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Uneven abundance of the invasive sun coral over habitat patches of different orientation: An outcome of larval or later benthic processes?



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ARTICLE INFO

Article history:

Received 28 March 2013

Received in revised form 18 November 2013

Accepted 28 November 2013

Available online 28 December 2013

Keywords:

Competition

Habitat orientation

Larval behavior

Sedimentation

Settlement

Tubastraea coccinea

ABSTRACT

Larval behavior in the water column and preference among natural benthic habitats are known to determine initial spatial distribution patterns in several sessile marine invertebrates. Such larval attributes can be adaptive, promoting adult benthic distributions which maximize their fitness. Further benthic processes may, however, substantially change initial distribution of settlers. In this study, we first characterized spatial distributions of adult colonies and single-polyp recruits of the invasive azooxanthellate coral *Tubastraea coccinea* over substrates of different orientation, and evaluated their consistency at both small (several tens of meters) and intermediate (a few km) spatial scales. We then assessed, through field and laboratory experiments, larval preferences and relative settlement and recruitment rates on surfaces with different orientations to determine whether processes taking place during the larval and early post-larval stages could help explain the distribution patterns of recruits and adult colonies. Results suggest that larval passive buoyancy and active larval behavior, unrelated to light conditions, determine a clear settlement distribution pattern, in which the density of settlers is highest at undersurfaces and almost nil at upward facing horizontal substrates. Except for an almost absence of settlers, recruits and adult individuals on upward facing horizontal habitat, there is substantial mismatch between the distribution of settlers and that of recruits and adult colonies. The latter were also common in vertical substrate in the field. We speculate that coastal runoff at the study area and subsequent sedimentation may inhibit coral development on flat upward facing habitat, and that competitive interference and pre-emptive interactions with other azooxanthellate corals could constrain abundance of *T. coccinea* in underface horizontal habitat.

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1. Introduction

The native range of the sun coral *Tubastraea coccinea* Lesson comprises the Pacific and Indian Ocean (Cairns, 2000), but this species has been introduced in shallow tropical habitats at many locations worldwide (Glynn et al., 2008), including the southeastern Brazilian coast (da Silva and Barros, 2011; Ferreira, 2003; Mantelatto et al., 2011; Paula and Creed, 2005). The rapid invasion of *T. coccinea* in this region is likely due to the expansion of the oil industry and associated shipping activity (Ferreira, 2003; Paula and Creed, 2005). As many other alien sessile invertebrates and algae, *T. coccinea* has probably benefited from the provision of bare hard substrates found in pipelines and oil platforms where they establish colonies that can seed nearby natural habitat patches. Indeed, surveys and experiments conducted at Ilha Grande, RJ, Brazil, have shown that the sun coral readily settles on different man-made hard substrates (Creed and Paula, 2007; Mangelli and Creed, 2012). The new colonies can resist extreme environmental conditions (Robinson, 1985), making this species an efficient colonizer not only of artificial substrates, but also of free patches of natural

habitat. In natural substrate, colonies can attain substantial surface cover and cause important modifications in native benthic communities (Lages et al., 2011), often through establishing negative interactions with the closely-related species *Mussismilia hispida*, endemic to south-eastern Brazil (Creed, 2006).

Substrate selection by settling larvae can shape, to some extent, the spatial distribution patterns of adult benthic populations, especially over small to moderate spatial scales (Chabot and Bourget, 1988; Harrington et al., 2004; Pineda et al., 2010). For instance, larvae of several azooxanthellate coral species, including *T. coccinea*, concentrate in downward facing (negative) and vertical surfaces, or crevices, where they can find release from competition with fast-growing coral species that use symbiont microalgae and light as an energy source (Bak and Engel, 1979; Birkeland, 1977; Fenner and Banks, 2004; Ferreira, 2003; Glynn et al., 2008; Lewis, 1974; Rogers et al., 1984; Vermeij, 2005). In the case of invading species, information on larval substrate selection is particularly important to establish environmental policies to help control their spread and understand potential effects on native communities. A basic selective larval behavior is whether to settle preferentially on vertical or horizontal, upward (positive) or downward facing surfaces. Because the latter two are particularly abundant in artificial habitat, such as piers, jetties or oil platforms, selective settlement

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behavior for different orientations can increase or decrease the negative impact of such artificial structures (e.g. Glasby, 2000; Salinas-de-León et al., 2011), but it can also determine the impact on natural communities where overhangs and vertical walls are a common topographic feature. While colonization of new (artificial) habitats may strongly reflect larval preferences and settlement behavior, spatial distribution patterns of natural habitats may largely depend on biological interactions with pre-established species assemblages. In order to disentangle larval and later benthic processes it is first important to estimate larval preferences and compare results to the natural distribution of early recruits and adults in the field. As far as we are aware of, this has not been attempted in this invasive species.

In spite of being considered primitive larvae lacking specialized organs for perception of environmental change (Barnes et al., 1993; Lewis, 1974; Permata et al., 2000), coral planulae exhibit responsive behavior to different stimuli, reinforcing the idea that their distribution can be modulated by individual's own movement (Babcock and Mundy, 1996; Harrison and Wallace, 1990; Raimondi and Morse, 2000). Pressure and light are apparently key environmental factors determining larval swimming activity and substrate searching behavior, which may promote higher settlement rates at depth ranges where performance of adult coral colonies, in terms of survival and growth (Anthony and Hoegh-Guldberg, 2003; Fricke and Meischner, 1985; Wellington, 1982), are more favorable. Larvae of some species can control their position in the water column by swimming upwards when exposed to increasing pressure and moving down when exposed to decreasing pressure. This type of barotactic response is found, for instance, in the zooxanthellate coral *Porites asteroides*, which allows larvae to remain within the euphotic zone, below surface waters where temperature and UV radiation are exceedingly high (Stake and Sammarco, 2003). Light responses are probably more elaborate. Mundy and Babcock (1998) found that settlement rates over light gradients of varying intensity and spectral composition are consistent with vertical distributions of adult colonies of several zooxanthellate coral species. Interestingly, no effects of light regime on larval behavior were found for *Platygyra daedalea*, a zooxanthellate species exhibiting a broad depth range. In agreement to these findings, settlement preferences in coral species which occur at different depths, but require specific light regimes, often shift from vertical to horizontal substrates with increasing depth (Bak and Engel, 1979; Rogers et al., 1984), indicating that behavior of competent larvae change according to ambient light-conditions.

Light-mediated settlement behavior, with higher incidence of substrate search and metamorphosis under darkness, may explain spatial settlement patterns of azooxanthellate corals like *T. coccinea*. However, larval behavior and active settlement selection described so far do not fully explain why coral recruits, of a great number of zooxanthellate species restricted to shallow waters, are almost exclusively found in vertical or under-surfaces (Rogers et al., 1984). In addition, settlement rates could also reflect the relative cost-efficiency of larvae in exploring substrates of different inclination, given that energetic reserves for swimming and searching are limited (Feng et al., 2010; Harii et al., 2002). In this sense, negatively buoyant larvae would more easily exploit horizontal upward facing surfaces, while positively buoyant ones would spend less energy probing horizontal under surfaces. Such differences would result in differential settlement rates, when provided adequate substrate texture for adhesion (rugosity) and equal habitat quality for both substrate orientations.

Post-settlement sources of mortality might, however, dramatically affect distribution patterns set at time of settlement (e.g. Gosselin and Qian, 1997; Hunt and Scheibling, 1997). In corals, the negative effects of sedimentation are relatively well understood. Sediments may inhibit recruitment to adult populations as observed in *Acropora millepora* (Birrell et al., 2005), or suffocate both founder polyps and colonies in *Pocillopora damicornis* (Harriott, 1983)—both zooxanthellate corals. This source of mortality is higher at patches where filamentous algae

dominate the substratum (Linares et al., 2012; Sato, 1985), because turfs can reduce water flow in the boundary layer and thus the resuspension of sediments (Carpenter and Williams, 1993). Thus, biological interaction can alter local physical regimes which in turn can determine adult coral distribution. Other factors commonly recognized as determinants of coral recruitment are competition for space (Chadwick, 1991; Glynn, 1976; Sheppard, 1979), exogenous chemical signals (de Nys et al., 1991; Heyward and Negri, 1999; Koh and Sweatman, 2000), and disturbance by grazers (Lirman, 2001; Sammarco, 1980; Sammarco and Carleton, 1981). One of the few field experimental studies attempting to evaluate the importance of biological interactions on the sun coral distribution conducted in Brazil concluded that predation on *Tubastraea* spp. by a guild of native fish is negligible (Moreira and Creed, 2012), at least at Ilha Grande, RJ, just 140 km northeast of the study area used for field observations in this study.

Considering the natural history of the sun coral, and the scarce available information about factors that determine recruitment patterns in southeastern Brazil, we document the distribution of adult colonies and single-polyp recruits in the field, and then investigate larval settlement selectivity through field and laboratory experiments. The majority of studies on *Tubastraea* along the Brazilian coast have focused on documenting its geographic distribution, range expansions and substrate occupation over coarse spatial scales. The species was recorded on rocky shores at different sites distributed along 2000 km of the Brazilian coast, between the states of Santa Catarina and Bahia (Creed et al., 2008; Ferreira, 2003; Mantelatto et al., 2011; Paula and Creed, 2005; Sampaio et al., 2012; Silva et al., 2011). These observations were always obtained from locations within a distance of 40 km from port terminals linked to petroleum activities. Colonies of this species are frequently found on vertical, undersurfaces and crevices (Ferreira, 2003; Mantelatto et al., 2011; Sampaio et al., 2012), although at some localities this pattern is not as clear, with many colonies found on upward facing surfaces (Paula and Creed, 2005). In southeastern Brazil, colonies are usually clumped in restricted areas (Mangelli and Creed, 2012; Paula and Creed, 2005), although larvae can settle over a variety of hard substrates (Creed and Paula, 2007). Two peaks of larval release and subsequent recruitment, one in April–May and the second in September–November, have been observed at four different sites, within 3 km, in Arraial do Cabo, RJ, Brazil (Mizrahi, 2008). Beyond these general observations on recruitment we are not aware of further information on the supply-side ecology of this species in this region.

In this study, we investigate the distribution of young recruits (<2 mo old) and adult colonies of the sun coral *T. coccinea*, in a recently invaded area within the Ilhabela Archipelago (Mantelatto et al., 2011), southeastern Brazil. We then assess the combined effects of larval preference and settlement success on resultant settler density observed on substrates of different orientations, and compared these patterns with recruit and adult distribution in the field. Mismatches between the distribution of early settlers and the distribution of recruits and adults were used to advance possible processes restricting the spread of colonies in the area.

2. Materials and methods

2.1. Study site

All field work was undertaken in 2011 at Búzios Island (23 48' 11" S; 45 08' 21" W), 7.5 km east of the main São Sebastião Island, São Paulo, Brazil (Fig. 1). Distant 25 km from mainland, this is an 755 ha island inhabited by about 200 residents, whose main economic activity is fishing.

The vertical distribution of *T. coccinea* in the study area ranges from the lower limit of the intertidal zone up to a depth of 16 m. Qualitative observations in this vertical range suggest that benthic assemblages at the Búzios Island are similar to those reported at more coastal sites within the region (Eston and Bussab, 1990; Vieira et al., 2012), with

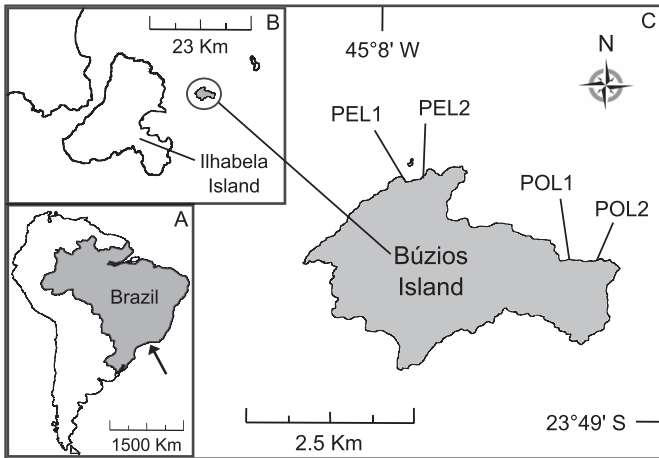


Fig. 1. (A) Regional and (B) local geographic position of Búzios Island where field sampling took place. (C) PEL and POL stand for sampling locations Pedra Lisa and Ponta Leste, respectively. Numerals 1 and 2 indicate positions of sampling sites.

a clear alternation in species dominance according to substrate inclination.

2.2. Field surveys: distribution of adult colonies and early recruits

2.2.1. Adults

Two locations 3 km apart, Pedra Lisa (PEL) and Ponta Leste (POL), where the occurrence of the sun coral was previously reported (Mantelatto et al., 2011), were chosen for all field work in Búzios Island (Fig. 1). Within each location, two different sites separated by several tens of meters were sampled to characterize distribution in different habitats and consistency at these two spatial scales. For calculations of percent cover, photographic records were obtained during SCUBA diving using a digital camera (Sony DSC W380 with a waterproof case) with a 60×40 cm frame. With the aid of a frame we fixed the focal distance at 1 m. At each site, we monitored an area of 2 to 3 km² and identified patches between 12 and 108 m² where at least some colonies of *T. coccinea* were observed. Then we photographed the entire area using the quadrats so as to cover all habitats (substrate inclinations) within these areas. The spacing between each photograph was between 0.5 and 1 m. Ten of these quadrats were randomly selected for each site, location and condition of substrate orientation, for analysis of colony cover using an orthogonal projection of the photographs and the intersection point method with 100 regularly spaced points. Then the total number of images analyzed for this section was 160. An inclinometer, adapted from Bak and Engel (1979), was used to measure surface inclination ($\pm 5^\circ$), which was classified as: positive horizontal (H+, 0° to 45° facing upward), positive vertical (V+, 45° to 90°, between vertical and slightly facing upward), negative vertical (V-, 90° to 135°, between vertical and slightly facing down) and negative horizontal (H-, 135° and 180°, facing downward), as illustrated in Fig. 2. All images were processed using the software CPCe v. 3.6 (Kohler and Gill, 2006) for calculations of percent cover of *T. coccinea*.

All sites were surveyed in February, April, June, September and December. We randomly selected 20 colonies from the 160 images taken in February, and measured their area using the CPCe software. The size of these colonies ranged from 4.6 to 56.7 cm². We tracked these colonies in photographs taken in December, and measured them again to obtain an estimate of colony growth. All colonies persisted over this 10-month period, but the average change in their size was minimal (0.70%), ranging from -2.33 to +5.79%. Thus we assume that adult colony cover and patterns of distribution were relatively invariant, and hence restricted spatial analyses to surveys conducted in February 2011.

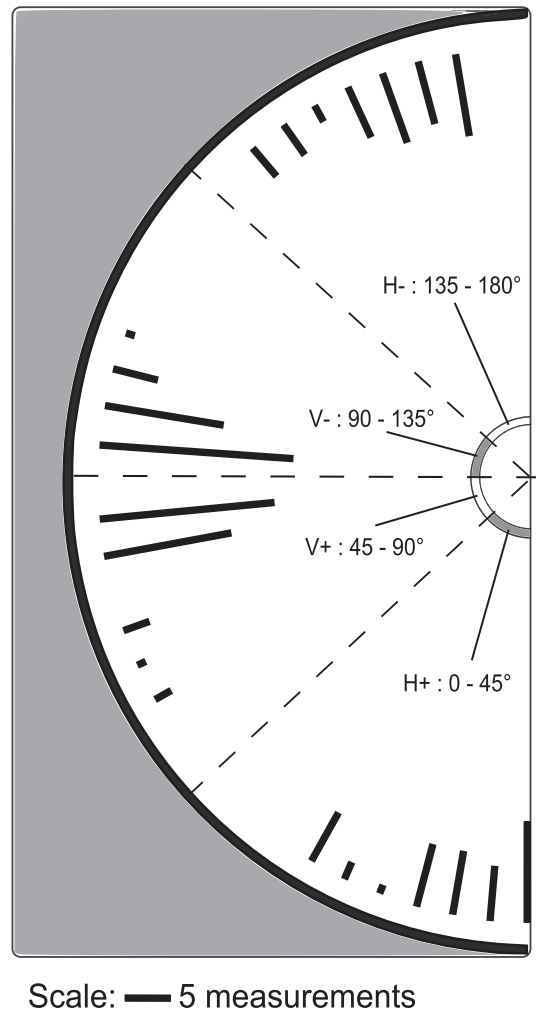


Fig. 2. Orientation categories used in this study to describe the distribution of *Tubastraea coccinea* early recruits and adult colonies in Búzios Island. Black bars indicate the frequency of surface angles at the sampling sites, measured in February 2011. Note that measurements cluster in negative horizontal (H-), vertical and positive horizontal (H+) orientations. In spite of a common cluster for vertical categories (V- and V+), we expected a sharp shift in conditions at 90°, with light incidence and potential for sedimentation due to gravity abruptly dropping in surfaces above this inclination (V-).

A mixed ANOVA model was used to analyze adult colony cover data, in which “site” (S) was considered a random factor, nested in “location” (L), and “substrate orientation” (O) a fixed factor orthogonal to both “site” and “location”. The SNK procedure was used for *a posteriori* comparisons among combination of factor levels when they were significant. The software WinGmav5 was used to undertake all analyses of variance in this study.

2.2.2. Recruits

Density of recruits was estimated using the same photographs. In this case, however, we obtained density estimates for all sampled months, by examining all 800 photographs and counting single-polyp recruits in five 5×5 cm quadrats, randomly allocated within each photograph. The area covered by adults was excluded since no recruits were ever observed both above the colonies and below their inferior borders, possibly due to negative allelopathy (Mizrahi et al., in prep.), and also because developing colonies at these sampling sites are rather massive, not leaving any available space underneath. The remaining cover consisted mostly of encrusting invertebrates and algae, and coralline turf. With varying frequency, recruits were found on all these biologic substrates. No bare rock was ever detected in photographs. We used the CPCe v. 3.6 software to digitally scale the images and randomly

position sampling units for recruit counting. Only recruits with a polyp diameter smaller than 5 mm were counted because this is the largest size of single founder polyps, corresponding to an approximate age of two months (Mizrahi, 2008).

The distribution patterns of recruits were examined at times when recruitment density was higher (February and June, see 'Results'). Average values of the 5 small quadrats within each photograph were considered as replicates in the analysis. The design was the same as that explained for adult cover, except that in this case 'Recruitment Event' was included as an orthogonal factor (with two levels) to all other factors. Data were converted to $\sqrt{(X + 1)}$ before running the analysis to reduce variance heterogeneity (Cochran's $C = 0.1283$, $p < 0.01$). Some level of heteroscedasticity persisted after transformation (Cochran's $C = 0.1029$, $p < 0.05$), but we proceeded with analyses because of the balanced structure and comparatively large sample size. Probabilities near significance level should be interpreted with caution, however.

2.3. Larval settlement experiments

2.3.1. Larval buoyancy

Determination of larval density (buoyancy) was found to be important for the interpretation of settlement rates and substrate preferences in the experiments described below, specifically to verify whether preferences can be explained by a passive process. A sample of 17 actively swimming larvae was obtained from live colonies in the laboratory, which were transferred in a plastic vial to a freezer ($-5\text{ }^{\circ}\text{C}$) for 20 min to kill them. Individual measurements of larval density started immediately after. Dead larvae were first introduced in a graduated 50 ml cylinder partially filled (30 ml) with seawater (salinity 34, density at $25\text{ }^{\circ}\text{C} = 1.023\text{ g cm}^{-3}$) and their buoyancy recorded (floating vs. sinking). For initially floating larvae, we then slowly introduced fresh water drops (salinity 0, density = 0.997 g cm^{-3}) until larvae descended. We recorded the fresh water volume added to cylinders and calculated final water (= larval) density.

2.3.2. Larval settlement preferences in the laboratory

To test whether larvae showed preferences to settle in substrates of different orientation and roughness, we used larvae released in June 2011 from a population of nearly 150 colonies, maintained for one month in the laboratory at the Centre of Marine Biology (CEBIMar) of the University of São Paulo. We hypothesized that adding some rugosity to an otherwise smooth surface would facilitate the fixation of larvae, reducing searching rate and potentially altering preferences according to surface orientation. The experiment was conducted using translucent PVC cubic-shape tanks ($10 \times 10 \times 10\text{ cm}$) so that the bottom (facing upward), top (underface) and all vertical sides were available for settlement and allowed larval counts from the outside during monitoring. Since no larvae settled on vertical sides (see Results section), comparisons were limited to the two horizontal surfaces and no standardization for surface area available was necessary. These tanks were held over a laboratory bench in complete darkness and at a temperature around $25\text{ }^{\circ}\text{C}$, typical of surface sea temperature in the region and about optimal for larval settlement (Mizrahi, 2008). Thus, larval settlement preferences took place in the absence of light cues. Larvae used in the experiment were collected from a supply tank during the day, using a plankton net and 5 ml plastic pipettes, and placed in 4 l aquaria for 6 h until dusk, when swimming activity began and healthy pyriform individuals could be selected. In less than 24 h after release, groups of 50 larvae were randomly allocated to experimental tanks filled with filtered sea water. The sides of each of the 32 tanks used in the experiment represented three treatments of substrate orientation; a) horizontal position facing up (0° inclination, bottom of the tank), b) vertical position (90° inclination, all 4 lateral tank walls) and c) horizontal facing down (180° inclination, underface of tank top). We did not split here vertical surfaces into V+ and V-, because light incidence and sediment

deposition, which are likely the main factors differing between these two orientation categories in the field, were maintained constant (no light) or are just not applicable (sedimentation) in the laboratory. In half of these tanks ($n = 16$) all the settlement surfaces were roughened with sandpaper and the other half were left smooth, in an attempt to mimic heterogeneity in rocky substrates. Twice a day, experimental tanks were monitored for settled larvae under a dim light and the experiment was terminated when no larvae remained swimming (10 d).

Because no settlement was observed in vertical surfaces, analyses considered only the two horizontal surfaces. To simplify analyses, we calculated the proportion of larvae settling at under surface (180°) of the total larvae settled (on upward plus downward facing) and compared this proportion between scrapped and smoothed surfaces. Variance was homogeneous between these two groups ($F_{\max} = 1.26$, $p > 0.05$) and thus proportions were compared using a two-tailed Student's t -test. A significant difference between them would indicate that preference depends on surface roughness.

2.3.3. Settlement in the field

To examine whether there is differential recruitment of *Tubastraea* to substrates with different orientations in the field, and to compare with settlement results obtained in the laboratory, we conducted an experiment at Pedra Lisa (PEL), the more sheltered location at Búzios Island. In June 2011, coinciding with a major recruit event (see Results section), we deployed square $10 \times 10\text{ cm}$ translucent PVC plates, 5 mm thick, in three ropes anchored at about 10 m from the shore and separated by a few hundred meters. Ropes were maintained in vertical position with sub-surface buoys. Five replicate plates of each of three orientations, 0° , 90° and 180° , were attached to each of the three ropes by knots that secured them through a small hole ($<2\text{ mm}$) drilled in the center. The position of plate orientation in each rope was randomly determined, along a vertical range from 4 to 12 m, to avoid eventual confounding effects related to depth. Distance between plates was always larger than 30 cm to avoid interference between neighboring units. After one month, plates were brought to the laboratory for recruit identification and counts under a dissecting microscope. Observations on color, number of septa and skeletal morphology confirmed that all coral recruits were *T. coccinea* individuals. Data were analyzed using a mixed-model, two-factor ANOVA, in which 'orientation' was considered a fixed factor (0° , 90° , 180°) and 'rope' a random factor. This model is equivalent to a randomized blocks design with replication, in which 'rope', the blocking factor, was needed to properly place settlement plates along the target depth range and over an adequate coastal stretch (i.e. a few hundreds of meters). Variance was heterogeneous among factor combinations ($C = 0.3636$, $p < 0.05$) and therefore data were transformed to $\sqrt{x + 1}$ to meet the criterion of homoscedasticity. The SNK procedure was used for *a posteriori* comparisons among treatments.

Table 1

Adult cover in the field. Results of the analysis of variance to assess effects of intermediate (between locations) and small (between sites) spatial scales on the distribution of adult sun coral colonies over substrates of different orientation. Values in bold highlight significant sources of variation ($p < 0.05$).

| SV | df | MS | F | P |
|----------------|-----|--------|-------|------------------|
| Orientation: O | 3 | 25,169 | 13.98 | 0.032 |
| Location: L | 1 | 14,213 | 5.48 | 0.144 |
| Site: S(L) | 2 | 2595 | 11.17 | <0.001 |
| O x L | 3 | 1939 | 1.36 | 0.342 |
| O x S(L) | 6 | 1427 | 6.14 | <0.001 |
| Res. | 144 | 232 | | |

Table 2

Recruit density in the field. Results of the analysis of variance to assess spatial effects of intermediate (between locations) and small (between sites) scales, and temporal effects (between recruitment events), on the distribution of early recruits over substrates of different orientation. Values in bold highlight significant sources of variation ($p < 0.05$).

| SV | df | MS | F | p |
|----------------|-----|--------|-------|------------------|
| Date: D | 1 | 0.006 | 0.01 | 0.938 |
| Orientation: O | 3 | 25.913 | 10.04 | 0.045 |
| Location: L | 1 | 5.457 | 21.26 | 0.044 |
| Site: S(L) | 2 | 0.257 | 1.12 | 0.329 |
| Re × O | 3 | 0.449 | 0.84 | 0.557 |
| Re × L | 1 | 0.613 | 6.94 | 0.119 |
| Re × S(L) | 2 | 0.088 | 0.38 | 0.682 |
| O × L | 3 | 2.582 | 1.15 | 0.404 |
| O × S(L) | 6 | 2.254 | 9.80 | <0.001 |
| D × O × L | 3 | 5.537 | 0.69 | 0.593 |
| D × O × S(L) | 6 | 0.783 | 3.40 | 0.003 |
| Res. | 288 | 0.230 | | |

3. Results

3.1. Distribution patterns of adult colonies and recruits in the field

3.1.1. Adult cover

The overall cover of adult colonies of the sun coral at the sampled locations was $32.24\% \pm 30.00$, with no overall differences between the two sampled locations, PEL and POL. However, there were differences at the smaller scale, between sites, which were not consistent across substrate orientations (Table 1, significant Orientation × Site interaction). Thus, although there was an overall highly significant effect of orientation on coral cover, the pattern was not consistent across sites (Fig. 3). While at all sites coral cover was zero or virtually nonexistent in the horizontal surfaces that face up (H+), and cover in the positive vertical surface (V+) was generally lower than in the other inclinations (although not always significantly so), the ranking between the negative horizontal (H−, facing down) and negative vertical (V−) inclinations varied from site to site (Fig. 3).

3.1.2. Recruit density

Overall recruit density (individuals < 5 mm) was much higher in the surveys conducted in February and June than in those in December, and were nearly nonexistent in April and September (Fig. 4). Considering the two months of peak recruit density, we found significant differences among the different substrate orientations, but the only consistent effect among sites and between dates was the near absence of recruits in horizontal surfaces facing upward (Fig. 5). Consequently, the three-way interaction between orientation, date and site was highly significant (Table 2). Slightly, but significantly higher recruit densities were observed at PEL than at POL ($p < 0.05$, Table 2), but such differences varied according to orientation and site (Table 2). Compared to adult cover (Fig. 3), and with exception of horizontal surfaces facing up, the density of recruits was much less consistent across orientations and sites (Fig. 5).

3.2. Larval experiments

3.2.1. Larval buoyancy

Of the 17 dead larvae tested, 13 (76.5%) floated in seawater and 4 (23.5%) sunk. Dilutions leading to final salinities ranging from 30.0 to 19.6 were needed to sink floating larvae, which translated to density estimates of $1.016 \pm 0.002 \text{ g cm}^{-3}$ larval density, i.e. larvae are positively buoyant. We suspect that the 4 individuals that sank were already close to metamorphosing and thus secreting skeletal tissue.

3.2.2. Larval settlement preferences in the laboratory

We did not observe any settlement on vertical surfaces, regardless of whether they were smooth or roughened to mimic the rock surface.

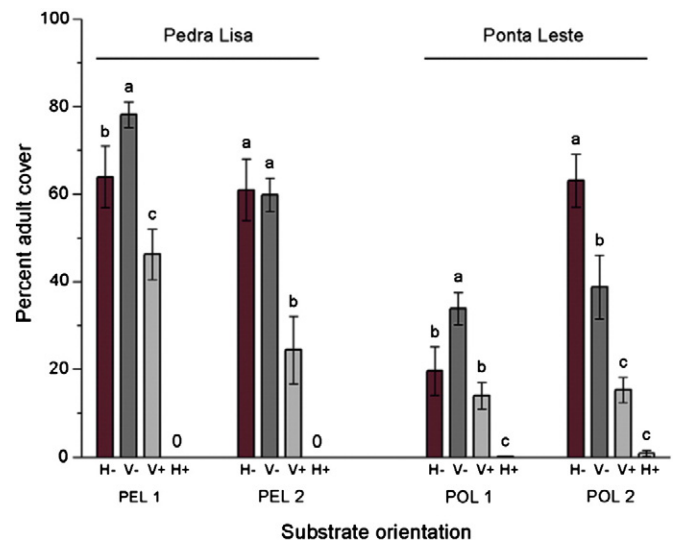


Fig. 3. Small scale spatial variation (= site) of the relative distribution of *Tubastraea coccinea* adult colonies over substrate orientations. Within sites, different letters above estimates of cover percentage (mean \pm 1SE) indicate significant contrasts ($p < 0.05$). Abbreviations of substrate orientations as in Fig. 2.

Overall larval loss was 38%, with no difference between rough (38.4%) and smooth boxes (38.5%). Missing larvae could have either died or settled in corners, where they could not be found.

The proportion of larvae that settled on the underface substratum (H−) did not differ between tanks with scrapped and smooth surfaces ($\bar{X}_{sc} = 0.59, \bar{X}_{sm} = 0.65, t = 1.59, p > 0.05$), indicating that roughness does not affect larval preference, which was slight but significant higher for undersurfaces in both cases (Fig. 6). Therefore, eventual settlement facilitation provided by adding texture to a smooth surface does not reduce preference between orientations.

3.2.3. Recruitment in the field

The field experiment showed a significant effect of plate orientation on the recruitment density of *T. coccinea* planulae, with very low density of recruits in horizontal plates facing up (H+) and highest in plates facing down (H−, Fig. 7, Table 3). In contrast to results obtained in the laboratory, recruitment in vertical plates was substantial, and on average

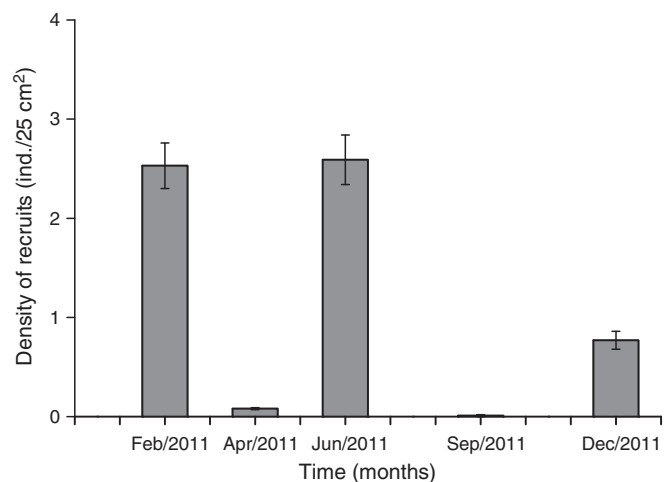


Fig. 4. Temporal variation of recruit density in the field (vertical columns and whiskers indicating mean values \pm 1SE).

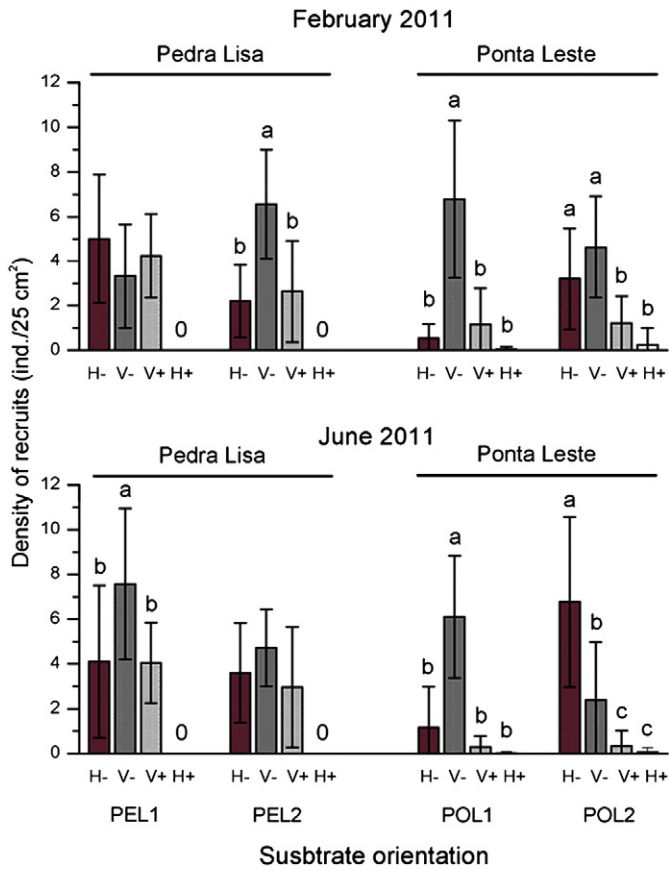


Fig. 5. Small scale spatial variation (= site) of the relative distribution of *Tubastraea coccinea* recruits over substrate orientations at major recruitment pulses detected in February and June 2011. Within sites, different letters above estimates of recruit density (mean ± 1SE) indicate significant contrasts ($p < 0.05$). Abbreviations of substrate orientations as in Fig. 2.

intermediate between upward and downward facing plates, but we could not statistically separate it from the other orientation treatments (Fig. 7).

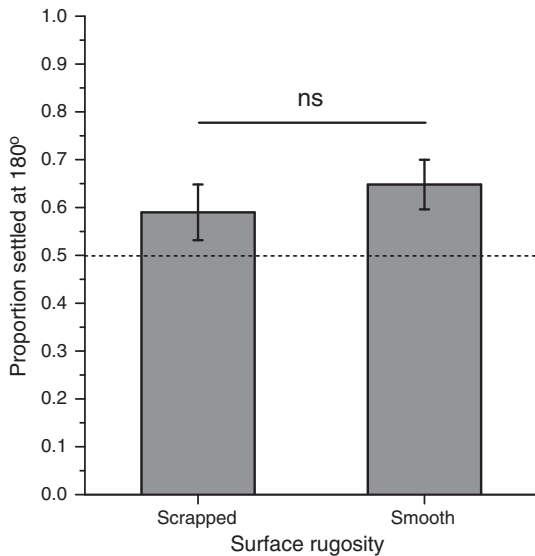


Fig. 6. Preference between horizontal surfaces, 0° and 180°, measured as proportion of larvae that settled at undersurfaces (180°), for both rough and smooth tanks. Bars indicate mean values and whiskers 95% confidence intervals.

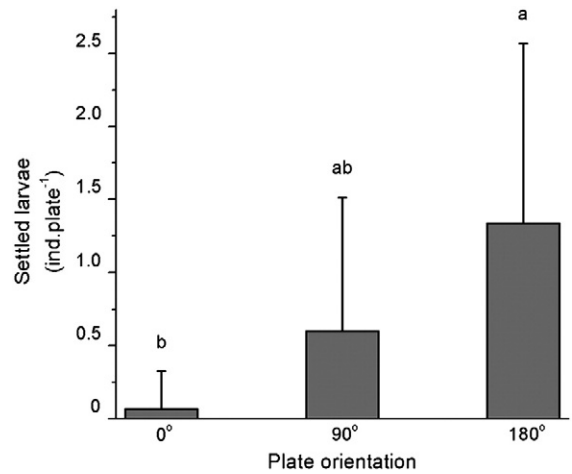


Fig. 7. Settlement rate (mean ± 1SE) according to orientation of artificial substrates deployed in the water column off Pedra Lisa, Búzios Island. Differences of settlement rate between orientation treatments sharing a given letter are not significant ($p > 0.05$). 0°: horizontal positive; 180°: horizontal negative.

4. Discussion

Our results of larval experiments represent the combined effect of larval behavior in the water column, benthic habitat selection and metamorphosis success. We did not attempt to separate these closely related processes, but, altogether, they promote a specific distribution pattern, favoring high densities at undersurfaces but only residual occupancy of upward facing horizontal habitat. There are several reasons to assume that such a distribution would favor the performance of adult colonies of *T. coccinea*. At horizontal surfaces facing downward, sedimentation is much reduced or absent (Babcock and Davies, 1991; Connell, 2005), UV radiation usually below coral damaging levels (Lesser et al., 1990; Gleason, 2001; Wellington and Fitt, 2003), and competition with zooxanthellate corals much relieved (Falkowski et al., 1990; Oren and Benayahu, 1997; Vermeij and Bak, 2002). In fact, the distribution of adult colonies at Búzios Island (this study), and other areas (Cairns, 1991; Fenner and Banks, 2004; Ferreira, 2003; Glynn et al., 2008; Vermeij, 2005), follows fairly well the pattern expected by larval processes alone when considering horizontal surfaces facing up versus facing down. But mismatch between our larval settlement experiments and field distribution were apparent when considering vertical surfaces, which were not at all colonized in the laboratory, but are frequently occupied in the field. The comparatively high recruitment in vertical plates after a month in the field are more in line with field distribution of recruits and adults, and suggest important differences in the environment experienced by larvae in the laboratory and in field conditions. Below we discuss these results and attempt to expand our understanding of the invasive ecology of *T. coccinea* in southeastern Brazil.

Table 3

Larval settlement rate in the field. Results of the analysis of variance testing larval settlement rates in artificial plates deployed at different orientations. A second factor, 'rope' to which plates were fastened to, is included to test for spatial consistency of orientation patterns within a few hundreds of meters. Values in bold highlight significant sources of variation ($p < 0.05$).

| SV | df | MS | F | p |
|----------------|----|-------|-------|--------------|
| Rope: Ro | 2 | 0.027 | 0.28 | 0.757 |
| Orientation: O | 2 | 0.768 | 10.02 | 0.028 |
| Ro × O | 4 | 0.077 | 0.80 | 0.533 |
| Res. | 36 | 0.096 | | |

4.1. Settlement rate and larval preferences

Among possible environmental variables affecting larval swimming behavior and habitat selection, light (Feng et al., 2010; Gleason et al., 2006) and pressure (Stake and Sammarco, 2003) are by far the most commonly identified. Field observations and manipulative experiments have led several authors to conclude that these two factors are used to maintain coral larvae at given depth intervals (Baird et al., 2003; Mundy and Babcock, 1998; Stake and Sammarco, 2003; Wellington, 1982), and that larval search behavior and metamorphosis is light-mediated to a great extent (Maida et al., 1994). This would explain why inclination of settlement surfaces in corals with broad depth range tend to vary from negative to positive with increasing depth (Bak and Engel, 1979; Rogers et al., 1984). Our results showing strong preference for negative horizontal surfaces were obtained from populations and environmental conditions restricted to shallow water, and thus pressure thresholds probably did not play a role in this study. But we can also reject the hypothesis that a light gradient is required to set preferential settlement between horizontal positive and negative substrates, since our laboratory experiment was conducted in complete and constant darkness. In the field, differences between recruitment in plates facing up versus down were even stronger than in the laboratory, suggesting either that light gradients can reinforce larval settlement preferences, or that post-settlement mortality occurring within a month after settlement is stronger in surfaces facing upward (see below). Two mechanisms help explain settlement selectivity in laboratory. Larvae could engage in active negative geotaxis, or they could simply benefit from passive flotation, allowing more frequent and durable contact with 'negative' surfaces, leading to higher settlement rates. Geotactic behavior is not frequently documented for coral larvae, but Vermeij et al. (2006) observed in the laboratory that early *Montastraea faveolata* larvae, formed 30 h after gamete release, concentrate at the surface but soon start descending, with most larvae swimming close to the bottom after 60 h in a salinity of 34. Settlement followed shortly after. Similarly *Oculina varicosa* larvae swim to the surface, but, after 18 h, they start moving to the bottom (Brooke and Young, 2005). Thus, geotactic behavior would better explain preferential settlement at upward facing (positive geotaxis) but not under surfaces. We argue that passive flotation may better assist larvae to settle on surfaces facing down. If swimming was vertically neutral throughout the experiment (10 d), then buoyancy alone would render higher settlement at negative than at positive surfaces, as observed in our laboratory experiment for tanks with both smooth and rough walls. Changes in floatability due to lipid consumption could explain why a considerable proportion of larvae settled in horizontal positive sides. Yet, a metabolic decline of lipid contents large enough as to cause sinking takes tens of days (Harii et al., 2007), which is far more than the few days most of our experimental larvae took to settle. Adding texture to experimental settlement plates could enable larvae to more rapidly find a suitable settlement spot and reducing swimming time. However, we found no differential response of larvae held at aquaria with smooth and rough surfaces, indicating that settlement patterns can be maintained with minimum physical complexity, at least in still water.

It is interesting to note that recruitment in vertical substrates was significant in the field (intermediate between horizontal upright and horizontal facing down), but nil in the laboratory. There are many possible explanations for this difference and, at this stage, we can only speculate on the more intuitive ones, related to the many differences between laboratory and field environmental conditions and the effects of post-settlement processes in the field. Plates deployed in the field suspended from a buoyed rope are undoubtedly exposed to horizontal currents and turbulence of varying magnitudes and many larvae may exhibit flow-mediated behaviors upon contact with benthic habitat, as found for barnacle cyprid larvae (Jonsson et al., 2004, and see Metaxas and Saunders, 2009). Also, larvae can undertake small-scale horizontal swimming along cross-shore light gradients, such as those reported by

copepods (Siebeck, 1979), since the open-ocean and the rocky environment reflect nearly opposite light intensity and spectra. A combination of changes in larval settlement behavior and post-settlement processes could also help explain differences between laboratory (settlement) and field observations (recruitment after a month). For instance, initial settlement in vertical surfaces in the field could be followed by increased early survival in these surfaces as compared to horizontal ones, further reinforcing the pattern of recruit density.

4.2. Processes affecting distribution patterns of early recruits and adult colonies

Natural densities at horizontal upward facing surfaces were almost nil for settlers, recruits and adults, suggesting that mechanisms inhibiting the colonization of the sun coral over these flat habitats may operate through all benthic ontogeny and across small and intermediate spatial scales, at least within our study region. Turbidity (= light attenuation) and sedimentation due to extensive coastal runoff characterizes long stretches of the southeastern Brazilian coast (Carvalho et al., 2002; Lima and Satyamurty, 2010), including the northern coast of São Paulo State. We suggest that the accumulation of sediments, facilitated by an ever-present cover of filamentous coralline algae of the genera *Jania* and *Amphiroa*, prevents colonization of flat upper habitat in our study area and increases the mortality of settlers that do settle there. Algal assemblages capable to retain large quantities of sediments are common in tropical and temperate regions (Steneck and Dethier, 1994), causing general structural changes in benthic communities (Piazzi et al., 2001), and specific negative impacts in several corals, such as *Pocillopora*, *Platygyra*, *Oxypora*, *Acropora* and *Eumicella* (Birrell et al., 2005; Harriott, 1983; Linares et al., 2012; Mundy and Babcock, 1998; Sato, 1985). This damage can be a result of burying (Harriott, 1983) or due to the loss of recruits that settled on sedimentary unstable habitat (Babcock and Davies, 1991; Hodgson, 1990).

The occurrence of recruits and adult colonies in negative horizontal substrates as compared to vertical surfaces were consistently lower than one would expect from settlement (laboratory) or early recruitment (field). We examined in more detail the H – habitats at the sites where *Tubastraea* adult colonies were particularly scarce (PEL1 and POL1). There, the relative abundance of the octocoral *Carijoa riisei* (at PEL1), and both the abundance of this species and the hexacoral *Astrangia rathbuni* (at POL1), were exceptionally high. We argue that competition between the invasive sun coral and azooxanthellate corals, such as *C. riisei*, a branching species well-established in the region, but native to the Indo-Pacific (Concepcion et al., 2010), and *A. rathbuni*, a native encrusting species, may be an important factor limiting the abundance of both recruits and adults of *Tubastraea*. Prevailing assemblages in H – habitats are probably the outcome of increased biological interactions, because these are preferred habitats for several species and their relative availability in natural sublittoral rocky substrates, as in our study region and many other areas, is relatively scarce.

Both chemical inhibition and tissue injury mediated by direct physical contact are likely mechanisms by which native species may impede that vast extensions of negatively oriented surfaces become monopolized by *T. coccinea*. There is no specific information on how encrusting corals such as *Astrangia* may interact with potential competitors, but it is known that *C. riisei*, a branching form, can produce secondary metabolites with strong antibiotic and cytotoxic activity (Seleghim et al., 2007), which potentially induce or inhibit larval settlement of other sessile benthic invertebrates (Sammarco et al., 1983). Except for some small sponges, we observed no direct contact between *C. riisei* and other species, including *T. coccinea*, suggesting a possible case of negative allelopathy. Further research framed to test these and other apparently relevant biological interactions should investigate this potential competitive interference and pre-emptive interactions.

Acknowledgments

We thank two anonymous referees for their comments and suggestions, which helped us preparing an improved version of this paper, and gratefully acknowledge the help of Joseilto Medeiros de Oliveira, Eduardo Honuma and Elso Alves da Silva, for their assistance in field surveys and laboratory experiments. We are also thankful to Alvaro E. Migotto for making available laboratory equipment and for his constant supportive attitude. Paula Kasten, Maisa Ito, Soledad Lopez, Sergio C. Souza, Fernando Freitas, Pedro Guerra, Rafael Duarte, Elias T. da Silva and, especially, Bernardette Saunier Rebori, provided general help and most valuable advice. This research was funded by the International Collaboration Program PC-PEG (Programa de Estudante-Convênio de Pós-Graduação), promoted by CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), through a PhD fellowship to DM, and by FAPESP (Fundação de Apoio à Pesquisa do Estado de São Paulo) through a visiting scientist grant conceded to SAN (# 2012/0519-3). This is a contribution of the Research Centre for Marine Biodiversity of the University of São Paulo (NP-Biomar/USP). [RH]

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