



Drivers of distribution of the parrotfish *Sparisoma frondosum* (agassiz, 1831) in Southwest Atlantic rocky reefs: Insights for management and conservation

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ABSTRACT

Understanding the effects of environmental drivers on fish distribution is of primary importance for designing effective conservation measures to protect endangered species. In this study, we investigated which habitat and spatial predictors enhance the abundance and biomass of the parrotfish *Sparisoma frondosum* in tropical rocky reefs from a Southwest Atlantic insular complex. Besides more than 170 islands, the Ilha Grande Bay (IGB) also harbors one of the most threatened Brazilian Marine Protected Area (MPA), the Ecological Station of Tamoios (ESEC-Tamoios). This no-take MPA became an emblematic area of the systematic dismantling of Brazilian environmental laws ongoing since the beginning of 2019 when the current government has declared intentions to recategorize and reduce the ESEC-Tamoios protection status. Our results revealed that distance from the coast and depth better explained the distribution of the iconic and vulnerable *S. frondosum*, regardless the presence of the no-take areas. An overall trend of increasing abundance and biomass with distance and depth was observed, except for sites with high cover of invasive coral *Tubastraea* spp. We also discuss the ESEC-Tamoios effectiveness and its current panorama to the Southwest Atlantic rocky reef's conservation. Finally, we identify strategies to protect parrotfishes and expand the ecological benefit of this MPA to adjacent areas.

1. Introduction

The identification of variables influencing the abundance and spatial distribution of species is fundamental to designing effective conservation strategies. Studies that adequately encompass the spectrum of environmental variability to which organisms are exposed help managers to focus conservation efforts in areas that maximize the representation of the most influential drivers for species spatial patterns (Connolly et al., 2005; Beger and Possingham, 2008). This is particularly critical for the establishment of marine reserves and for conservation programs of endangered species wishing to protect sites that could potentially sustain higher densities, enabling biomass exportation to the surrounding areas (Francini-Filho and Moura, 2008; Lester et al., 2009).

Effective models of species distributions should be based on good spatial coverage and present habitat and spatial variables including both

natural and anthropogenic components. In the case of reef fish, these variables include benthic composition (Bouchon-Navarro and Bouchon, 1989; McClanahan and Karnauskas, 2011; Chong-Seng et al., 2012), topographic complexity (Friedlander and Parrish, 1998; Bejarano et al., 2011), depth (Srinivasan et al., 2003), and spatially explicit predictors that represent an array of environmental influences such as wave exposure (Karnauskas et al., 2012), fishing activity (Advani et al., 2015; Teixeira-Neves et al., 2015), terrigenous sediment (Beger and Possingham, 2008; DeMartini et al., 2013; Neves et al., 2016) and thermal impact (Teixeira-Neves et al., 2012).

Parrotfishes are abundant and ecologically important members of the reef community playing an important role in controlling the growth of algae, grazing primarily on epilithic algal matrices (EAM) and detritus (Bellwood and Choat, 1990; Bonaldo et al., 2006; Ferreira and Gonçalves, 2006; Mendes et al., 2018). Foraging activity of these fishes

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provide areas of clean substrate that facilitates the settlement, growth, and survival of coralline algae and corals (Bonaldo and Bellwood, 2009; Green and Bellwood, 2009), contributing to the increase of structural complexity on the reefs (Hughes et al., 2007; Mumby 2009; Adam et al., 2015). Despite their contribution to these top-down process are not well understood for all reef environments, such as subtropical rocky-reefs with low coral cover, the fact is that parrotfishes represent a ubiquitous and ecologically important group that is increasingly prevalent in commercial and artisanal fisheries worldwide (Floeter et al., 2006; Taylor et al., 2014). In Brazil, for example, parrotfishes are targeted along the coast mainly by small-scale artisanal fishery with the use of different gears, including gillnets, handlines, and spearguns (Francini-Filho and Moura, 2008; Bender et al., 2014). Consequently, understanding the relative influence of anthropogenic and environmental drivers on parrotfish assemblages is of prime interest to reef ecologists and resource managers.

The factors known to influence the abundance, biomass, and size-class of parrotfishes are scale-dependent and variable according to the species, but generally related to reef attributes that provide potential habitats for species, related to their respective feeding modes and availability of shelter (Taylor et al., 2015; Roos et al., 2015, 2019). In Southwest Atlantic rocky reefs, the available study has reported small-scale topographic complexity (e.g. number of holes), depth, and wave exposure as important drivers of parrotfishes' spatial patterns (Cordeiro et al., 2015). Thus, few studies have investigated the drivers of parrotfishes' abundances for impacted coastal systems, where anthropogenic factors may overcome habitat features in influencing fish distributions (Neves et al., 2016), as levels of human influence (such as fishing) are frequently unique to particular sites or islands (Taylor et al., 2014).

The Agassiz's parrotfish (*Sparisoma frondosum*, Agassiz, 1831) is amongst the most abundant parrotfish species in the West Atlantic (Carvalho-Filho, 1999; Padovani-Ferreira et al., 2012; Lessa et al., 2016). It occurs from the tropical reefs (e.g., Amazon Reefs) (Moura et al., 2016) southwards to subtropical areas $\sim 27^\circ$ (Anderson et al., 2015), including the oceanic islands (Moura et al., 2001; Bonaldo et al., 2006; Francini-Filho et al., 2010; Longo et al., 2015). *Sparisoma frondosum* is a nominally herbivorous fish that feeds browsing (biting off parts of erect macroalgae), although large individuals may also feed grazing (scraping algae-covered substratum) (Ferreira and Gonçalves, 2006; Bonaldo et al., 2014). Despite the wide distribution range, *S. frondosum* is under increasing fishing pressure (Floeter et al., 2006; Roos et al., 2016) and was ranked as vulnerable in the Red List of Brazilian Fauna (Ferreira et al., 2018). Larger-bodied parrotfishes of the genus *Sparisoma* have become targeted by spearfishermen's as populations of top predators (mainly groupers and snappers) collapsed (Mumby et al., 2012; Bender et al., 2014). As for many other target species, well-established and enforced marine protected areas (MPAs) may increase the biomass or abundance of parrotfishes (Bellwood et al., 2003; Mumby et al., 2006; Bonaldo et al., 2017) and exportation of juveniles and adults across reserve boundaries (spillover effect) has been observed in some regions (da Silva et al., 2015; La Mesa et al., 2012; Garcia et al., 2014). In this sense, *S. frondosum* can be considered a valid model to examine the effect of an MPA in protecting target species, especially for reserves with low biomass of large predators, several of which prey on parrotfishes (Mumby et al., 2006).

Rocky-reefs represent the primary habitat for reef fishes and reef-associated biota on the tropical-subtropical transition zone of the Brazilian coast (Floeter et al., 2001). In the coastal insular complex of Ilha Grande bay (IGB), reefs are subjected to multiple gradients of physical, biological, and anthropogenic features (Teixeira-Neves et al., 2015; Neves et al., 2016). IGB was the starting point of the invasive coral *Tubastraea* spp. in the Brazilian in the late 1990s. This scleractinian coral is well succeeded in competing for space on consolidated substrates due to its allelopathic interference that, among other effects, have been reducing the habitat heterogeneity in rocky reefs (Lages et al., 2011; da

Silva et al., 2014; Mizrahi et al., 2017). Since 1990, the IGB harbors one of the most threatened Brazilian MPA, the Ecological Station of Tamoios (ESEC-Tamoios). Besides the increasing threats in which coastal areas are worldwide subjected (e.g., tourism, shipyards, private marinas, and fisheries), the ESEC-Tamoios became an emblematic area of the systematic dismantling of Brazilian environmental laws ongoing since the beginning of 2019 (Escobar, 2018; Abessa et al., 2019; Levis et al., 2020) when the current government has declared the intentions to reduce the protection status of this MPA. In this complex scenario, this study aimed to identify the most influential drivers on the spatial variation of the vulnerable parrotfish *Sparisoma frondosum* in the Ilha Grande bay. We selected *S. frondosum* due to its higher abundance in the IGB compared to other parrotfishes' species. We examined habitat attributes (i.e., benthic cover composition, reef height, number of holes, crevices, depth) and spatial variables (distance from the coast, MPA) of 39 sites and identified which set of these predictors optimize the abundance and biomass of *S. frondosum*. Specifically, this study aims to investigate the effect of a no-take MPA on the abundance and biomass of *S. frondosum*, one of the remaining target reef fish of the region after the intense fishing pressure on large predators.

2. Materials and methods

2.1. Study area

This study was conducted on rocky reefs of Ilha Grande Bay (IGB), southeastern Brazil ($23^\circ 04' 36$ S; $44^\circ 01' 18$ W) (Fig. 1). The bay covers an area of about 1.000 km² and has approximately 170 islands surrounded by shallow water, typically no more than 8 m in depth (Neves et al., 2016; Johnsson and Ikemoto, 2015). The main physiographic structure of the study area is characterized by narrow rocky shores covered by granite boulders, ending in a sand bottom (interface). The local water is influenced by winds and tides with a mean amplitude of 1.6 m (Nogueira et al., 1991) and receives a significant contribution of freshwater from the rivers in some locations (Neves et al., 2016). The water temperature ranges from 20 °C to 31 °C, the salinity from 29 to 36 (Dias and Bonecker, 2008), and presenting an average annual accumulation of rainfall of 1770 mm, ranging from 180 mm during the dry/winter season (June–August) to 750 mm during the wet/summer season (January–March).

The IGB has a Marine Protected Area (MPA) at the Ecological Station of Tamoios (ESEC – Tamoios) that comprises twenty-nine islets, islands, rocks, and slabs and their respective marine surroundings in a 1 km radius. Fishing is prohibited in Ecological Stations, which allow only scientific research and environmental education actions (SNUC, 2000). Progressively increasing threats to the bay include tourism, power generation (thermonuclear power plants), shipyards, private marinas, oil terminals, a commercial port, and fisheries, including destructive bottom trawling and recreational fishing targeting rocky reef fishes (spearfishing and hook-and-line fishing) (Freret-Meurer et al., 2010; Teixeira-Neves et al., 2016). In addition to these threats, the bay exhibits a high susceptibility to biological invasions, especially the invasive corals of the genus *Tubastraea* (*Tubastraea coccinea* e *T. tagusensis*) which are responsible for changes in community structure of rocky reefs in IGB (de Paula and Creed, 2004; de Paula et al., 2014; Lages et al., 2011; da Silva et al., 2014).

This study was part of a larger fish survey conducted at IGB, during the winters of 2010 and 2011, which investigated the structure and dynamics of reef fish assemblages (Teixeira-Neves et al., 2015; Neves et al., 2016). Thirty-nine sites were selected to encompass the environmental conditions in IGB, including reefs with variable habitat structure (benthic cover and topographic complexity) and subjected to distinct levels of disturbances, mainly related to fishing pressure and damage to benthic communities by trampling, such as the constant access of tourists and proximity of marinas and harbors. The intensity of these impacts varies according to distance from the coast and to distance from the

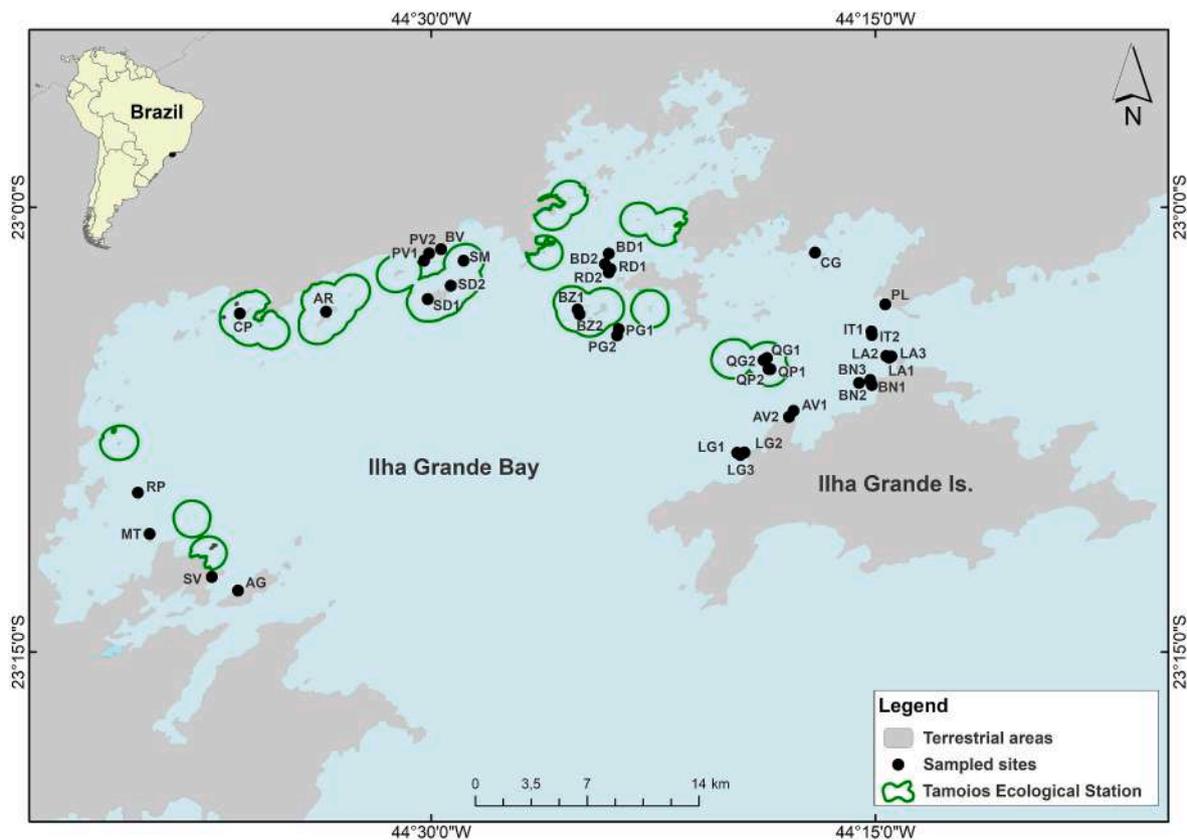


Fig. 1. Study sites at Ilha Grande Bay, southwestern Atlantic, Brazil. Green areas indicate islands of the no-take marine reserve Tamoios Ecological Station. Sites codes according to distance from the coast: PL, Ponta Leste; SV, Saco da Velha; PV1, Praia Vermelha (1); BV, Barlavento; PV2, Praia Vermelha (2); MT, Mantimento; CG, Cataguazes; CP, Comprida; AG, Algodão; SM, Samambaia; AR, Araraquara; IT2, Itacuatiba (2); IT1, Itacuatiba (1); SD2, Sandri Island (2); SD1, Sandri Island (1); LA3, Lagoa Azul (3); BD2, Brandão (2); RP, Rapada; LA1, Lagoa Azul (1); LA2, Lagoa Azul (2); RD2, Redonda (2); BD1, Brandão (1); BZ1, Búzios (1); BZ2, Búzios (2); BN3, Bananal (3); RD1, Redonda (1); BN2, Bananal (2); BN1, Bananal (1); PG1, Papagaio (1); QG2, Queimada Grande (2); PG2, Papagaio (2); QG1, Queimada Grande (1); QP1, Queimada Pequena (1); QP2, Queimada Pequena (2); AV1, Alvo (1); AV2, Alvo (2); LG2, Pta da Longa (2); LG1, Pta da Longa (1); LG3, Pta da Longa (3). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

main cities of the region (Angra dos Reis and Paraty). A total of five sites was sampled in the mainland, twelve in unprotected islands, eleven in the MPA (ESEC – Tamoios), and eleven around Ilha Grande (Fig. 1). Overall, these sites were distributed across three distance from the coast ranges (<3 km, 3 – 6 km, and > 6 km). For the eleven MPA sites, 5 were located near the coast (<3 km), 2 in an intermediate distance (3 – 6 km), and 4 far from the coast (~10 km). To avoid confounding effects and better assess the influence of the habitat structure and human influences, sites were chosen in areas sheltered from wave activity, far from point sources such as river discharges, mangroves, sewage outfalls, and thermal discharges.

2.2. Sampling program

Fish were sampled using underwater visual census by scuba diving along transects 20 m long and 2 m wide (40 m²). At each site, 6–15 transects were sampled in two different depth strata; shallow (shallower areas closer to shore) and interface (deeper areas near to rock and sand interface), totaling 340 transects. The number of individuals and total length (TL) body sizes were recorded for each transect. Samples were performed under stable oceanographic conditions, between 9:00 and 15:00 h, during neap tide, near quarter moon.

Benthic communities and topographic complexity of each site were quantified using high-resolution digital images. A housed digital camera was mounted on a 60 × 60 cm photoquadrat frame. Photoquadrats were taken randomly along the same fish transect on a single sampling occasion, resulting in 20 photos per transect and 120 photos per site. In

some sites, however, less than 20 photos per transect were taken due to logistical constraints or inclement weather. The number of transects and photoquadrats per site are given in Table S1[†]. Topographic complexity variables measured on rocky reefs consisted of two scales: i) small-scale complexity, that was considered to be the number of holes and crevices in each quadrat, and ii) large-scale complexity, that was considered to be the size of rocky boulders. Small-scale complexity was measured by counting the total number of holes and crevices (gaps between structures that could provide a path for a fish to escape a predator) from each photograph. At the same position from which each photo was taken, we estimated the height in meters of the tallest rocky boulder (reef height), following Neves et al. (2016).

The percentage of benthic cover was analyzed using the software Coral Point Count with Excel Extensions – CPCe 3.4 (Kohler and Gill, 2006) by overlaying 20 random points on each image and identifying the organism under each point. Benthic sessile and semi-sessile organisms, expressed as percentage of benthic cover, were grouped as follows (adapted from Steeneck and Dethier, 1994): epilithic algal matrix (EAM, i.e., aggregate with less than 3 cm high of filamentous algae); the invasive corals of the genus *Tubastraea* (*Tubastraea coccinea* e *T. tagusensis*); fleshy algae, comprised mainly by brown algae such as *Sargassum* and *Dictyopteris* genera; crustose calcareous algae (CCA); and zoanthids, soft corals represented by *Palythoa caribaeorum* and *Zoanthus sociatus*. Other invertebrates, such as hard coral (scleractinians such as *Mussismilia hispida*), crinoidea, tunicate, hydrozoa, octocoral, sessile polychaetes (e.g., the genus *Phragmatopoma*) were also measured but not included in the analysis due to its low percentage cover. We also

recorded the depth of each transect and measured the distance from each sampled site to the coast (Table S1).

2.3. Data analyses

The data from habitat surveys (percentage cover of selected benthic categories, number of holes, number of crevices, reef height, depth, and distance from the coast) and fish transects (number of individuals and biomass) were analyzed considering reef stratum (shallow and interface) as the lowest level of replication. A single value for each stratum in each site was calculated (average) for the habitat variables and fish data. Fish biomass was estimated by transformations of weight-length and allometric conversions: $W = a \cdot L^b$ where parameters a and b are constants in equation of growth allometric. The Fishbase was used as a source for this information (Froese and Pauly, 2014). The size class distribution of *S. frondosum* was plotted using five 10-cm TL body size categories (<10, 10–20, 21–30, 31–40, >40 cm). The Kruskal-Wallis and Dunn's pos-hoc tests were conducted on length measurements to determine whether the size frequency of *S. frondosum* differed among three distance from the coast ranges (<3 km, 3–6 km, >6 km). These analyses were performed using the R Language for Statistical Computing (R Core Team, 2020).

The existence of highly correlated predictors and the need for data transformation was assessed using a draftsman plot. The predictors EAM, zoanths, *Tubastraea* spp. and reef height had a high degree of skewness and were log $x+1$ transformed following Clarke and Gorley (2006). The number of holes and crevices had an intermediate degree of skewness and was square-root transformed. As the predictors distance from the coast and depth had a low degree of skewness, raw data were used for the analysis following Anderson et al. (2008). The abundance and biomass variables were log $x+1$ transformed to minimize the influence of extreme values and zeros. Pairwise correlation coefficients were calculated between all continuous predictors (percentage cover of EAM, zoanths, and *Tubastraea* spp.; number of refuges, reef height, depth, distance from the coast) and only *Tubastraea* spp. and reef height were collinear ($r > 0.7$; Zuur et al., 2007). These variables were collinear because four MPA sites (Queimada Grande and Queimada Pequena islands) with the highest reef heights (mean of 3.2 ± 0.14 m) also had the highest *Tubastraea* spp. cover (mean of $16.6 \pm 2.66\%$). MPA was treated as categorical variable with two levels (protected x unprotected reefs).

A correlation-based principal component analysis (PCA) on the habitat variables (reef height, cover of EAM, fleshy algae, zoanthid and *Tubastraea* spp., number of crevices and holes), distance from the coast and depth was performed to better describe the studied sites. For this analysis, data were normalized to standardize the contribution of variables measured on different scales. Samples in PCA were labeled according to three distance from the coast ranges (<3 km, 3–6 km, >6 km).

The relationships between abundance and biomass of *S. frondosum* and reef attributes were investigated using distance-based linear models (DistLM; Legendre and Anderson, 1999; McArdle and Anderson, 2001) through two complementary explanatory models. The first model (hereafter called "model 1") tested all predictors together (MPA, distance from the coast, depth, reef height, number of holes and crevices, percentage cover of EAM, zoanths and *Tubastraea* spp.) using the data of 35 sites (without the *Tubastraea* spp.-dominated sites). This approach avoided the collinearity between *Tubastraea* spp. and reef height and allowed us to examine the effect of the MPA while controlling for the influence of the invasive coral. The second model (model 2) considered the data from all 39 sites excluding the predictor reef height.

DistLM analysis was used to identify which of the potential examined predictors explained most of the variability in fish abundance and biomass. The "best" selection method, according to the Akaike Information Criterion (AIC), was used to select the final model. Multiple partial correlations of the selected predictors according to DistLM analysis with the first distance-based redundancy analysis axis (dBRDA,

Legendre and Anderson, 1999; McArdle and Anderson, 2001) were also examined to interpret the strength and direction (positive or negative) of the relationship between fish abundance and biomass and the environmental variables. We used permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) as a complementary approach to explore the effect of MPA on fish abundance and biomass, while accounting for variability between sites, selected predictors, and interaction between these continuous predictors. P values were calculated using 9999 permutations of residuals under a reduced model and Type I (sequential) sums of squares. MPA was a fixed factor, Site was considered a random factor and selected predictors according to DistLM analysis (model 1) were covariates. To explore the amount of overlap in the explained variability among terms because of the unbalanced design (MPA, 11 sites; unprotected, 28 sites) with covariates, we changed the order of the terms in the analysis and re-run de model to see how this affected the results, following Anderson et al. (2008). DistLM and PERMANOVA analyses were based on Euclidean similarity matrices. These analyses were conducted using PRIMER 6.0 + Permanova software (Anderson et al., 2008).

3. Results

Our study sites were mainly covered by epilithic algal matrix (EAM) and zoanths but showed differences in the coverage of fleshy algae and the invasive coral *Tubastraea* spp. (Fig. 2, Table S1). Near shore sites (<3 km) comprised of shallower and less complex reefs (<reef height, number of holes and crevices), covered by a high proportion of fleshy algae in comparison to other areas. Sites at intermediate distances (3–6 km) consisted of high cover of Zoanths (mainly *Palythoa caribaeorum*) and the highest topographic complexity at the small scale (>number of holes and crevices) in comparison to the other areas. Sites further from the coast (~7–12 km) consisted of deeper rocky reefs (~10 m deep) comprised by large boulders (>reef height), covered by of EAM or covered by the highest proportion of *Tubastraea* spp. (Fig. 2, Table S1).

3.1. *Sparisoma frondosum* abundance and biomass

A total of 167 *Sparisoma frondosum* individuals comprising 42,869 g was observed in 340 transects (40 m² each) performed at 39 sites of Ilha Grande Bay. The highest abundance was observed in six sites located between 6 and 13 km from the coast, which ranged from ~2 to 5 individuals/40 m² (Table S1). Fish abundances were relatively low in sixteen sites, ranging from 0.16 to 0.88 individuals/40 m², while no individuals were observed in twelve sites located near the coast (<3 km) and in four sites far from the coast (6–13 km). Overall, one site of the no-take marine reserve Tamoios Ecological Station (Búzios island) had more individuals than any other site of IGB (5.3 ± 2.87 individuals/40 m²), followed by sites of Ilha Grande island (~2–4 individuals/40 m²). Fishes ranged in size from 8 to 45 cm (total length, TL) and were represented mainly by juveniles (median TL of 16 cm). The distribution of length data differed between intermediate (3–6 km) and far from the coast reefs (~6 km–12.5 km) according to Kruskal-Wallis ($P < 0.001$; $\chi^2 = 18.617$) and Dunn's pos-hoc ($P < 0.001$) tests. A modal length of 10–21 cm TL was observed for all distance ranges (<3 km, 3–6 km, >6 km), while individuals from 21 to 45 cm TL were more abundant at greater distances from the coast (Fig. 3).

The distance from the coast was the best predictor of spatial changes in *S. frondosum*' abundances and biomasses for both DistLM models, explaining between 21 and 34% of the variance (Table 1). Depth was the second most important predictor for fish abundance (12%, model 1) and fish biomass (13 and 8%, model 1 and model 2, respectively). The invasive coral *Tubastraea* spp. was the second most important driver for fish abundance in the model 2 (10%), followed by depth (5%), while for fish biomass, *Tubastraea* spp. explained 4% of the variance. There was also a significant effect of EAM cover and the number of crevices for fish biomass, which explained between 1 and 7% of the variance

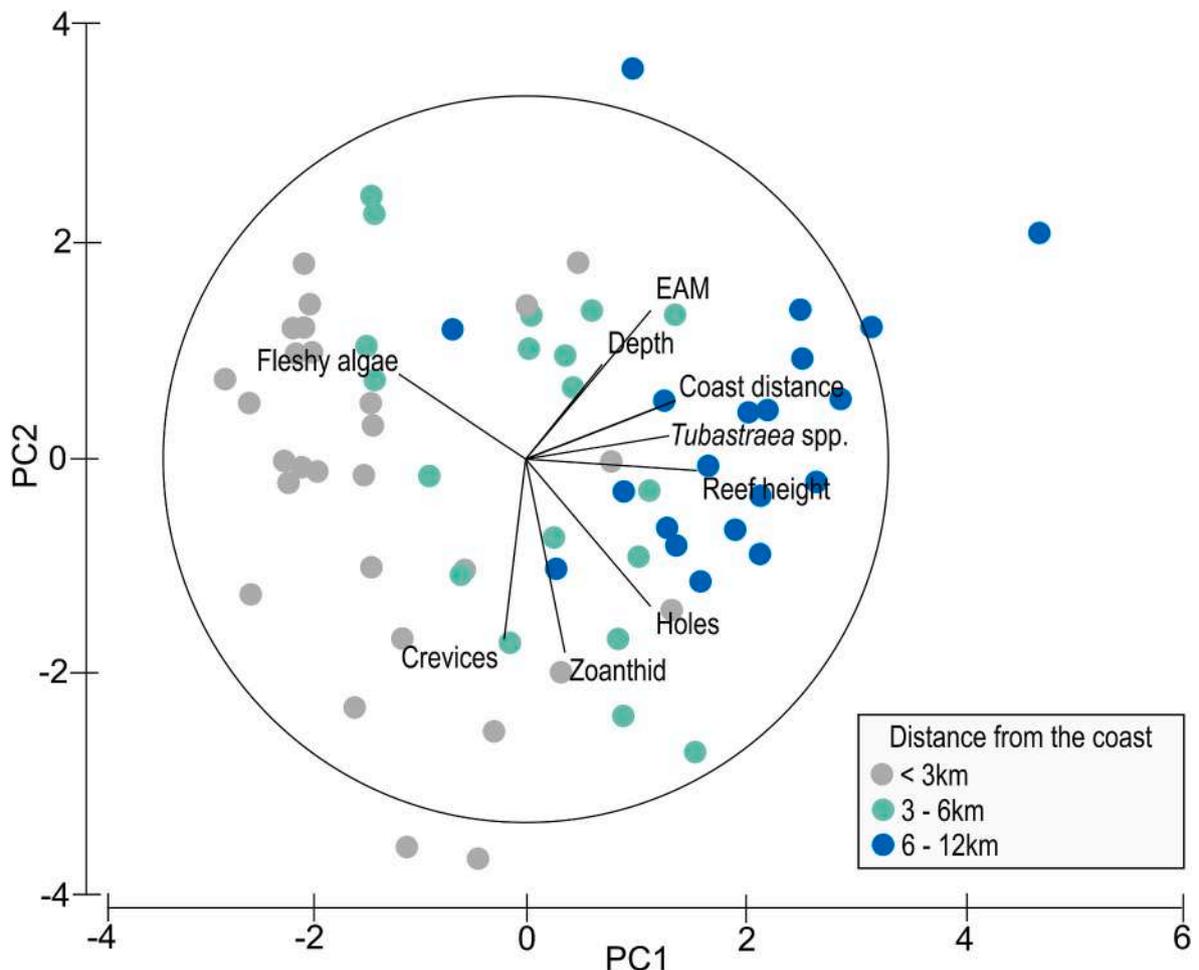


Fig. 2. Principal component analysis (PCA) of relative contribution of 9 predictors observed in the study area. Colors represent the three groups based on the distance from the coast: Grey, close reefs located <3 km; green—intermediate reefs, located from 3 to 6 km and blue—far reefs, located from ~6 km to 12.5 km. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Table 1). In total, DistLM models explained between 39 and 53% of the variation in fish abundance and biomass. MPA, zoanthids, reef height and number of holes were not selected by any model. The relationships between *S. frondosum*' abundance, biomass and selected predictors (variation explained > 10%) is showed in Fig. 4.

Distance from the coast, depth, number of crevices, and EAM cover are positively related with *S. frondosum*' abundance and biomass (Table S2, Fig. S1), while *Tubastraea* spp. cover had the opposite trend. There was no significant effect of protection from MPA and sampling sites, given the influence of distance from the coast and depth as covariates in the PERMANOVA model (Table 2). The interaction between distance from the coast and depth was significant, indicating that the greater depths maximize the positive effect of distance on fish abundance (Table 2, Fig. 4).

4. Discussion

This study investigated the drivers of abundance and distribution patterns of a nominally herbivorous fish across several reefs subjected to different environmental conditions and levels of anthropogenic disturbances. The overall abundance of *S. frondosum* in IGB was low considering the sampling effort (167 fish recorded from 340 transects performed in 39 sites). Besides that, some islands of this study showed higher densities of *S. frondosum* (e.g. Búzios island; mean of 5.33 ind. 40 m⁻², see Table S1) compared to other reefs of the Brazilian coast (e.g. 0.28–0.39 ind. 40 m⁻²; Floeter et al., 2007; ~1–3 ind. 40 m⁻²; Roos

et al., 2019). Although parrotfishes' abundance in this southwest Atlantic bay is expected to be lower than tropical reefs northwards (Ferreira et al., 2004). Despite the greater number of sites sampled, most individuals were concentrated in two small islands (Papagaio and Búzios) and two areas of the largest island of IGB (Ponta da Longa and Alvo sites), which together accounted for 88% of total abundance. On the other hand, no individuals were observed at sites located on the coast. *Sparisoma frondosum* has a wide distribution on the Brazilian coast and can succeed in establishing populations in a range of habitat conditions (Carvalho-Filho, 1999; Humann and DeLoach, 2002). However, our findings demonstrated that *S. frondosum* had a restricted occurrence on a local scale (within a bay), which is likely related to environmental and habitat constraints on spatial patterns.

Distance from the coast was the best predictor of occurrence and biomass of *S. frondosum* in the IGB. The higher abundance and biomass in reefs less subjected to human activities, mainly tourism, boat traffic and fishing (Teixeira-Neves et al., 2016; Cardoso, 2019) and the scarcity of larger individuals (>30 cm TL) indicate a heavy fished system. Coast distance is a good overall predictor of fishing effort (Jackson et al., 2001; Stelzenmüller et al., 2008; Cinner and McClanahan, 2006; Teixeira et al., 2017), and nearshore fishing spots are more subjected to long-term artisanal and recreational fishing effort than reefs further from the coast (Begossi et al., 2006; 2011). Unlike the northeastern Brazilian coast, where most fishers use gillnets and handlines to catch *S. frondosum* (Roos et al., 2015), spearfishing is the primary method of harvesting for parrotfishes in reefs of IGB (LMN personal observation)

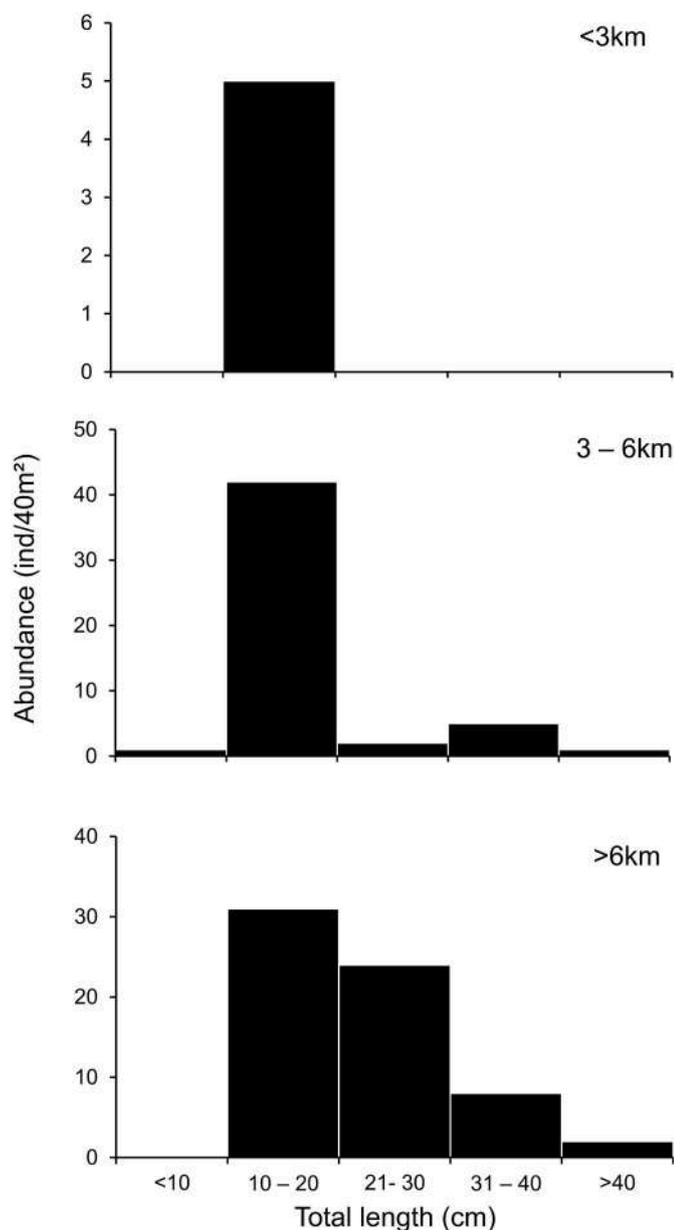


Fig. 3. Length–frequency histogram depicting the size structure of *S. frondosum* at increasing distances from the coast in the Ilha Grande bay, Brazil.

Table 1

Results of the distance-based linear model (DistLM) demonstrating the percentages of variation explained by each variable for the abundance and biomass. AIC, Akaike's information criterion; RSS, Residual sum of squared errors.

	AIC	R ²	RSS	N° Groups	Predictors Selected (%)
Model 1					
Abundance	–119.9	46	6.97	2	Distance from the coast (34), Depth (12)
Biomass	81.45	53	198	4	Distance from the coast (34), Depth (13), Crevices (5), EAM (1)
Model 2					
Abundance	–133.5	39	8.09	3	Distance from the coast (24), <i>Tubastraea</i> spp. (10), Depth (5)
Biomass	102.7	43	259.6	5	Distance from the coast (21), Depth (8), Crevices (7), <i>Tubastraea</i> spp. (4), EAM (3)

and is commonly used worldwide to catch parrotfish at considerable amounts (Frisch et al., 2012; Lindfield et al., 2014). The distance effect detected cannot be uncoupled from ontogenetic variability in habitat use. Parrotfishes adults are most observed in reefs further from the coast with high wave energy, while juveniles tend to occur in more sheltered reefs (Roos et al., 2019), which is related to benthic resource distribution and species-specific feeding modes (Johnson et al., 2019). Besides that, sediment deposition on benthos, which is higher nearshore (Neves et al., 2016), affects parrotfishes by suppressing their foraging (Goatley and Bellwood, 2012; Gordon et al., 2016). In this study, we avoided areas under strong river influence and wave activity to minimize the influence of these factors.

The higher abundance and biomass of *S. frondosum* in deeper reefs observed is likely related to substrate area availability for fish foraging, reproduction, or resting. Shallow rocky-reefs are generally narrower and less structured than deeper reefs, and depth is used as a proxy of substrate area availability (Gibran and Moura 2012; Teixeira-Neves et al., 2015). Parrotfishes exhibit an intense foraging behavior, especially during the juvenile phase, feeding continuously throughout the day (Bonaldo et al., 2006). Also, the initial phase of *S. frondosum* grazes frequently on crustose calcareous algae (Francini-Filho et al., 2010), which increase with depth (Amado-Filho et al., 2018). Thus, deeper and larger reefs may have relatively higher abundances. Another possible explanation is that depth is inversely related to spearfishing pressure due it is only allowed to free-divers by the Brazilian laws. The influence of depth on the biomass of herbivorous species is often attributed to temperature, the effect of light intensity on algal assemblages, and wave action variation (Garrabou et al., 2002; Ferreira and Gonçalves, 2006; Fox and Bellwood, 2007), especially for systems with a greater depth range (Cordeiro et al., 2015). Unlike these systems, our study sites are characterized by sheltered and shallow islands (most no more than 8 m depth) and abundance-peaks were associated with higher depth, irrespective of coast distance (e.g. sites BUZ2, PAG2, LG3, Fig. 4). It indicates that depth minimized the negative influence of human activities. Depth can act as a buffer for fish community changes along a distance gradient from impact sources (Araújo et al., 2017).

The highest cover of *Tubastraea* spp. negatively affected abundance and biomass of *S. frondosum*, possibly related to the reduction of the available substrate for foraging. To our knowledge, this is the first empirical evidence of the invasive coral, *Tubastraea* spp., negative effect on the distribution patterns of an herbivore fish. A recent study showed that *Tubastraea* spp. species reduce feeding rates of roving herbivores, which may increase their home ranges, consequently requiring a higher energetic demand and increasing the predation risks (Miranda et al., 2018). In this study, *Tubastraea* cover was higher at sites deeper and further from the coast of the no-take Tamoios Ecological Station (Queimada Grande and Pequena islands), where we would expect higher *S. frondosum* abundances. Conversely, abundance was comparatively higher in reefs with low *Tubastraea* spp. cover situated near these islands (Papagaio, Longa and Alvo sites). Sun corals species are widespread distributed along more than 3500 km of the Brazilian southwest Atlantic coastline (Soares et al., 2016). Management actions have been taken to control their expansion on Brazilian reefs (Creed et al., 2017), but their effectiveness remains to be verified by long-term monitoring. Yet, the correct control of vectors is the most effective approach for management and prevention of new invasions (Davidson et al., 2008; Capel et al., 2019) with the implementation of immediate eradication protocols (Creed et al., 2017). Additionally, local efforts to control invasive levels at reefs with the highest *Tubastraea* cover may be not effective to protect *S. frondosum*. Instead, ongoing monitoring on the effects of invasive levels on reef processes should be taken at sites with higher parrotfish abundance.

DistLM models explained between 39 and 53% of the variance and evidenced that distance from the coast, depth and *Tubastraea* spp. were the best predictors. In addition, high number of crevices and EAM cover may contribute to enhance the biomass of *S. frondosum*, possible related

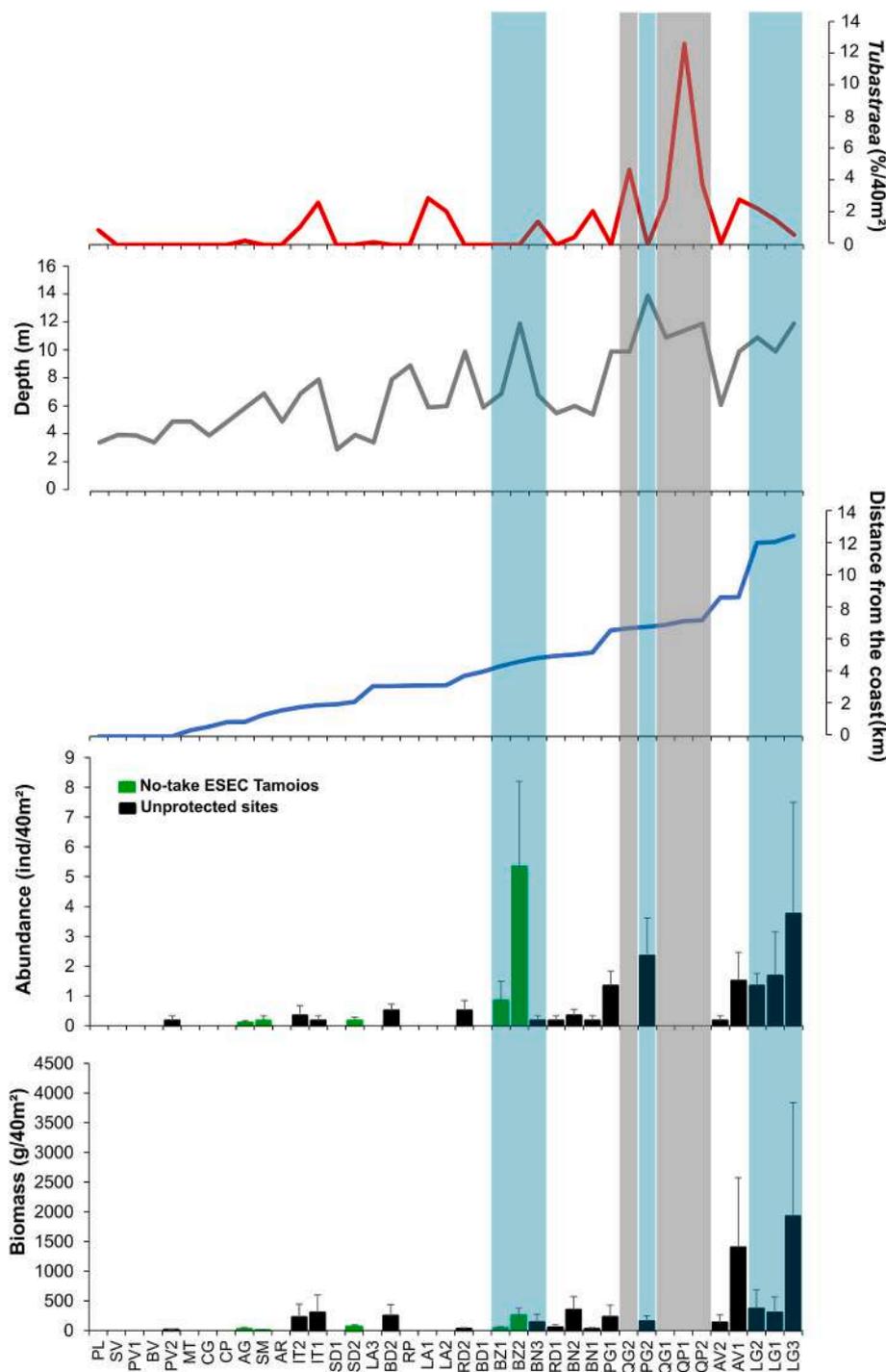


Fig. 4. Relationships between selected predictors, *S. frondosum'* abundance and biomass (Mean ± SE) for the thirty-nine sites classified according to distance from the coast (km) in the Ilha Grande bay, Brazil. Site codes are given in Fig. 1. Green bars represent sites of the no-take Ecological Station of Tamoios. Blue areas indicate that abundance-peaks were associated with higher depth, irrespective of coast distance; and grey areas highlight the invasive coral effect on *S. frondosum'* distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
PERMANOVA results based on Euclidian distance measures for *S. frondosum'* a. abundance and b. biomass.

a. Fish abundance						b. Fish biomass				
Source	df	SS	MS	Pseudo-F	P	df	SS	MS	Pseudo-F	P
Distance	1	4.41	4.41	38.87	***	1	147.94	147.94	35.21	***
Depth	1	1.55	1.55	13.68	***	1	56.13	56.13	12.58	***
Distance*Depth	1	0.90	0.90	7.75	**	1	2.22	2.23	0.48	ns
MPA	1	0.31	0.31	3.14	ns	1	0.05	0.05	0.09	ns
Site	33	3.11	0.10	0.78	ns	33	113.60	3.54	0.72	ns
Residuals	22	2.71	0.12			22	108.51	4.93		
Total	58	12.94				58	428.44			

(df = degrees of freedom, SS = sum of squares, MS = mean sum of squares, * = p < 0.05, ** = p < 0.01, ***p < 0.001, ns = non-significant.

to availability of shelter habitat and preferred food sources. It is well documented that EAM cover is one of the main foraging substrates for *Sparisoma* fishes (Choat, 1991; Bonaldo et al., 2006; Francini-Filho et al., 2010) and shelters are a particularly important resource for juvenile fishes (Steele, 1999; Ford et al., 2016). However, given the observed effect of distance, which, is mainly associated with fishing activities highly variable at small-spatial scales (between islands apart for ~3 km), we would not expect structural and benthic predictors to explain much variation in terms of abundance and biomass. Future studies should examine the effect of fishing on parrotfishes while accounting for the influence of distance from the coast on ontogenetic variability in habitat use.

Our results have not demonstrated a significant effect of the no-take marine reserve Tamoios Ecological Station on *S. frondosum* variability in IGB, but the largest abundance was recorded for one MPA site (Búzios island, mean of 5.3 ind. 40 m⁻²) which is larger than reported for some rocky-reefs of the southwest Atlantic (Floeter et al., 2007; Roos et al., 2019). The lower abundance of *S. frondosum* in non-protected reefs near to Búzios island (e.g. Redonda island, Table S1) indicates a local effect of protection possibly related to effective enforcement and the reduced individuals mixing between reefs of near islands. In fact, parrotfishes of the *Sparisoma* genus may have a small preferential site; although, natural barriers (large areas of the sandy substrate) are crossed by some individuals (La Mesa et al., 2012; Garcia et al., 2014), limiting the effectiveness of fragmented reserves. Consequently, the recovery of target fish depends on the implementation of fisheries management measures in the open-access area. In 2018, the Brazilian government issued an Executive Order (Portaria 63/2018) that regulated *S. frondosum* fishing under strict rules, including the ban of recreational spearfishing, the control of specific gears (e.g. traps) and the establishment of slot sizes. Beyond that, *S. frondosum* can only be fished in management areas linked to spatial planning measures. Nevertheless, parrotfishes remain targeted by recreational spearfishing in IGB since control over commercialization and better-informed consumption are major gaps for reef fish (Freitas et al., 2019). Scientific evidence to implement fishery management areas are scarce for most regions of the Brazilian coast. Here, we demonstrated that sites deeper and further from the coast should be considered in spatial planning to protect *S. frondosum* within a length range between 10 and 40 cm TL. Therefore, we are unable to recommend specific suggestions for smaller juvenile fishes (<10 cm), which were largely absent in this study. It is important to identify the nursery grounds of *S. frondosum* in the region and incorporate them to MPA planning and management. However, the protection of the main nursery areas is not enough to prevent the species from declining, probably because of intensive fishing pressure on adults (Roos et al., 2020).

Our results suggest that *S. frondosum* would benefit from extending MPAs towards deeper areas. In fact, a mosaic of no-take, restricted take, and fished zones already exists in IGB, where the no-take ESEC-Tamoios is interconnected with Environmental Protected Areas (e.g. APA Tamoios, APA de Cairuçu and APA Paraty), but it needs baseline information, strategic planning, and regular monitoring to become effective (Roff, 2014; Stratoudakis et al., 2019). We observed that sites near Búzios island (Papagaio, Longa and Alvo sites) which concentrate most of *S. frondosum* occurrences in the bay are good candidates for effective management measures. Despite the well-documented benefits of no-take MPA in protecting endangered species targeted by fisheries (Edgar et al., 2014), to expand no-take areas in coastal systems marked by their conflicts between fisheries and tourism is challenging (Lopes et al., 2015; de Freitas et al., 2017). Therefore, mobilizing resources for better enforcement of MPA sites with habitat features that maximizes parrotfish abundances is needed.

In conclusion, this study highlighted a strong influence of distance from the coast and depth on the distribution patterns of *S. frondosum*, which can be related to less fishing pressure and increased surface area for fish use (e.g. foraging, resting). Also, the effect of reduced surface

area for fish foraging was indicated by the negative influence of the invasive coral *Tubastraea* spp. on both fish abundance and biomass and needs further investigation. In the context of harvesting and diffuse sources of disturbances, few sites concentrated most of *S. frondosum* individuals in IGB and adjacent sites (e.g. less than 3 km from each other) sharply varied in fish abundance. It indicates the need for conservation practices that act at relatively small spatial scales, such as increasing enforcement efforts on sites that maximize the representation of the most influential drivers for species occurrence. Also, expand protection from these most representative sites in terms of abundance or biomass of target species to adjacent areas may contribute to improving MPA design.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ocecoaman.2021.105642>.

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