

Allelopathic effects on the sun-coral invasion: facilitation, inhibition and patterns of local biodiversity

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Abstract In spite of growing concerns about the invasion of the sun-coral *Tubastraea coccinea* along the tropical Southwestern Atlantic, the biological interactions mediating this species' establishment and spread are largely unknown. Here, we identified species associations with *T. coccinea* by comparing community structure between invaded and non-invaded areas at Búzios Island, SP, Brazil. We also investigated effects of chemical cues from representative benthic species on sun-coral larval performance in the laboratory and quantified the density of sun-coral recruits across different microhabitats in the field. Field surveys showed that the invasion of the sun-coral is more intense at reef areas of higher species richness and diversity, putting at risk a

higher number of native species than anticipated and suggesting that local richness offers little resistance to invasion. Highest density of *T. coccinea* recruits observed on the least bioactive encrusting corallines suggests this taxonomic group may constitute doorways to the establishment of this coral. In contrast, field patterns of sun-coral colonies and recruits, as well as laboratory trials, suggest that cnidarian-dominated habitats represent obstacles to the sun-coral invasion. Thus, while areas dominated by the snowflake coral *Carijoa riisei*—which showed the greatest negative allelopathic effect on *T. coccinea*—likely provide resistance to the invader spreading, areas covered by encrusting coralline algae and 'barren substrates' probably facilitate its establishment. Because these latter, less-structured microhabitats often prevail after disturbance, damage assessment following human-mediated impacts should include detection and control of sun-coral populations.

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Introduction

Reef habitats are generally inhabited by diverse communities of sessile invertebrates and macroalgae, usually covering most of the available space (Witman et al. 2004; Linares et al. 2012). In these environments, interspecific interactions are expected to be strong and play a significant role on the structure of benthic assemblages (Cornell and Lawton 1992; Witman et al. 2004). Under these circumstances, theory predicts that the chances for the successful establishment of exotic species would be facilitated by positive interactions (e.g. species that facilitate larval settlement) and curtailed by intense local negative interactions, especially when species diversity is high (Elton 1958; Stachowicz et al. 1999; Fridley et al. 2007). Therefore, species successfully invading diverse shallow reef habitats are expected to be either strong

competitors or good colonizers, making an efficient use of resources not fully exploited by native assemblages and to be resistant (or resilient) to predation and other sources of mortality. The sun-coral, *Tubastraea coccinea*, is likely one of such species, having remarkably colonized and expanded over a variety of shallow hard-bottom habitats along most of the tropical coasts (reviewed in De Paula 2007), although its original distribution range was restricted to the Pacific and Indian Oceans (Cairns 2000). Along the Brazilian coast, this invasive species has been recorded on natural substrates from Santa Catarina to Bahia (Castro and Pires 2001; Mantelatto et al. 2011; Sampaio et al. 2012). The possibility of occasional long-distance dispersal through polyp clustering (Mizrahi et al. 2014a) and the transportation by sea of sun-coral fouled man-made structures (Creed et al. 2017) have probably enhanced connectivity among invaded areas, while the apparent unpalatability to local predators (Moreira and Creed 2012) may have favored the persistence of sun-coral in colonized areas. Compared to processes that help spread the sun corals, the local mechanisms that may enhance successful colonization or otherwise restrain the establishment and development of sun-coral colonies at recently invaded sites have received much less attention. Interspecific competition can be important, to some extent, since recent studies have shown that sun-coral colonies may be overgrown by sponges (Meurer et al. 2010; Lages et al. 2012) and possibly removed by nesting pomacentrid fish (Mizrahi et al. 2016). During early ontogenesis, from settling larvae to small few-polyp colonies, exposure to metabolites released by a wide array of benthic organisms may play a particularly important role, but the relevance of this sort of interactions remains largely unknown.

Mizrahi et al. (2014b) undertook laboratory experiments showing that positive buoyancy combined to active habitat selection promotes higher sun-coral settlement rates on undersurface habitat (i.e. negatively oriented). These laboratory results were consistent with sun-coral distribution patterns at shallow reefs in Búzios Island, SP, Brazil. Given this pattern, the impact of *T. coccinea* is expected to more directly affect assemblages of sessile invertebrates and macroalgae developing on reef walls and overhang surfaces. Bare space in those substrate orientations is scant at Búzios Island and at most shallow rocky reefs in the region. Thus, the establishment and expansion of sun-coral colonies should largely depend on the occurrence of biogenic substrates that either inhibit or facilitate larval settlement and subsequent growth of colonies. Identifying these benthic organisms may allow more accurate risk assessments at areas still not invaded and assist conservation efforts to protect established native species that hold back or slow down the spread of this exotic species.

Facilitation and inhibition mechanisms at the settlement stage, and over the early post-settlement phase, are usually

critical processes in the establishment of many coral species (Doropoulos et al. 2015). Successful settlement is expected to occur over benthic substrates of comparatively low structural complexity, where colonies can grow fast to a size at which they are less vulnerable to predators and overgrowing. Patches of bare rock, encrusting algae and dead coral skeletons are usually important settlement substrates (Heyward and Negri 1999; Edmunds 2000), probably because biofilm coating on these otherwise inert substrates provide strong settlement cues for planula larvae (Morse and Morse 1984; Hadfield and Paul 2001). Biofilm settlement-inducing substances are composed mostly of small peptides, soluble proteins and carbohydrates, which are highly soluble in seawater and can be detected at distance by competent larvae of many invertebrate groups (Zimmerfaust and Tamburri 1994). Substrate searching behaviors are typically triggered upon detection of these substances (Whittaker and Feeny 1971), ultimately facilitating settlement and the establishment of developing coral colonies. In contrast, other reef biogenic habitats are predictably unfavorable. For instance, turf or erect macroalgal patches are generally inadequate for settlement because they may not provide stable substrates and often retain large quantities of sediments that might clog coral polyps (Hodgson 1990; Babcock and Davies 1991). Similarly, small polyps recruiting near rapidly growing algae, ascidians, bryozoans and sponges face a high risk of dislodgment or overgrowth (Bruno and Witman 1996; Lapointe et al. 2007). Coral planulae may be able to detect chemical cues signaling the presence of such adverse substrates and actively avoid them, therefore inhibiting settlement. Moreover, several sessile invertebrates and macroalgae can produce bioactive substances that might impair approaching larvae in many ways (Whittaker and Feeny 1971; Dworjanyn 2001). These are usually non-polar compounds of varying toxicity, such as furanones and terpenoids, located over the surface of the organisms producing them (De Nys et al. 1995; Dworjanyn 2001). These substances are candidate inhibitors of sun-coral larval settlement.

In this study we combined field and laboratory observations and experiments to improve our understanding of interspecific interactions mediating the sun-coral invasion at Búzios Island, SP, Brazil. In this island, *Tubastraea coccinea* was first observed in 2008 (Mantelatto et al. 2011) and colonization is still an ongoing process, with both the scale of invaded areas and overall density of coral colonies still much lower than what is presently verified at other places, such as Ilha Grande, RJ, where the first records of this species date back to the late 80s (Castro and Pires 2001). We structured the study around three main objectives. First, we compared benthic assemblages over different substrate orientations, both at reef extensions already colonized by the sun-coral and at areas

still free from this invading species, to assess whether abundance was related to local species richness and diversity and to identify species which are positively and negatively associated with sun-coral colonies. Second, we measured the density of coral recruits (<2 months old) on biogenic substrates, within invaded reef areas, to identify possible species interactions affecting early sun-coral stages. Third, to provide a first-hand evaluation of the potential for chemically mediated interactions, we carried out laboratory bioassays to quantify settlement success of sun-coral planulae and survival of early recruits exposed to crude extracts of representative benthic species identified in the study area. Taken together, our results provide an assessment of the possible role of allelopathic interactions in the determination of successful recruitment in the field and how these early-stage interactions may endure through ontogeny and underlie local distribution patterns of fully developed coral colonies. This study shows how evidence can be integrated to identify key-role species determining patterns of the sun-coral invasion. In addition, researchers from other regions may use these results to assess reef vulnerability, provided adequate information on assemblage structure, since most of the species addressed in this study are distributed along tropical coasts around the world.

Materials and methods

Study site

- Fieldwork was undertaken at Búzios Island (23°48'11"S, 45°08'21"W), which is part of the Ilhabela Archipelago (Fig. 1), located 25 km offshore the main coast. We sampled shallow reef habitat (<20 m) inhabited by sessile assemblages of invertebrates and macroalgae similar to those described at other rocky reefs within the northern coast of São Paulo state (Ghilardi 2007; Vieira et al. 2012). These assemblages are generally dominated by fine red algae forming short turfs (less than 2 cm tall). Other important components include a suite of a few red and brown erect macroalgae growing to a short canopy of a few centimeters and a complex and diverse assemblage of marine invertebrates, composed mostly of hydrozoans, anthozoans, sponges, ascidians and bryozoans. Scleractinian corals are much less abundant than in the more tropical habitats from the State of Rio de Janeiro and northwards, but *Mussismilia hispida*, *Astrangia rathbuni* and *Madracis decactis* are commonly found. The sun-coral is now well established at Ilha de Búzios and its abundance is clearly increasing since it was first recorded in the area. At present, the density of coral colonies is highest at undersurface

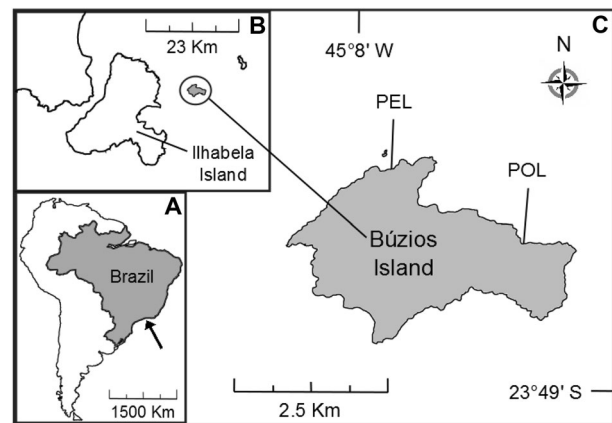


Fig. 1 Regional (a) and local (b) geographic position of Búzios Island, with the indication of sampling sites (c). PEL and POL stand for sampling locations Pedra Lisa and Ponta Leste, respectively

substrates and lowest at upper surfaces where algal turfs prevail (Mizrahi et al. 2014b).

Comparisons of species assemblages between invaded and non-invaded reef areas

The structure of benthic assemblages was estimated using SCUBA diving at two sites separated by 3 km (Pedra Lisa and Ponta Leste, Fig. 1) during February 2011. At each site, replicate plots (60 × 40 cm, $n = 12$) were photographed at invaded and non-invaded patches with surface areas ranging from 12 to 108 m² and at each of the four main surface orientations [horizontal upper surfaces (H+, 0°–45°), horizontal undersurfaces (H–, 135°–180°), vertical upper surfaces (V+, 45°–90°) and vertical undersurfaces (V–, 90°–135°), see Mizrahi et al. 2014b for details]. We considered non-invaded patches all bedrock extensions in which characteristically bright-orange sun-coral colonies (>5 cm in diameter) were not found after diving for several minutes. Invaded areas were immediately recognized at distance at negative orientations, and also at V+ surfaces in Pedra Lisa, since they form conspicuous patches with average coral cover ranging from 23 to 68% (see Table S1). Plots were haphazardly allocated while swimming along sites, maintaining a minimum distance of 3 m between them. The reefs at Pedra Lisa and Ponta Leste were surveyed from the surface to a maximum depth of 16 m, covering an overall reef area of ca. 3 km². At both sites, there were several invaded and non-invaded patches at any given sampled reef orientation, and sampling encompassed at least four of those patches, thus incorporating important spatial variability. All photographs were processed using the software CPCe v. 3.6 (Kohler and Gill 2006). To estimate percentage cover of each biogenic substrate we used a grid of 100 regularly spaced points for each plot. In the

case of invaded patches, the relative cover of each species was recalculated after removing the points covered by *T. coccinea* to allow direct comparisons of community structure between invaded and non-invaded habitats. Species richness and Shannon diversity indices were also calculated for each plot. Small samples of species difficult to identify in the field were collected and sent to specialized taxonomists for correct species identification.

Separate three-way analyses of variance were used to analyze the univariate variables 'species richness' and the 'Shannon diversity index'. The ANOVA model considered substrate 'orientation' (O) and 'coral presence' (CP) in the invaded or non-invaded patches as fixed factors, **and 'site' (S) as a random factor, which served as a test for spatial consistency of assemblage patterns at the scale of a few km. Richness data were log-transformed to meet homoscedasticity. The same design was applied to analyze community structure (on root-transformed cover data), but in this case using permutational analysis of variance, PERMANOVA (PRIMER software v. 6.), with a Bray Curtis similarity matrix, with 9999 permutations. Significant sources of variation were further examined using the SIMPER procedure to discriminate the main species responsible for 10% or more of the dissimilarity between groups.

Early sun coral recruits on natural substrates

We used the same quadrat photographs described above, at invaded areas, to estimate sun-coral recruit density on patches of the different sessile species. In each photograph, five subquadrats (5 × 5 cm) were randomly located over the portions of the plot free of adult *Tubastraea* using the CPCe software. The species dominating these 5 × 5 cm subquadrats and the number of single-polyp sun-coral recruits smaller than 5 mm (<2 months old, Mizrahi et al. 2014b) were recorded. Based on earlier estimates of recruit density in the same region, February is likely within the peak recruitment season at Búzios Island (Mizrahi et al. 2014b).

The size of the habitat patch where recruits are found could potentially play an important role on the distribution of *T. coccinea* recruits and blur any effects of chemically mediated settlement and early recruitment. For instance, negative correlations between patch size and recruit density could indicate intensified settlement at habitat types that are in limited supply (Pineda and Caswell 1997), while positive correlations could take place when settlement rate responds to cues in a dose-dependent way (Morse and Morse 1984; Dworjanyn et al. 1999). However, correlations at two scales (within biogenic substrates using single-subquadrat data, and across substrates using average patch size and recruit density), were never significant (Figure S1), except for a positive association in *Diplosoma listerianum*

(1 out 12 cases). Variation of recruit densities across habitat types was thus assumed to be mostly a result of chemical allelopathic responses, without large artifact effects due to habitat patch size. Because data were heteroscedastic even after transformation, a Welch ANOVA (Quinn and Keough 2002) was used to compare the density of recruits among treatments. To simplify the analysis, data from the two sites were pooled and separate analyses were performed for each substrate orientation followed by Tukey a posteriori tests. Biogenic substrates where recruit density was always zero (eight cases), or those counting with less than five observations (two cases), were removed from analyses.

Allelopathic effects on larval settlement in the laboratory

Preparation of settlement surfaces

Bioassays measuring settlement and mortality of sun-coral larvae were conducted using extracts of nine different benthic organisms collected at the study sites during the field surveys described above: the anthozoans *Carijoa riisei* (Cr), *Parazoanthus* sp (Psp) and *Tubastraea coccinea* (Tc), the bryozoan *Bugula dentata* (Bd), the sponges *Scovalina reutzleri* (Sr) and *Dragmacidon reticulatum* (Dr), the turf of articulated coralline algae dominated by *Jania* sp and *Amphiroa* sp (Art), and the red algae *Falkenbergia hillebrandii* (Fh) and *Wrangelia argus* (Wa). Underwater photographs and spare samples preserved in 70% alcohol were used to confirm identifications. These organisms were chosen because they are among the most common species in the study area. Because collections were carried out at invaded reef areas and at a time when sun-coral planulation was taking place, production of secondary metabolites with allelopathic potential should be intense (Padilla 2001). It is important to note that our assays must be regarded as an evaluation for the potential occurrence of such chemically mediated interactions. More realistic effects would require adequate information on the production and release rates of such substances by target species, local flow around individuals, velocity fields, turbulence and corresponding diffusion rates close to the sea bottom, among other variables (as reviewed in Briand 2009), which are not available for our study system.

Samples were placed in sealed plastic bags and frozen (−18 °C), avoiding any contact with contaminants or exposure to light. After being thawed, samples were examined under a dissecting microscope to remove all non-target species, lyophilized and weighed. In order to extract any metabolites with allelopathic potential, samples were immersed in a solution of methanol and dichloromethane (1:1) for 24 h, which was then filtered and the solvent evaporated with the aid of a rotary evaporator (Büchi R) and a

Speed Vac (Genevac—SF50), following the protocols of Da Gama et al. (2003). The immersion–filtration–evaporation cycle was repeated two more times to obtain sufficient precipitated material from the sample. Extracts obtained through this procedure were dissolved in 20 ml of the same extraction solvent and incorporated into filter papers (9 cm diameter). The crude extracts were incorporated into the filter papers considering concentrations in tissues in vivo, to simulate natural conditions in bioassays. Extracts, or plain solvent (in the case of control surfaces), were then evenly incorporated into filters and placed in a camera with laminar air flow for 24 h to allow solvent evaporation.

Settlement trials

Nine replicate Petri dishes (9 cm diameter, 1.5 cm height) were prepared for each of the nine test species listed above. A single impregnated filter was fitted to the bottom of each Petri dish and filtered seawater was used as medium. Nine additional control dishes were prepared the same way, but using filter papers permeated with the dilution solvent alone, making up a total of 90 experimental units. Ten larvae of *T. coccinea*, obtained from a population of 150 adult colonies kept in captivity, were added to each one of these replicate dishes. Only active pyriform larvae released within the 24 h preceding the experiment were used. In order to test the consistency of allelopathic responses for all treatments, sequential trials were run using larvae released in three different batches over 1 month (July 2011). Three replicate petri dishes for each treatment plus the control were monitored in each of these three trials. Petri dishes assigned to the different treatments were randomly interspersed over bench space and held for 16 days at constant environmental conditions (28 °C in the dark) favoring settlement (Mizrahi 2008). Each day, the cumulative number of settled and dead larvae was recorded.

Three response variables were computed for each replicate Petri dish: number of settled larvae (NS) over the experiment, time to 50% cumulative settlement (S_{50}) and time to 50% mortality (M_{50}). A two-way ANOVA design was then used to compare larval responses among treatments, at three different times. The design thus included ‘species’ as a fixed factor and ‘larval batch’ as a random one, which tested for temporal consistency of treatments. Extract treatments with invariable mortality rate (one case) or leading to no settlement in at least one larval batch (five cases) were removed from M_{50} and S_{50} . Owing to exceedingly high mortality in several replicates belonging to some treatments, the two-way design could not be used to analyze S_{50} data. In this case, a one-way procedure (across extract treatments only) was carried

out. The SNK procedure was used for post hoc comparisons when applicable.

Results

Comparisons of species assemblages between invaded and non-invaded reef areas

Invaded reef areas were characterized by a high abundance of *Tubastraea coccinea*, which reached an average cover of 25% (± 2.7 SE), with peak abundance at negatively oriented substrates (Table S1). Excluding the sun-coral coverage, differences in community structure between invaded and non-invaded reef areas depended on both ‘site’ and substrate ‘orientation’, as indicated by the significant three-way interaction in PERMANOVA tests (Table 1). Post-hoc pairwise comparisons (9999 permutations) between invaded and non-invaded reef patches, at each substrate orientation within each site, indicated significant differences in all cases ($p < 0.05$), except positive substrates (V+ and H+) at Ponte Leste. Non-metric multidimensional scaling further showed these differences, with more evident effects of *T. coccinea* on community structure at negatively oriented surfaces, especially in Pedra Lisa (Stress 2D: 0.13, Fig. 2). Weak differentiation in composition between invaded and non-invaded areas was observed at positively oriented surfaces at this site and no differentiation at all at Ponta Leste ($p > 0.05$; Fig. 2). SIMPER analyses indicated ten negative and four positive different cases of species associations with *T. coccinea*, including all orientations (Fig. 3). The largest

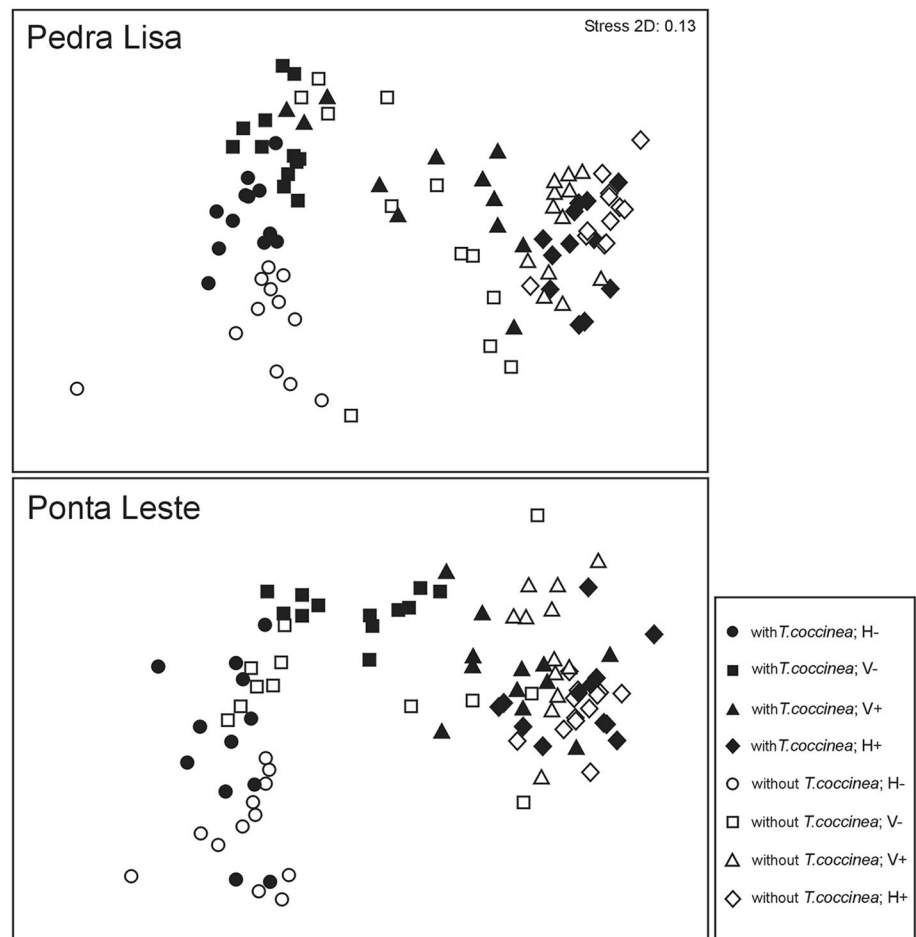
Table 1 Results of 3-way permutational analysis of variance (PERMANOVA) assessing differences of benthic assemblages according to sampling site (Ponta Leste, Pedra Lisa), substrate orientation (H+, H−, V+, V−) and the presence of the sun-coral (present, absent) at Búzios Island

SV	df	MS	Pseudo-F	p (perm)
Site (S)	1	8093	5.8	<0.001
Orientation (O)	3	87702	18.6	<0.05
Coral presence (CP)	1	23249	3.9	0.244
S × O	3	4726	3.4	<0.001
S × CP	1	5898	4.2	<0.001
O × CP	3	8385	1.8	0.127
S × O × CP	3	4650	3.3	<0.001
	176	1395		

At invaded reef areas, species abundances (as percent cover) were calculated after excluding sun coral entries, p values are based on 9999 permutations

df degrees of freedom, MS mean sum of squares, Pseudo-F F value by permutation

Fig. 2 Variation of the benthic community structure at Búzios Island, SP, Brazil, according to sampling site, substrate orientation and the presence or not of the invasive sun-coral *Tubastraea coccinea*. Sample clusters result from non metric multi-dimensional scaling (NMDS). The overall plot was split in two different panels, separating the data of each sampling site, for a clearer reading. *H* and *V* stand for horizontal and vertical surfaces. Negative and positive inclinations are indicated by ‘+’ and ‘−’, respectively



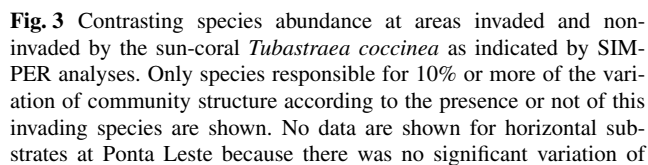
differences observed were for native corals and hydrozoans, which attained significantly higher cover at non-invaded undersurfaces of both sites (H−, Fig. 3). For instance, the hydrozoan *Obelia dicothoma* covers nearly half of the available space at non invaded areas of Pedra Lisa and nearly 25% at Ponta Leste, while it was scarce (<2%) in invaded areas. Similarly, the soft coral *Carijoa riisei* and the colonial zoanthid *Parazoanthus* sp were more abundant in non-invaded areas at Ponta Leste. In contrast, at H− reef patches, the sponge *Mycale escarlatai* was found only at invaded areas. In other substrate orientations, associations were all related to algal species and were less consistent. Turfs of coralline articulated algae were important at Pedra Lisa but their associations to the sun-coral were both negative (V−, V+) or positive (H+). Seemingly, the red seaweed *Falkenbergia hillebrandii* was positively associated at Ponta Leste V− orientations, but negatively associated with *T. coccinea* at Pedra Lisa positive surfaces, with the opposite trend found for encrusting coralline algae.

Species richness was significantly higher at areas invaded by *T. coccinea* for most comparisons (six of eight). Similarly, half of the comparisons suggested

higher diversity (H') at invaded areas (Fig. 4a, b). However, the magnitude of those effects varied between sites and across substrate orientations (e.g. no differences in H+ substrates), rendering a significant three-way interaction (Table 2). At most substrate orientations and sites, over 50% more species were observed in invaded *Tubastraea* areas than in non-invaded ones, with a sharp three-fold increase in richness in V+ surfaces (Fig. 4; Table 2). Exceptions were V− and H+ substrates in Ponta Leste, where numerical trends were not backed by statistical significance. Differences in diversity, as measured by Shannon H' , were less pronounced, but followed the same general trend observed in richness, with no effects at H+ substrates. The only opposite trend was observed at V− areas of Ponta Leste, where diversity was significantly lower at *Tubastraea* invaded areas, despite a non-significant trend to increased richness in these same areas.

Early sun coral recruits on natural substrates

As expected, recruit density varied significantly among the different biogenic substrates at almost all reef orientations (Fig. 5, H−: $F_{8, 30.8} = 11.12$, $p < 0.001$; V−: F_6 ,



The relative abundance of recruits across substrates was compared by first multiplying the average percent cover observed in a given substrate (Table S1) by

the respective recruit density in that substrate and then expressing these data as percentage of total recruit abundance. This comparison suggests that encrusting coralline algae form the most important substrate type for the establishment of sun-coral colonies at the study sites (Fig. 5), although covering considerable less space than other species. Conversely, we observed low density of sun-coral recruits on H— surfaces with high cover of anthozoans and hydrozoans (especially *Carijoa riisei* and *Parazoanthus* sp, Fig. 5).

The allelopathic mediation of sun coral settlement was clearly different among tested extracts, with no effects of larval batches (Table 3), indicating consistent larval responses for each treatment. By combining results of the

Fig. 4 Community richness and diversity (Shannon H) at sun-coral invaded and non-invaded areas. Separate comparisons are presented for each of the tested substrate orientations, at the two sampled sites. Data represent average values per plot \pm 1 SE. * $p < 0.05$, ** $p < 0.01$, *ns* not significant. Abbreviations as in Figs. 1 and 2

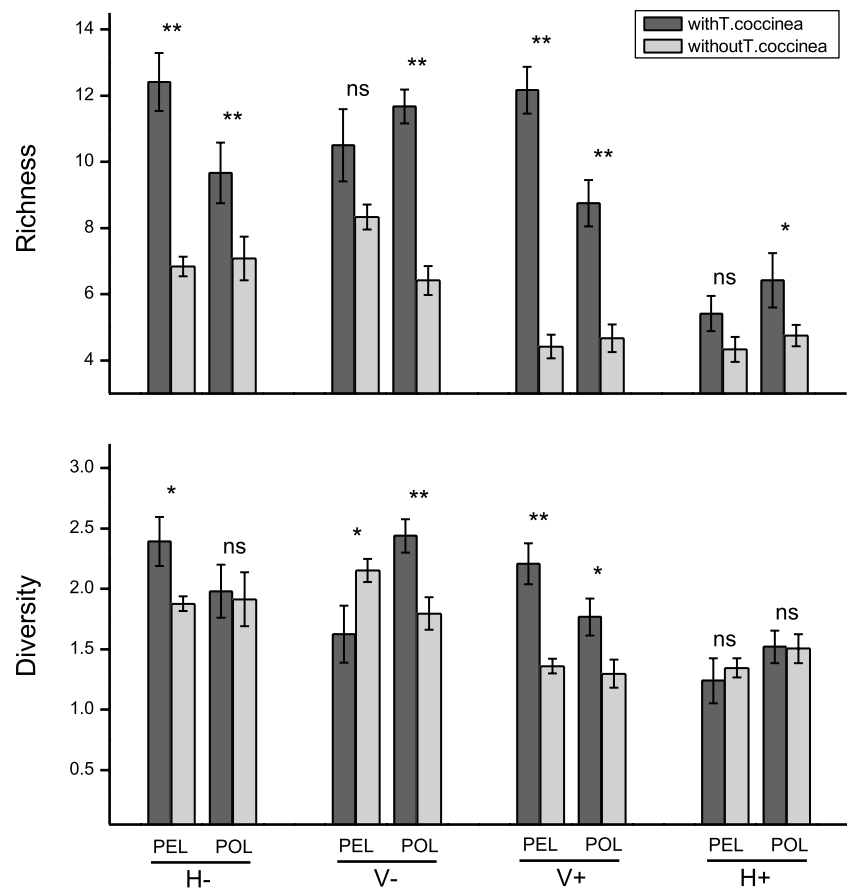


Table 2 Summary results of 3-way analyses of variance testing differences of species richness (S) and diversity (Shannon H) according to sampling site (Pedra Lisa and Ponta Leste), substrate orientation (negative horizontal, negative vertical, positive horizontal and positive vertical) and presence of the sun-coral (present/absent) at Búzios Island

SV	Richness (S)			Diversity (H)		
	df	F	p	df	F	p
Site (S)	1	127.35	<0.001	1	9.58	<0.05
Orientation (O)	3	4.33	0.13	3	3.75	0.15
Coral presence (CP)	1	6.81	0.23	1	0.00	0.98
S × O	3	9.11	<0.001	3	4.04	<0.01
S × PC	1	0.25	0.62	1	0.55	0.46
Or × PC	3	0.51	0.70	3	0.47	0.72
S × O × PC	3	4.93	<0.05	3	5.80	<0.001
Res.	176			176		
Transformation Ln (X)						
		C = 0.1639, ns			C = 0.1439, ns	

Values in bold highlight significant sources of variation ($p < 0.05$)

C stands for the Cochran's statistic, *ns* non-significant

three different larval parameters and comparing the effects of extracts to the control treatment, we classified responses as (1) facilitation, (2) low inhibition, (3) high inhibition, (4) toxicity and (5) high toxicity (Fig. 6). Except for the case of settlement rate, allelopathic responses were generally null or negative. M_{50} responses to extracts were classified as generally non-toxic (Fig. 6a, groups 1, 2 and 3), toxic

(Fig. 6a, group 4, significantly lower than the control), or highly toxic (Fig. 6a, group 5, significantly lower than the control and group 4). Mortality rate of larvae exposed to *Tubastraea coccinea* (Tc) extracts was nearly double that observed on the toxic sponge *Scopalina reutzleri* (Sr), but close to half of the larval mortality observed upon exposure to extracts of *Carijoa riisei* (Cr), which invariably died

Table 3 Summary results of analyses of variance to assess the allelopathic mediation of sun-coral settlement

SV	M ₅₀			NS			S ₅₀		
	df	F	p	df	F	p	df	F	p
Species (S)	8	10.0	<0.001	7	20.4	<0.001	4	13.0	<0.05
Batch (B)	2	1.1	0.382	2	0.7	0.523	–	–	–
E × B	16	1.2	0.991	14	0.3	0.987	–	–	–
Res.	54			48			29		
				Transform. Ln (X)					
		C = 0.182, ns			C = 0.145, ns			C = 0.346, ns	

Replicate larval batches (B) were used to obtain settlement metrics in response to species extracts (S) of common macroalgae and invertebrates. *p* values for significant sources of variation ($p < 0.05$) are highlighted in bold

M₅₀ time at 50% larval mortality, NS number of settlers, S₅₀ time at 50% larval settlement, C stands for Cochran's statistics testing for variance homogeneity, ns Not significant ($p > 0.05$)

within the first day (Fig. 6a). There were no extract treatments significantly exceeding the total number of settlers observed in controls. Numbers of settlers on *Falkenbergia hillebrandii* (Fh) and *S. reutzleri* treatments were similar to those observed in controls (Fig. 6b), but all other extracts apparently inhibited larval settlement. Among inhibitory species, settlement was higher on extracts of articulate coralline algae and *Parazoanthus* sp (Psp) (Fig. 6b, group 2) than on extracts of the sponge *Dragmacidon reticulatum* (Dr), the bryozoan *Bugula dentata* (Bd) or the red alga *Wrangelia argus* (Wa) (Fig. 6b, group 3). All larvae exposed to extracts of *Tubastraea coccinea* (Tc) or *Carijoa riisei* (Cr) died without having settled (in the water column). For all extract treatments for which settlement records were obtained over periods of 2 days or more, time to 50% settlement was lower compared to the control treatment (Fig. 6c). Unfortunately, we could not estimate time to 50% settlement for species in group 3 because no settlement was observed in a large number of replicates, making statistical analysis unworkable. It is noteworthy that extracts of *Scopalina reutzleri* (Sr), despite its apparent toxicity, resulted in similar total settlement and higher settlement rate compared to the control treatment.

Discussion

Community structure at invaded and non-invaded reef areas

An important result of our community surveys, which has important consequences on the dynamics of the sun-coral invasion in Southeastern Brazil, and our understanding of invasive ecology in general, show that *Tubastraea coccinea* either colonizes more frequently natural reef habitats with higher species richness or that the establishment of sun-coral colonies somehow facilitates the co-occurrence of a

larger number of species. The pattern was too consistent across sites and substrate orientations, and too strong to be a simple sampling artifact, deserving further attention. If sun-corals settle primarily on areas of high species richness they are actually putting at risk a potentially larger number of shallow benthic species than could have been anticipated. At a first glance, this interpretation would contradict generally accepted theory on the role of species interactions in preventing invasions, as well as several empirical studies in which species richness was experimentally manipulated and found to halt or reduce invasion rates (Stachowicz et al. 1999; White and Shurin 2007). However, some other studies had converged in that at larger spatial scales, beyond the range of direct species interactions, habitat heterogeneity may favor the coexistence of native and exotic species (Davies et al. 2005; Melbourne et al. 2007). In this study, the distance between invaded and non-invaded areas (hundreds of meters) probably encompass considerable environmental heterogeneity. This variability may lead to increased local richness at habitat patches where conditions are favorable to both the sun-coral and a considerable number of local filter-feeding invertebrates (see Table S1 for the full species list), all of which are common under low light intensity (possibly preventing fast macroalgal growth) and low sedimentation. This pattern resembles the change from negative to positive correlations between native and invasive species richness observed at the 'metacommunity scale' in springtail soil fauna of cold-temperate systems, with both species groups clustering at more benign low-altitude sites, where the soil is frost-free for longer periods (Terauds et al. 2011). Because *Tubastraea* spp promptly deter neighboring individuals through negative chemical mediation (Creed 2006; Lages et al. 2010), the alternative explanation, i.e. that the presence of sun corals actually facilitates the establishment of a diverse assemblage of native encrusting species, seems less plausible. However, it cannot be ruled out that modification of surface

Distribution of recruits

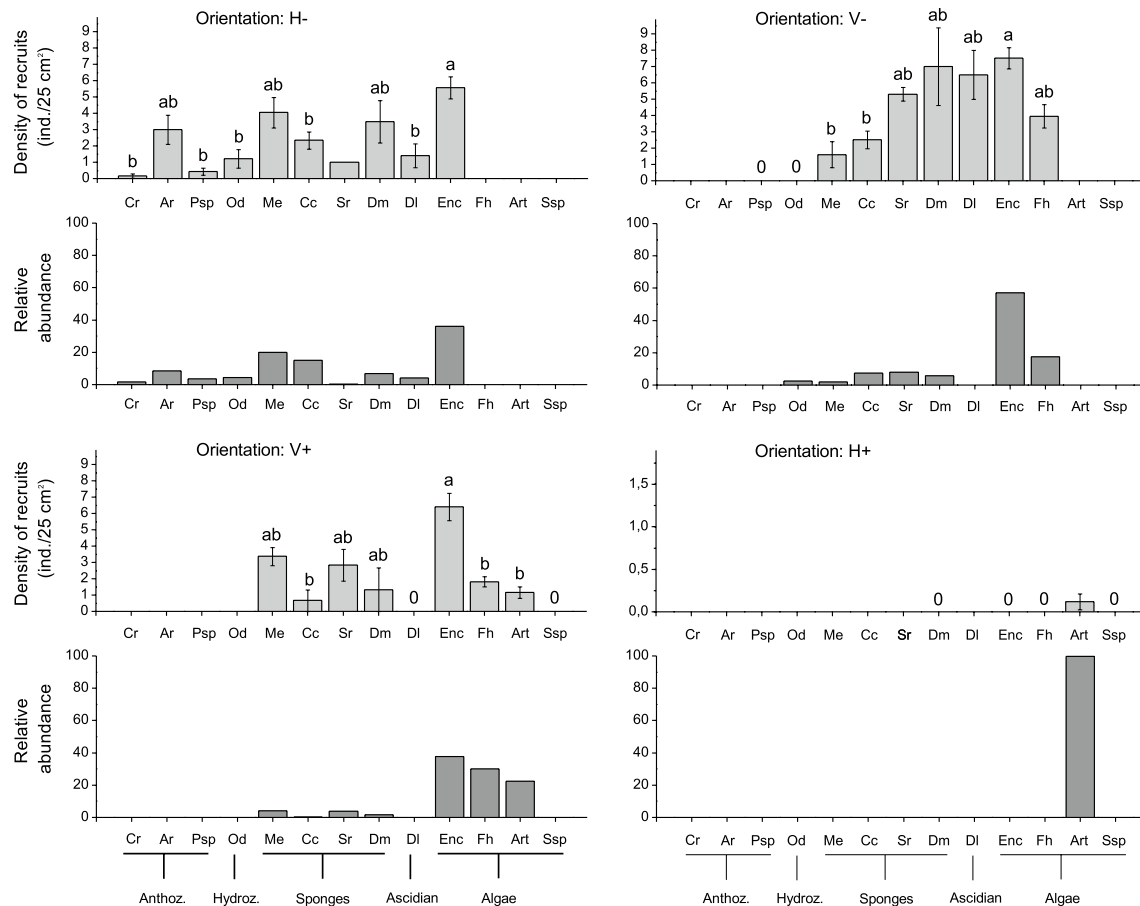


Fig. 5 Density and relative abundance (%) of sun-coral recruits on patches of the more representative sessile species. Data from the sites Pedra Lisa and Ponta Leste are pooled, and separate comparisons were carried out for each substrate orientation (abbreviations as in Fig. 2). In density plots, bars and whiskers represent average values \pm SEs. Differences between any two biogenic substrates sharing at least a single letter are not statistically significant ($p < 0.05$). Abundance data were first computed by multiplying average densities of *Tubastraea coccinea* recruits by the percent cover of respective biogenic substrata (shown in Figure S1) and then recalculated as

relative percentages. Abbreviations for taxonomic groups—Cr: *Carijoa riisei*, Ar: *Astrangia rathbuni*, Psp: *Parazoanthus* spp, Od: *Obelia dichotoma*, Dl: *Diplosoma listerianum*, Me: *Mycale escarlatei*, Cc: *Clathria campecheae*, Sr: *Scopalina reutzleri*, Dm: *Desmanthus meandroides*, Enc: Encrusting coralline algae, Fh: *Falkenbergia hillebrandii*, Art: Articulated coralline algae, Ssp: *Sargassum* spp. The sponges *Scopalina reutzleri* and *Clathria campecheae* were removed from analyses because data were only available for a single subquadrat

characteristics around colonies may alternatively facilitate the establishment of other species; a possibility that should be tested experimentally.

Chemically active cnidarians seemingly exert a strong influence on assemblage structure at areas already colonized by the sun-coral. Consistent negative associations with patches dominated by the snowflake coral *Carijoa riisei*, the presence of the zoanthid *Parazoanthus* sp and the sea thread hydroid *Obelia dichotoma* is a first indication of direct negative interactions between these species and the sun-coral. This implies that interpretation of results may be the opposite if one moves from a large (tens to hundreds of meters) to a small (tens of cm) spatial scale.

For instance, while comparisons between invaded and non-invaded reef areas support colonization of more speciose reef habitat, chemical deterrence within invaded reefs may favor the persistence of diverse patches of mostly colonial species. However, two lines of evidence suggest that such pockets of resistance may not prevail. First, abundance and distribution patterns of sun-coral colonies at Búzios island (Mizrahi et al. 2014b) indicate that colonization is still an ongoing process in the area. At other places in South-eastern Brazil, where colonization started long before, the sun-coral reaches higher abundances at vertical walls and has already successfully spread over less commonly impacted flat positive substrates, clearly monopolizing

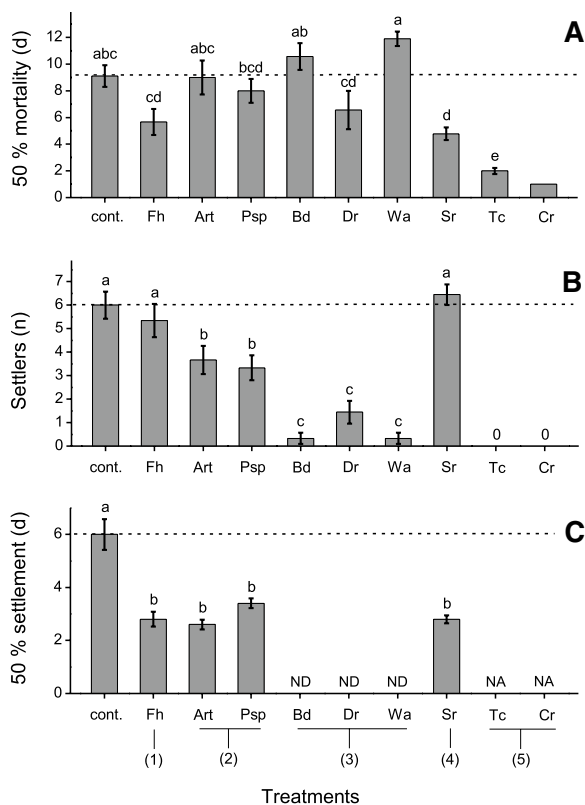


Fig. 6 Results of bioassays with crude extracts of representative reef species testing allelopathic effects on the settlement of *T. coccinea* larvae. Means and standard errors are represented for the three variables tested: **a** time at 50% mortality, **b** number of settled larvae, **c** time at 50% settlement. Tested species were grouped according to response categories based on combinations of all three measured variables (see main text): (1) facilitation, (2) low inhibition, (3) strong inhibition, (4) toxicity, and (5) high toxicity, as shown at the bottom of panel C. For all variables, differences between species extracts sharing the same letter are not significant ($p > 0.05$), according to a posteriori tests. Groups that share one or more letters cannot be discerned from each other. Species abbreviations: Fh: *Falkenbergia hillebrandii* (red alga), Art: Articulated coralline algae, Psp: *Parazoanthus* sp (anthozoan), Bd: *Bugula dentata* (bryozoan), Dr: *Dragmacidon reticulatum* (sponge), Wa: *Wrangelia argus* (red alga), Sr: *Scopalina reutzleri* (sponge), Tc: *Tubastraea coccinea* (anthozoan), Cr: *Carijoa riisei* (anthozoan), cont: control. Other abbreviations: ND no data, NA not applicable. Mass mortality within 1 day for all larvae exposed to *Carijoa riisei* precluded the inclusion of this treatment in mortality analyses. Dashed lines correspond to average estimates for the control treatment in all three panels

large extensions of entire shallow-water rocky reef habitats (Paula and Creed 2005). Second, diversity trends reversed at V— walls at Pedra Lisa, where the coverage of sun-coral was the highest recorded at Búzios island (on average 68%, Mizrahi et al. 2014b; Table S1). This result suggests space limitation within dense sun-coral for the development of native assemblages.

To date, effects on positively oriented reef areas are not clear at Búzios Island. In contrast to H— and V— substrates,

differences in community structure between invaded and non-invaded areas on positively orientated substrates are much less clear at Pedra Lisa and undetected at Ponta Leste. Also, differences in species diversity and richness tended to be less important at H+ habitat for both sampled sites, where the abundance of *Tubastraea* is much lower and its impact on local diversity likely less important.

Potential factors facilitating recruitment

The likelihood of a given community to be impacted by an invading species may largely depend on processes leading to facilitation and inhibition of settlement and early juvenile recruitment (Hay et al. 1998; Hadfield and Paul 2001). In tropical shallow reef habitats, where interspecific competition for space is often keen (as reviewed in Hart et al. 2012), allelopathic mechanisms affecting settlement are expected to be common (Morse 1992; Hay et al. 1998). Overall, our results support such a view. Sun-coral larvae may settle and recruit, as small single polyps, on a range of biogenic substrates, independent of their patch size. However, the only taxon consistently hosting a larger number of coral recruits was encrusting coralline algae, which invest very little in chemical defenses (as reviewed by Morse 1992; Hadfield and Paul 2001), providing a relatively inert substrate and apparently representing no obstacle to competitive overgrowth. Because encrusting algae are ubiquitous at shallow subtidal rocky habitats in our study region, as well as in many other tropical and subtropical reefs worldwide (Steneck 1997; Vermeij et al. 2010), they maybe a natural gateway for the sun-coral introduction in many different areas. In our sampled area, the sun-coral may well had overgrown substantial extensions of encrusting coralline algae, reducing its cover from around 30% (as estimated at similar non-invaded reefs) to 15% in invaded V— habitat at Ponta Leste. It is also important to note that coralline crustose algae become especially abundant in disturbed habitats (Dethier 1994; Steinbeck et al. 2005). Since human-mediated impacts may select for less-structured reef habitat with predominance of exposed algal crusts, devoid of any secondary cover, care should be taken to detect, and ideally eradicate, settling sun-coral colonies. This issue naturally extends to man-made structures deployed in the sea, such as ship hulls, oil platforms and piers (e.g. Cairns 2000; Castro and Pires 2001), which are appropriate for the development of bacterial biofilms, known to induce larval settlement of many invertebrates, including corals (Morse and Morse 1984; Hadfield and Paul 2001).

Negative allelopathic effects likely blocking the sun-coral spread

Generally, with the exception of the encrusting coralline algae noted above, responses of sun-coral planula larvae

to extracts of native invertebrates and macroalgae were negative in comparison to responses observed in controls. Considering effects of settlement and mortality combined, our results strongly suggest that the virtual absence of sun-coral recruits on snowflake coral *Carijoa riisei* patches is due to chemical deterrence. The action of a number of cytotoxic and antimicrobial byproducts produced by this species, which effectively eliminate protozoa, fungi and bacteria (Reimão et al. 2008; Maia et al. 2000), may have been responsible for prompt mass mortality of sun-coral larvae in our bioassays. It is important to note that *C. riisei* has itself been accidentally introduced in different coastal regions of the world (e.g. Padmakumar et al. 2011; Dhivya et al. 2012), including the Brazilian coast (Concepcion et al. 2010), and that once established, this coral is capable of dominating large reef areas overgrowing several other coral species, including *T. coccinea* (Grigg 2003; Sanchez and Ballesteros 2014). In spite of being frequently attacked by specialized nudibranch species, predation on polyps is never sufficient to control *C. riisei* populations (Wagner et al. 2009), which may persist for a long time. At areas still not invaded by *Tubastraea* in Búzios Island, *C. riisei* was found to be one of the most abundant species, ranking third on H- and V- surfaces in Pedra Lisa and Ponta Leste, respectively, and first at H- surfaces in the latter location, covering 34.8% of the substrate. The snowflake coral was also relatively common at areas where the sun-coral was already present, ranking second behind *Tubastraea* at Ponta Leste H- reef areas (16.2%, Table S1). Added to the fact that several species capable of remarkable chemical defense are associated with the branches and stolons of *C. riisei*, including the sponge *Desmapsamma anchorata*, which is known to negatively affect *T. coccinea* (De Paula 2007), there is substantial evidence indicating that the snowflake coral is a major obstacle for the sun-coral invasion and that negative chemical interactions may be important processes mediating the settlement dynamics of these two species.

Response to extracts of adult *Tubastraea* conspecifics was as negative as observed upon contact with *C. riisei* extracts, with 50% larval mortality after 2 days and no settlement. This result is very consistent with field data, since no recruits were ever recorded on, or in contact with, conspecifics, or on patches of *C. riisei*. Contrary to the distribution of adult colonies, which tend to aggregate and form a rather homogeneous cover when occupancy is high (ca. >40%, Paula and Creed 2005; Glynn et al. 2008; Mantelatto et al. 2011), small *T. coccinea* colonies up to a few polyps tend to be uniformly distributed at the recently invaded areas (unpublished personal observations), typically more than 5 cm apart. This is approximately the maximum distance over which sun-coral colonies can inflict tissue necrosis on different organisms (Creed

2006; Lages et al. 2010). It is likely that negative chemical mediation, eventually leading to halos around individual colonies, will be no longer effective as colonies grow larger and get closer. Changes in chemical reactions, or production of allelopathic substances mediated by colony density, will be interesting to investigate. Regarding the invasive process, settling at some distance may maximize space occupancy and increase colonial growth and colonization of newly invaded areas. It is important to note that the occurrence of negative interactions in our experiments must be considered as a first-hand indication for the potential of chemically mediated interactions in the field. First, whole cell extracts may have contained several byproducts involved in chemical defense (Nylund et al. 2007) and high mortality in trials may reflect enduring exposure to chemically active substances in still water; a condition hardly observed in nature. Partly to increase realism of this trials authors have used running sea water tanks (e.g. Tamburri et al. 1996), which clearly represent a step forward towards realistic conditions. But without some indication of local scale velocities, turbulence and particularly diffusivity around biological structures, it is difficult to reproduce realistic field conditions in the laboratory. Unfortunately, in our case there was a further complication to run experiments in flow-through tanks circulating water: *Tubastraea* planulae clustered together even at very low flow velocities, making it impossible to make individual records. Field experiments get around many of these problems, but conducting controlled field trials can be nearly impossible except for the shallow and calm environments. It should be noted that in our experiments conditions were the same for all extract treatments and, therefore, comparisons should still reflect the potential for allelopathic effects. Further studies should proceed towards the evaluation of these effects under field conditions.

Field data on early recruit distribution support the classification of articulate coralline algae and *Parazoanthus* sp as weak settlement inhibitors. Both species lie on the low settlement rate group in laboratory bioassays and on the group with low density of *T. coccinea* recruits at field, except for accidental records of sun-coral recruits on articulate coral-lines in H+ surfaces. The species we classified as strong inhibitors, other than *C. riisei*, were not among the most abundant in photographed plots and, therefore, we could not examine their effect in the field. However, our results showing inhibition of settlement are generally concordant with findings of the broad studies comparing chemically mediated bioactivity on a wide array of marine organisms conducted by Munro et al. (1989) and Uriz et al. (1991). Red algae and cnidarians, which include weak inhibitors *Parazoanthus* sp and articulate coralline algae, are regarded on both studies as less active taxa compared to bryozoans

and sponges, which include our strong inhibitors *Bugula dentata* and *Dragmacidon reticulatum*. The exception was the response to the red weed *Wrangelia argus*, which strongly inhibited sun-coral settlement. Chemical activity of red algae should, however, be examined with caution since antibiosis in this group can be extremely variable and complex, as shown by Robles-Centeno et al. (1996) in a study investigating responses to extracts of three different species, including the congener *W. bicuspidata*.

Together with the presumably facilitating alga *Falkenbergia hillebrandii* and the sponge *Scopalina reutzleri*, which showed toxic effects in our laboratory tests, the relatively few sun-coral larvae that managed to settle on extracts of the low-inhibition group did it faster than the control treatment. Without additional results, we regarded this as a positive response, assuming that rapid settlement may correlate to a shorter pelagic larval duration in the field and hence a reduced chance of pelagic predation or larval loss due to advection to non-reef habitat. Alternatively, higher settlement rates may be caused by stress, resulting in premature metamorphosis and ultimately leading to small size of first recruits and lower early survival rate (Vermeij et al. 2006). This could explain the particular response of larvae to extracts of *S. reutzleri*, classified as toxic, in which both settlement rate and total number of settlers were among the highest, but mortality rate was exceedingly high.

Overall, this study suggests some of the directions that scientific studies should further pursue in order to inform conservation policies and management strategies to control or at least contain the invasion of the sun-coral in South-eastern Brazil. In particular, we stress the importance of monitoring inert substrates, especially new artificial habitats and especially if covered with coralline algae, which may work as stepping stones in the spread of the sun-coral to still undisturbed areas. We also highlight the need to protect native coral species, and other cnidarians, which apparently could chemically (or perhaps mechanically) resist or slow down the spread of *Tubastraea* through reducing larval settlement. These species are often embedded in species-rich reef patches. As an ecosystem engineer potentially providing structurally complex habitat, the sun-coral invasion may also strongly affect the composition of vagile invertebrate assemblages and thus the feeding resources for predatory fish, which constitute a very important consumer guild in the region (Ferreira et al. 2012). Such trophic interactions are also and most certainly promising lines of research.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Informed consent Informed consent was obtained from all individual participants included in the study.

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