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Do invasive corals alter coral reef processes? An empirical approach evaluating reef fish trophic interactions

Ricardo J. Miranda[a,b,*], José de Anchieta C.C. Nunes[a], Eduardo Mariano-Neto[c], James Z. Sippo[b], Francisco Barros[a]

[a] Laboratório de Ecologia Bentônica, Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Federal da Bahia, Salvador, BA, CEP 40170-115, Brazil
[b] National Marine Science Centre, Southern Cross University, Coffs Harbour, NSW 2450, Australia
[c] Laboratório de Estudos de Vegetação, Instituto de Biologia, Universidade Federal da Bahia, Salvador, BA, CEP 40170-290, Brazil

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ABSTRACT

Understanding how invasive species affect key ecological interactions and ecosystem processes is imperative for the management of invasions. We evaluated the effects of invasive corals (*Tubastraea* spp.) on fish trophic interactions in an Atlantic coral reef. Remote underwater video cameras were used to examine fish foraging activity (bite rates and food preferences) on invasive cover levels. Using a model selection approach, we found that fish feeding rates declined with increased invasive cover. For Roving Herbivores (RH) and Sessile Invertivores (SI), an abrupt reduction of fish feeding rates corresponded with higher invasive cover, while feeding rates of Territorial Herbivores (TH) and Mobile Invertivores (MI) decreased linearly with cover increase. Additionally, some fish trophic groups, such as RH, SI and Omnivores (OM), had lower densities in reef sections with high invasive cover. These findings demonstrate that invasive corals negatively impact fish-benthic interactions, and could potentially alter existing trophic relationships in reef ecosystems.

1. Introduction

Biological invasions can influence the structure and function of natural systems (Strayer, 2012). Ecosystem impacts of invasive species can be associated with changes to processes altering the pools, fluxes, and mass balance of materials and energy (Ehrenfeld, 2010; Simberloff, 2011). For instance, invasive species can change ecosystem processes through their resource acquisition, by altering disturbance regimes, or by altering trophic structure and/or food webs of the invaded system (Vitousek, 1990). These effects may have severe consequences for human well-being through the loss of goods and services (Pejchar and Mooney, 2009). Understanding how invasive species affect key ecosystem processes and ecological interactions is central to managing invasions and is one of the main challenges for the conservation of ecologically diverse ecosystems, such as coral reefs (Albins and Hixon, 2008; Coles and Eldredge, 2002; Mumby and Steneck, 2008).

In coral reefs, the effects of invasive species on ecological interactions remain poorly understood. Predator-prey interactions which influence community structure and ecological processes can be strongly modified by biological invasions (Grosholz et al., 2000; Rilov, 2009). Two contrasting hypotheses have been proposed to explain the mechanisms and effects of invasive species on predator-prey interactions (Mitchell et al., 2006). The enemy release hypothesis (ERH) predicts that introduced species experience less regulation from natural predators than natives, resulting in an increase in distribution and abundance (Keane and Crawley, 2002). This hypothesis has been often proposed to explain invasive success (Keane and Crawley, 2002). The biotic resistance hypothesis (BRH) can be affected by native consumers that could control the abundance of the invader by actively predate on it, which limits their invasiveness (Elton, 1958). Therefore, fundamental to alien invasion theory, investigating the interactions between native and introduced species is imperative to understanding how invasive species alter trophic relationships and ecological processes.

ERH and BRH have been used to examine effects of species invasions in different ecosystems (Parker and Hay, 2005). However, the consequences of benthic invaders on fish-benthos interactions on coral reefs remain relatively understudied. Fish are commonly classified into functional trophic groups by their foraging activities on the benthos, which helps to understand their roles in the reef ecosystem (Bellwood et al., 2006; Hoey and Bellwood, 2009; Longo et al., 2014). Studies of invasions on reef ecosystems show that native algae can be preferentially consumed by fishes over invasive algae, thereby facilitating

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[*] Corresponding author. Laboratório de Ecologia Bentônica, Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Federal da Bahia, Salvador, BA, CEP 40170-115, Brazil.

E-mail address: ricardojdemiranda@gmail.com (R.J. Miranda).

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invasion success and contributing to changes in benthic cover and fish grazing activity (Stimson et al., 2001; Woo et al., 2000). Fish-benthos interaction is a critical ecosystem process, regulating the cycling of materials and energy fluxes on coral reefs (Bellwood et al., 2004; Mumby, 2006). A shift in benthic composition is shown to lead to changes in functional roles performed by fishes (Nash et al., 2016), and may thereby lead to flow on effects within reef ecosystems.

The invasion of the alien Sun corals (*Tubastraea coccinea* and *T. tagusensis*) in the Southwestern Atlantic is well documented (Creed et al., 2017) and represents a valuable opportunity to improve knowledge of alien invasion theory. Natives of the Indian Ocean, *Tubastraea* spp. (Scleractinia, Dendrophylliidae) have successfully invaded Caribbean, Western Atlantic, Gulf of Mexico and Brazilian reefs (Creed et al., 2017). The biological characteristics of *Tubastraea* spp. are typical of opportunistic species, demonstrating high fecundity (de Paula et al., 2014; Glynn et al., 2008), rapid growth, efficient recruitment (Creed and de Paula, 2007), competitive aggressiveness (Creed, 2006; Miranda et al., 2016b; Santos et al., 2013) and survival strategies to escape adverse environmental conditions (Vermeij, 2005). In Brazilian reefs, evidence suggests that *Tubastraea* spp. have low palatability to generalist fish predators due to the production of allelochemicals (Lages et al., 2010a; Moreira and Creed, 2012). Generally, these benthic chemical cues can strongly influence the foraging strategies, feeding choices and habitat use of fishes (Choat and Clements, 1998; Hay, 2009, 1996). This suggests that reef fishes may avoid patches dominated by invasive corals, thereby modifying fish-benthic interactions on the reef.

Sun corals occupy rocky shores and tropical coral reefs as well as artificial substrates (Creed et al., 2017). In Brazil, Sun corals were first reported on oil platforms and rocky shores in the southeast (Castro and Pires, 2001; de Paula and Creed, 2004; Ferreira, 2003) where they became the most abundant taxa on substrate to the detriment of algae and other invertebrates (Lages et al., 2011). Miranda et al. (2016b) described negative impacts of the Sun coral on native reef coral assemblages, where *T. tagusensis* caused an increase in tissue necrosis on some native coral species. However, there are no evaluations of the potential impacts of Sun corals to ecosystem processes and functioning in tropical reefs.

This study evaluates the influence of the alien Sun coral (*Tubastraea* spp.) invasion on reef fish-benthic interactions, examining relationships between the feeding rates of fish trophic groups and invasive coral cover. We hypothesize that invading Sun corals will be avoided by native fish species in accordance with ERH, thereby negatively influencing fish feeding rates in areas with elevated invasive cover. We also investigate whether the effects of the invading corals can change to fish feeding preferences and fish community structure.

2. Material & methods

2.1. Study area

The study was conducted at Cascos Reef (CR, 13°07′S, 38°38′W), a reef patch complex 11–13 m in height and 1–100 m in length, located at depths of approximately 21 m in the outer part of Todos os Santos Bay (TSB), a region on the east coast of Brazil (Fig. 1). This region has relatively high endemism and diversity of species in the South Atlantic Ocean, and is considered a priority for conservation (Cruz et al., 2015; Leão et al., 2003; Vila-Nova et al., 2014). *Tubastraea tagusensis* and *T. coccinea* has been reported in TSB since 2008 and actually they are broadly distributed (Miranda et al., 2016a, 2016b; Sampaio et al., 2012, Fig. 1a). In CR these species were firstly reported in 2011. CR was the first coral reef site where these species were documented in the Southwestern Atlantic. In March 2013, *Tubastraea* spp. cover in CR was approximately 9% and was concentrated in a relatively small area located on south section of reef (Miranda et al., 2016b, Fig. 1b). The samples of the present study were collected on the 29th of February and the 2nd of March 2016, three years after the first assessment was conducted.

2.2. Benthic community structure

To sample benthic community (mean % cover) 26 plots of 1 m^2 (using quadrats) were distributed randomly along three reef sections at CR: High ($n = 9$), Medium ($n = 8$ one sample lost during field work) and Low ($n = 9$) (Fig. 1b). These reef sections were spatially selected based on the chronology of invasion, Sun coral cover mean (%) on substrate and similarity in size. Each plot was sampled independently by 5 photo quadrats (25 × 25 cm) using a digital camera (CANON G12, USA). Photographs were analyzed using the software Coral Point Count with Excel Extensions Software (CPCe) (http://www.nova.edu/ocean/cpce/) (Kohler and Gill, 2006), where the mean percentage of benthic cover was estimated through 20 randomly distributed points per photo.

2.3. Foraging activity: bite rates and selectivity

Remote underwater video was used to record fish foraging activity (i.e. bites rates and food selection) in the same 26 reef plots of 1 m^2 where photo quadrats were taken (Video S1). Video frames were taken by remote cameras (GOPRO Hero 3 + Black Edition, USA) on 25-cm length stems placed on the substratum after photo quadrat recordings (Fig. 1c). We used a 1 m^2 quadrat to delimit the recorded plot which was removed after 1 min. Each plot was recorded for 30 min and the central 25 min of each video was analyzed. All videos were recorded between 9:00 and 15:00 h in two days (29th February and 2nd March 2016). All fish species that foraged on the benthos were identified and the number of bites were counted for each fish specimen on the different benthic categories (*Tubastraea* spp. Turf Algae, Crustose Coralline Algae, Calcareous Articulated Algae, Fleshy Algae, Native Hermatypic Corals, and Sponge). A total of 650 min was analyzed.

Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2018.03.013.

The fish were classified into five trophic groups based on previously described trophic categories and feeding behaviors, Roving Herbivores (RH), Territorial Herbivores (TH), Mobile Invertivores (MI), Sessile Invertivores (SI) and Omnivores (OM) (Ferreira et al., 2004; Halpern and Floeter, 2008; Longo et al., 2014). Several authors have highlighted positive aspects that functional approaches can provide to better understand ecosystem functioning (e.g. Bellwood et al., 2006; Hoey and Bellwood, 2009; Longo et al., 2014).

RH, including Scarids (parrotfish), Acanthurids and Kyphosids, feed primarily on turf algae and detritus, but some species also feed on scleractinian corals (Ferreira et al., 2004; Francini-Filho et al., 2010; Halpern and Floeter, 2008). They influence the biomass and productivity of algae and the structure of coral assemblages (Bonaldo et al., 2014) and play important roles in reef bioerosion, production, reworking, transport of sediment and the facilitation of coral recruitment (Bellwood, 1996; Bonaldo et al., 2014; Bruggemann et al., 1996; Goatley and Bellwood, 2012). TH, such as pomacentrids, graze on farmed turf algae and have an important role in structuring algae community (Ceccarelli, 2007). MI, such as labrids, and SI, such as tetraodontids, transfer energy from first consumers to higher trophic levels through predation. This energy transfer is mainly through small mobile microcrustaceans and sessile invertebrates, such as corals, sponges and octocorals (Jones et al., 1991; Kramer et al., 2015). OM forage on a wide variety of items and contribute broadly to the trophic web.

2.4. Fish community structure

We conducted visual census on 10 × 2 m transects (20 m^2), whereby individual fish were counted and each specimen was identified. The density of each species was obtained for each transect. Transects were located independently at least 5 m apart in the same areas as photo and video samplings along the same three reef sections. A total of 30

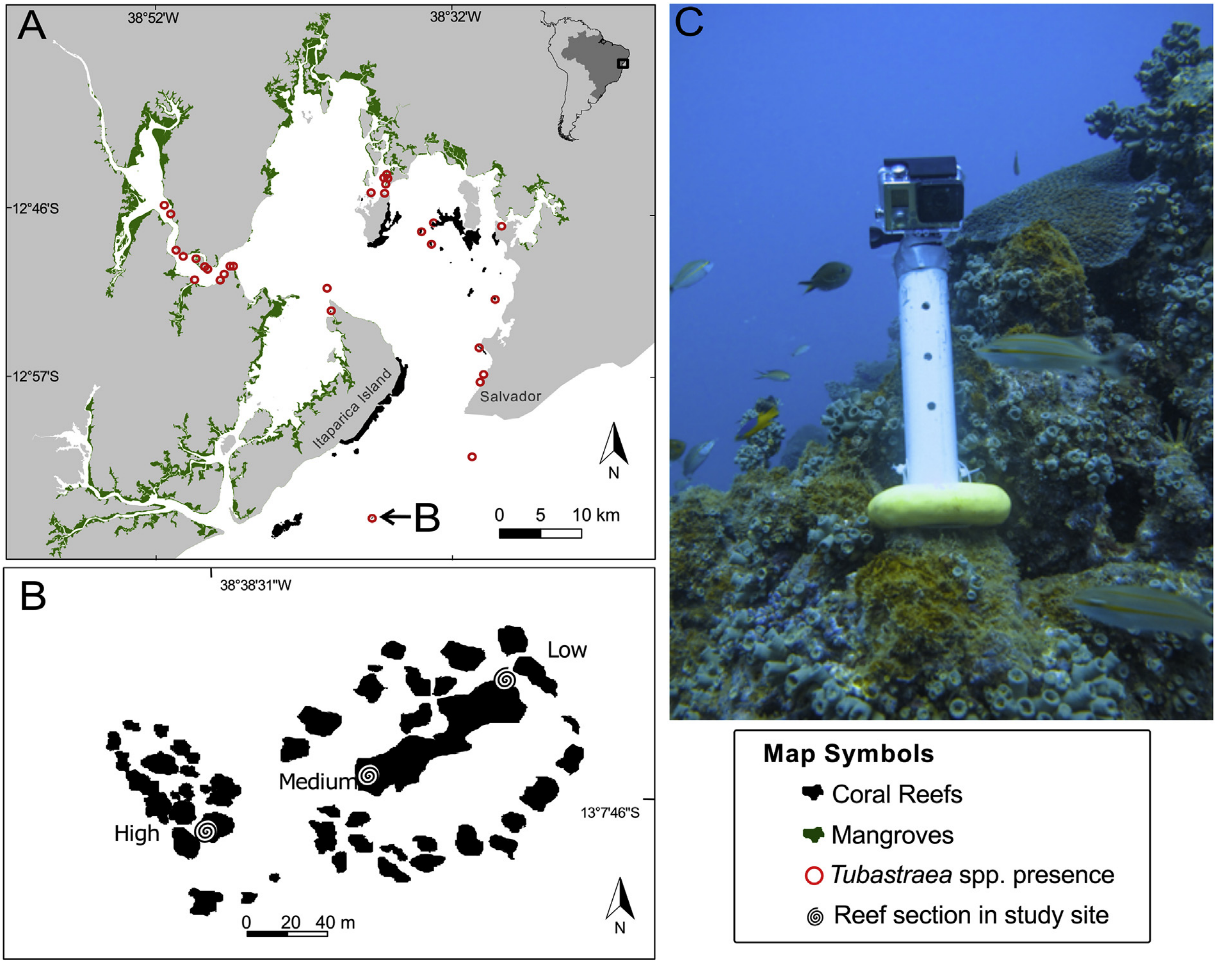

Fig. 1. Map of study site and sample method of fish foraging activities: a) location of Cascos Reef at Todos os Santos Bay, Southwestern Atlantic, b) Cascos Reef and reef sections sampled based on *Tubastraea* spp. cover levels (High, Medium and Low), c) set up of the remote underwater camera.

transects were conducted: 10 replicates at the High section, 10 at the Medium section, and 10 at the Low section.

2.5. Data analysis

The invasive cover mean was calculated for each reef section and differences were tested using Kruskal-Wallis and post hoc Tukey test. The biological characteristics of the two *Tubastraea* species (*T. tagusensis* and *T. coccinea*) are very similar (e.g. morphology, ahermatypic and allelochemical production) in comparison to the native coral species of the South Atlantic (de Paula and Creed, 2004; Lages et al., 2010a, 2010b). For this reason we analyzed the combined effect of *Tubastraea* spp. percent cover on native fishes, which we have considered as one single coral invasion phenomenon. A model selection approach was used to evaluate the relationship between invasive coral cover and fish bite rates. Three models were assessed: null, linear and non-linear negative. The null model was used to test the absence of effects, whereby a linear model represented the constant effect of invasive coral cover on the fish bite rates. A non-linear negative exponential model was used to investigate a potential more intensive response of the effect on fish bites (Pinheiro and Bates, 2000). The model selection approach was also used to analyze the relationship between invasive cover and algae turf cover and to assess a potential mechanism of competitive interference on an important food consumed by reef fishes. The models assessed were: null, linearized, and quadratic.

We used the Akaike Information Criterion corrected to small samples (AICc) and Akaike information weights (AICc weights) to select the most plausible model (Anderson, 2008). The best fitting model had the lowest AIC value, and models with up to 2 values of ΔAICs were considered equiprobable. To determine the best model for our data we used residual analyses and parsimony. Models that did not present convergence during parameter estimates were excluded from the model selection procedure.

The Ivlev's electivity index was used to verify fish preference or rejection of each food type on each reef section. The electivity index was calculated as $Ei = (ri - ni)(ri + ni)^{-1}$ in which Ei is the electivity measure for the i food type; ri is the percentage of bites of each species on the i food type and ni is the percentage of the i food type in the studied reef sections. Electivity index varies from +1 to −1, where values close to +1 indicate higher preferences and values close to −1 indicate lesser preference or avoidance (Krebs, 1989).

To test for differences between fish community structure between the reef sections, data of fish composition and density were analyzed by permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) based on Bray–Curtis dissimilarities using 10000 random permutations. We also used Generalized Linear Models (GLMs) with poisson distribution to test for potential differences in fish total density (community) and fish density of each individual trophic group between reef sections. A categorical approach was used to represent results of fish density by reef sections considering differences in size of sampled areas between transects ($20\,m^2$) and photo quadrat ($1\,m^2$) recordings.

All analyses were performed using the R software (R Development

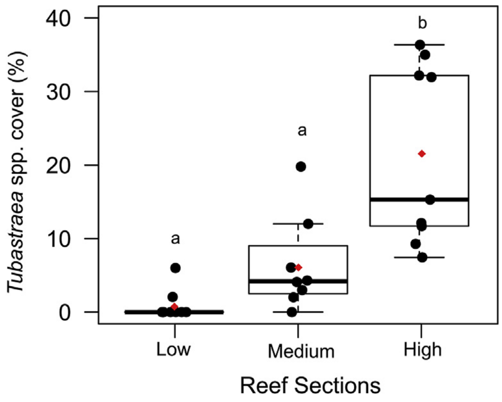

Fig. 2. *Tubastraea* spp. cover (%) in three reef sections (Low, Medium and High) at Cascos Reef. Box-plot represents the median, Q_1, Q_3, minimum and maximum values; red diamonds represent mean values; each point represents a quadrat plot of 1 m^2. Letters denote significant differences. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Core Team, www.r-project.org): the package *bbmle* and *nlme* were used for model selection, the package *vegan* was used for PERMANOVA and GLM.

3. Results

3.1. Benthic community structure

Benthic cover at CR was composed mainly of Turf (44%) and Crustose Coralline (27%) Algae, Native Hermatypic Corals (13%, e.g. *Montastraea cavernosa* 9%, *Siderastrea stellata* 2%, *Madracis decactis* 1%, *Mussismilia hispida* 1%), Fleshy Algae (7%), Sponges (0.3%), and Calcareous Articulated Algae (0.2%), as well as Invasive Corals (10%, *T. tagusensis* 9.1% and *T. coccinea* 0.6%) (Table S1). Sun corals were found along all reef sections of CR but the cover pattern varied significantly from 21% at High, to 6% and 1% at Medium and Low sections, respectively (Kruskal-Wallis, chi-squared = 17.708, df = 2, p = 0.0001; post hoc Tukey test High ≠ Medium, High ≠ Low, Medium ≈ Low) (Fig. 2). Turf algae cover showed no relationship with the percent cover of invasive corals (best fit model: null, see Fig. S1). Turf algae was well distributed and cover was relatively high along all reef sections, even in areas with High invasive coral cover (Table S1).

3.2. Fish bite rates

RH (*Scarus zelindae, Acanthurus bahianus, Sparisoma frondosum, Acanthurus chirurgus, Sparisoma amplum* and *Sparisoma axillare*) and TH (*Stegastes fuscus*) were the most representative trophic groups, contributing to 41% and 40% of the total fish bites, respectively. Fish groups representing smaller percentages of the total community include: MI 9% (*Bodianus rufus, Halichoeres brasiliensis, Halichoeres poeyi* and *Haemulon aurolineatum*), SI 5% (*Cantherhines pullus, Holocanthus tricolor* and *Cantherhines macrocerus*), OM 3% (*Abudefduf saxatilis, Cantigaster figueredoi* and *Pomacanthus paru*) and others 1% (*Chromis multilineata* and *Amblycirrhitus pinos*).

Overall, invasive cover was negatively associated with fish bite rates (Table 1, Fig. 3). Invasive cover increase led to an abrupt reduction on total bite rates, mainly for RH and SI (best fit model: negative exponential) (Fig. 3). The bite rates of TH and MI decreased linearly with invasive cover increase (best fit model: linear). The frequency of OM bites rates was very low (Fig. 3) and was excluded from the model selection procedure.

Table 1
Models explaining the relationship between invasive coral cover and bite rates of the fish trophic groups. The most parsimonious models are shown in the first line of each group.

Trophic group	Model	ΔAICc	Df	Weight
Total Fish	Exponential	0.0	3	1
	Linear	207.8	2	< 0.001
	Null	484.6	1	< 0.001
Roving Herbivores	Exponential	0.0	3	1
	Null	855.6	1	< 0.001
Territorial Herbivores	Linear	0.0	2	0.52
	Exponential	0.2	3	0.48
	Null	13.0	1	< 0.001
Sessile Invertivores	Exponential	0.0	3	0.9
	Null	9.2	1	0.01
Mobile Invertivores	Linear	0.0	2	0.7
	Exponential	2.9	3	0.1
	Null	3.3	1	0.1

3.3. Food selectivity

Turf algae was the most frequently grazed item by all fish trophic groups (93.2% of all bites) (Fig. S2). Much less frequently chosen items were native corals (4.1%), fleshy algae (1.1%), invasive coral *Tubastraea tagusensis* (1.1%), and crustose coralline algae (0.5%). *T. coccinea* was not bitten by any reef fish. All fish trophic groups showed a preference for foraging on turf algae while *T. tagusensis* was largely avoided (Fig. 4; Video S1). RH avoided foraging over turf algae on reef plots with an elevate percentage of invasive cover (≥10%). Two trophic groups (TH and MI) bit over *T. tagusensis*; however in general, the bite number on *T. tagusensis* was relatively low and the electivity index was closer to −1 on plots with ≥10% of invasive coral cover (Fig. 4).

3.4. Fish community structure

MI were the dominant trophic group, accounting for 79.0% of all fish density, followed by RH (8.7%), OM (6.7%), SI (2.9%) and TH (2.7%). Overall, fish community structure was not significantly different along the three reef sections (PERMANOVA, $p > 0.05$; Table S2). However, fish total density and density of RH, SI, MI and OM were significantly different between reef sections (GLMs, $p < 0.05$; Fig. 5 and Table S3). The groups RH, SI and OM had lowest densities (median) in High or Medium sections where invasive coral cover was higher. In contrast, the MI group had higher density in the High reef section (median) where invasive cover was higher (GLMs, $p < 0.05$; Fig. 5 and Table S3).

4. Discussion

4.1. Invasive coral effects on fish foraging activity

Sun coral invasions are influencing fish community foraging activities at studied site. Fish feeding rates had an exponential decrease when invasive cover increased, especially RH which was the group with the highest contribution of bite rates on substrate. Furthermore, no evidence of tissue damage on the invasive coral by fish predation was found on Sun corals and most fish avoided them when foraging. These findings can be interpreted as evidence of the Enemy Release Hypothesis, where native species are unable to regulate the alien coral invasion (Keane and Crawley, 2002). The production of allelochemicals in *Tubastraea* colony tissue and their low palatability to generalist fish predators are important mechanisms that explain these results (Lages et al., 2010a; Moreira and Creed, 2012). This observation is supported by several studies, which suggest that chemical cues used by benthic species can influence the foraging strategies, feeding choices and habitat use of fishes (Choat and Clements, 1998; Hay, 2009, 1996).

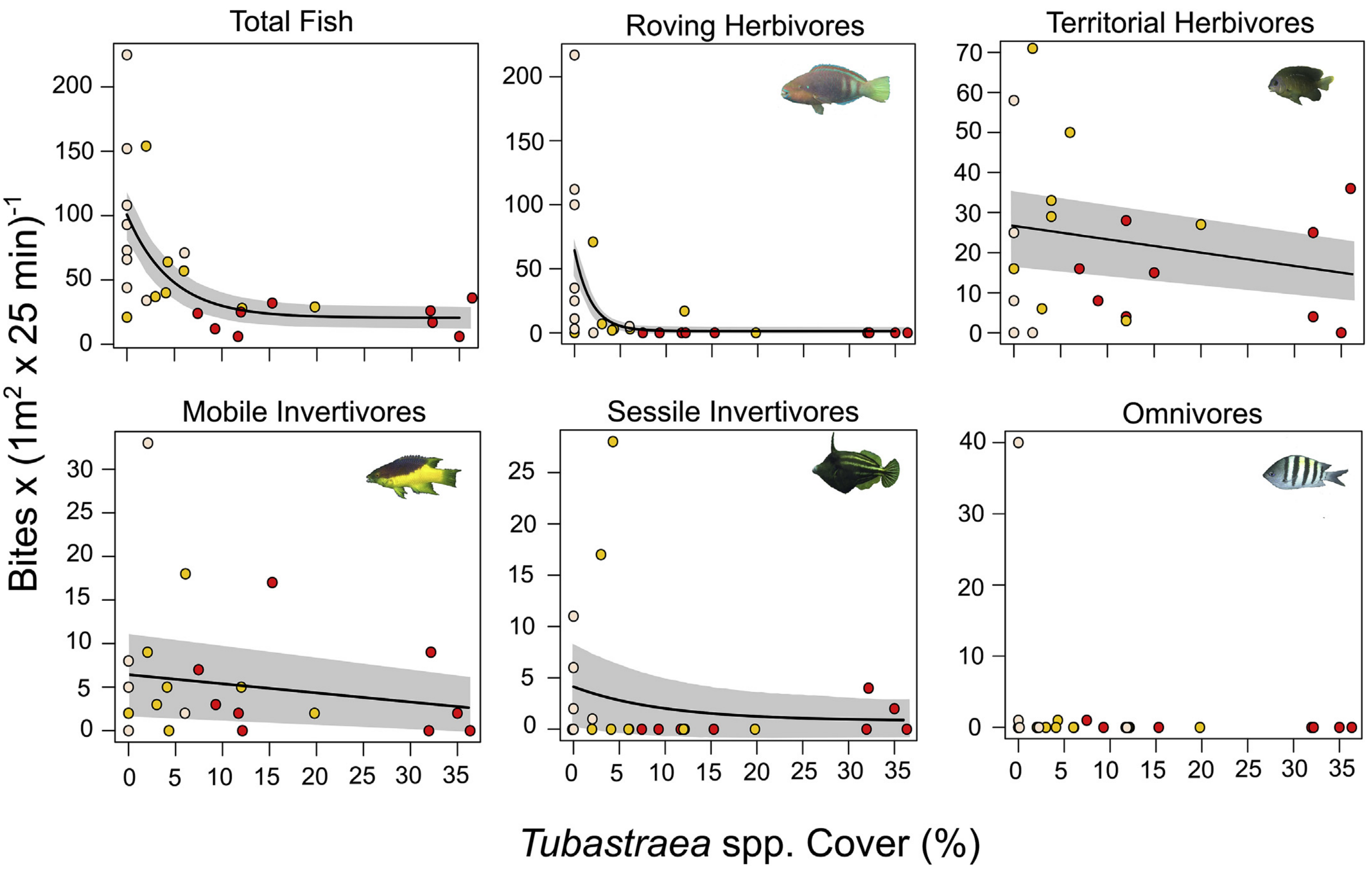

Fig. 3. Relationship between bite rates of fish trophic groups and *Tubastraea* spp. cover (%). Curves and lines represent the most parsimonious selected models. Each point represents a remote underwater camera, colors indicate reef section where video was recorded based to *Tubastraea* spp. cover level (beige = Low, yellow = Medium, red = High). Fish images represent species with the highest bite rates from each group: Roving Herbivores (*Scarus zelindae*), Territorial Herbivores (*Stegastes fuscus*), Mobile Invertivores (*Bodianus rufus*), Sessile Invertivores (*Cantherhines pullus*) and Omnivores (*Abudefduf saxatilis*); grey areas are 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

4.2. *Effects on Roving Herbivores*

The RH group responded to the benthic changes associated with alien coral invasion with a reduction of RH bites in plots with elevated invasive coral cover. This may have important consequences, since RH species provide critical energy exchange within coral reef ecosystems (Bellwood et al., 2003; Hoey and Bellwood, 2008). Within the RH trophic group, parrotfishes are important consumers of algae and detritus, thereby contributing to reef primary productivity and nutrient cycling (Hay, 1991; Horn, 1989). The most abundant parrotfish in the study area, *Scarus zelindae,* can remove corals and leave noticeable scars (Francini-Filho et al., 2010; Pereira et al., 2016). The reduction of bite rates by parrotfishes and surgeonfishes may cause a release of grazing pressure on algae and a subsequent decrease in detrital cycling. Coral recruitment may also be affected since RH provide open space to recruit and settle on substrate which directly alters reef resilience (Hoey et al.,

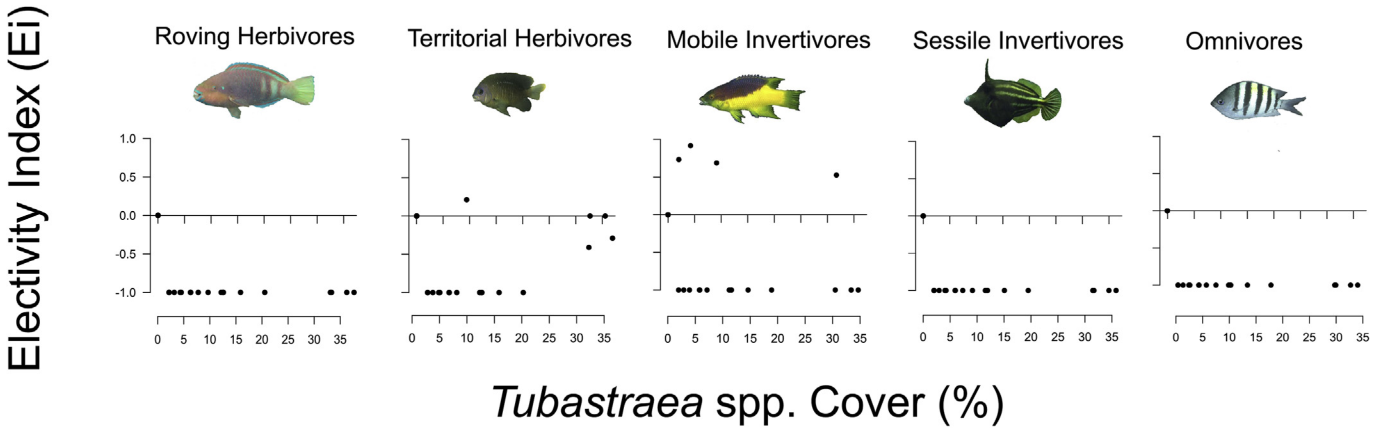

Fig. 4. Grazing selectivity (Ivlev's electivity index) of each fish trophic group for *Tubastraea* spp. cover (%). Images represent the species that contributed the highest feeding pressure within each group: Roving Herbivores (*Scarus zelindae*), Territorial Herbivores (*Stegastes fuscus*), Mobile Invertivores (*Bodianus rufus*), Sessile Invertivores (*Cantherhines pullos*) and Omnivores (*Abudefduf saxatilis*).

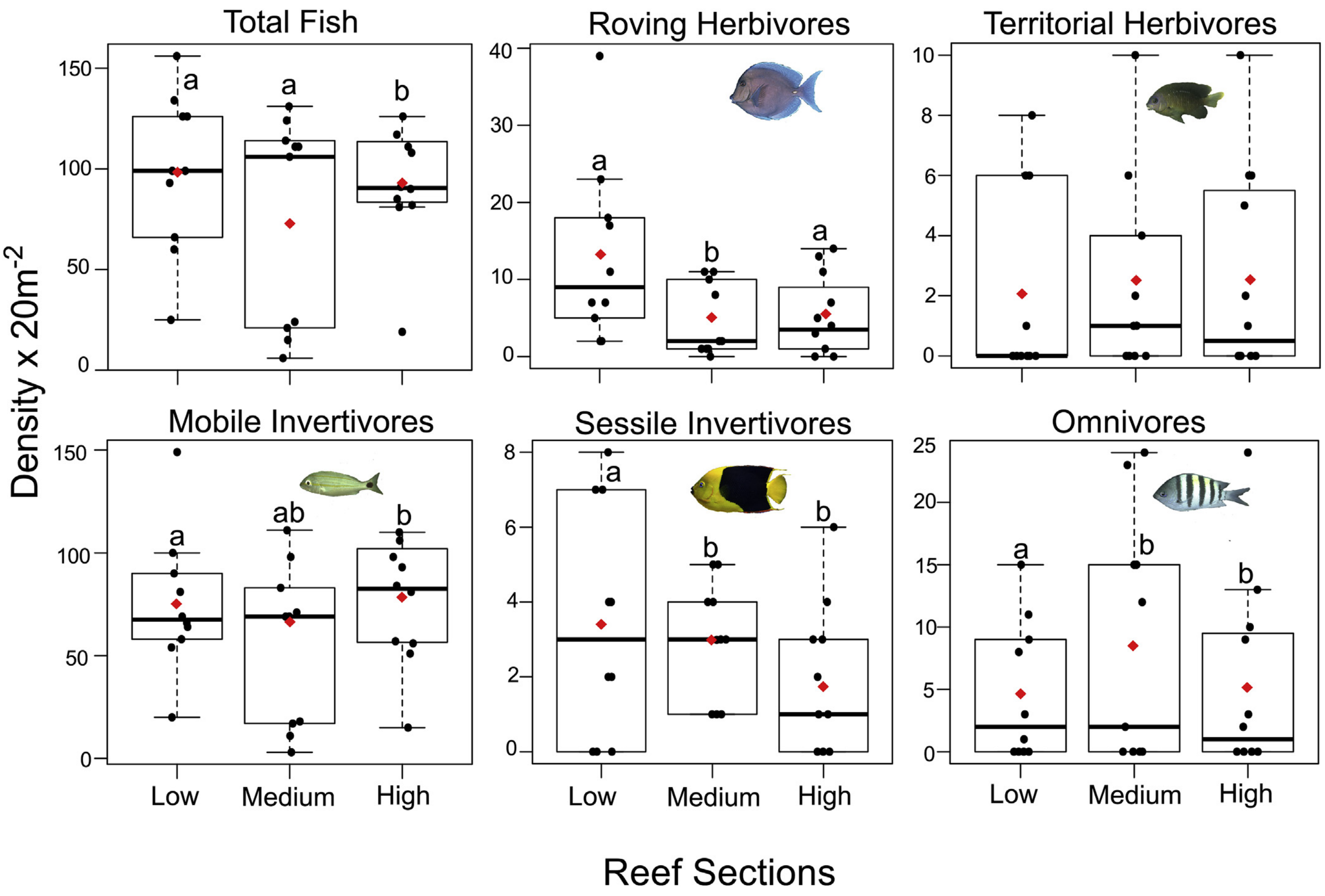

Fig. 5. Fish density on three reef sections based on *Tubastraea* spp. cover levels (Low, Medium and High). Box-plots represent the median, Q_1, Q_3, minimum and maximum values; each point represents a visual census. Images represent the species with the highest density within each trophic group: Mobile Invertivores (*Haemulon aurolineatum*), Roving Herbivores (*Acanthurus coeruleus*), Omnivores (*Abudefduf saxatilis*), Territorial Herbivores (*Stegastes fuscus*) and Sessile Invertivores (*Holocanthus tricolor*). Letters denote significant differences.

2011).

Foraging activities of RH are primarily based on turf algae (Bonaldo et al., 2014; Bonaldo and Bellwood, 2011; Francini-Filho et al., 2008; Hoey et al., 2011; Pereira et al., 2016; Rotjan and Lewis, 2006; Russ, 2003; Wilson et al., 2003). While Sun corals are replacing turf algae in some sites (Lages et al., 2011), it is unlikely that the observed reduction in RH bites in elevated invasive cover plots was associated with turf algae cover decline in this case, since turf algae is broadly abundant along the studied site and algae cover showed no relationship with the invasive coral cover (Table S1, Fig. S1). *Tubastraea* spp. has extensive polyps (reaching up to 7 cm in height) with a yellow/orange color, containing allelochemicals that can inhibit fish predation. While some RH species may be facultative coralivores (e.g., zooxanthellate corals), we did not observe any evidence of RH foraging on Sun corals. Therefore, we suggest that the rapid growth and gregarious spatial distributions exhibited by large colony patches of invasive corals hide turf algae and detritus, inhibiting RH grazing in areas with high invasive cover.

Consequences of invasive coral effects on RH foraging activities could increase the home range of RH or displace RH to non-invaded reefs. According to the optimal foraging theory, larger home ranges require a higher energetic demand and increases predation risks (Macarthur and Pianka, 1966; Nunes et al., 2013; Webster and Laland, 2012). RH density was lower in the High section where mean invasive cover was highest (21% mean) and RH are a group with species threatened by overfishing in Brazil (Padovani-Ferreira et al., 2012). Habitat change caused by alien coral invasions may be an additional stressor to RH species in coral reefs.

4.3. Effects on Territorial Herbivores and Mobile Invertivores

The feeding rates of TH and MI were negatively related with invasive cover. However, these relationships were weak (best fit model: linear) and the fish density of TH species was not different between reef sections. This is likely because territorial feeding behavior and algae cover were unaffected by the percentage cover of the invasive corals (Fig. S1). For example, TH species such as *Stegastes fuscus* feed primarily on farmed turf algae within a vigorously defended territory (Ceccarelli, 2007; Ferreira et al., 1998b; Francini-Filho et al., 2010). Due to their small size and great capacity of feeding choice (Ferreira et al., 2004) *S. fuscus* individuals were able to graze on turf algae between invasive colony patches less accessible to other fish grazers.

While increased invasive coral cover did not decrease algal turf cover, it may change food availability to some fish groups by hiding turf and detritus. This change in food visibility may increase the competition between TH and RH. For example, we observed interference competition from TH to RH in a plot with high invasive cover (Video S1). Grazing competition from TH has been found to limit RH access to algal resources (Robertson et al., 1979), reduce RH feeding rates (Robertson et al., 1976), increase RH grazing pressure (Hixon and Brostoff, 1996) and consequently increase ingestion of inferior food types (Bruggemann et al., 1994). Change in food availability caused by these invasive corals has the potential to influence the interactions between these groups.

MI were the dominant trophic group, represented mainly by *Bodianus rufus* and *Haemulon aurolineatum*. This result supports findings from Ferreira et al. (2004), who found that MI was the most abundant group in different sites along the Brazilian coast. MI density was significantly higher in reef sections with higher invasive coral cover. Moreover, we observed that MI selected turf algae even on plots with high invasive cover (36%) and eventually bit on native coral and *Tubastraea* colonies. MI feed preferentially on small benthic mobile invertebrates (e.g. harpacticoid and siphonostomatoid copepods), a high caloric food resource which is abundant on turf algae and scleractinian coral colonies, such as native and *Tubastraea* species (Ferreira et al., 1998a; Humes, 1997; Kramer et al., 2015, 2013; Menezes, 2012; Nogueira et al., 2015; Stella et al., 2010). It is possible that the abundance of microinvertebrates that live within turf algae and native corals is higher than those in *Tubastraea* colonies, but it needs to be properly evaluated.

4.4. Conclusions and implications

This study reveals that Sun coral invasion has negative effects on fish feeding regimes. Importantly, invasive corals had the strongest effect on the RH trophic group. The RH group were the second most abundant species at the study site and play important functional roles (e.g. grazing, coral predation, browsing, bioerosion and sediment transport) fundamental to coral reef energy exchange (Bonaldo et al., 2014). These effects could be particularly relevant to coral-algae interactions, and reduction in RH feeding and abundance may trigger long-term changes at the ecosystem level such as shifts in benthic group dominance (Lirman, 2001; Mumby, 2009).

Given that climate change scenarios are causing the redistribution of many marine species and altering species functions and interactions (Dukes and Mooney, 1999; Stachowicz et al., 2002), the synergetic impacts of strong invasive species, such as Sun corals, and climate change should be taken into account when modelling ecosystem state in future scenarios. A key challenge for research is to determine how invasive species respond to warming scenarios and to adopt management strategies to reduce impacts on reef ecosystems (Hellmann et al., 2008). We highlight the importance of developing a trophic approach for invasions and ecosystem management, such as the ecological threshold approach. The ecological threshold is defined as a point or zone where a sudden change in the condition or dynamics of a biological system occurs (Nichols et al., 2014). The ecological threshold approach has clarified previously unanswered questions regarding the boundaries between ecosystem states impacted by biological invasion (Briske et al., 2006; Friedel, 1991; Jeschke et al., 2014; Stringham et al., 2003), and would aid in the management of this Sun coral invasion.

Several studies have recommended actions to control the expansion of *Tubastraea* on Brazilian coast (Costa et al., 2014; Lages et al., 2011; Miranda et al., 2016a, 2016b; Sampaio et al., 2012; Santos et al., 2013; da Silva et al., 2014) and recently governmental environmental agencies have recognized the importance of creating a management plan. We reinforce these recommendations, particularly management focused on vectors (i.e. oil and gas platforms) which are largely responsible for Sun coral introduction and expansion in Brazil (Creed et al., 2017). Avoiding the large scale expansion of Sun corals may avoid establishment success and ecological impacts on fish-benthic interactions demonstrated in present study. Ongoing monitoring of invasive cover levels and fish interactions is fundamental to assess the ecological threshold of *Tubastraea* invasion.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2018.03.013.

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