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Hierarchizing biological, physical and anthropogenic factors influencing the structure of fish assemblages along tropical rocky shores in Brazil

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Abstract Understanding the distribution patterns of reef fish and the relationships between those patterns and habitat and anthropogenic factors is important for the development of conservation policies by environmental managers. Fish assemblage structure was studied over 22 rocky shores with different physical complexity and benthic cover in Ilha Grande Bay, Southeastern Brazil. We aimed to test the relative influences on rocky reef fish assemblage descriptors (richness, density and biomass) of three categories of predictors: 1) biological features as dominant benthic cover (in percentage), i.e., fleshy algae, turf algae and soft coral; 2) physical factors, i.e., depth and a physical structure index; and 3) anthropogenic factors, i.e., distance from the coast, population of the nearest city, and influence of a marine protection area. The main explanatory variables determining fish assemblage structure according to the distance based linear model (DistTLM) were depth (explaining 16.7 % of the variation) and distance from the coast (14.0 %), followed by population of the nearest city (3.7 %) and turf algae (2.9 %). Similarly, fish species richness was positively associated with deeper areas and greater distance from the coast, thus being less accessible to human influence. Fish density and biomass increased with distance from the coast, and this relationship is likely linked to the presence of large top predators and herbivores. Moreover, fish richness and density increased with the physical complexity indicated by the physical structure index, suggesting that the presence of a variety of refuges enhances the availability of shelter. We recommend that areas farthest from the urban centres and with higher physical complexity should be prioritised in conservation policies.

Keywords Fish assemblage · Habitat structure · Shallow waters · Anthropogenic impacts · Conservation

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Introduction

Responses of marine assemblages to habitat components can be used to identify the specific physical or ecological attributes influencing distribution patterns (Moore et al. 2010). Factors known to influence the spatial patterns of reef fish assemblages include the biological, such as benthic cover (Chittaro et al. 2005; McClanahan and Karnauskas 2011), physical, such as depth (Srinivasan 2003) and wave exposure (Floeter et al. 2007), and anthropogenic, such as sewage pollution (Azzurro et al. 2010), fishing pressure (Floeter et al. 2006) or proxies of human influences such as distance from a specific source (e.g., discharge of sewage or thermal effluent) and demographic metrics (Nguyen and Phan 2008; Vincent et al. 2011; Gibran and Moura 2012). Hierarchizing the influences of these various factors on the responses of species and assemblage structures to major environmental gradients requires the use of spatial models that incorporate the combined influence of those factors. Identifying the most important factors that determine spatial patterns of marine organisms is an essential step in helping environmental managers design effective conservation measures.

Habitat structure (biological and physical) is known to be among the main factors structuring fish communities (McGehee 1994; Lara and Gonzalez 1998; Wantiez and Chauvet 2003). Further, benthic composition is an important factor structuring habitat complexity (Bouchon-Navarro and Bouchon 1989; Jones et al. 1991; Munday 2002; Floeter et al. 2007), adding niches to a diverse fauna of mobile and sessile invertebrates. Benthic organisms may also contribute to structural complexity provided by boring and arborescent organisms on a scale of centimetres and can provide meso-scale habitat modification for small benthic fishes (Stephen et al. 2006). Physical structure (Luckhurst and Luckhurst 1978; Roberts and Ormond 1987; Ohman and Rajassuriya 1998; Teixeira et al. 2012) is closely related to fish species richness and can reduce predation and competition by providing more refuges, contributing to decreased encounter rates between predators and prey prey, and increasing the availability of resources such as food, shelter, and spawning areas (Murdoch and Oaten 1975; Letourneur 1996; Friedlander and Parrish 1998; Almany 2004; Grober-Dunsmore et al. 2008). Relationships of physical characteristics of the habitat such as depth (Williams 1991; Srinivasan 2003) and complexity with fish community structure have been reported elsewhere (Carpenter et al. 1981; Mcmanus et al. 1981; Grigg 1994; Chabanet et al. 1997; Lewis 1997; Adjeroud et al. 1998).

The process of human development, with the growth of urban centres and demand for natural resources, is increasingly affecting coastal environments. Fish assemblages may not respond directly to human population density but may respond instead to a variety of direct and indirect factors, such as urban development, tourism, fishing, sedimentation, and habitat degradation, that are related to human population density (Benjamin et al. 2012). Fish assemblages may respond to disturbances such as sewage discharges (Russo 1982; Smith et al. 1999; Guidetti et al. 2002; Islam and Tanaka 2004) and fishing (Grigg 1994; Chabanet et al. 1995; Otway et al. 1996) that influence the diversity, dominance, biomass, abundance, reproductive inhibition or failure and trophic structure. Therefore, variables such as distance from the coast (Williams 1982; Green et al. 1987; Adjeroud et al. 1998; Lecchini et al. 2003) and population of the nearest city (Vincent et al. 2011) can be used as a proxy for changes in spatial structure and distribution of fish assemblages. Concerns have been raised regarding the increasing degradation of coastal areas. Marine protected areas (MPAs) are an alternative for managing and conserving littoral resources (Lester et al. 2009; Halpern et al. 2010). One objective of unfished zones in MPAs is to help maintain viable fisheries in adjacent areas by increasing the density and size of fish, providing centres for dispersal of individuals and larvae, and augmenting local fishery yields through biomass exportation from the protected area (García-Charton et al. 2008). Although this region has an MPA, it is poorly managed and is affected by factors including coastal development (e.g., port activity, thermal pollution, sewage discharge) and fishery activities (bottom trawling, recreational fisheries targeting reef fishes). Consequently, quality assessment and monitoring of marine ecosystems has become increasingly important to ensure their sustainability (Spatharis and Tsirtsis 2010; Borja et al. 2012).

In Brazil, the vast majority of the literature on rocky shores fish assemblage is focused on describing fish composition and its relationship with habitat structure (Ferreira et al. 2001; Floeter et al. 2007; Krajewski and Floeter 2011). However, few studies have been conducted to assess the influences of anthropogenic factors (Floeter et al. 2006) and both biotic and abiotic variables, exploring their eventual interactions, and hierarchizing their influence on fish assemblages. In this study, we aimed to test the relative influences of these three categories of predictors (biological, physical and anthropogenic factors) on descriptors (richness, density and biomass) of fish assemblages.

Material and methods

Study area

Ilha Grande Bay (IGB) is located in the southern tip of Rio de Janeiro state (23°06 S, 44°42 W), SE Brazil, and covers an area of approximately 600 km^2, containing approximately 350 islands surrounded by shallow water (typically no more than 8 m in depth) (Ignacio et al. 2010). The bay is an oligotrophic system that is

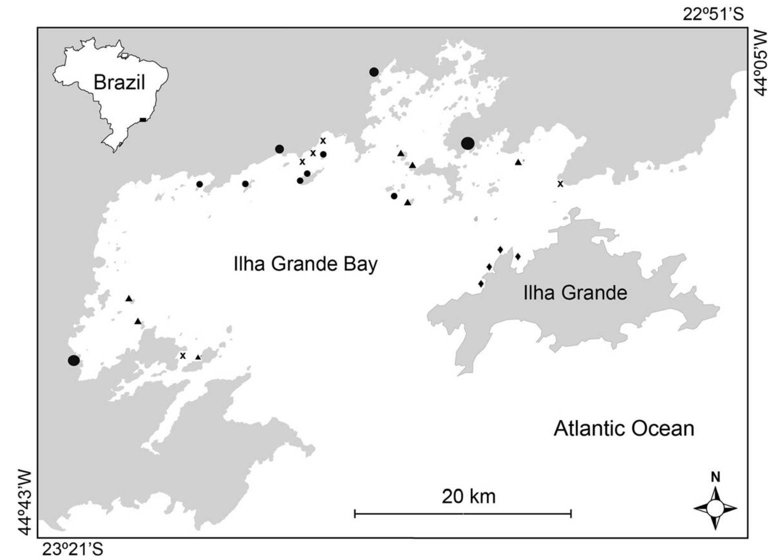

Fig. 1 Map of Ilha Grande Bay showing the study sites. Mainland sites are represented by axes, MPA sites by *circles*, islands by *triangles*, and Ilha Grande Island rocky shores by trapezoids. *Large circles* in the mainland represent most populous cities in the area

freely connected to the Atlantic Ocean (Fig. 1), receiving no significant input of freshwater from rivers. The shoreline is highly jagged, and coastal mountains reach the coastline, leaving little space for coastal plain evolution (Guerra and Soares 2009). Economic activities conducted in IGB include tourism, power generation (nuclear power plants), shipyards, private marinas, oil terminals and fisheries. Despite its economic and ecological importance, IGB has not been the subject of systematic biological studies. The main physiographic structure of the study area is characterised by narrow rocky shores covered by granite boulders, ending in a sand bottom (interface). The sampled rocky shores had average depths ranging from 2.1 (shallow) to 5.1 m (interface). IGB has an MPA at the Ecological Station of Tamoios that began to operate in 1990 and comprises twenty-nine islets, islands, rocks and slabs. Progressively increasing threats to the bay include sewage discharge from coastal development, industrial fisheries (including destructive bottom trawling) and recreational fishing targeting rocky reef fishes (harpoon and hook-and-line fishing).

Sampling surveys

Fish assemblages and habitat characteristics of twenty-two rocky shores (sites) were selected: five in the mainland, seven in the islands, six in the MPA and four around Ilha Grande. Sampling was conducted in the winters of 2010 and 2011. Rocky shores were chosen in areas sheltered from wave activity, far from point sources such as river discharges, mangroves, sewage outfalls and thermal discharges; thus, confounding effects were avoided, and the influences of the selected environmental variables could be better assessed. Underwater visual censuses were performed along transects of 20×2 m (40 m^2) following current practice along the Brazilian coast (Ferreira et al. 2001; Floeter et al. 2006, 2007; Krajewski and Floeter 2011), at “shallow” (the upper limit of the low tide) and “interface” (situated on the consolidated substrate, at least 2 m from the sand/rocky interface) zones at each site. The depth of the “shallow” zone varied from 1.2 to 2.9 m, whereas that of the “interface” area varied from 3 to 7.2 m. At each site, six evenly spaced transects were performed (three transects at each depth zone), totalling 114 transects in the entire study area. Each transect was sampled twice for fish counts. In the first pass, the diver swam along the transect and recorded all mobile fishes in water column. In the second pass, the observer focused on searching beneath rocks and in crevices to observe the more cryptic species (e.g., Blenniidae, Gobiidae, Muraenidae). The sampling unit, number of fish per 40 m^2, was defined as the pooled number of mobile and cryptic fishes.

Physical structure

The quantitative assignment of physical structure was based on depth and a physical structure index. The depth was obtained through the average of three measurements for each fish transect, evenly spaced along the length of the transect. Twenty photographs were taken at each fish sampling and were used to quantify the variables describing physical structure following Chapman et al. (1995). A digital camera was mounted onto a 0.36 m^2 polyvinyl chloride (PVC) photo quadrat frame, and the following physical characteristics were quantified posteriorly: (1) number of refuges (holes and crevices); (2) percentage of hard substratum; (3) number of rocks of different sizes. The fourth characteristic, (4) substratum height, was estimated during the sampling. Number of refuges and number of rocks were grouped in three size ranges (<30 cm; 30 cm-1 m; >1 m) following the method proposed by Aburto-Opereza and Balart (2001). Holes, crevices and rocks of different sizes form gaps between structures that can provide paths for fish to escape from predators. "Hard substratum" refers to the percentage of substratum that was not sand, rubble or shell-sand patches. Substratum height was a subjective visual estimate taken at an intermediate position between the top of the rocks and the lowest point for each transect. The physical structure index was adapted from Gratwicke and Speight (2005). The scores were 1 for lowest, 3 for intermediate and 5 for the highest physical complexity. For example, rocky shores with a single refuge size receive scores of 1, whereas those with refuges of all different size categories receive scores of 5. A total score was calculated by adding the scores of each of the four physical characteristics to give an estimate of the overall degree of complexity of the sites (Table 1).

Benthic cover

Photographs were also analysed to measure the percentage of benthic cover using Coral Point Count with Excel Extensions-CPCe 3.4 (Kohler and Gill 2006) by overlaying 20 random points on each image and identifying the substratum under each point. Benthic organisms, expressed as percentage of benthic cover, were grouped as follows: 1) fleshy algae, comprised mainly of crustose carbonate algae, coenocytic thalli, and *Sargassum* spp.; 2) turf algae, composed of a matrix of small macroalgae mainly belonging to the orders Corallinales, Ceramiales and other green and red filamentous algae (Thrush et al. 2011); and 3) soft coral, represented by the Zoanthids *Palythoa caribaeorum* and *Zoanthus sociatus*. Other invertebrates, such as tunicates, cirripedia, sponges, hydrozoa, Echinodermata, bryozoans and hard coral (scleractinians such as *Mussismilia hispida* and the invasive corals of the genus *Tubastraea*) occurred rarely in this area and were not included in the analyses.

Anthropogenic factors

The following variables related to anthropogenic influence were included in this study: 1) distance from the coast; 2) population of the nearest city; and, 3) whether the site was inside or outside an MPA. The distance from the coast (measured in kilometres) was included as a proxy of anthropogenic influences because the rocky shores were comparatively less accessible to human influence. For the rocky shores closer to the coast, where there are ramps, marinas and beaches, access to the islands by small boats in the bay also means greater influence of anthropogenic activities. The population of the nearest city can characterise the influence of urban disturbances on the marine environment in relation to the intensity of exploitation of nearby coastal resources. The MPA was also characterised as a factor related to anthropogenic influence. Although the enforcement of

Table 1 Scoring system for the physical structure index and the recorded values for each physical characteristic

Descriptors	Physical structure score		
	1	3	5
(1) Number of refuge size categories (holes and crevices in the following size categories for each refuge type: <30 cm; 30 cm-1 m; > 1 m)	0–1	2–4	4–6
(2) Hard substratum (%)	0–20	20–40	40–50
(3) Substratum height (visual estimate of height of physical structure-cm)	0–50	51–100	>100
(4) Number of rocks of different sizes (in the three following size categories: <30 cm; 30 cm-1 m;> 1 m)	0–1	2	3

restrictive measures is inadequate, we expect that areas inside the MPA may be better preserved than areas outside the MPA because they are legally protected.

Data analyses

The following response variables derived from the fish assemblage data were used: fish assemblage structure, fish richness, density and biomass. Total numbers of species (richness) and individuals (density) were calculated based on observations from each transect. Total fish biomass per transect was estimated by length-weight relationship curves and allometric conversions: $W=a\times L^b$, where parameters 'a' and 'b' are constants for the allometric equation from FishBase (www.fishbase.org), Macieira and Joyeux (2008) and Camilato et al. (2010). When coefficient values were not available for the species, we used coefficients for the most closely related species. For the other parameters, the size range and nearest region were chosen. Prior to analyses, fish assemblage, fish richness, density and biomass data were square-root transformed. Bray-Curtis similarity matrices were calculated for multivariate data (fish assemblage), while Euclidean similarity matrices were used for univariate variables (fish richness, density and biomass). Pairwise correlation coefficients were calculated between all predictors to detect eventual co-linearity ($r<0.7$; Sleeman et al. 2005; Leathwick et al. 2006), but no significant associations were found among these variables.

The relationships between fish assemblage descriptors (fish assemblage structure, fish richness, density and biomass) and the explanatory variables were analysed using distance-based linear models (DistLM; Legendre and Anderson 1999; McArdle and Anderson 2001) in the software PRIMER-E+. DistLM analysis was used to identify which of the potential examined variables explained most of the variability in fish assemblage. The "best" selection method, according to the Akaike Information Criterion (AIC), was used to select the final model. Moreover, a distance-based redundancy analysis (dbRDA, Legendre and Anderson 1999; McArdle and Anderson 2001) was used to detect patterns between the selected variables and fish assemblage. This routine performs a constrained ordination of the fish assemblage data using the most parsimonious DistLM model. To validate the interpretation of the dbRDA, a distance-based principal coordinate analysis (PCO) was used following Anderson et al. (2008). Species raw Pearson correlations with the first two dbRDA axes were then examined to identify the dominant species driving the response of the fish assemblage structure to the physical, biological and anthropogenic predictors. The strength and direction (positive or negative) of the associations between the univariate fish assemblage descriptors (fish richness, density and biomass) and the selected variables according to DistLM analyses were identified using the multiple partial correlations of the variables with the first dbRDA axis and scatterplots.

Results

A total of 67 fish species, distributed over 34 families, were identified during the entire survey. The distance-based multivariate linear model (DistLM) analysis indicated significant relationships between fish assemblage and six of the predictors: depth, distance from the coast, population of the nearest city, percentage of turf algae, percentage of fleshy algae and percentage of soft coral. Together, these factors accounted for 39.2 % of the variance in the fish assemblage. Depth was the most important environmental factor, explaining 16.7 % of the total variation, followed by distance from the coast (14.0 %) (Table 2). The remaining variables contributed a small but significant component of the variance. These included the population of the nearest city (3.7 %) and the percentages of turf algae (2.9 %), fleshy algae (1.6 %) and soft coral (0.3 %). Turf algae, fleshy algae and soft coral occurred almost in all sampling sites. In fact, turf and fleshy algae were found at 100 % of the sites surveyed and accounted for approximately 36.9 and 23.9 % of the benthic cover of the habitat, respectively. Soft corals were also common, identified at 94.7 % of the sites and accounting for 25.1 % of the benthic cover.

The first dbRDA accounted for 16.7 % of the total variation in the fish assemblage and distinguished sites dominated by depth (shallow and interface sites) (Fig. 2a). The first dbRDA axis was positively correlated with the percentages of turf algae ($r=0.57$), the percentage of soft coral ($r=0.49$), the population of the nearest city ($r=0.35$) and the percentage of fleshy algae ($r=0.23$) and was negatively correlated with depth ($r=-0.49$). The second dbRDA axis was positively correlated with depth ($r=0.62$) and distance from the coast ($r=0.68$). The first axis clearly represented the gradient of depth on the rocky shores studied, with the right side

Table 2 Results of the distance-based multivariate linear model (DistLM) for the fish assemblage, showing the percentage of variation explained by significant environmental variables ($P<0.001$)

Axis	Percentage of variation explained by individual axes			
	% Explained variation (fitted model)		% Explained variation (total variation)	
	Individual	Cumulative	Individual	Cumulative
Depth	42.62	42.62	16.73	16.73
DistCoast	35.79	78.41	14.05	30.78
Population of nearest city	9.46	87.87	3.71	34.49
% Turf algae	7.38	95.25	2.90	37.39
% Fleshy algae	4.00	99.25	1.57	38.96
% Soft coral	0.75	100.00	0.29	39.26

DistCoast Distance from the coast

characterised by shallow sites with increasing depth towards the left (Fig. 2a). Two groups were defined a posteriori – shallow areas and deeper areas (near the interface). As an additional way method of validation, the dbRDA, a constrained ordination that uses the model results, was compared to an unconstrained Principal Coordinates Analysis plot (Fig. 2b). The two plots approximate each other, indicating that our model is capturing the main patterns of variation (Anderson et al. 2008).

To determine which environmental variable or combination of environmental variables were represented by the dbRDA axes, raw Pearson correlations of each variable with each dbRDA axis were examined (Table 3). The omnivores with shoal distribution, *Diplodus argenteus* and *Abudefduf saxatilis*, along with the territorial herbivore *Stegastes fuscus*, were positively correlated (Pearson correlations of>0.3) with axis 1, associated with the percentages of turf algae, fleshy algae and soft coral. The groupers with heavy fishing pressure, *Mycteroperca bonaci* and *Mycteroperca acutirostris*, along with the invertivores *Anisotremus virginicus* and *Serranus flaviventris*, were negatively correlated with axis 1, indicating that they are associated with deeper areas. Axis 2, associated with depth, distance from the coast, percentages of turf algae and soft coral and population of the nearest city, was positively correlated with 17 species, whereas the puffer fish *Sphoeroides greeleyi* showed the opposite pattern (Table 3).

The DistLM showed that 53.3 % of the variation in the richness was attributed to the three following variables: physical structure index, depth and soft coral. Physical structure index and depth were negatively correlated with the first dbRDA axis, indicating a positive association with species richness (Fig. 3). Depth was strongly correlated with the first dbRDA axis (multiple partial correlation=–0.91). Physical structure index and soft coral were correlated with the first dbRDA axis (multiple partial correlations=–0.40 and –0.01, respectively) (Table 4). Density showed significant correlations with the physical structure index and distance from the coast. This model explained 30.2 % of the variance. The highest fish density was found in sites with the highest values of the physical structure index (–0.546) and the highest distance from the coast (–0.838). The biomass was strongly inversely correlated with the distance from the coast (–1.0), with this model explaining 27.4 % of the variance (Fig. 3 and Table 4).

Discussion

Our data indicate that depth, distance from the coast, population of the nearest city and the dominant benthic cover are the best predictors of rocky reef coastal fish assemblage structure in the rocky shores of IGB. Moreover, the physical structure index and distance from the coast explained most of the variation in fish richness, density and biomass. There was a positive relationship between the physical structure index, richness and density, whereas distance from the coast was positively correlated with density and biomass.

We found higher fish richness in the deeper sites than in the shallow sites. Deep sites are located in areas between the consolidated substrate and the sandy bottom, a transition zone that favours increases of species richness where species pass through for foraging and

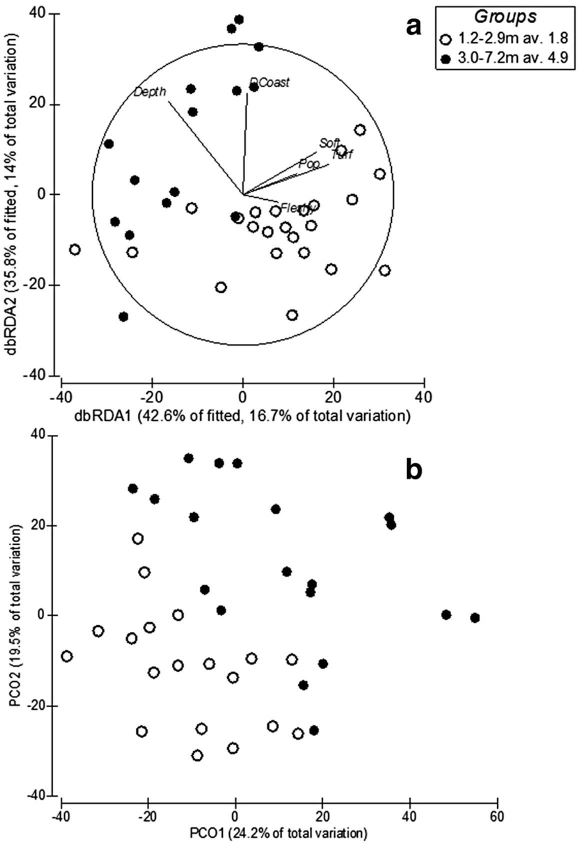

Fig. 2 Ordination diagrams of the first two axes of the Distance-Based Redundancy Analysis (dbRDA) (**a**) and Principal Coordinates Analysis (PCO) (**b**), showing samples from the shallow (*empty circles*) and interface (*filled circles*) sites. Axes describe the percentage of variation of the selected model in terms of the total variation of the fish assemblage. Vectors in dbRDA represent the environmental variables comprising the best selected models (from Akaike's information criterion). Codes for variables: *DCoast* Distance from the coast, *Pop* population nearest city, *Turf* % turf algae, *Fleshy* % Fleshy algae, *Soft* % Soft coral

camouflage in the sand. Moreover, these sites are suitable for predators such as serranids to search for prey. By contrast, shallow sites are characterised by consolidated substrate only, thus offering less habitat diversity for fishes. Mendonça-Neto et al. (2008) also found that species richness increases from shallow to interface areas in a tropical region along the southeastern coast of Brazil. The vertical distribution of reef fish assemblages is highly correlated with the vertical distribution of benthic organisms, and it appears to be determined by factors such as habits and feeding behaviours, refuge from predation and social interactions (Ferreira et al. 2001). García-Charton and Pérez-Ruzafa (1998) also found a strong correlation between fish assemblage structure and depth for Mediterranean rocky shores, and Gibran and Moura (2012) found a similar correlation across a gradient from nearshore areas to coastal islands in Southeastern Brazil. In these studies, the direct effects of depth are associated with pressure, low temperature and lowlight intensity, as reported by Srinivasan (2003).

Because microhabitat structure often changes with depth (Done 1982), distributions of fishes may be explained by the availability of preferred microhabitats (Srinivasan et al. 2010). However, in shallow rocky shores of IGB, the influence of depth on the fish assemblages may be more closely related to its indirect effects on increasing availability of substrate (by increasing the surface area of the shore). Availability of rocky surface is a critical factor for reef fishes, and reef sites with higher depths present greater hard surface area and more diverse structures in which marine life can settle. Increases in habitat area often create a mosaic of microhabitats that are separated by barriers such as corridors and patchily distributed resources. These factors play an important role in altering competition, predation and dispersion rates in different species (Kareiva 1990) and thus have consequences on overall diversity. This highlights the importance of depth in structuring the distribution of the fish species in this study.

The highest fish densities were also found in sites with the highest values of the physical structure index. This index was designed in a robust manner to compare a range of physical complexities such as the number of refuges of various size categories (holes and crevices), the percentage of hard substratum, and the height and number of rocks of different sizes. Possible explanations for the increased number of fishes in rugose areas include increased refuge from predators or increased primary productivity on the hard surfaces that can support more fishes (Gratwicke and Speight 2005). Physical complexity has been widely used in coral reefs worldwide as a good predictor of fish diversity (Chabanet et al. 1997). Increasing the variety of refuge sizes would enhance species richness by increasing the availability of refuges to species with differing body sizes (Luckhurst and Luckhurst 1978), thereby reducing predation and competition, contributing to decrease encounter rates between predators and preys, and increasing resource availability (Almany 2004). Physical features such as rocks and holes of various sizes provide shelter and reproductive grounds for fish species (Aburto-Opereza and Balart 2001). Therefore, the

Table 3 The first two axes for best discriminating fish species (>0.3) of the fish assemblage, based on with heavy fishing pressure (Floeter et al. 2006)* and trophic category classification (Ferreira et al. 2001, 2004)

Species	RDA1	RDA2	Trophic category
Mycteroperca bonaci	−0.457	–	Piscivore*
Anisotremus virginicus	−0.530	–	Mobile invertebrate feeder*
Mycteroperca acutirostris	−0.561	–	Pscivore*
Serranus flaviventris	−0.591	–	Mobile invertebrate feeder
Diplodus argenteus	0.512	–	Mobile invertebrate feeder
Abudfduf saxatilis	0.433	–	Omnivore
Stegastes fuscus	0.390	0.377	Territorial herbivore
Coryphopterus glaucofraenum	–	0.370	Mobile invertebrate feeder
Chromis multilineata	–	0.394	Planktivores
Cantherhines pullus	–	0.394	Omnivore
Epinephelus morio	–	0.407	Carnivore*
Epinephelus marginatus	–	0.445	Carnivore*
Haemulon aurolineatum	–	0.448	Mobile invertebrate feeder
Sparisoma axillare	–	0.474	Roving herbivore*
Stegastes pictus	–	0.475	Territorial herbivore
Serranus baldwini	–	0.502	Mobile invertebrate feeder
Elacatinus figaro	–	0.512	Mobile invertebrate feeder
Halichoeres poeyi	–	0.514	Mobile invertebrate feeder
Odontocion dentex	–	0.539	Carnivore
Acanthurus chirurgus	–	0.549	Roving herbivore
Canthigaster figueiredoi	–	0.562	Sessile invertebrate feeder
Sparisoma frondosum	–	0.619	Roving herbivore*
Pomacanthus paru	–	0.626	Omnivore
Sphoeroides greeleyi	–	−0.442	Mobile invertebrate feeder

physical structure index is an important predictor for fish assemblage structure and density in IGB coastal reefs.

Densities of individual species were notably higher at greater distances from the coast, likely representing reduced levels of disturbance and impacts from various sources on the mainland (e.g., sedimentation, sewage pollution, and discharge from the rivers). Coastal areas at the sites close to the mainland have been degraded, and those waters were very turbid compared to the offshore areas. These findings are consistent with previous studies, which demonstrated that high sedimentation and low transparency indirectly influence fish distribution (Letourneur et al. 1998) or directly reduce coral diversity and coverage (Loya 1976). Benjamin et al. (2012), studying environmental factors affecting coral reef fish in the Mariana Archipelago, found that proximity to areas of high human population is likely to affect the distribution of large-bodied fishes that have a negative association with population density. Species correlated positively with distance from the coast belonged to the most important families of the herbivorous and carnivorous fishes. Species such as parrotfishes (*S. frondosum* and *S. axillare*) and groupers (*E. marginatus, E. morio, M. bonaci* and *M. acutirostris*) suffer from heavy fishing pressure all along the Brazilian coast (Floeter et al. 2006). The association of these species with distance from the coast indicates the importance of human action in populations of reef fishes. This trend is consistent with the expectation that harvesting pressure is lower in areas away from the coast, due to the increasing difficulty of human access (Floeter et al. 2007). Distance from the coast of the mainland (source of impacts from the mainland) is also important in structuring fish communities (Nguyen and Phan 2008).

The fish biomass was also correlated with the distance from the coast. The low abundance of large predators and herbivores found in this study indicates that fishing is an important factor structuring fish populations on IGB. Historically, this bay was well populated

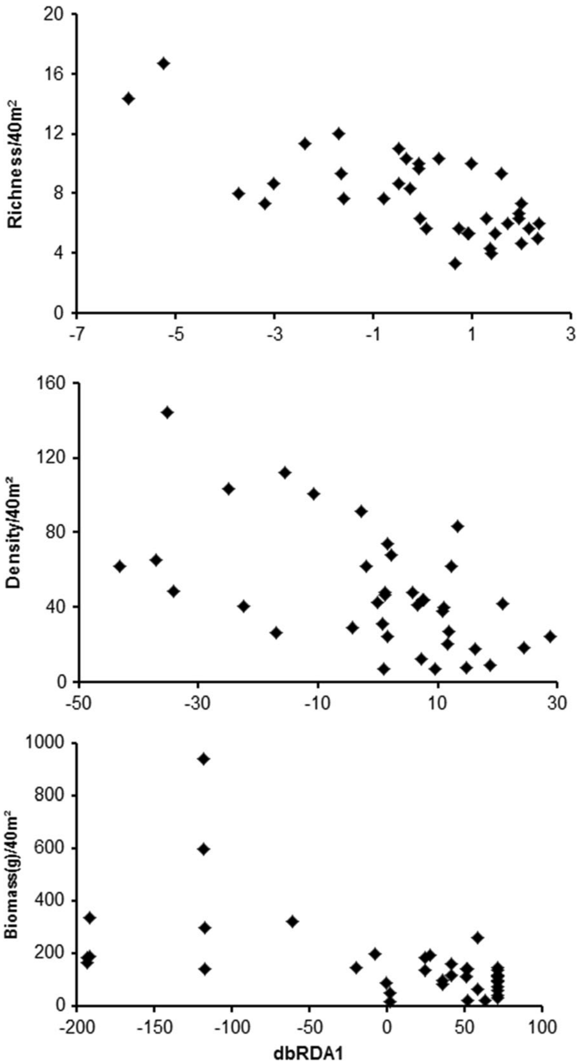

Fig. 3 Scatterplot diagram comparing fish response variables (richness, density and biomass) and the first Distance-based Redundancy Analysis (dbRDA) axis

with larger groupers (pers. obs.), all of which were prized as food fish. Local resources exploited by the artisanal fisheries in the region include rocky reef species such as groupers (*Epinephelus* spp. and *Mycteroperca* spp.) and snappers (*Lutjanus* spp.) (Begossi et al. 2011). Fisheries appear to be affecting the population size and size structure of fish populations in studies on other coastal reefs in Brazil (Ferreira and Gonçalves 1999; Frédou 2004; Gasparini et al. 2005; Floeter et al. 2006). Stuart-Smith et al. 2008, studying fishing impacts and the relationship with distance from the nearest boat launching ramp, found low numbers of large fish and a greater number of smaller fish at the sites closest to access points.

Fish biomass is likely the most important factor in accessing the status of reefs (Sabater and Tofaeono 2007; Francini-Filho and Moura 2008); thus, this variable has direct implications for management. Reef sites with the highest number of human communities are those that have the poorest water quality, the lowest coral cover and the lowest fish biomass (Dinsdale et al. 2008). In the Brazilian National Park at the Abrolhos Reef, a system with predominant coral cover, significant spatial variability was recorded, with the highest values for fish biomass occurring in protected areas (Leão et al. 1988; Floeter et al. 2001; Francini-Filho and Moura 2008; Bruce et al 2012). This confirms that MPAs help maintain viable fisheries by augmenting local fishery yields through biomass exportation from the protected area (García-Charton et al. 2008).

Biological factors such as benthic organisms may interfere in reef relief by increasing the structural complexity provided by boring and arborescent organisms, which, on a scale of centimetres, can provide mesoscale habitat modification for small benthic fishes (Stephen et al. 2006). In IGB, benthic cover the percentages of turf algae, fleshy algae and soft coral) represented a small (<5.0 %) influence on fish assemblage structure. Although benthic cover on rocky shores is very important in determining the habitat structure, when analysed with other variables, it appears to have only limited influence on fish assemblages. Previous studies on fish community structure have shown high levels of variance explained by benthic cover (Chabanet et al. 1997;

Table 4 Results of the distance-based multivariate linear model (DistLM) for the univariate variables richness, abundance and biomass. AIC, Akaike's information criterion; RSS, Residual sum of squared errors

Descriptors	AIC	R^2	RSS	N° Groups	Selections
Richness	59.619	0.5333	147.82	3	Physical structure index, depth and soft coral
Density	254.42	0.3022	26,235	2	Physical structure index and distance from the coast
Biomass	380.43	0.2743	761,910	1	Distance from the coast

Ferreira et al. 2001; Gratwicke and Speight 2005; Floeter et al. 2007). However, Kuffner et al. (2010) found a weak relationship between benthic cover and fish assemblage variables. The lack of relationships is consistent with several mechanisms, including stochastic larval dispersal, priority effects of early colonisers, and human disturbance (fishing) (Kuffner et al. 2010). Moreover, studies on benthic cover influences determined "a priori" as a factor (e.g., levels of a given benthic cover; incrusting versus arborescent algae/coral; flat vs. complex coral) are more likely to have confounding results. Furthermore, potential generalisations may be obscured due to a number of factors. These include the enormous variation in the magnitude of changes to habitats observed, restrictive assumptions about the forms of relationships between fish and benthic variables, inadequate descriptions of habitat and fish community structure, a heavy reliance on 'natural', pseudoreplicated experiments and a plethora of different numerical and analytical techniques (Syms and Jones 2000).

In this study, we observed high similarity in the benthic cover among the sites, which likely reduces the variability of this factor. The high frequency in the sampled sites of turf, fleshy algae and soft coral were likely associated with the weak relationship between benthic cover and fish assemblage. However, the sites with the highest percentage of soft coral showed the lowest richness. Rocky shores dominated by soft coral such as *P. caribaeorum* may reduce the amount of shelter available to fishes by overgrowing reef crevices and by reducing benthic diversity, consequently limiting food resources (Mendonça-Neto et al. 2008). Zoanthids do not generate complexity, and by covering huge portions of the reef substratum, they can actually flatten the available complexity (Mueller and Haywick 1995; Haywick and Mueller 1997). The absence or low abundance of *P. caribaeorum* provides more space in those sites for algal growth, which potentially benefits herbivores. In addition to soft coral, small fouling organisms that do not form large structures, including algae mostly composed of turf, were common in IGB. Although turf algae does not form complex structures, it provides strong effects on the distribution of macrofaunal organisms that live in the turf matrix and is very important for invertivore fish species as well as herbivores (Giangrande 1988; Sarda 1991; Kelaher et al. 2001).

The Ecological Station of Tamoios MPA, despite having been in place for 24 years, has not shown responses to the biological, physical or anthropogenic variables tested in this study. Perhaps the lack of oversight prejudices the efficiency of these islands as protected area. Most areas of the Tamoios MPA are subject to insufficient enforcement measures, and some of them must even be considered merely as "paper" reserves. As is often the case in Brazilian protected areas, this MPA was created through a top-down approach, by a governmental decree that delimits its boundaries but does not resolve pending resource conflicts (Begossi et al. 2011). Although nominally under federal management and protection, as are most such areas created by governmental fiat, its legitimacy and credibility among artisanal fishers are weak (Begossi et al. 2010). Local conflicts include rules for the use of fishing areas established by artisanal fishers inside the MPA and the advent of protected areas that close access to some fishing areas used by artisanal fisheries (Begossi et al. 2011).

We assigned the characteristic of "in" or "out" for the sites within and outside the MPA together with other habitat structure and anthropogenic variables in the model. This approach is important to avoid overestimate the effects of the MPA on fish assemblage compared with studies that consider only the site location within or outside the MPA. Protected and non-protected areas differ in accessibility, exploitation intensity, and fisheries activities, as well as in the effectiveness of enforcement measures (García-Charton et al. 2004; Claudet et al. 2010). Côté et al. (2001) compared data for 19 marine reserves worldwide and concluded that the effect on fish abundance is highly variable, based on factors such as intensity of exploitation outside protected areas, variation in enforcement efficiency, and habitat characteristics. Therefore, caution is required when designing and developing programs to test the efficiency of MPAs, considering the potential influences of anthropogenic activities and habitat structure.

In the case study of IGB, we found that the distance from the coast was the predictor that best explained the response variables, showing the importance of preserving coastal areas that are losing species diversity. The areas near the coast showed low levels of richness, density and biomass, whereas areas farther from the coast or more difficult to reach showed the opposite pattern. These areas should be constantly monitored to avoid human disturbance. Moreover, re-organisation and expansion of the MPA should be an important management practice to protect fish species, especially large predators and herbivores.

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