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ORIGINAL ARTICLE

Recruitment, habitat selection and larval photoresponse of *Paraleucilla magna* (Porifera, Calcarea) in Rio de Janeiro, Brazil

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Abstract

Little is known about the recruitment and behaviour of sponge larvae, especially of the class Calcarea. The calcareous sponge *Paraleucilla magna* is very common in Southeast Brazil, where it is considered a cryptogenic species. This study quantified recruitment rates in shaded and illuminated habitats for 2 years in Rio de Janeiro, Brazil, and analyzed larval photoresponses of this species. Four structures, each containing a shaded and an illuminated surface, were exchanged every 3 months for 2 years. The number of recruits was quantified on each plate. In the laboratory, larvae of *P. magna* were placed in half-shaded Petri dishes and the number of settlers in each side was counted after 24 h. *Paraleucilla magna* recruited continuously throughout the experiment. Recruits occurred in greater abundance on shaded surfaces than on illuminated surfaces, and the larvae were negatively phototactic *in vitro*. Despite the possible influence of other factors in the recruitment of sponges (such as sedimentation, competition and predation), the prevalence of *P. magna* in shaded habitats may also be related to larval choice.

Introduction

The colonization of habitats by sessile marine organisms with planktonic larvae can be divided in four phases: dispersal, active habitat choice by the larvae, settlement and recruitment (Keough & Downes 1982). During this whole process, but especially in the recruitment phase, many biotic and abiotic factors may interact at various temporal and spatial scales to determine the intensity of the recruitment and the success of the population (Pawlik 1992; Hunt & Scheibling 1997; Perkol-Finkel & Benayahu 2007; Pineda *et al.* 2009).

Sponges are sessile organisms that possess a planktonic larval stage and are important members of benthic marine communities (Muricy 1989). Despite their importance, few recruitment studies have been conducted with these organisms. Most studies have been on temperate water demosponges (McDougall 1943; Hartman 1958; Wells *et al.* 1964; Fell 1976; Fell *et al.* 1978; Lewandrowski & Fell 1981; Barthel 1986). Consequently, our knowledge of sponges in the class Calcarea and particularly of tropical sponges is even scarcer. So far, only six studies have examined the recruitment of calcareous sponges (Pronzato 1972; Johnson 1978, 1980; Vacelet 1980, 1981; Pansini & Pronzato 1981) and all of them were conducted in temperate regions of the Northern hemisphere. In those works, the only abiotic stimuli analyzed were temperature, depth and substratum composition. The effects of light and sediment, although mentioned by some authors, have never been tested for calcareous sponges (Johnson 1980; Vacelet 1981).

Light is considered one of the most important stimuli for the settlement of sponge larvae, guiding the sponges to illuminated or shaded places (Ettinger-Epstein *et al.* 2008). The preference of most sponges for shaded habitats (*e.g.* Sarà & Vacelet 1973; Jokiel 1980) is frequently explained by competition with macroalgae, protection against predators and intolerance to sedimentation and

UV radiation (Vacelet 1976; Jokiel 1980; Harmelin 1985; Rützler *et al.* 2000; Maldonado *et al.* 2008). Like demosponges, calcareous sponges are more commonly found in shaded environments such as burrows, caves and under rocks (Klautau & Borojevic 2001). However, there have been no studies comparing the recruitment of calcareous sponges between shaded and illuminated habitats.

Paraleucilla magna Klautau *et al.* 2004 is a calcareous sponge very common on rocky shores of Rio de Janeiro, São Paulo and Santa Catarina States in Brazil and also along the Mediterranean coast (Italy, Malta and Spain; Longo *et al.* 2007; Zammit *et al.* 2009; Guardiola *et al.* 2011). Adults of this sponge can be found in both illuminated and shaded environments (Monteiro & Muricy 2004) but no studies on preferential recruitment of this species have been done. *Paraleucilla magna* is considered cryptogenic on the Brazilian coast (Klautau *et al.* 2004), but in the Mediterranean Sea it is considered invasive because it causes damage in mussel farms (Longo *et al.* 2007). Therefore, a knowledge of recruitment rates of this species is important for predicting its capacity to maintain existing populations and establish new ones. In addition, it is important to understand how cryptic populations are established (either by differential settlement between shaded and illuminated surfaces, or by differential mortality).

We compared recruitment rates of *Paraleucilla magna* in Rio de Janeiro, Brazil over a 2-year period to test whether there was differential recruitment between illuminated and shaded surfaces. Additionally we tested whether larvae of *P. magna* display photoresponses that could help to explain differential recruitment rates between illuminated and shaded environments.

Material and Methods

Study area

The recruitment experiment was undertaken at Vermelha Beach, in Rio de Janeiro, Brazil (22°57′18″S – 43°09′42″W; Fig. 1). This is a semi-enclosed bay at the entrance of Guanabara Bay (Lanna *et al.* 2007). The study was performed at the eastern rocky shore of Vermelha Beach, at approximately 6 m depth. Individuals of *Paraleucilla magna* obtained for the larval phototaxis experiment were collected at Urca, an area of artificial rocky shores with an intense transport of fishing boats and input of organic matter located approximately 700 m from Vermelha Beach (Fig. 1).

Recruitment experiment

To study the recruitment of *Paraleucilla magna* we used 15 × 15 cm acrylic plates with both sides roughened. Each plate was supported horizontally on four legs, with the lower surface 5 cm above a concrete block that was haphazardly positioned on the bottom at Vermelha Beach. Therefore, each plate offered an illuminated and a shaded surface for *P. magna* to recruit. At the beginning of the experiment, four plates, each on a separate block, were placed underwater. Every 3 months each plate was removed and exchanged for a new one until the end of the study. The experiment lasted 2 years, from January 2007 to 2009. After removal, the plates were fixed in 93% ethanol and observed under a stereomicroscope at the laboratory, where *P. magna* recruits were counted.

Larval phototaxis

To determine whether the larvae of *Paraleucilla magna* respond to light, adult individuals of *P. magna* were collected in September 2009 at Urca and placed in a plastic container filled with seawater. At the laboratory, the specimens were observed under a stereomicroscope and the released larvae were collected with a Pasteur pipette and distributed among four Petri dishes. Approximately 20 ml of seawater containing larvae were placed in each dish (353, 209, 830 and 336 larvae, respectively). Each Petri dish had two different halves, one covered with black tape

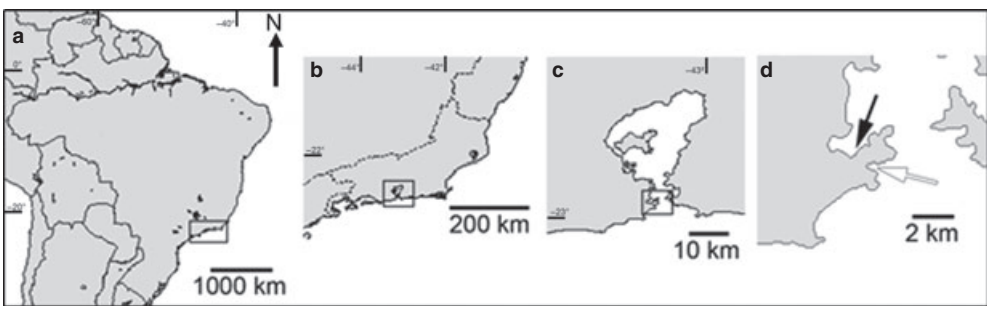

Fig. 1. Location of the recruitment experiment. (a) Brazil, Rio de Janeiro State; (b) Rio de Janeiro. State showing the specific location of Guanabara Bay; (c) Guanabara Bay and Vermelha Beach; (d) black arrow – Urca, where the individuals were collected for the larval experiment; white arrow – Vermelha Beach, where the recruitment experiment was performed.

to block light and the other clear, artificially creating a shaded and an illuminated environment in each dish.

A source of fluorescent light (0.16 $W \cdot m^{-2}$ of intensity) was positioned approximately 40 cm above the dishes. The number of larvae settled in each half of the Petri dishes was counted after 24 h using a Nikon Eclipse TS100 inverted microscope. Larvae still swimming at the end of the experiment (2.7%) were excluded from the analyses.

Data analyses

A two-way blocked ANOVA with square-root transformed data was applied to compare the recruitment rates between illuminated and shaded surfaces over the 2-year experiment. The factors analyzed were: habitat preference (illuminated or shaded) and immersion period (trimesters). Each plate was the blocking factor, within recruitment treatments (illuminated and shaded) being applied. Both analyses were performed using R 2.9.0® software (R Development Core Team, 2009). A chi-squared analysis using INSTAT (GraphPad Software, Inc., San Diego, CA, USA) was performed to test whether the number of settled larvae in illuminated and shaded environments was random.

Results

Recruitment and habitat selection

Paraleucilla magna recruited during every trimester over the 2 years of the experiment. The period with the highest recruitment rate was January–April 2007 (101.3 recruits ± 34.6) and the lowest was October 2008–January 2009 (1.8 recruits ± 1.4; Fig. 2). Recruitment in the second year of the experiment (2008) was much lower than observed in 2007, with the highest recruitment rate being April–July (5.1 recruits ± 2.9; Fig. 2). Although individuals of *P. magna* were found on both illuminated and shaded sides of plates, the number of recruits on the shaded plates (550 recruits, 94.8%) was significantly higher than on the illuminated ones (30 recruits, 5.2%; $F = 45.15$; $df = 1$; $P < 0.001$; Fig. 2). The two-way blocked ANOVA showed that the blocking factor (the illuminated and shaded surfaces) was not significant ($F = 1.17$; $df = 21$; $P = 0.359$). This indicates that the recruitment on one surface was not dependent on the recruitment on the other and, therefore, on the structure. The interaction between habitat preference (illuminated or shaded) and immersion period (trimesters) was significant, meaning that the habitat selection was dependent on the sampling period ($F = 11.11$; $df = 7$; $P < 0.001$). This interaction occurred because of the larger number of recruits in the first trimester.

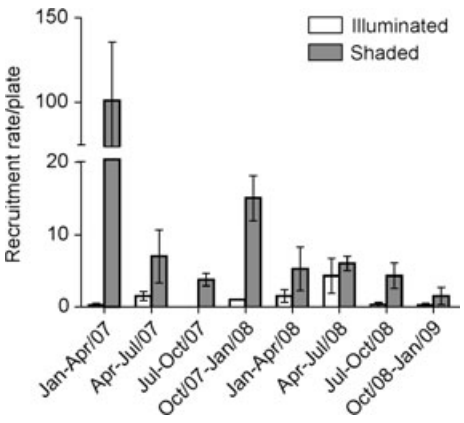

Fig. 2. Recruitment rate of *Paraleucilla magna* in shaded and illuminated surfaces for each trimester (means and standard errors) during the whole experiment period.

Larval photoresponse

After their release from the sponge, the amphiblastula larvae of *Paraleucilla magna* swam to the water surface, where they kept swimming in spiral movements. The larvae did not stay very long in the water column, settling and metamorphosing approximately 3 h after release. The chi-squared test showed that the settlement differed significantly between illuminated and shaded sides ($\chi^2 = 25.4$; $df = 3$; $P = 0.0001$), with settlement being higher in the shade (Fig. 3).

Discussion

Recruitment of *Paraleucilla magna*

Paraleucilla magna recruited continuously over the 2 years of the experiment, showing the highest recruitment rate in the first trimester (summer) of 2007 (Fig. 2). In a previous study, *P. magna* reproduced mainly during the summer (Lanna *et al.* 2007), however, despite the highest recruitment rate during the summer of 2007, the same

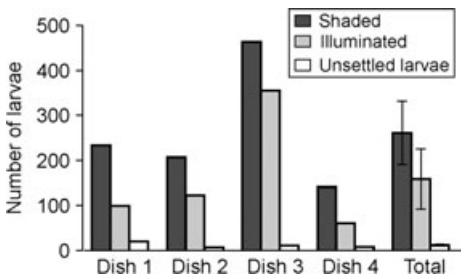

Fig. 3. Number of settled and unsettled larvae of *Paraleucilla magna* in each Petri dish in the photoresponse experiment.

was not observed in the summer of 2008. In fact, the population density of *P. magna* at Vermelha Beach was visibly lower throughout 2008 than during 2007. It is possible that the lower number of individuals settled on the experiment plates in 2008 reflected a reduced number of individuals reproducing on the rocky shore. The interannual difference in recruitment may be the result of natural fluctuations intrinsic to this species or could be related to its adaptation to a new habitat as it is a putative exotic species in Brazil. In the Mediterranean Sea, where this species is considered to be invasive, its recruitment showed no temporal pattern (Pierri *et al.* 2010).

The only prior study of sponge recruitment conducted in a tropical region (northeast Colombia) demonstrated that the recruitment of demosponges occurred during most of the year, with maximum rates in summer and spring (Zea 1993). Calcareous sponges have been studied only in temperate regions, where they also recruited the whole year, but mainly in winter and spring months (Pronzato 1972; Johnson 1978, 1980; Vacelet 1980, 1981; Pansini & Pronzato 1981).

Recruitment of *Paraleucilla magna* was significantly higher on shaded than illuminated plates. In general, calcareous sponges are much more common in shaded habitats (crevices, under caves and rocks; Klautau & Borojevic 2001). Even though specimens of *P. magna* have already been found in high abundances in illuminated environments, these sponges were present in vertical habitats, which are less exposed to light than horizontal ones (5.9 individuals·m^{-2}; Monteiro & Muricy 2004 as *Paraleucilla* sp.). Sponges are frequently dominant in protected and shaded habitats and on the undersides of plates without light and/or sediment (Jokiel 1980; Zea 1993; Klautau & Borojevic 2001; Maldonado 2006; Maldonado *et al.* 2008). Spatial distribution is a consequence of larval choice or post-settlement factors such as predation, competition, turbulence and sedimentation (Maldonado & Young 1996; Maldonado & Uriz 1998; Carballo 2006; Maldonado *et al.* 2008; Miller & Etter 2008). Therefore, when larvae are able to choose their settlement sites, they may increase their chances of survival (Maldonado & Young 1996).

Although we cannot discount differential mortality of recruits in illuminated habitats caused by competition, predation and sedimentation, the photonegative behaviour of *Paraleucilla magna* larvae *in vitro* suggests that the recruitment of this species in shaded environments is at least in part influenced by larval choice. The importance of larval behaviour in recruitment has already been demonstrated for demosponge species (Maldonado & Young 1996; Abdul Wabab *et al.* 2011) and phototaxis of sponge larvae has already been observed in numerous species (*e.g.* Maldonado *et al.* 1997, 2003; Uriz *et al.* 1998; Leys & Degnan 2001; Mariani *et al.* 2005). However, only one calcareous sponge has been studied so far and, similarly to *P. magna*, the larvae of *Sycon coactum* also demonstrated a negative response to light (Elliot *et al.* 2004).

In summary, *Paraleucilla magna*, as other tropical sponges already studied, is capable of recruiting all year round, and it prefers shaded habitats. Although other factors, such as sedimentation, predation and competition may be important to the recruitment of this species, larval phototaxis seems to contribute to the observed distribution of this species in shaded habitats.

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