764	0.0001*
<i>Sycon sp.</i>	11	6.938	0.0001*
<i>Sycon bellum</i>	11	6.981	0.0149
<i>Paraleucilla incomposita</i>	11	1.530	0.0131
<i>Leucandra serrata</i>	11	1.332	0.0010*
<i>Leucilla sp.</i>	11	0.625	0.8040
<i>Heteropia glomerosa</i>	11	1.530	0.1312
(b)			
Whole assemblage	11	6.662	0.0001*
(c)			
Temperature	11	1569	0.0001*
Photoperiod	11	74.85	0.0001*

\*Indicates significant values after Bonferroni correction for biological variables ( $\alpha = 0.006$ ) and for environmental variables ( $\alpha = 0.025$ ).

### Influence of the environmental parameters on recruitment

Data were log transformed before applying the multiple regression analysis to verify whether changes in the recruitment of calcareous sponges occurred according to the environmental parameters. None of the tested relationships was significant. It seems that there was a greater total number of recruits of *Sycon avus* (Figure 5) in warmer months but it was not significant.

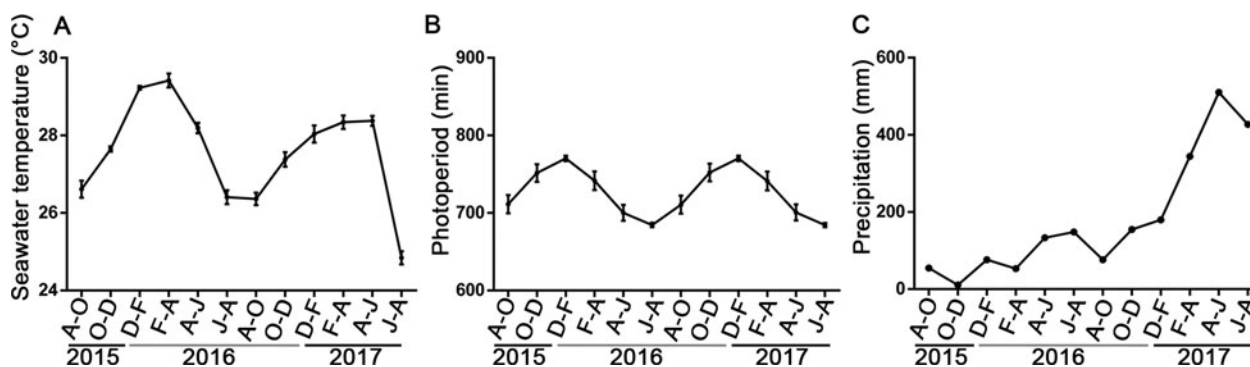
### Discussion

#### Recruitment of calcareous sponges over time

In the present work, only sponges of the subclass Calcaronea were found on the plates and significant differences in the number of recruits over time were observed for three out of the seven identified species. No significant relationship with precipitation, temperature or photoperiod was observed despite the historical recognition that dry and rainy seasons are important biological drivers in the region.

*Sycon avus*, *Paraleucilla incomposita*, *Leucilla sp.* and *Heteropia glomerosa* showed the highest number of recruits at February/April 2016 (mostly within dry season; Figure 3). Recruitment peaks occurred at different bimesters for *Sycon sp.* (December 2015/February 2016; dry season), *Leucandra serrata*





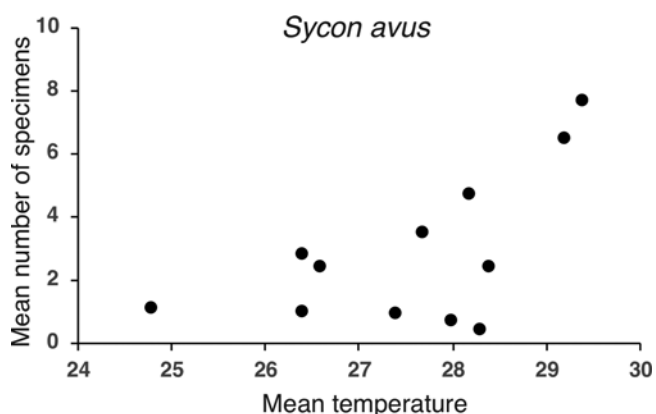
**Fig. 4.** Temporal variations in the environmental parameters. (A) Average and standard deviation of the seawater temperature over time, (B) Average and standard deviation of the photoperiod over time, and (C) Bimonthly accumulated precipitation. A–O = August–October; O–D = October–December; D–F = December–February; F–A = February–April; A–J = April–June; J–A = June–August.

(August/October 2016, mostly within dry season) and for *Sycon bellum* (June/August 2017; rainy season). In comparison with other calcareous sponges from tropical areas, the results obtained here for *Sycon avus*, *P. incomposita*, *Leucilla* sp. and *Heteropia glomerosa* were similar to those previously reported to *Paraleucilla magna*, as its highest recruitment occurred in the middle-late summer (more specifically in January/April 2007) (Padua et al., 2013). Another tropical species to which data are available is *Clathrina aurea* (subclass Calcinea). Ribeiro et al. (2016) monitored one of its populations *in situ* over 13 months and a clear seasonality was reported, with two peaks of abundance and coverage – in January 2013 and August 2013. They were explained by the recruitment of additional individuals, possibly resulting from two events of sexual reproduction (Ribeiro et al., 2016). To the best of our knowledge, among the species studied in the tropics, the only exotics are *P. magna* and *H. glomerosa*, but number of specimens of *H. glomerosa* found on the plates were extremely low. Further studies on the recruitment over time are needed to elucidate if native and exotic calcareous sponges have different recruitment patterns.

Most of the previous studies on calcareous sponges were performed in temperate regions. The available data show that, as observed here, the period of peaks in the number of recruits varies among sympatric species (regardless of whether they belong to Calcinea or Calcaronea). In populations of *Clathrina blanca* (Miklucho-Maclay, 1868) and *C. coriacea* (Montagu, 1814) from Santa Catalina Island, for example, the highest number of recruits of these species was observed from March to May 1975 and from February to July 1975 (spring/summer), respectively (Johnson,

1979). Differences in the number of recruits were also reported by Pansini et al. (1974) for several species from the Italian coast. *Leucandra aspera* (Schmidt, 1862), the most abundant on the recruitment plates, recruited mainly from July to August (summer, year not provided), although recruits of other sympatric species were not found in this same period (Pansini et al., 1974). In the present work, the lack of a similar recruitment pattern to all the species composing the studied assemblage is reinforced by the results found for *Sycon bellum*, *Paraleucilla incomposita*, *Leucilla* sp. and *Heteropia glomerosa*, which did not vary significantly over time (Figure 3; Table 1).

An intriguing point of the present results is the rarity with which *Heteropia glomerosa* was found on the plates (up to  $0.5 \pm 0.4$  specimens per plate; Figure 3G). This is an exotic species widely distributed along the Brazilian coast, occurring mainly in marinas and harbours along an extent of ~2900 km, and its reproductive effort is amongst the highest observed for sponges (Calazans & Lanna, 2019; Klautau et al., 2020). In the studied site in Todos os Santos Bay, it is easily found along the year, colonizing ropes and a plethora of surfaces composed of different types of artificial substrates (wood, plastic, concrete and so on; Chagas & Cavalcanti, 2017; Barros et al., 2018). Differences in the abundance of *H. glomerosa* on the ropes used by the marina to dock the vessels and on the ropes used as experimental plates cannot be attributed to their composition/material as they are exactly the same kind of nautical cable. Nevertheless, time of immersion of the original ropes of the marina and that of the plates are probably different, the former potentially remained immersed for very much longer periods. Therefore, it seems that *H. glomerosa*, differently from most of the calcareous sponges, is not a pioneer in the colonization. Its recruitment may be hampered by the use of new/recently immersed substrates, with a preference for those sustaining a more developed/complex fouling community and/or a higher biofilm complexity. The ability for occupying colonized surfaces could facilitate the dispersion of *H. glomerosa* attached to artificial substrates. The need for longer periods of immersion of the substratum had already been reported for calcareous sponges living in the Mediterranean Sea. Vacelet (1981) compared plates immersed during 44 or 48 months and showed that the former were preferred by *Amphoriscus chrysalis* (Schmidt, 1862) and *Leucandra aspera* (Schmidt, 1862), while *Sycon quadrangulatum* (Schmidt, 1868) recruited mainly on plates immersed for 48 months. In the Italian coast, the number of species on plates sunk for 47 months was two, three or five times higher than on those immersed for 26 months depending on the type of artificial substratum (Pansini & Pronzato, 1981). Further studies are needed to test this hypothesis of ‘higher biofilm/ fouling complexity’ and to



**Fig. 5.** Relationship between recruitment of *Sycon avus* and the seawater temperature (°C).

provide a better understanding of the colonization and/or development capabilities of the exotic *Heteropia glomerosa* in Brazil. A putative competition between this species and *Sycon avus*, the most abundant on the plates, does not seem to be a plausible explanation as uncolonized areas were commonly observed. In the case of the remaining species, we could not evaluate whether their abundance on the plates over time agreed with their occurrence in the marina as, unlike *H. glomerosa*, they are not easily recognized in the field.

### Environmental parameters and recruitment

The factors influencing the population dynamics of sponges remain poorly understood. For the calcareous sponges *Sycon ciliatum*, *Paraleucilla magna* and *Sycettusa hastifera*, abundance of recruits may depend on the substratum orientation (Vacelet, 1981; Cavalcanti *et al.*, 2013), immersion time of the substrates (Pansini *et al.*, 1974; Pansini & Pronzato, 1981; Vacelet, 1981), depth (Vacelet, 1981), light (Cavalcanti *et al.*, 2013; Padua *et al.*, 2013), or larval behaviour (Padua *et al.*, 2013). Reproductive cycles, sedimentation, seawater temperature and biological interactions have been discussed, but not tested, to explain differences in the recruitment of *Clathrina blanca*, *C. coriacea*, *S. ciliatum*, *Leucosolenia variabilis* and *P. magna* (Pronzato, 1972; Johnson, 1979; Padua *et al.*, 2013).

During the development of the present work, some preliminary analyses were performed with data obtained after the first year of study. The results indicated that, for *Sycon avus* and the whole pool of recruits (i.e. the total number of calcareous sponges), recruitment would be regulated by changes in the seawater temperature. Nevertheless, after two years of the experiment, no significant results were found. It reinforces the relevance of continuing the experiment for more than one year to avoid erroneous generalizations about the temporal pattern of recruitment and its drivers.

Zea (1993) analysed the recruitment of demosponges in Santa Marta, Colombian Caribbean. In his work, the young sponges were not identified at the species level, but a significant and positive effect on the general number of recruits was found, although the seawater temperature varied little over time (from 24–26°C during the dry upwelling season to 27–28°C during the rainy outwelling season; Zea, 1993). In the present work, we observed a greater variation of seawater temperature (from 24.6–29.2°C) but no correlation with recruits of calcareous sponges. Possibly, recruitment was driven mostly by biological processes related to the fecundity of each species, and/or by endogenous controls, but further studies are needed to test these hypotheses. The influence of juvenile predation and the incidence of light were not analysed, and we could not assume that they are irrelevant factors. Additionally, we cannot refute that the seawater temperature could be important for larval settlement (as for the demosponge *Rhopaloeides odorabile*; Whalan *et al.*, 2008) but not for recruits. This correlation could be masked by factors such as mortality (Pineda *et al.*, 2009), and be undetectable when looking at the number of recruits. Recently, Calazans & Lanna (2019) showed that the reproduction of one of the species found here, *Heteropia glomerosa*, may be regulated by photoperiod. According to our results, this same factor was not correlated to the number of recruits of this species. Pineda *et al.* (2009) argued that the lack of correlation sometimes observed between drivers of reproduction and those of recruitment may be caused by the mortality of larvae and juveniles, differences in the fecundity rate among the species, dependence on abiotic factors that may or may not be an environmental parameter, among others. The influence of seawater temperature, photoperiod and also other variables must then be investigated by experiments considering larval settlement and recruitment success.

### Final considerations

The identification of recruits at the lowest taxonomic rank is important to evaluate the existence of patterns of recruitment among different species sharing the same habitat. As mentioned by Zea (1993), the difficulty linked to this task is the absence, in young sponges, of some of the morphological features used in taxonomic identification. In the present work, most of the recruits could be identified at the species level after the preparation of microscope slides. Our results contributed to improve the current knowledge on the dynamics of each species found on the plates and reinforced the general view that the pattern of recruitment varies greatly in Calcareia, even amongst sympatric species. It has been reported since the pioneer work by Pronzato (1972) and is evidenced here for tropical species.

Particularities of each species in the assemblage became evident, and drivers of their recruitment may not be the same, even though they live so close to each other in the substratum. Also, factors triggering the reproduction of the adults may not be the same as those regulating the initial steps of the benthic juveniles, but more work is needed particularly for *Heteropia glomerosa* as it is an exotic species for which data on its reproductive biology is now available (Calazans & Lanna, 2019).

The integration of data about the production and settlement of the larvae with information on the recruitment of the same species would fill an important gap of knowledge on the biology and population dynamics of calcareous sponges. To the best of our knowledge, currently, these complementary data are available only for *Paraleucilla magna* and *Clathrina aurea* (Cavalcanti *et al.*, 2013; Padua *et al.*, 2013; Lanna *et al.*, 2015; Ribeiro *et al.*, 2016). In this context, two of the species studied here could be used as models in future works aiming for a broader understanding on the biology and dynamics of Calcareia: *Heteropia glomerosa*, for which data on the reproductive biology are available (Calazans & Lanna, 2019); and *Sycon avus*, as it was the most representative on the plates, a crucial feature for model species. Data on the reproduction and larval behaviour of *S. avus* would complement our understanding on its recruitment dynamics and elucidate whether the seawater temperature is an important driver.

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