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Impact of invasive corals *Tubastraea* spp. on native coral recruitment

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ABSTRACT: Understanding how invasive species affect ecosystem processes of coral reefs can assist reef conservation. Recruitment is a key population parameter and an important consideration in the invasive potential of non-native species. We evaluated the effects of the invasive corals *Tubastraea tagusensis* and *T. coccinea* on native coral recruitment and adult populations within distinct habitats in a southwestern Atlantic reef off the Brazilian coast. We investigated the relationships adult–adult and adult–recruit between invasive and native corals. Sixty experimental plates (20 × 20 cm) were installed for 13 mo in 2 reef habitats (reef wall and reef top) along a gradient of *Tubastraea* invasion. Using zero-inflated negative binomial regression models, we found that native recruit density declined with increased cover of adult invasive corals. Additionally, native adult coral cover also declined with elevated invasive cover. No significant differences were observed for native recruits (density) between habitats (reef wall and reef top) along the gradient of invasion. However, differences of native and invasive adult coral cover were found between habitats, with native coral more often found on the reef top and invasive coral widely dominant on the reef wall. Furthermore, the relationship between invasive recruitment and adult cover was significant on the reef wall. These findings reveal that coral recruitment is generally inversely related to the cover of the invasive coral *Tubastraea*. Unless management actions are undertaken to slow the invasion of *Tubastraea*, it will likely continue to impact native corals and degrade the natural values of the reef ecosystems they support.

KEY WORDS: Non-native species · Biological invasion · Orange cup coral · Ecosystem processes · Larval settlement · Todos os Santos Bay · Brazil

INTRODUCTION

Biological invasions threaten biodiversity and ecosystem function (Strayer 2012) and can impact ecosystem integrity, goods, and services (Pejchar & Mooney 2009). Invasive species can change entire ecosystems by impacting ecological processes, especially when they differ from natives in resource acquisition or use, alter trophic pathways, or change disturbance regimes (Vitousek 1990). Understanding how invasive species affect ecosystem processes may be central to managing invasions, particularly in ecosystems subject to multiple stressors, such as coral reefs (Mumby & Steneck 2008).

Reef-building corals create complex physical structures that support high levels of associated biodiversity (Graham & Nash 2013, Rogers et al. 2014). Coral mortality has increased substantially in the last 3 decades due to a combination of stressors (e.g. global warming, acidification, pollution, diseases, and over-

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fishing), to which species invasion has been a key contributor to coral reef decline in some parts of the world (Hughes & Connell 1999, Gardner et al. 2003, Creed 2006, Bruno & Selig 2007, Miranda et al. 2016). Although it is fundamental to understanding the mechanisms behind declining coral reef functioning and resilience, the effects of reef invaders on coral recruitment have not been evaluated to the same extent as impacts from other stressors (Miranda et al. 2016).

Coral recruitment is a complex process involving a bipartite life history with pelagic larvae and benthic recruits (Ritson-Williams et al. 2009, Doropoulos et al. 2017). Following their settlement on benthic substrata, the survival and growth of coral larvae is often influenced by environmental factors (e.g. temperature and wave action), species-specific characteristics, predation, and the presence of other benthic organisms (Maida et al. 1995, Hughes & Connell 1999, Vermeij et al. 2006). It is well known that once benthic invaders (e.g. oysters and barnacles) have been established, occupying the primary substratum, they may influence recruitment patterns of native species by reducing the available space, intensifying competition, or increasing mortality of newly settled native recruits (Wilkie et al. 2013, Vye et al. 2017). However, the potential effects of hard coral invaders on native coral recruitment are virtually unknown.

In reef ecosystems, corals represent a group with unusual examples of invasive species (Coles & Eldredge 2002). However, azooxanthellate corals of the genus *Tubastraea,* originally from the Pacific, have successfully invaded Atlantic reefs (Sampaio et al. 2012), threatening the functioning of ecosystem processes (Miranda et al. 2016, Creed et al. 2017). In the southwestern Atlantic, the non-native sun corals *Tubastraea coccinea* and *T. tagusensis* were first reported in the 1980s. Since their establishment, sun corals have extended their distribution along the Brazilian coast on rocky and coral reefs, where they have dominated (e.g. 80–100% cover) the hard substratum in some reef areas (Creed et al. 2017). These invasive corals have increased mortality rates on some native coral species and altered the benthic community structure on Brazilian reefs (Creed 2006, Lages et al. 2011, dos Santos et al. 2013, Miranda et al. 2016). The success of *Tubastraea* spp. as an invasive species has, in part, been associated with competitive and reproductive advantages over native corals (Miranda et al. 2016).

Sun corals have a relatively high reproductive output compared to most native corals, including higher oocyte production, early reproductive age, short embryonic incubation time, and hermaphroditism (Szmant 1991, Pires et al. 1999, de Barros et al. 2003, Neves & Da Silveira 2003, Glynn et al. 2008, de Paula et al. 2014, Mizrahi et al. 2014a). They also have at least 2 reproductive peaks per year (Glynn et al. 2008) but can continuously reproduce throughout the year (de Paula et al. 2014). In contrast, native corals usually reproduce only once per year. Furthermore, *Tubastraea* spp. planulae can remain competent in the water column for 3 to 14 d (Glynn et al. 2008, de Paula et al. 2014, Mizrahi et al. 2014a) and can settle on a range of substrata and orientations but particularly on vertical surfaces (e.g. reef walls) (Creed & de Paula 2007, Mizrahi et al. 2014b, 2017, Miranda et al. 2016). Vertical surfaces in benthic habitats usually are darker than horizontal surfaces, which can favour the establishment of azooxanthellate species such as *Tubastraea* in Brazil (Creed & de Paula 2007, Miranda et al. 2016, Mizrahi et al. 2017). *Tubastraea* spp. can also increase the production of allelochemical substances in response to competition with coral recruits of different species (Koh & Sweatman 2000, Lages et al. 2012). Thus, understanding how sun corals and habitat affect coral recruitment patterns is important to the evaluation of invasion impacts on coral reefs and their associated ecosystem services and functions.

Here, a field experiment was carried out to evaluate whether the effects of sun coral invasions can be related to recruitment patterns of native coral species. Specifically, we tested the hypothesis that elevated invasive adult coral cover will reduce native and increase invasive recruitment density on experimental settlement plates. Additionally, we also tested the hypothesis that *Tubastraea* spp. recruitment will be higher on vertical (reef wall) than on horizontal (reef top) habitats.

MATERIALS AND METHODS

Study site

The field experiment ran from December 2015 to January 2017 (13 mo) at Cascos Reef (13° 07′ S, 38° 38′ W), a coral reef complex in the outer part of Todos os Santos Bay, Brazil (Fig. 1). The reefs consist of patches 11 to 13 m high and 1 to 100 m long, located around 20 m deep. These reefs have reef tops (horizontal surfaces; 11–13 m deep) and near-vertical walls (vertical surfaces; 12–20 m deep) (Miranda et al. 2016). The benthic communities of those reefs comprise algal turfs, crustose coralline algae, her-

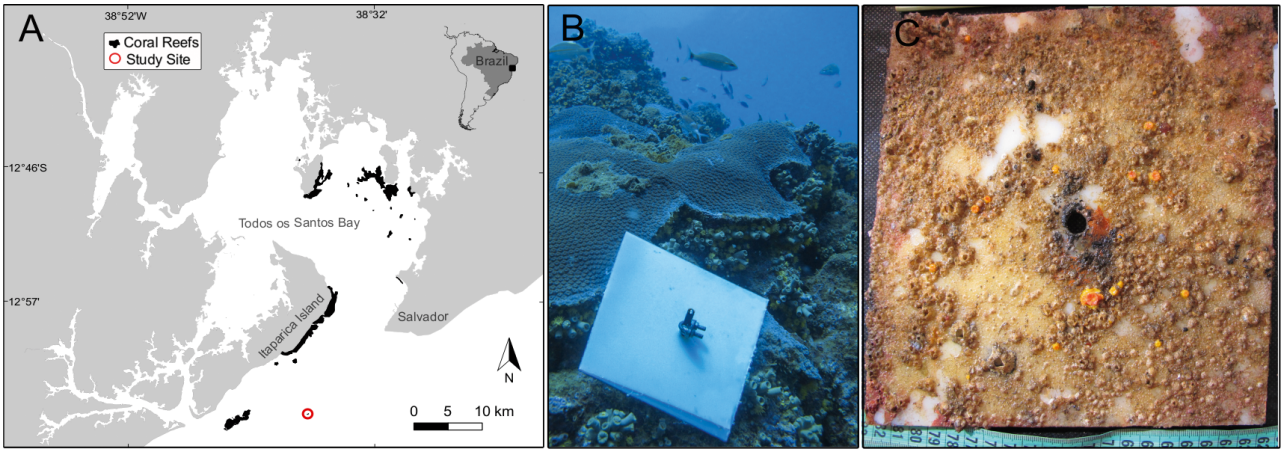

Fig. 1. Study region and recruitment experiment: (a) location of the study site Cascos Reef (indicated by red circle) at Todos os Santos Bay, Brazil; (b) experimental unit fixed in the study site; and (c) experimental plate showing *Tubastraea* spp. recruits (bright orange polyps) and other benthic organisms after 13 mo. Photos by Ricardo J. Miranda

matypic corals (*Montastraea cavernosa, Madracis decactis, Mussismilia hispida, Mussismilia leptophylla, Siderastraea stellata, Phyllangia americana, Astrangia* spp., *Meandrina braziliensis, Millepora alcicornis*), sponges, macroalgae, octocorals, ascidians, and bryozoans. Sun corals *Tubastraea tagusensis* and *T. coccinea* (hereafter denoted as *Tubastraea*) were distributed along the reef, with average cover ranging from 1 to 21% (Miranda et al. 2018).

Experimental design

To evaluate the effect of sun coral invasion and habitat on recruitment patterns, 60 settlement plates were attached to the reef substrate (n = 30 on the horizontal reef tops in 11–13 m depth and n = 30 on the vertical reef walls in 12–15 m depth). Settlement plates were randomly positioned along the study site, which had a gradient of *Tubastraea* cover that ranged between 1 and 21% in different reef zones (Miranda et al. 2018). Each settlement plate was composed of 2 polyethylene sheets (approximately 0.20 × 0.20 m) fixed with a steel screw (0.25 m long × 0.008 m thick) (Fig. 1b). Settlement plates were attached at least 5 m apart from each other within each habitat (reef top and reef wall).

At the end of the experiment, 15 plates were recovered from the reef wall and 11 plates were recovered from the reef top. The remaining plates could not be found despite extensive searching. The recovered plates were transported in seawater to the laboratory and stored in a freezer at −1°C for 24 h. Both sides of each plate were inspected under a stereomicroscope (Leica LED2500), and all recruits of native and invasive corals were quantified and identified to the lowest possible taxonomic level using available literature.

Adult coral cover patterns around settlement plates

To estimate the cover of the adult coral population on natural substrates, 4 photo-quadrats (0.25 × 0.25 m) were taken around 1 m of each settlement plate recovered (104 photos in total). This sampling method was developed to account for the gregarious nature of *Tubastraea* on southwestern Atlantic reefs (de Paula & Creed 2005, Mizrahi et al. 2014b). Photographs were taken using a digital camera (Canon G12) and analysed using the software Coral Point Count with Extensions (www.nova.edu/ocean/cpce/) (Kohler & Gill 2006). Adult coral cover was estimated using 20 randomly distributed points per photo-quadrat, totalling 80 points (4 photo-quadrats) around each settlement plate. Coral cover was represented by the total number of points under which it was observed, and these count data were used for statistical analysis.

Data analysis

To model the relationship between invasive coral cover and reef habitat type (reef wall and reef top) (predictor variables) on native recruit density, invasive recruit density, and native coral cover (response variables), we used zero-inflated negative binomial

(ZINB) regressions. This model was also used to test for relationships between native adult coral cover (predictor variable) on native recruit density (response variable). ZINB was ideal for this analysis because (1) the response variable was continuous and overdispersed (i.e. the variance exceeds the mean) due to the natural aggregated distribution of invasive corals (Creed & de Paula 2007, Mizrahi et al. 2014b, Miranda et al. 2016) and (2) coral settlement samples often have an excess of zeros due to stochasticity of coral recruitment. The ZINB model accounts for the excess of zeros in the sample data, by modelling zeros as a mixture arising from a dual process. The first process was from the low detection probability, due to a lack of availability of competent larvae and/or clumped or aggregated distribution patterns, or even a physical factor, and the second was from the predictor variables. The data in the binomial process are divided into a zero mass component, containing only zeros from the aggregated distribution, and a count component that may also contain zeros as well as other values, with the count component linked and modelled using an appropriate count variance structure (Zuur et al. 2009).

ZINB was compared using Chi-square for the null model. The interaction term of invasive coral cover with the covariate habitat (fixed factor, 2 levels: top and wall) was included because there is a marked difference in the orientation and light between habitats (top and wall). Thus, invasive coral cover and habitat could affect the overall outcome (i.e. the influence of invasive coral cover could be habitat dependent). All analyses were performed using R software (R Development Core Team 2008); the packages bbmle, MASS, ggplot2, pscl, and boot were used for the ZINB model.

RESULTS

Coral recruitment patterns

A total of 243 coral recruits were identified on the settlement plates after being deployed for 13 mo. Of these, 23 were from native corals (9.5%) and 220 were from the invasive *Tubastraea* (90.5%) (Table 1). Most settlement plates (62%, n = 16), however, did not have coral recruits. The genus and family of coral recruits identified on the settlement plates were *Tubastraea* spp., *Astrangia* spp., *Siderastraea* spp., and Faviidae.

Adult coral cover patterns

Overall, adult corals occupied 25.3 ± 2.8% (mean ± SE) of the natural substrate (Table 1). Native coral cover was 13.0 ± 3.7% of the total area surveyed and comprised *M. cavernosa* (9.3 ± 2.5%), *M. decactis* (2.1 ± 0.9%), *Siderastraea* spp. (1.2 ± 0.7%), and *M. hispida* (0.4 ± 0.2%). The average native coral cover was 8.1 ± 2.5% on the reef wall and 18.7 ± 5.3% at the reef top. In contrast, invasive coral cover represented 12.3 ± 2.6% of the total area surveyed, of which 11.7 ± 2.5% was *T. tagusensis* and 0.6 ± 0.3% was *T. coccinea*. In terms of the 2 habitats, *Tubastraea* occupied 13.4 ± 3.7% of the reef walls and 10.5 ± 3.4% of the reef top.

Effects of invasive adult cover on coral recruitment (native and invasive) and on native adult cover

Native recruit density and adult cover were negatively related to *Tubastraea* adult cover on the sur-

Table 1. Recruits (total individuals and density) and adult cover (points and percentage, mean ± SE) of coral species in different reef habitats (wall and top). (*) Recruits identified up to family level (Faviidae); (–) no data

Species	Recruits						Adult cover					
	Ind.			Density (ind. 0.04 m^{-2})			Points			%		
	Total	Wall	Top	Total	Wall	Top	Total	Wall	Top	Total	Wall	Top
Native corals	23	16	7	0.9	1.5	0.5	9.9 ± 2.9	6.4 ± 1.9	14.7 ± 4.2	13.0 ± 3.7	8.1 ± 2.5	18.7 ± 5.3
*Montastraea cavernosa**	5	4	1	0.2	0.4	0.1	7.2 ± 2.0	3.7 ± 1.6	12.0 ± 3.7	9.3 ± 2.5	4.7 ± 2.1	15.2 ± 4.6
Madracis decactis	0	0	0	0.0	0.0	0.0	1.4 ± 0.7	2.4 ± 1.1	0.0 ± 0.0	2.1 ± 0.9	3.1 ± 1.4	0.0 ± 0.0
Siderastraea spp.	4	4	0	0.2	0.4	0.0	1.0 ± 0.5	0.3 ± 0.2	1.9 ± 1.1	1.2 ± 0.7	0.3 ± 0.2	2.5 ± 1.4
Mussismilia hispida	0	0	0	0.0	0.0	0.0	0.3 ± 0.2	0.0 ± 0.0	0.8 ± 0.5	0.4 ± 0.2	0.0 ± 0.0	1.0 ± 0.6
Astrangia spp.	14	8	6	0.5	0.7	0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Invasive corals	220	134	86	8.5	12.2	5.7	9.6 ± 2.0	10.3 ± 2.8	8.5 ± 2.6	12.3 ± 2.6	13.4 ± 3.7	10.5 ± 3.4
Tubastraea tagusensis	–	–	–	–	–	–	9.1 ± 1.9	9.7 ± 2.7	8.3 ± 2.6	11.7 ± 2.5	12.6 ± 3.5	10.5 ± 3.3
Tubastraea coccinea	–	–	–	–	–	–	0.5 ± 0.2	0.6 ± 0.3	0.3 ± 0.2	0.6 ± 0.3	0.8 ± 0.4	0.4 ± 0.2
Scleractinian corals (total)	239	150	93	9.2	13.6	6.2	19.5 ± 2.2	16.7 ± 2.3	23.3 ± 3.8	25.3 ± 2.8	21.6 ± 3.0	29.3 ± 4.9

rounding reef (Table 2, Fig. 2). The effect of habitat was significant for the relationship between adult cover of native and invasive corals. However, no habitat effect was found for the relationship between native recruits and invasive adult cover, probably due to the low number of recruits in both habitats. There was no significant relationship between invasive recruits and adult cover, meaning that the model without an interaction (*Tubastraea* adult cover effect) did not explain more variance in the data than null models (no effect) (Table 2, Fig. 3a). However, the relationship between invasive recruit density and adult cover had a significant interaction with habitat, suggesting that the model with the interaction term (*Tubastraea* adult cover × habitat) better explains the patterns with adult cover than a model without an interaction term.

Effects of native adult cover on native coral recruitment

There was no significant relationship between native recruit density and adult cover. Similarly, there were no significant effects of habitat or no significant interactions (adult cover × habitat) associated with native coral recruitment (Table 2, Fig. 3b).

Table 2. Zero-inflated negative binomial regression model (count data) explaining the relationships between native coral recruits and *Tubastraea* spp. adults; native coral adults and *Tubastraea* spp. adults; *Tubastraea* spp. recruits and *Tubastraea* spp. adults; and native coral recruits and native coral adults. *p < 0.05

	Estimate	SE	*z*-value	Pr (>|*z*|)
Native coral recruits				
Intercept	1.42	0.49	2.85	0.004*
Tubastraea adult cover	−0.06	0.02	−2.20	0.027*
Habitat	−0.41	0.63	−0.64	0.518
Tubastraea adult cover × Habitat	0.05	0.04	1.15	0.247
Native coral adults				
Intercept	2.38	0.11	20.44	0.000*
Tubastraea adult cover	−0.06	0.01	−3.87	0.000*
Habitat	0.86	0.15	5.72	0.000*
Tubastraea adult cover × Habitat	0.00	0.01	0.32	0.745
Tubastraea spp. recruits				
Intercept	2.50	0.22	11.16	0.000*
Tubastraea adult cover	0.01	0.00	1.58	0.112
Habitat	0.48	0.28	1.67	0.094
Tubastraea adult cover × Habitat	−0.04	0.01	−3.24	0.001*
Native coral recruits				
Intercept	0.49	0.49	0.99	0.320
Native adult cover	−0.00	0.04	0.09	0.926
Habitat	0.05	0.92	0.05	0.955
Native adult cover × Habitat	0.01	0.05	0.34	0.729

DISCUSSION

The effects of sun coral invasion likely change native coral recruitment patterns. The numbers of *Tubastraea* recruits on settlement plates and adults on the natural substrate were greater than those of native corals on vertical walls. This supply-side advantage (sensu Lewin 1986) can contribute to *Tubastraea* dominance in adult cover over native coral species. The successful settlement and recruitment of *Tubastraea* reflects the high propagule pressure associated with its high reproductive output, such as high oocyte production and early reproduction age (de Paula et al. 2014). This is likely to be one of the reasons that *Tubastraea* has successfully expanded its range along the Brazilian coast (Creed & de Paula 2007, Riul et al. 2013, Creed et al. 2017). Additionally, the invasive coral's successful settlement could also be the result of asexually produced larvae (Ayre & Resing 1986, Capel et al. 2017). Overall, we show the potential for *Tubastraea* to change native coral population dynamics, and affirm previous suggestions of the impacts on ecological processes, such as recruitment of native species (Miranda et al. 2016, 2018).

The number of native recruits on experimental plates was low and negatively related to the adult cover of *Tubastraea*. Efficient competitive strategies of invasive corals could be increasing the mortality of recently settled native coral larvae. Following settlement on the substrate, juvenile *Tubastraea* can elongate their thin tissues, which increases colony survival when facing competition from other coral species (Vermeij 2005). *Tubastraea* adults also use elongated polyps and allelochemical products to impact competitors, as well as asexual reproductive strategies such as polyp bailout to survive and establish on the substrate (Creed 2006, dos Santos et al. 2013, Capel et al. 2014, Hennessey & Sammarco 2014, Sammarco et al. 2015, Miranda et al. 2016). Once colonies of *Tubastraea* are established, they spread out into the surrounding area, reducing the space available for settlement of native coral species (de Paula & Creed 2005, Mizrahi et al. 2014b). This was shown in the present study, as native corals tended not to settle in areas with high covers of adult *Tubastraea*. This may be a

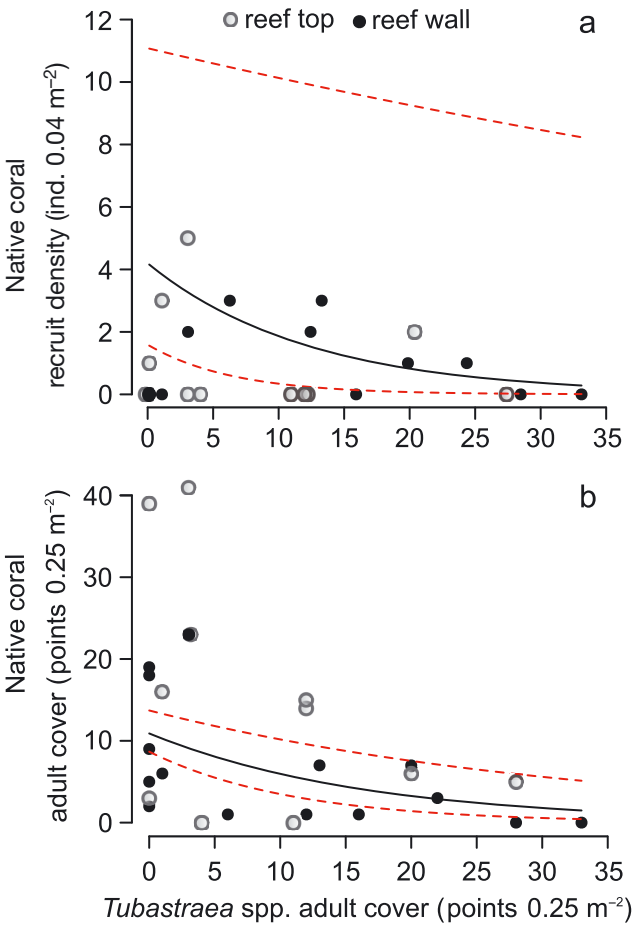

Fig. 2. Relationship between (a) native coral recruits (density) and *Tubastraea* spp. adult cover (no. of points) and (b) native coral adult cover (no. of points) and *Tubastraea* spp. adult cover (no. of points). Black circles represent experimental units on reef wall, and grey circles represent units on reef top. Black line represents curve of zero-inflated negative binomial regression model. Red dashed lines represent 95% confidence interval of the model

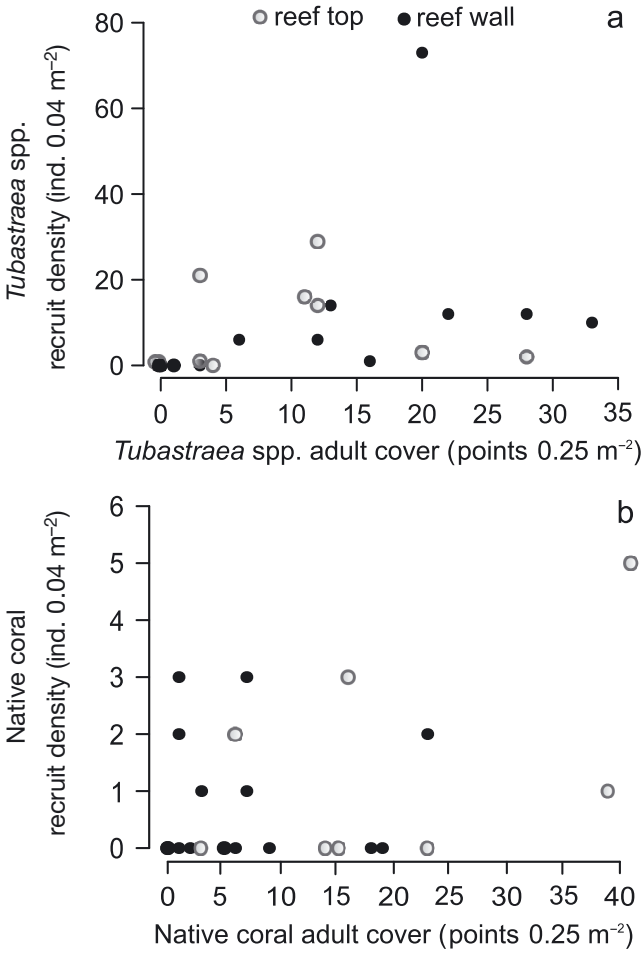

Fig. 3. Relationship between (a) *Tubastraea* spp. recruit density and adult cover and (b) native recruit density and native adult cover. Black circles represent experimental units on reef wall, and grey circles represent units on reef top

response to the toxic chemical compounds produced by *Tubastraea*, which might be impacting larval settlement (Koh & Sweatman 2000). Additionally, it is unlikely that the observed reduction in native recruitment was associated with native adult coral decline, in this case, since native recruit density showed no relationship with the native adult cover.

We have demonstrated that native adult coral cover was negatively related to *Tubastraea* adult coral cover. It is possible that these results are associated with sampling artefacts, considering the small scale of our study (see Fridley et al. 2004). On the other hand, these results also can be explained by the competitive dominance of invasive corals over the native species (dos Santos et al. 2013, Miranda et al. 2016). Endemic species, such as *Siderastraea stellata* and *Mussismilia hispida*, experience a significantly greater percentage of mortality when opposed to *Tubastraea tagusensis* and *T. coccinea* in competitive encounters (dos Santos et al. 2013, Miranda et al. 2016). By reducing the vitality of native adult corals through competition, *Tubastraea* could also impact the production of native coral larvae released during reproductive peaks. In the short term this could impact recruitment success of native coral, but over time this might drive reproductive failure of populations (Levitan & Petersen 1995).

The adult cover of *Tubastraea* was relatively high in companion to all native species, especially on the reef wall. The relative success of this azooxanthellate invader on the reef walls could be due to the environmental conditions in this habitat, such as lower light intensity and more available space because of the lower cover of native zooxanthellate competitors,

which are found more often on the well-lit reef tops. According to the niche theory, one species can dominate a community, leading to either resource partitioning between the species or elimination of the weaker competitor from the habitat (Colwell & Fuentes 1975, Diamond 1978). As such, common interpretations of this theory suggest that successful invasion requires the invader to occupy different niche space than most of the resident species or to just outcompete them (Fargione et al. 2003, MacDougall et al. 2009), which appears to be the case for *Tubastraea* on Brazilian reefs.

Overall, there was no significant relationship between the invasive recruits and adult cover. This is possibly due to the intense competitive conditions around adult colonies, which could increase juvenile mortality. These competitive conditions could lead *Tubastraea* to produce more larvae with the capacity to travel longer distances than larvae able to settle rapidly near the parental colony (Mizrahi et al. 2014a). However, the relationship between invasive recruit density and adult cover had a significant interaction with habitats. The characteristics of the different habitats assessed may be important for *Tubastraea* recruitment dynamics because there was a positive relationship between recruit density and cover of adults on reef walls but not on reef tops. *Tubastraea* larvae usually settle near the adult colonies, favouring self-recruitment and promoting gregarious spatial patterns, especially in habitats with negative and vertical orientation, such as reef walls (de Paula & Creed 2005, Glynn et al. 2008).

Given that coral recruitment is important to the maintenance and recovery of coral populations (Vermeij & Sandin 2008, Ritson-Williams et al. 2009, Bauman et al. 2015, Doropoulos et al. 2017), the effects of *Tubastraea* invasion on native recruits and adult corals are likely to impact the demography of native coral populations. Considering that coral reefs in the southwestern Atlantic are facing multiple local (e.g. pollution and sedimentation, see Dutra et al. 2006, Cruz et al. 2015) and global (e.g. ocean warming, see Leão et al. 2008, Hoegh-Guldberg & Bruno 2010, Miranda et al. 2013) stressors, the compounding impacts of the invasive *Tubastraea* to native coral recruitment will likely drive an overall change in the natural values and resilience of these reef ecosystems. Unlike the global challenge of climate change, it is possible to implement localised strategies (e.g. wrapping method, single or multiple manual removals, and low-salinity treatments) (Moreira et al. 2014, Mantelatto et al. 2015, de Paula et al. 2017) to reduce the spread and impact of *Tubastraea*. To be effective, however, these management interventions should be evidence based and assessed with robust coral reef monitoring.

Finally, we show that the invasion success of the coral *Tubastraea* can be related to the recruitment and population dynamics of corals in a southwestern Atlantic coral reef. Since the first observation of *Tubastraea* on the southwestern Atlantic coast over 30 yr ago, these invasive species have successfully colonised coral and rocky reefs along the Brazilian coast. These invaders are responsible for increasing mortality of native corals and altering ecological processes (Lages et al. 2011, dos Santos et al. 2013, Miranda et al. 2016, 2018, Creed et al. 2017). Our study highlights the importance of considering early life history processes when assessing the effects of invasive species on ecological functioning in coral reef ecosystems.

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