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ORIGINAL PAPER

Effects of the alien coral *Tubastraea tagusensis* on native coral assemblages in a southwestern Atlantic coral reef

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Abstract The alien coral *Tubastraea* spp. has invaded Atlantic coral reefs since 1940s, but their effects on native coral assemblages are poorly understood. In this study the effects on coral assemblage structure and tissue mortality in native competitors by alien coral were investigated. We compared native coral cover in zones with and without *T. tagusensis* and evaluated the mortality of native coral species in natural encounters with *T. tagusensis*. Additionally, we evaluated the effects of contact with this invader on two native corals, *Siderastrea stellata* and *Montastraea cavernosa*, using a manipulative experiment. Multivariate analyses detected significant differences between coral assemblages in invaded and non-invaded zones. In the invaded zone, we observed greater cover of *T. tagusensis* on reef walls (34.9 ± 4.2 %) than on reef tops (18.5 ± 4.1 %). *Madracis decactis* and *Mussismilia hispida* were significantly less abundant in invaded zone than in non-invaded zones at the reef walls. Manipulative experiments showed a significant increase in tissue mortality of *S. stellata* (3.2 ± 1.4 cm^2) after 60 days of contact with *T. tagusensis* and no effects on *M. cavernosa* after 90 days of contact. In natural encounters, 52 and 0.1 % of the *S. stellata* and *M. cavernosa* colonies, respectively, showed tissue mortality. These results indicate that competitive interactions with native competitors are important to understand alien coral establishment on coral reef. Our study documents the negative effects of the alien coral on coral reef assemblages and reinforces the urgent need for monitoring and management actions to control the expansion of this invader on Brazilian reefs.

Introduction

Biological invasion is a primary threat to global biodiversity and ecosystem function (Ruiz et al. 1997; Molnar et al. 2008; Seebens et al. 2013). Invasive species have had extensive effects on marine systems worldwide (Carlton and Geller 1993), and a large number of studies have demonstrated the negative impacts of invasive species on marine benthic assemblages (Hollebone and Hay 2007; Caralt and Cebrian 2013). However, coral reefs, one of the most biodiverse and productive marine systems in the world (e.g., Birkeland 1977; Connell 1978), have been the subject of relatively few rigorous studies evaluating the potential consequences of invasions on coral assemblages (Coles and Eldredge 2002; Fernández and Cortés 2005; Ávila and Carballo 2009; Pérez-Estrada et al. 2013). Coral reef systems are highly dependent on hermatypic corals which build complex three-dimensional physical structures (Jones et al. 1994; Graham and Nash 2012), creating a large variety of microhabitats and leading to a high diversity and abundance of organisms (Crowder and Cooper 1982; Coni et al. 2013; Leal et al. 2013; Graham 2014; Rogers et al. 2014; Leal et al. 2015). Thus, understanding how invasions

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affect these ecosystems is crucial for the well-being of the coral reefs and the organisms that depend of them.

The ahermatypic coral *Tubastraea* (Scleractinia, Dendrophylliidae), commonly known as cup coral, is a native genus from the Indo-Pacific region likely introduced by ships and/or oil platforms in the Atlantic Ocean in the 1940s (Cairns 2000; Castro and Pires 2001; Fenner 2001; Fenner and Banks 2004). Three species of *Tubastraea* genus were reported in the Atlantic (*T. micranthus*, *T. coccinea* and *T. tagusensis*). *Tubastraea* spp. is a successful invader due to its high fecundity (Glynn et al. 2008; De Paula et al. 2014), rapid growth (Wellington and Trench 1985), allelochemical defenses (Lages et al. 2010a, b) and competitive aggressiveness (Wellington and Trench 1985; Dos Santos et al. 2013). However, there are no reports of the ecological impacts of this invader on native coral species in coral reefs (Fenner and Banks 2004). Recent biological invasions by the species *T. coccinea* and *T. tagusensis* are threatening coral reefs along the northeast Brazilian coast in the southwestern Atlantic (Sampaio et al. 2012). These species were first reported on the subtropical southwest coast of Brazil (De Paula and Creed 2004) on rocky shores, where they can change the structure of benthic assemblages (Lages et al. 2011). However, there is an urgent need to assess the potential effects of these alien species on Brazilian corals, especially on the northeast coast, the region with the richest hermatypic coral fauna in the southwestern Atlantic (Leão et al. 2003). The orange cup coral represents a serious threat to the local marine biodiversity (Creed 2006) because Brazilian reefs are relatively poor in coral species but have high endemism (Castro and Pires 2001; Leão and Kikuchi 2001; Neves et al. 2006; Nunes et al. 2008). Direct interactions of *T. tagusensis* and *T. coccinea* with a Brazilian endemic coral (*Mussismilia hispida*) result in the tissue necrosis of native coral, but the effect is not reciprocal (Creed 2006; Dos Santos et al. 2013). These evidences suggest that the alien coral *Tubastraea* spp. can reduce or exclude the native coral species by space competition (Dos Santos et al. 2013).

Competition for space is an important process on coral reefs determining patterns of distribution, abundance and species diversity in benthic communities (Connell et al. 2004). Competitive processes regulate reef structure, since the space on hard substratum is limiting resource for the settlement, growth and reproduction of reef-building corals (Lang and Chornesky 1989; Connell et al. 2004; Chadwick and Morrow 2011). Competition among corals can occur (1) indirectly by overtopping, when growth by one colony (e.g., branching, tabular or foliaceous forms) overshadows another or (2) directly, when tissues of different colonies come into contact, resulting in necrosis of one or both competitors (Connell 1973). Direct interactions among corals are frequent in coral communities, especially those dominated by massive corals (e.g., Leão et al. 2003). These interactions may involve several mechanisms including, sweeper tentacles (Hidaka and Yamazato 1984), sweeper polyps (Peach and Hoegh-Guldberg 1999), mesenterial filaments (Lang 1973) and the secretion of mucus (Chadwick 1988). The competitive outcomes are complex and can lead to fitness reduction of the subordinate coral, cessation of growth along the margin of damaged and/or even competitive reversal. In the cases, the most aggressive coral species may impact the structure of reef communities (Dai 1990).

Dos Santos et al. (2013) showed that tissue necrosis caused by the alien coral species *T. tagusensis* and *T. coccinea* on the native coral *M. hispida* occurred mainly due to physical mechanisms in direct encounters. Thus, effects of direct encounters between *Tubastraea* spp. and native corals should be considered to understand biological invasions on Brazilian coral reefs. In this study, we evaluate whether *T. tagusensis* negatively affected the hermatypic coral assemblage in Brazil. To achieve this, we tested whether (1) sites with a high cover of *T. tagusensis* would have different structure of native coral assemblages compared with non-invaded sites and (2) whether direct encounter with *T. tagusensis* would cause tissue damage on native coral species. Therefore, we combined mensurative and manipulative experiments to provide an important baseline that will serve as a starting point for future monitoring and management actions.

Materials and methods

Study area

The study was conducted at Cascos Reef (13°07′46″S, 38°38′31″W) in the outer part of Todos os Santos Bay (TSB), east coast of Brazil (Fig. 1). Cascos Reef is the first coral reef site where *T. tagusensis* was documented in the southwestern Atlantic (Sampaio et al. 2012). This reef, at depths of approximately 20 m, consists of reef patches 11–13 m in height and 1–100 m in length (Fig. 1). Two main habitats are clearly distinguished on Cascos Reef: the reef top (horizontal surfaces; 11–13 m deep) and the walls (vertical surfaces; 12–20 m deep).

Eight species of native hermatypic coral occur on Cascos Reef, the scleractinians *Montastraea cavernosa*, *Madracis decactis*, *Phyllangia americana*, *M. hispida*, *Mussismilia leptophylla*, *Siderastrea stellata*, and *Meandrina braziliensis* (the last four species are endemic to Brazilian reefs: e.g., Leão et al. 2003; Neves et al. 2006; Nunes et al. 2008; Budd et al. 2012) and the hydrozoan fire coral *Millepora alcicornis*. There is only one zone

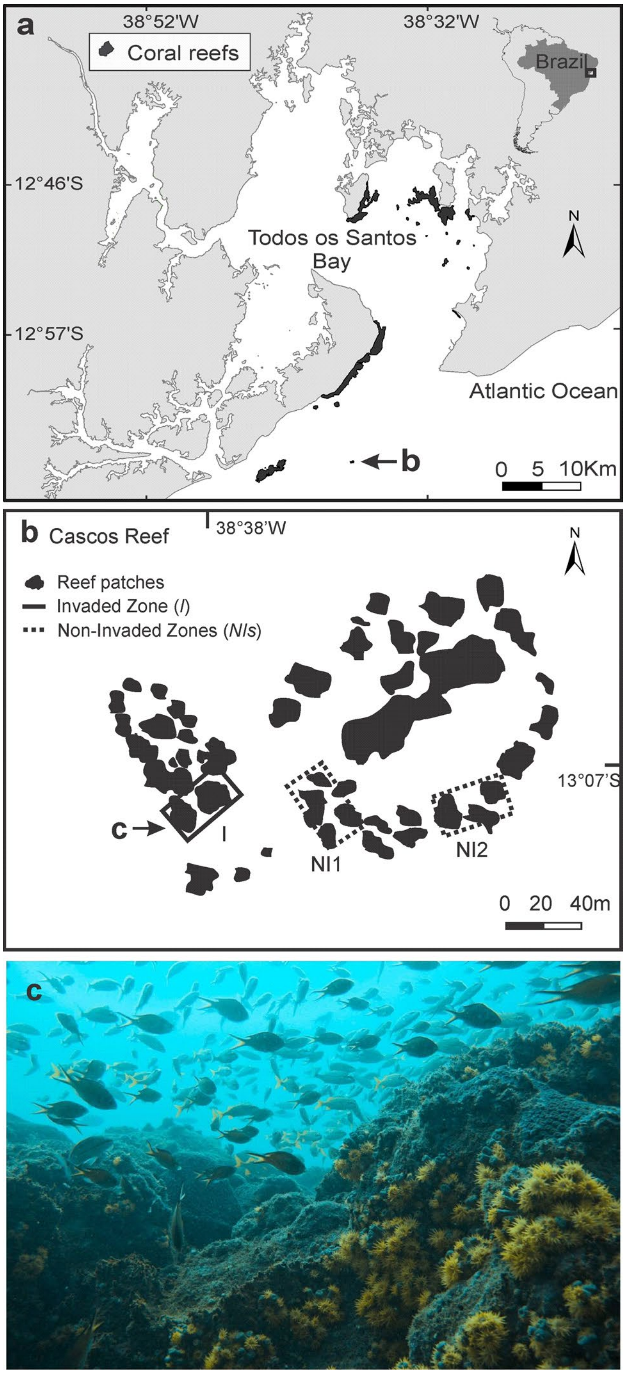


Fig. 1 Location map of coral reefs in Todos os Santos Bay, Brazil (**a**): (**b**) Cascos Reef, with sampling zones (I = invaded zone; NI1 and NI2 = non-invaded zones) and (**c**) reef assemblages of the invaded zone

on Cascos Reef where the population of *T. tagusensis* is aggregated over approximately 800 m^2 (Fig. 1b, "Invaded Zone"). This population is dense, with patches measuring approximately 4 m^2. *T. coccinea* was not found in field samples in the study area, and therefore, only *T. tagusensis* was used in our study.

Assemblage structure in invaded and non-invaded zones

We compared the structure of coral assemblages in the invaded zone (hereafter indicated as *I*) with that in non-invaded zones (NI1 and NI2, hereafter denoted *NIs*; Fig. 1b) to evaluate whether the presence of *T. tagusensis* affected the native coral assemblage structure. We selected the non-invaded zones based on their similarity in size (800 m^2) and environmental conditions (i.e., wave exposure and depth) to the invaded zone. The non-invaded zones, where *T. tagusensis* did not occur, were 20 m apart. We sampled two distinct habitats, reef walls and reef tops, within each zone because of the marked differences in abiotic conditions (e.g., light incidence and substrate inclination, Francini-Filho et al. 2013).

We used an asymmetrical design to compare the coral cover between *I* and *NIs*. This design, with two non-invaded ("control") locations (*NIs*), produces better estimates of natural variability than the use of a single "control" area, which was appropriate for this situation in which there was only a single impacted location (*I*) that could not be replicated (see Underwood 1992; Glasby 1997; Terlizzi et al. 2005a, b). Therefore, our design had three factors: Treatment (*I* and *NIs*, fixed and orthogonal), Zone (I, NI1 and NI2 random, nested in Treatment) and Habitat (Wall and Top fixed, nested in Zone).

During the summer of 2012/2013 (December–March), we characterized the coral assemblages using photo-quadrats (0.25 m^2) of the reef tops and walls. We haphazardly took 80 photographs per zone (I, NI1 and NI2), 40 in each habitat (top and wall). We estimated the percentage of coral cover per species through 30 randomly distributed points per photo-quadrat (2400 points per zone, 1200 per habitat) using the Coral Point Count with Excel Extensions Software (CPCe) (http://www.nova.edu/ocean/cpce/) (Kohler and Gill 2006).

We analyzed the data using a combination of multivariate and univariate procedures to evaluate the variations in the structure of coral assemblages and native hermatypic species, respectively. We used a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) to test for differences between assemblages of corals in *I* and *NIs*, based on Bray–Curtis dissimilarities using 9999 random permutations, with arc-sine square root transformation of the data to achieve homogeneity of dispersions using the software PRIMER 6. The significance level (α) adopted in this analysis and the other analyses was 0.05.

We used analysis of variance (ANOVA) to test for differences in cover of each native coral species in *I* and *NIs* using the software STATISTICA version 8.0. A Cochran's *C* test (Underwood 1997) and the Kolmogorov–Smirnov test were used to check for homogeneity of variance and normality, respectively. If necessary, data were arc-sine square root transformed to remove variance heterogeneity. If there was no suitable transformation, we performed analyses on the untransformed data. Previous studies argued that ANOVA was robust to departures from the assumption of homogeneous variances when there were many independent estimates of sample variance (e.g., Underwood 1997; Terlizzi et al. 2005a), as in the present study.

Natural encounters

We investigated the natural encounters between the alien coral and any native coral species in *I* (described above and shown in Fig. 1b) to estimate the percentage of native colonies with tissue damage. We estimated the total number of colonies of each native species contacting *T. tagusensis* in 80 photographs taken as previously described. We considered it a natural encounter when one colony of *T. tagusensis* was in contact with, or closer than 5 cm to, a native coral colony and when tissue lesions and algae overgrowth were observed (Dai 1990; Van Veghel et al. 1996). The distance between 1 and 5 cm was defined based on the different mechanisms of competition (e.g., sweeper tentacles, sweeper polyps, elongated polyps and mesenteric filaments) that can cause tissue damage on neighboring corals within this range (Lapid et al. 2004; Lapid and Chadwick 2006; Dos Santos et al. 2013). We also conducted a night dive to observe coral competitive morphological structures (e.g., sweeper tentacles and elongated polyps) in open polyps acting during natural encounters.

Manipulative experiment

We selected two well-distributed coral species of the Brazilian reefs (*M. cavernosa* and *S. stellata*) to evaluate the direct competitive encounter effects of the invasive coral *T. tagusensis*. These two native species were chosen because they occurred in the study area and were abundant in several other coral reefs (non-invaded, see Ferreira and Maida 2006; Cruz et al. 2009) susceptible to invasion in the northeastern and northern regions of the Brazilian coast. We established a manipulative experiment in the field (Cascos Reef) using paired species (alien-native) and corresponding controls (single colony of one species) attached to polyethylene plates (20 cm × 20 cm) as experimental units. Overall, we collected 42 colonies (18 of *T. tagusensis*, 12 of *M. cavernosa* and 12 of *S. stellata*) with diameters between 8 cm and 12 cm to minimize potential size effects (e.g., Zilberberg and Edmunds 2001). We attached the colonies to experimental plate units with non-toxic marine epoxy (Tubolit Men) immediately after collection. After allowing the epoxy to harden in a tank for 1 h, we attached the plate units to 20 cm × 20 cm × 40 cm cement blocks, which we had previously placed on the coral reef substrate at a depth of 21 m, with cable ties. We distributed the experimental units randomly on the substrate. We used two treatments: (1) Contact, where paired alien-native colonies (*T. tagusensis* with *M. cavernosa* and *T. tagusensis* with *S. stellata*) were placed 5 mm apart to avoid skeletal contact, but allowing tissue contact when their tentacles were expanded; (2) No Contact, where a single colony of each of the three species was placed alone one in the experimental unit. Each treatment had six replicates ($n = 6$).

The experiment lasted for 90 days, and our observations were made on days 5, 15, 30, 60 and 90 using SCUBA diving and underwater photography (high-resolution digital images). After 3 months, we performed a night dive to observe competitive morphological structures when the coral polyps were expanded. We quantified tissue necrosis of the native species by measuring the necrosed area (cm^2) with photographs taken at each time, using CPCe (Kohler and Gill 2006). We used a one-way repeated measures ANOVA to assess the possible differences in the mortality of native species with the following factors: Treatment (fixed, two levels: Contact and No Contact) and Time (fixed, five levels: 5, 15, 30, 60 and 90 days), with time as a repeated measurement factor. To test the homogeneity of variance and normality, we used Cochran s C and the Kolmogorov–Smirnov statistic, respectively, using STATISTICA software, version 8.0. We applied a square root transformation to the mortality data prior to the analysis to remove variance heterogeneity. A post hoc Tukey test was used when significant differences were found.

Results

Assemblage structure in invaded and non-invaded zones

The top five most abundant coral species (mean cover ≥1 %) in the Cascos Reef were *M. cavernosa* (14.1 ± 1.3, mean ± SE), *T. tagusensis* (8.9 ± 1.3), *M. decactis* (5.1 ± 0.7), *M. hispida* (2.8 ± 0.4) and *S. stellata* (1.4 ± 0.2). In the invaded zone, *T. tagusensis* was dominant (26.7 ± 3.1) and its cover was higher on reef wall (34.9 ± 4.2) than on reef top (18.5 ± 4.1). In the non-invaded zones, the native coral *M. cavernosa* was dominant (11.6 ± 1.7 in NI1 and 16.8 ± 2.2 in NI2) and more abundant on reef top (18.6 ± 2.7 in NI1 and 27.8 ± 3.4 in NI2) than on reef wall (4.5 ± 1.5 NI1 and 5.7 ± 1.6 NI2). The PERMANOVA showed significant differences in the cover pattern of coral assemblages between *I* and *NIs* (Table 1). No significant differences were detected between *NIs*, although the assemblages differed significantly between habitats (top and wall, Table 1; Fig. 2 "Native Hermatypic Corals").

The ANOVA analysis showed significant differences for *M. decactis* and *M. hispida* between reef walls at *I* and *NIs* ($F_{(1,239)} = 4.96$, $p < 0.05$ and $F_{(1,239)} = 7.53$, $p < 0.01$, respectively), and four native corals showed differences between habitats (*M. decactis*, $F_{(2,237)} = 31.38$, $p < 0.01$; *M. hispida*, $F_{(2,237)} = 7.43$, $p < 0.01$; *M. cavernosa*, $F_{(2,237)} = 45.75$, $p < 0.01$; and *S. stellata*, $F_{(2,237)} = 13.63$, $p < 0.01$, Fig. 2).

Table 1 Asymmetrical PERMANOVA based on the Bray–Curtis dissimilarities (arcsine square root data transformed) of the coral assemblages (5 taxa)

Source	DF	MS	Pseudo-F	Unique perms	*p* (MC)
Treatment	1	23,779	98.833	3	0.004**
Zone (treatment)	1	240.6	0.892	9953	0.467
Habitat (zone (treatment))	3	9967.3	36.967	9938	0.0001**
Res	234	269.63			
Total	239				

** $p < 0.01$

Natural encounters

We observed 141 natural encounters between the invasive coral and the four most abundant native coral species (*M. cavernosa*, *M. decactis*, *M. hispida* and *S. stellata*). Colonies of native corals showed partial mortality on the side facing the neighboring invader in 21 % of the encounters ($n = 30$). *S. stellata* and *M. hispida* had the highest percentage of colonies with partial mortality, 52 % ($n = 10$) and 50 % ($n = 7$), respectively (Fig. 3). *M. cavernosa* and *M. decactis* had the lowest percentage of colonies with partial mortality, 0.1 % ($n = 2$) and 20 % ($n = 11$). At night, we observed *M. cavernosa* and *M. decactis* using sweeper tentacles against the elongated polyps of *T. tagusensis* (Fig. 4).

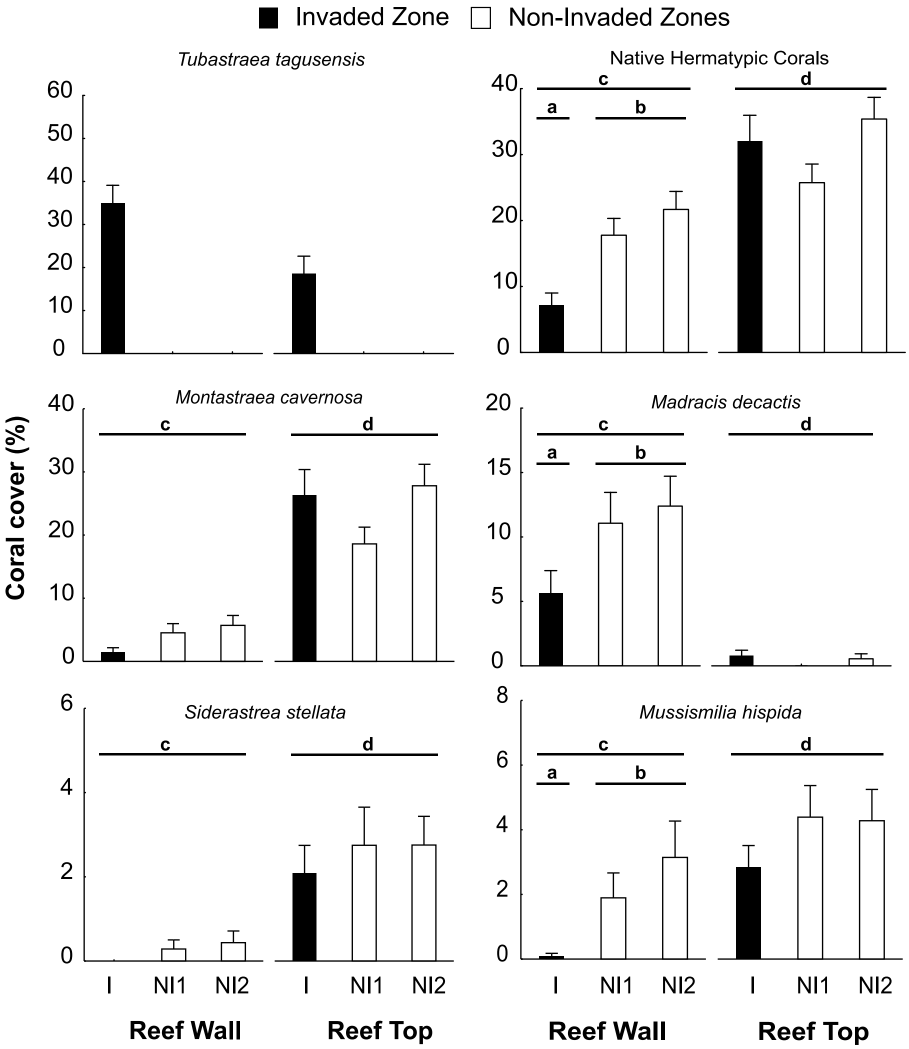


Fig. 2 Mean coral cover (±SE) within habitats in invaded and non-invaded zones. The *different letters* denote significant differences. Native Hermatypic Corals represent the sum of native species covers

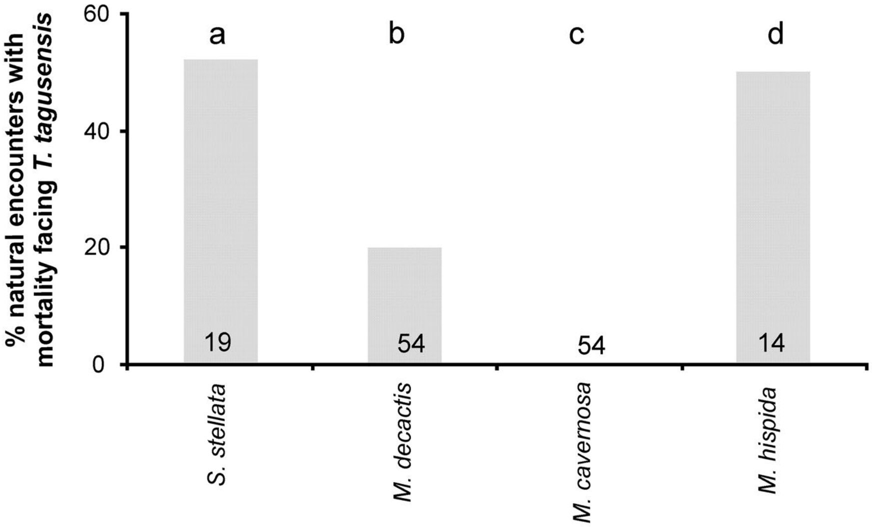
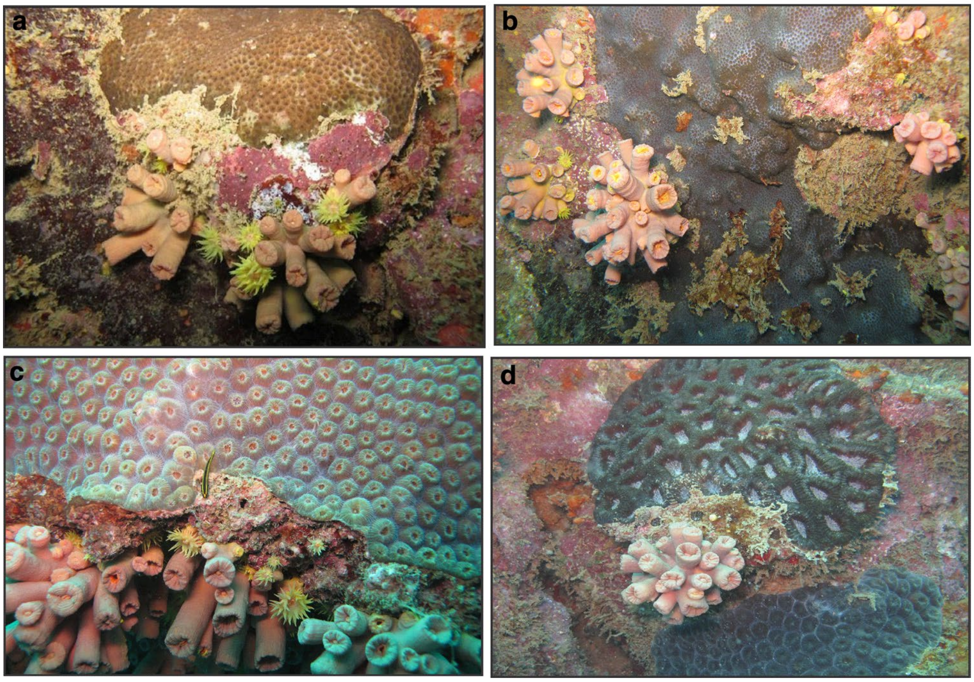


Fig. 3 Percentage of natural encounters with mortality in each native coral species on the side facing *Tubastraea tagusensis*: **a** *Siderastrea stellata*, **b** *Madracis decactis*, **c** *Montastraea cavernosa* and **d** *Mussismilia hispida*. The *number* at the base of each *bar* represents the total number of colonies of each species in contact with *T. tagusensis*

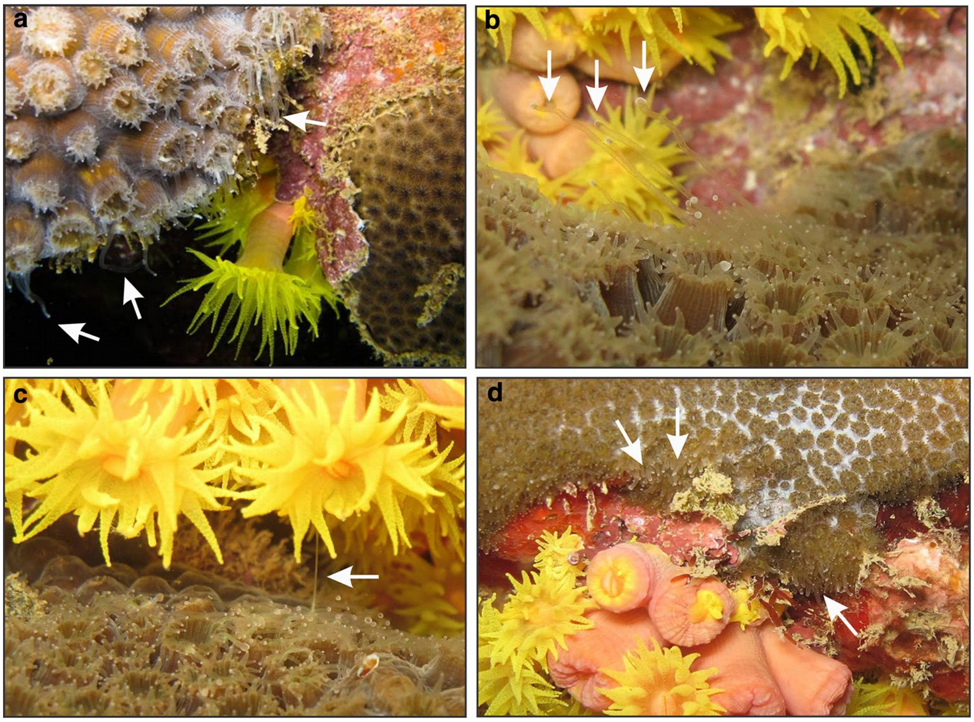


Manipulative experiment

During the first 15 days of the experiment, the native coral *S. stellata* was healthy and no significant mortality was found between Contact and No Contact treatments (Fig. 5). However, after the 30th day, the area with tissue necrosis in *S. stellata* became more pronounced (1.3 ± 1.1 cm^2), and bleaching and turf algae growth was also observed in the Contact treatment. At this time, we frequently observed hermit crabs in the contact zones between corals. At night, we also recorded elongated polyps of open *T. tagusensis* between dead and living zones in the *S. stellata* colonies. The mortality area of *S. stellata* increased significantly on the 60th and 90th days (3.2 ± 1.4 and 3.4 ± 1.3 cm^2, respectively, Fig. 5; Table 2) and no tissue necrosis was observed in the colonies of *T. tagusensis* on the side facing *S. stellata.* Furthermore, all colonies of the No Contact treatment were healthy during the entire experiment.

On the 5th day of the experiment, the mortality of *M. cavernosa* was 0.04 ± 0.03 cm^2 (Fig. 5) and no necrosis was observed in *T. tagusensis* during this period in the Contact treatment. On day 15, the necrosis in *M. cavernosa* increased slightly (0.1 ± 0.04 cm^2), followed by the growth of turf and fleshy algae; however, this pattern was also observed in *T. tagusensis*. Over time, mortality area on *M. cavernosa* was insignificant (Table 2) and only a small portion of its colony tissue was lost during the entire experiment (0.2 ± 0.1 cm^2). We also observed that the number

Fig. 4 Sweeper tentacles (*arrows*) observed in natural encounters involving competition: **a**–**c** *Montastraea cavernosa* and **d** *Madracis decactis*



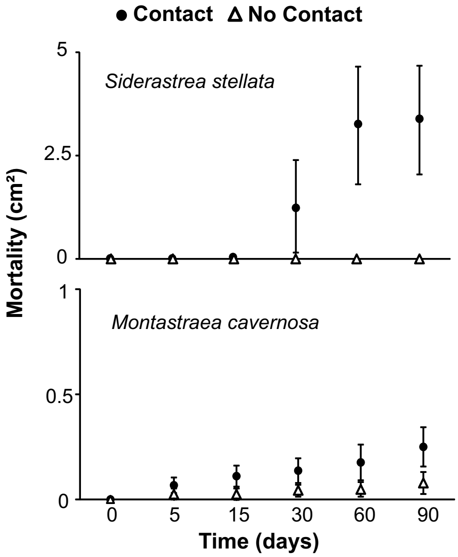


Fig. 5 Mortality (mean and SE) of native species in treatments (Contact and No Contact) in a manipulative experiment over 90 days ($n = 6$)

Table 2 One-way repeated measures ANOVA of mortality area in native species (*Siderastrea stellata* and *Montastraea cavernosa*) over time, with time as the repeated measure

Source of variation	DF	MS	*p*
Siderastrea stellata			
Treatment	1	47.124	0.046*
Time	3	7.829	0.015*
Treatment (time)	3	7.829	0.015*
Post hoc Tukey tests	TIME60: Contact > No Contact TIME 90: Contact > No Contact		
Montastraea cavernosa			
Treatment	1	0.179	0.211
Time	4	0.017	0.161
Treatment (time)	4	0.007	0.430

Treatment ($n = 2$) was "Contact" with colonies of the invasive coral *Tubastraea tagusensis* versus "No Contact". The times were the sampling periods 5, 15, 30, 60 and 90 days following the start of the experimental contact ($n = 5$ periods, Fig. 5). *S. stellata*: one level of the factor time (Day 5) was removed due to mortality = 0. $n = 6$ native colonies per treatment

* $p < 0.05$

of polyps increased (one to seven polyps) by budding in all six replicates. These observations indicated that *M. cavernosa* remained in good condition during the experiment. In addition, *M. cavernosa* showed the ability to attack the alien coral. We recorded the sweeper tentacles of *M. cavernosa* reaching the living edge of *T. tagusensis* colonies at night (Fig. 4) that resulted in progressive tissue necrosis in the alien coral over time. By day 30, we observed the growth of turf algae in the mortality area of *T. tagusensis* colonies and occurrences of hermit crabs in contact zones. At 60–90 days, additional *T. tagusensis* polyp mortality occurred together with coenosarc discoloration, deterioration of the skeleton, growth of epibionts (crustose coralline algae and turf algae) and occurrences of polychaetes and hermit crabs.

Discussion

We showed that the structure of coral assemblages in Cascos Reef were different in reef zones with and without the presence of the alien coral. The invaded zone in Cascos Reef was dominated by *T. tagusensis*, especially on the vertical surfaces (i.e., reef wall), and this zone showed significantly lower abundances of the native hermatypic corals, *M. decactis* and *M. hispida*. We also found natural differences in patterns of native coral cover between habitats (as observed by Glynn 1976; Francini-Filho et al. 2013) with higher cover of the native zooxanthellate coral on horizontal surfaces, indicating that the alien coral likely found less free space in this habitat than on vertical surfaces. On vertical surfaces, we found a high number of natural encounters between alien and native corals with tissue mortality in colonies of *S. stellata*, *M. hispida* and *M. decactis*, indicating a large number of competitive interactions. A manipulative experiment confirmed that the tissue mortality on *S. stellata* was significantly higher when in contact with *T. tagusensis* than without contact. This was similarly observed for *M. hispida* by Dos Santos et al. (2013). However, our experiment also showed that *M. cavernosa* had insignificant mortality and reacted to the presence of *T. tagusensis* developing sweeper tentacles and damaging the alien colonies. This native coral was dominant on all reef tops and its cover did not differ between invaded and non-invaded zones, suggesting possible resistance to the invader effects.

A similar pattern was reported on the rocky shores of southeast Brazil, where the high cover of the alien coral (e.g., on vertical surfaces) was positively correlated with changes in native assemblage structure (Lages et al. 2011). Vertical surfaces, with less light than horizontal surfaces, seems to have optimal conditions for the rapid growth of azooxanthellate *T. tagusensis* in Brazilian rocky and coral reefs (De Paula and Creed 2005; Mizrahi et al. 2014; present study). Light is a key source of energy for reef-building, zooxanthellate corals via photosynthesis (autotrophy) for successful growth and competition in horizontal habitats (Muscatine 1990). This could explain the preference of the alien coral for shaded habitats where they can find greater release from competition with native zooxanthellate corals than in high-irradiance habitats (Mizrahi et al. 2014). The traditional niche-based models of interspecific competition propose that one species can dominate a community, leading to either resource partitioning between the species, or elimination of the weaker competitor from the habitat (Colwell and Fuentes 1975; Diamond 1978). However, this hypothesis needs further testing.

Our results showed that alien coral dominance in the invaded zone (e.g., reef wall) can be related, at least in part, to their competitive abilities. We observed in natural encounters a high percentage of colonies of the native corals *M. hispida* and *S. stellata* with partial mortality on the side facing the neighboring invader. Several authors have suggested that cup coral species from the Dendrophylliidae family (i.e., *T. tagusensis*, *T. coccinea*, *T. micrantha* and *Balanophyllia elegans*) are aggressive competitors using tentacular contact that can frequently cause tissue damage to neighboring corals (Wellington and Trench 1985; Creed 2006; Dos Santos et al. 2013) or prevent overgrowth by ascidians (Bruno and Witman 1996). Creed (2006) and Dos Santos et al. (2013) demonstrated by mensurative and manipulative experiments that despite the ability of *M. hispida* to extrude mesenteric filaments a defense mechanism, high mortality rates were observed on this native coral species when in direct contact with the alien corals *T. tagusensis* and *T. coccinea.* This may explain why cover of *M. hispida* was significantly lowest in the invaded zone. These observations corroborate previous suggestions that the endemic Brazilian coral *M. hispida* can be reduced or competitively excluded by *T. tagusensis* (Creed 2006; Dos Santos et al. 2013).

Our experiments also confirmed a negative effect of alien coral contact on the endemic coral *S. stellata*. We registered tentacular contact of *T. tagusensis* on native *S. stellata* by the use mechanism of elongated polyps which likely caused a significant increase of the mortality area observed in this native species 60 days after contact. Despite the fact that there was no test for the effects of mechanical contact on tissue necrosis (coral mimic control as in Box and Mumby 2007; Diaz-Pulido et al. 2011; Lages et al. 2012), our experiment strongly suggests that competition was the important mechanism causing tissue necrosis. The polyps of *S. stellata* are relatively small, and this may explain its lower ability to compete against the large and extensive polyps of *T. tagusensis*. This native species showed the lowest cover in the invaded zone, along with *M. hispida* and *M. decactis,* but cover was also very low at reef walls on non-invaded zones (Fig. 2), which might impede the detection of significant differences. An alternative explanation for the absence of significant variation in cover variation of *S. stellata* between zones is the compensation of high adult mortality by high settlement and recruitment rates. Reproductive characteristics of *S. stellata* (e.g., early reproductive age and brooding) enable mature colonies of small size to release planulae larvae able to settle rapidly on substrate, favoring high recruitment rates in shallow reefs (Barros et al. 2003). This supports the competition–colonization trade-off model (Levins and Culver 1971; Horn and MacArthur 1972). This model proposes that species that are inferior competitors are better colonizers and vice versa (Levins and Culver 1971; Horn and MacArthur 1972). Following this model, inferior competitors are better at colonizing vacant space; however, superior competitors can generally displace the subordinates in time (Amarasekare et al. 2004). Furthermore, the high reproductive capacity of the alien coral (Glynn et al. 2008; De Paula et al. 2014) would accelerate the displacement of *S. stellata* by strong competition between recruits, and therefore additional studies are needed to assess this issue.

T. tagusensis seemed competitively superior to most of the endemic species when competing for space; however, their aggressive mechanism had no effect on *M. cavernosa*. This native species had a low percentage of colonies with mortality in natural encounters and the tissue necrosis of this native species did not significantly increase when it was in contact with the invasive coral in the manipulative experiment. This result was most likely due to the ability of *M. cavernosa* to use sweeper tentacles (Richardson et al. 1979), as observed in the present study. It is probable that these tentacles developed in response to contact with the neighboring invasive coral (Richardson et al. 1979). In fact, 30 days after the beginning of the experiment, the alien coral began to show tissue necrosis. Several authors recorded the development of sweeper tentacles 20–30 days after contact with a neighbor (Wellington 1980; Chornesky 1983; Langmead and Chadwick-Furman 1999; Lapid et al. 2004; Lapid and Chadwick 2006). This ability to retaliate against invasive corals can explain why this species did not show differences in cover between invaded and non-invaded zones, as observed in our manipulative experiment. The cosmopolitan species *M. cavernosa* appears to offer resistance to competition from this invasive species. However, development of competitive mechanisms such as sweeper tentacles requires high energetic demands to coral which in turn cause a trade-off between the allocation of energy to aggressive interactions versus coral growth or reproduction (Tanner 1997). Thus, long-term competition against the alien coral could alter fitness of the native *M. cavernosa*.

Overall, our study confirmed negative effects of an alien coral on endemic hard corals as suggested by Creed (2006) and Dos Santos et al. (2013). This may be the trigger for a change in the functional benthic group dominance (Cruz et al. 2014) from hermatypic to ahermatypic coral. This would be dramatic for reef integrity, because hermatypic corals are ecological engineers accumulating high rates of calcium carbonate (Birkeland 1977) that increase reef structural complexity and facilitate the occurrence of a large number of species (Graham and Nash 2012; Graham 2014; Rogers et al. 2014). Thus, alien ahermatypic corals could indirectly affect the physical structure and biodiversity of the reef ecosystem. Due to the importance of biodiversity for ecosystem properties (Hooper et al. 2005), these impacts may represent the loss of ecological function and services (Micheli et al. 2014; Pratchett et al. 2014). Future experiments must address how this invasive species affects coral reef functioning.

Several studies suggested that highly diverse communities were more resistant to invasion than communities with low diversity (Elton 1958; Levine and D'Antonio 1999; Stachowicz et al. 1999). The biotic resistance is the ability of a native community to resist change in the face of an invasion (Elton 1958; Kimbro et al. 2013). When compared with Caribbean or Indo-Pacific reefs, Brazilian coral reefs may have low resistance to alien coral impacts due to lower species richness and a higher level of endemism. These characteristics may facilitate the establishment of *Tubastraea* spp. in other Brazilian reefs and explain the absence of impacts of *Tubastraea* spp. on the coral assemblages of Caribbean reefs (Sammarco et al. 2012).

Our findings showed that the expansion of the invader to other Brazilian coral reefs along the coast could be extremely negative for the most important coral system on the South Atlantic Ocean. Species distribution modeling showed that habitats occupied by native species along the entire Brazilian coast were suitable for *Tubastraea* spp. (Riul et al. 2013). The Abrolhos reef complex, the most important marine hotspot of the southern Atlantic (the largest and richest coral reef system, Leão et al. 2003), has not yet been invaded by *Tubastraea* spp., but a recent study reported this invader on oil platforms south of the Abrolhos Bank (Costa et al. 2014). The recent introduction of this species on Brazilian coral reefs requires the implementation of immediate eradication or control protocols with long-term monitoring in order to better understand the effects on Brazilian reefs. In addition, given that the introduction of *Tubastraea* spp. in Brazil most likely occurred by ships and oil/gas platforms (Fenner 2001; De Paula and Creed 2004), there is a need for the appropriate rules to supervise maritime trade to reduce the flow of this invasive species to the region.

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