Impact of invasive Tubastraea spp. (Cnidaria: Anthozoa) on the growth of the space dominating tropical rocky-shore zoantharian Palythoa caribaeorum (Duchassaing and Michelotti, 1860)

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Abstract

Competition for space directly affects the structure of the sessile benthic communities on hard substrates. On the Brazilian coast Palythoa caribaeorum is an abundant shallow water mat-forming zoantharian and has fast growth rates. The objective of the present study was to assess the zoantharian’s biotic resistance by investigating changes in growth rates when interacting with the invasive sun corals Tubastraea tagusensis and T. coccinea on a tropical rocky shore in southeast Brazil. In the experimental design, eight blocks were arranged along the rocky shore where the growth treatment was applied with four different levels: empty, skeleton, live T. coccinea and live T. tagusensis. We opened up 10 × 10 cm² spaces in the P. caribaeorum mat into which treatments were transplanted with epoxy putty. Growth measures of the zoantharian were obtained using photographs. During the 184 day experiment, P. caribaeorum had the highest total growth rate in the empty treatment with an average value of 2.124 ± 0.189 mm.mo⁻¹; the treatment with the lowest total growth rate was T. coccinea with mean value of 1.104 ± 0.117 mm.mo⁻¹. The presence of T. coccinea influenced the growth rate of the zoantharian, unlike its congeneric T. tagusensis, which did not significantly influence the growth rate of P. caribaeorum. The negative interactions between P. caribaeorum and the invasive Tubastraea spp. were species specific in nature, and the native zoantharian exhibited quite some biotic resistance to the invasive species, especially to T. tagusensis.

This was due to competition, probably mediated both through physical and/or chemical mechanisms and preemptive occupation of space. Growth rates of P. caribaeorum were dependent on the degree of competitive interaction as well as seasonal differences in light and/or temperature which remain to be elucidated. From a management perspective, the manual removal of Tubastraea spp. will allow native species such as P. caribaeorum to recover space and thus foster ecosystem recovery.

Key words: benthos, competition, growth, interaction, space-limited, Tubastraea coccinea, Tubastraea tagusensis

Introduction

Invasive species interact with one another and with native species in ecological networks, which means they may induce a wide variety of direct and indirect changes (reviewed by Jackson 2015). Most of these are...
negative for the original receptor community. In sessile marine benthic communities on hard substrates in shallow tropical waters, space is usually at a premium. The pre-emption of space by the native community, along with predation and disease, may offer biotic resistance to invasion (Olyarnik et al. 2009). Substantial attention has been paid to the ongoing invasion by sun corals (genus *Tubastrea*) throughout the tropical Atlantic Ocean, Caribbean Sea and Gulf of Mexico (Miranda et al. 2016; Brito et al. 2017; Creed et al. 2017a, b). In Brazil, the first record of the species occurred in the 1980s, on oil and gas platforms in the Campos Basin, in the north of the state of Rio de Janeiro (Castro and Pires 2001; Creed et al. 2017a). Currently these species have been recorded on natural and artificial substrates at points along a large extension of the Brazilian coast, from 2.49° to 27.28° South (De Paula and Creed 2004; Creed et al. 2008; Mantelatto et al. 2011; Sampaio et al. 2012; Batista et al. 2017; Creed et al. 2017a).

Sparse knowledge is available regarding the associations and interactions of these sun corals with other species within their native range in the Pacific Ocean (Hermosillo-Nuñez et al. 2016; Ponti et al. 2016). In contrast there is more information regarding their associations and interactions as non-indigenous species (NIS) with native species outside their native range (De Paula 2007; Meurer et al. 2010; Santos et al. 2013; Hennessey and Sammarco 2014; Mantelatto and Creed 2014; Hoeksema and Hove 2017; Miranda et al. 2016, 2018a, b; Luz and Kitahara 2017; Skinner 2018; Vinagre et al. 2018). This is not surprising as it is desirable to identify the multiple biological effects of invasive species in order to understand their impact, predict their spread and propose management action. Novel associations and interactions have been reported between *Tubastrea coccinea* and *T. tagusensis* and other benthic (Luz and Kitahara 2017) and demersal (Miranda et al. 2018a) species on coral reefs (Miranda et al. 2016), on tropical rocky shores (De Paula 2007) and artificial substrates including vectors of introduction (Page et al. 2006). These invasive sun corals can occur up to 110 m and 43 m depth (*Tubastrea coccinea* and *T. tagusensis* respectively, Creed et al. 2017a). However, according to Paula and Creed (2005), they are more abundant from the littoral fringe and shallow subtidal (0–5 m) along the Brazilian coast.

*Palythoa caribaeorum* is very common, native sessile colonial anthozoan in shallow waters along the west coast of the Atlantic Ocean. It has a large geographical distribution because it is tolerant to a wide range of environmental conditions (reviewed by Durante et al. 2018). As it is a zooxanthellate it is a shallow water species, depending on sunlight for growth, that may form extensive continuous mats. According to Suchanek and Green (1981), *P. caribaeorum* acquires and dominates space using physical (e.g., overtopping) and chemical means. On Brazilian reefs *P. caribaeorum* mats are well developed and widespread (reviewed by Mendonça-Neto et al. 2008). It is an important taxon determining large-scale patterns in
shallow water benthic communities in the southwest Atlantic Ocean (Aued et al. 2018; Durante et al. 2018; Mantelatto et al. 2018) as well as the zonation of reef fishes (Mendonça-Neto et al. 2008). Within the Ilha Grande Bay, *P. caribaeorum* is one of the most abundant (areal cover) and frequently occurring shallow subtidal taxons [site frequency 59% (17/29 sites, Castro et al. 1999); site frequency 71% (30/42 sites, Pires et al. 2007); site frequency 100% (8/8 sites) and mean cover 47.21% (Lages et al. 2011)]. With the arrival and invasion of *Tubastrea* spp., we expect to find *Tubastrea-Palythoa* interactions throughout the region. The incorporation of new species can create novel communities with new ecosystem properties (Hobbs et al. 2009) causing a variety of local changes. Luz and Kitahara (2017) reported possible negative effects of *T. coccinea* and *T. tagusensis* on *P. caribaeorum*. However, in a manipulative experimental study Paula et al. (2017) found little evidence of the effect of sun corals on *P. caribaeorum*. Luz and Kitahara (2017) mention that *P. caribaeorum* is a community structuring species on Brazilian rocky shores and that its replacement with the invasive sun corals may change biodiversity and community dynamics of shallow waters. Where *Tubastrea* spp. are invading, *P. caribaeorum* is ubiquitous and a major space occupying species (mean frequency of occurrence = 100%; mean cover = 47.21%, compared to mean frequency 65% and cover of 1% for *Tubastrea* spp; Lages et al. 2011) so interactions are common (Luz and Kitahara 2017).

According to invasion theory (the biotic resistance hypothesis, or diversity-invasibility hypothesis; Jeschke 2014), invasibility will depend on biodiversity, at least at the local scale (Shea and Chesson 2002). In native communities dominant benthic space occupying species are usually competitively superior within their own community; theoretically, they also suppress biological diversity by depressing evenness (MacArthur and MacArthur 1961; Lloyd and Gjelardi 1964). In contrast, single resident species are occasionally important in excluding invaders (Olyarnik et al. 2009). Both *Tubastrea* spp. and *Palythoa caribaeorum* have physical and chemical attributes which make them formidable competitors for space. The mat forming *P. caribaeorum* preempts space very successfully so that space may only be taken if *Tubastrea* spp. is able to outcompete the native species in close contact. If this were to happen, we would expect depressed growth in *P. caribaeorum*, avoidance of overgrowth and facilitation of further expansion, which would result in substantial change in community structure and function (Davis et al. 2018). Alternatively, *P. caribaeorum* may stand off, continue to hold space or even outcompete the invasive coral by overgrowth. To investigate this we used the growth rates of *P. caribaeorum* together with experimental transplants of *Tubastrea* spp. in order to predict whether *P. caribaeorum* will lose space to the invasive corals over the long term.
Materials and methods

Study area

The study was conducted between August 2016 and January 2017 at Abraãozinho on Ilha Grande (23.133333°S; 44.151389°W, Datum WGS84), Ilha Grande Bay, Brazil. Abraãozinho is an inlet formed by a 500 m long sand beach with two adjacent rocky shores. The study site was no deeper than 6 m, easily accessible, protected from waves and had benthic communities dominated by Palythoa caribaeorum, algal turfs and T. coccinea and T. tagusensis (Lages et al. 2011 and personal observations). The water temperature at the study site can vary from 16.5–29 °C over the year, and extreme minimum temperatures can occur in summer due to periodic coastal upwelling; mean monthly minimum temperatures occur in August (22.4 °C) and October (23.4 °C) maximum in April (26.1 °C) (JCC unpublished data).

Natural encounters

To quantify general patterns in the natural encounters between T. coccinea × P. caribaeorum and T. tagusensis × P. caribaeorum, SCUBA dives were performed at sites covering 18 km within the study region (Ponta Longa 23.13725°S; 44.32144°W and Laje Branca 23.1368°S; 44.34496°W). During the dives, active searches were made for up to n = 60 individual encounters between the invasive and native species ≤ 7 cm distance from one another. We considered that colonies > 7 cm distant would not influence one another either by physical or chemical means. All encounters were photographed using a PowerShot G16 camera, Canon WP-DC52 in a waterproof case and a ruler graduated in centimeters for scale. Photo analysis was carried out to find the shortest linear distance between species encounters, the major space occupying taxon between (if present) and the aspect of the P. caribaeorum border nearest the Tubastraea spp. in terms of color (discolored or normal) and edge (tapering or not tapered, Figure 1) using the open software CPCe (Kohler and Gill 2006). For comparison we randomly selected n = 60 boarders of P. caribaeorum with no encounter with either Tubastraea spp.

Experimental design

To estimate the effects of the invasive corals on the growth rate on P. caribaeorum, experimental transplants were performed underwater using SCUBA. Individual live colonies (4–6 cm diameter) of both T. coccinea and T. tagusensis were collected locally with a hammer and chisel. Same-size clean skeletons of Tubastraea spp. were obtained from dead material from previous eradication actions. We cut and removed 10 × 10 cm squares from the central region of mats of P. caribaeorum. Eight blocks were arranged along the rocky shore where treatments were applied with four different levels (total n = 32): a) Em, open empty space in P. caribaeorum colony with
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Guilhem et al. (2020), Aquatic Invasions 15(1): 98–113, https://doi.org/10.3391/ai.2020.15.1.07

Figure 1. Experimental treatments (A) Empty, (B) Skeleton, (C) live *T. coccinea* and (D) live *T. tagusensis*, and observed features (E) Discoloring (arrow), (F) Border type (White arrow = non-tapered, Black arrow = tapered). Note a founding polyp of *Tubastraea* spp. circled in F recently recruited into the stand-off zone. Scale bars = 2 cm. Photos by Bruno P. Masi.

no transplant, the control; b) Skeleton, were a skeleton of *Tubastraea* spp. (haphazard mix of either species, or both, as colonies can fuse) was fixed into the center of the *P. caribaeorum* colony to evaluate the potential physical influence of a same volume but non-living colony; c) Tc, where a living colony of *T. coccinea* was transplanted into the center of the *P. caribaeorum* colony; d) Tt, where a living colony of *T. tagusensis* was transplanted into the center of *P. caribaeorum* (Figure 1A–D). Transplants were fixed to the rock using Tubolit MEM underwater epoxy putty. Additionally, discoloring at the encounters was also recorded (Figure 1E), and we made observations about the appearance of the edges of encounters between *P. caribaeorum* and *Tubastraea*, classifying them as tapered or non-tapered (Figure 1F). Photographs were taken of each experimental unit monthly with a PowerShot G16 camera and Canon WP-DC52 waterproof case. Photoquadrats were analyzed using CPCe software (Kohler and Gill 2006) to estimate the planar area and perimeter of the manipulated zone and the area occupied by *Tubastraea* spp. (or skeleton) over time. Each measurement was performed
three times and the mean used to increase confidence in the integrity of data generated by analytical methods. To determine the scaling in each image, a five-centimeter ruler was used.

Calculating the growth rate

To estimate a monthly growth rate, we used a formula of Silva et al. (2015) modified from Garrabou (1999), in which the difference of the planar area between two subsequent months (growth) was divided by the perimeter of the previous month (available free edge). At treatment levels where the skeleton or living colonies of Tubastraea are attached, the planar area occupied by them was subtracted from the total planar area. Total growth rate (used in comparisons between treatments) was calculated in the same way, using the values between the first and last months of the experiment. The values were expressed as mm.mo⁻¹.

\[
\text{Growth} = \frac{\text{planar area } t_2 - \text{planar area } t_1}{\text{perimeter } t_1} \times \frac{\text{days } t_1 - t_2}{d \text{ays}}
\]

Statistical analyses

Welch’s unequal variances t-test was used to compare the distances recorded in the encounters of T. coccinea × P. caribaeorum and T. tagusensis × P. caribaeorum. Pearson’s chi-squared test was used to determine whether discoloration or tapered (%) differed between Tubastraea species. With regard to the hypothesis testing, the assumptions were checked using Bartlett’s test of homogeneity of variances and the Shapiro-Wilk normality test. We tested differences in growth rates between treatment levels in the experiments using the nonparametric Kruskal-Wallis test, followed by post-hoc pairwise comparisons using Wilcoxon rank sum test. All analyses were carried out in R (R Core Team 2015).

Results

In natural encounters the two species of Tubastraea showed significantly different patterns of distance from P. caribaeorum (t = -9.2634, df = 91.515, p-value = < 0.001). Considering all encounters up to 7 cm distance, the mean distance of T. tagusensis from P. caribaeorum was 1.516 cm while it was 4.101 cm for T. coccinea encounters, so T. tagusensis was more often found closer to P. caribaeorum (Figure 2). Short benthic forms were able to occupy the space between encounters. Between T. coccinea and P. caribaeorum the main space occupying organisms were turf algae (53%), sponges (37%) and crustose coralline algae (10%); for T. tagusensis crustose coralline algae (40%) and sponges (35%) were most commonly found occupying this microhabitat. Rarely was the space unoccupied (8%). With regard to the edge of the colonies of Palythoa closest to Tubastraea spp., P. caribaeorum...
was discolored in 29% of encounters with *T. tagusensis* and 55% with *T. coccinea*, but no discoloring was found in *Palythoa* when not in proximity to the invaders. We accepted the null hypothesis and concluded that the two *Tubastrea* species exhibit a significantly different impact on the coloration of *P. caribaeorum* ($\chi^2 = 2.4384, \text{df} = 1, p\text{-value} = 0.1184$). With regard to the shape of the edge of the *P. caribaeorum* colony nearest the invasive encounter, with *T. coccinea* 33% were tapered and with *T. tagusensis* 62% were tapered. We accept the null hypothesis that the two *Tubastrea* species cause a significantly different edge shape of *P. caribaeorum* ($\chi^2 = 2.8155, \text{df} = 1, p\text{-value} = 0.09336$).

Over the 184 day experiment, the control plot of *P. caribaeorum* grew twice as quickly into empty space with an average value of (mean ± SE) $2.12 \pm 0.19 \text{ mm.mo}^{-1}$ as it did into space occupied by *T. coccinea*, the treatment with the lowest total growth rate of $1.09 \pm 0.12 \text{ mm.mo}^{-1}$ (Figure 3). There were significant differences (Kruskal-Wallis, $\chi^2 = 23.912, \text{df} = 3, p < 0.001$) between treatments, as growth rates into space occupied by *T. coccinea* were significantly lower than those into other treatments. Based on the post-hoc investigation, there was a statistically significant difference between treatments Em vs. Tc ($p < 0.0001$), Sk vs. Tc ($p < 0.01$) and Tc vs. Tt ($p < 0.0001$) (Figure 3). Regarding the temporal analysis of growth rates across all treatments, the highest mean value was recorded from November to December in the empty treatment ($8.1695 \pm 1.1877 \text{ mm.mo}^{-1}$), and the lowest average value was from September to October in the skeleton treatment (Figure 4). Overall mean negative values (retraction) were recorded for *T. coccinea* from August to September and for all treatments from October to November (Figure 4). The nonparametric Kruskal-Wallis test showed significant differences between treatments in August and September.

![Figure 2](image-url)
Figure 3. Box plot of growth rates (mm month$^{-1}$) of \textit{Palythoa caribaeorum} growing into empty space (Em), skeleton of \textit{Tubastraea} spp. (Sk), space occupied by living \textit{T. coccinea} (Tc) or \textit{T. tagusensis} (Tt) (n = 8 per treatment). Plots show the median (mid line), 25th and 75th quartiles (box edges), full range of the data (whiskers) and outliers (dots).

Figure 4. Monthly growth rates (mm month$^{-1}$) of \textit{Palythoa caribaeorum} between treatment levels (Em = empty, Sk = skeleton, Tc = \textit{Tubastraea coccinea} and Tt = \textit{T. tagusensis}) over each period (a) August to September, (b) September to October, (c) October to November, (d) November to December and (e) December to January. Boxplots show the median (mid line), 25th and 75th quartiles (box edges), full range of the data (whiskers) and outliers (dots).
Table 1. Results of nonparametric Kruskal-Wallis tests and Wilcoxon rank sum tests for all pairwise comparisons of the growth rate of *Palythoa caribaeorum* over monthly periods from August 2016 to January 2017 in the four treatments: Em = empty space; Sk = skeleton of *Tubastraea* spp.; Tc = living *T. coccinea*; Tt = living *T. tagusensis*.

| Period            | Kruskal-Wallis Chi-squared | df  | P       | Wilcoxon Pairwise comparisons | P       |
|-------------------|---------------------------|-----|---------|--------------------------------|---------|
| August to September | 18.434                    | 3   | < 0.001 | Em vs. Sk                      | < 0.05  |
|                   |                           |     |         | Em vs. Tc                      | < 0.0001|
|                   |                           |     |         | Em vs. Tt                      | ns      |
|                   |                           |     |         | Sk vs. Tc                      | ns      |
|                   |                           |     |         | Sk vs. Tt                      | ns      |
|                   |                           |     |         | Tc vs. Tt                      | < 0.01  |
| September to October | 2.3294                    | 3   | Ns      | Em vs. Sk                      | ns      |
|                   |                           |     |         | Em vs. Tc                      | ns      |
|                   |                           |     |         | Em vs. Tt                      | ns      |
|                   |                           |     |         | Sk vs. Tc                      | ns      |
|                   |                           |     |         | Sk vs. Tt                      | ns      |
|                   |                           |     |         | Tc vs. Tt                      | ns      |
| October to November | 5.1837                    | 3   | Ns      | Em vs. Sk                      | ns      |
|                   |                           |     |         | Em vs. Tc                      | ns      |
|                   |                           |     |         | Em vs. Tt                      | ns      |
|                   |                           |     |         | Sk vs. Tc                      | ns      |
|                   |                           |     |         | Sk vs. Tt                      | ns      |
|                   |                           |     |         | Tc vs. Tt                      | < 0.05  |
| November to December | 7.9231                    | 3   | < 0.05  | Em vs. Sk                      | ns      |
|                   |                           |     |         | Em vs. Tc                      | ns      |
|                   |                           |     |         | Em vs. Tt                      | < 0.05  |
|                   |                           |     |         | Sk vs. Tc                      | ns      |
|                   |                           |     |         | Sk vs. Tt                      | < 0.05  |
|                   |                           |     |         | Tc vs. Tt                      | < 0.01  |
| December to January | 22.336                    | 3   | < 0.0001| Em vs. Sk                      | < 0.01  |
|                   |                           |     |         | Em vs. Tc                      | < 0.01  |
|                   |                           |     |         | Em vs. Tt                      | ns      |
|                   |                           |     |         | Sk vs. Tc                      | ns      |
|                   |                           |     |         | Sk vs. Tt                      | < 0.01  |
|                   |                           |     |         | Tc vs. Tt                      | < 0.01  |

(Table 1, Figure 4a), November and December (Table 1, Figure 4a–d) and December and January (Table 1). Based on the post-hoc investigation using Wilcoxon rank sum test pairwise comparisons, there was a statistically significant difference between August and September, October and November, November and December and December and January (Table 1).

**Discussion**

Our results, taken as a whole, indicate that *T. coccinea* had a significant negative effect on the growth of *P. caribaeorum* at Ilha Grande, while the effects of the congener *T. tagusensis* on the zooantharian were less clear (Figure 5). The island Ilha Grande, which consists of tropical rock shores and shallow subtidal hard grounds, was the first known location to be invaded in Brazil (Silva et al. 2014; Creed et al. 2017a, b), after the introduction of *Tubastraea* spp. by oil platforms being serviced in the region in the late 1990s (Silva et al. 2014). The mean values of the growth rate of *P. caribaeorum* into the empty space observed in the present study (2.12 mm.mo⁻¹) were half of those recorded by Silva et al. (2015) in the
northeast of Brazil (4.5 mm mo⁻¹, in a coral reef ecosystem). As Palythoa is a zooxanthellate, this difference may be explained by local light (Tun et al. 1997) and/or seawater temperatures, as both will influence the metabolic processes behind growth (e.g. Coles and Jokiel 1977). The northeast region of Brazil is nearer to the equator and presents higher temperatures throughout the year when compared to the southeast where Ilha Grande Bay is situated. Ilha Grande Bay is also subjected to periodic seasonal upwelling in summer (Valentim et al. 1987) resulting in up to a 10 °C decrease in seawater temperature over a few hours.

Palythoa caribaeorum also presented different growth rates over time. Silva et al. (2015) found differences in the growth of P. caribaeorum between dry and rainy seasons in some specific situations; we also found interactions between environmental factors in this study. Silva et al. (2015) mentioned that the flux of tourists might result in the differences they observed, but we suggest here that temperature and/or light may be major factors that caused differences in the present study. Mean monthly minimum temperatures at the study site occur in August (22.4 °C) and October (23.4 °C) (JCC unpublished data), which is the time period at which the minimum growth rate was found. Kordas et al. (2011) mentioned how temperature as a physical phenomenon influenced the ecology of individuals by influencing the rates of biochemical reactions. According to Lord (2017), temperature influences competitive abilities through growth and reproduction rates. Growth in P. caribaeorum is a function of photosynthesis (P) and respiration (R) rates. There were points during the experiment in which
the P:R ratios became less than 1, perhaps due to low light levels or high temperatures, both of which can reduce P:R ratios. Further studies, such as those carried out by Tun et al. (1997) and Coles and Jokiel (1977), are needed to better explain the seasonal patterns we found.

We found highly significant evidence of negative effects of *T. coccinea* on *P. caribaeorum* and marginal evidence for an effect of *T. tagusensis*. These negative effects on *P. caribaeorum* include discoloring, increased distance from competitor and decreased growth rates (Figure 5). Tapering occurred when *P. caribaeorum* polyps at the edge of the colony projected both vertically and horizontally (Figure 1F) thus representing a margin actively extending horizontally. No tapering occurred when polyps were projected only vertically, forming a colony wall with no horizontal extension. The manifestation of less tapering, or the wall formation (see Figure 1F), was therefore interpreted to be due to the inhibition of *P. caribaeorum* growth in the direction of the invasive sun corals in natural encounters. The fact that less tapering occurred in proximity to *T. coccinea* in natural encounters was concordant with the experimental results.

Both invasive sun coral species produce chemicals, such as alkaloids (Maia et al. 2014a, b), which have antifouling properties and are deterrents to predation by fish (Lages et al. 2010a, b) and invertebrates (Lages et al. 2010a; Santos et al. 2013). *P. caribaeorum* is also considered an aggressive competitor due to the production of palytoxin (Moore and Scheuer 1971), but when in direct contact with sun corals, *P. caribaeorum* colonies recede or necrose (Luz and Kitahara 2017). The community occupying the microhabitat between the invasive species and zoantharian was also specific to each invasive species, so other native species in the receptor community may also react differently to the physical and/or chemical effects of each *Tubastrea* species.

Interestingly Lages et al. (2010a) reported that *T. tagusensis* had a stronger deterrent effect on fish than *T. coccinea* which would suggest greater biological activity by *T. tagusensis*, the opposite conclusion to that found for *P. caribaeorum* in the present study. Obviously predation deterrence and the competitor suppression found here are very different types of interaction. Most other previous comparative studies between the two invasive sun coral species have shown that, with regard to most biological and ecological features, they behave very similarly; so much so that the two species are often (~ 17%, see data in Creed et al. 2017b) found growing together in fused colonies (interspecies level chimera). Notwithstanding, when compared to *T. tagusensis*, *T. coccinea* is slightly more resistant to necrosis from freshwater (Moreira et al. 2014) and vinegar (Creed et al. 2018), genetically more diverse (Capel et al. 2017) and proportionally more abundant on artificial substrates than on natural ones (Mangelli and Creed 2012). In contrast *T. tagusensis* is about twice as abundant as *T. coccinea* throughout the studied region and expands its range more quickly. Silva et
al. (2014) attributed these last attributes to the fact that both species are relatively reproductively precocious; the larvae of *T. tagusensis* are viable for up to 18 days, contrasting to 14 days in *T. coccinea* (De Paula 2007). *Tubastraea tagusensis* is also more resistant to control by wrapping (a management method of smothering) (Mantelatto et al. 2015). Therefore it may not be surprising that the congeners had somewhat different effects on *P. caribaeorum*.

In the current study, only one invasive colony (of *T. tagusensis*, personal observation) was actually overgrown by the native zoantharian. *P. caribaeorum* is a fast-growing species (Rabelo et al. 2013; Silva et al. 2015), which allows it to dominate the available hard substrata and impede the settlement and recruitment of non-native species. As such *P. caribaeorum* is recognized as an aggressive competitor of neighboring benthos (reviewed by Mendonça-Neto et al. 2008). *P. caribaeorum* has been documented as overgrowing a number of other scleractinian corals in studies undertaken at numerous locations (reviewed by Rabelo et al. 2013). However with the evidence here (predominance of non-tapered edge, discoloration and reduced growth rate in contact with *T. coccinea*), we would predict that if the experiments were run longer the other colonies of *T. tagusensis* would also have been overgrown but there would have been a stand-off with *T. coccinea*.

Although not investigated here, it is important to highlight that the mat-forming nature of *P. caribaeorum* presumably pre-empts space, not only for adult colonies of the invasive corals around the edges of colonies and also hinders larval settlement to the substratum. These two processes provide *P. caribaeorum* with more substantial biotic resistance to *Tubastraea* spp. than many other native species or functional groups. Despite this we would expect the gradual retraction of *P. caribaeorum* over time due to negative competitive interactions with *Tubastraea* spp. Inadvertently, we registered a process of enhancement, due to both the slow lateral grow of adult invasive corals at the border, pushing back the native, and the recruitment of the corals into the stand-off zone between *P. caribaeorum* and *Tubastraea* spp. (see detail in Figure 1F). A similar positive feedback mechanism was found in interactions between *Tubastraea* spp. and the native coral *Mussismila hispida* (Verrill, 1902) in the same region (Creed 2006).

Comparing a potential invader’s performance to that of natives in a community at risk of invasion increases our ability to predict whether that particular exotic will successfully invade the community (Olyarnik et al. 2009). Here we have added to the understanding of how the biological invasion of *Tubastraea* spp. will steadily advance over the next decades. The negative interactions between *Palythoa caribaeorum* and the invasive *Tubastraea* spp. were species specific in nature, and the native zooantharian exhibited quite some biotic resistance to the invasive species, especially to *T. tagusensis*. This was due to competition, probably mediated both...
through physical and/or chemical mechanisms and the preemptive occupation of space. Growth rates of *P. caribaeorum* were dependent on the degree of competitive interaction as well as seasonal differences in light and/or temperature which remain to be elucidated.

**Acknowledgements**

We thank the financial support of Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro – FAPERJ – through research support programs Pensa Rio (E-26/010.003031/2014) and Cientista de Nosso Estado (E-26/201.286/2014) (JCC) and postdoctoral support program PAPD (E-26/202.097/2015, E-26/202.075/2015) for BPM. This article is no. 32 from the Projeto Coral-Sol. We thank Drs. Alejandro Bortolus, Amy Fowler and the anonymous reviewers for their useful comments.

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