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Depth, hard coral, and turf cover as predictors of micro-scale spatial distribution of fishes in a subtropical rocky reef

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Abstract The combination of the physical structural heterogeneity of the environment, oceanographic characteristics, and the benthic assemblage composition structures the habitat, consequently shaping the associated diversity of fish. Understanding the spatial variability of fish assemblages and how it relates to environmental factors is essential to identify potential variables that determine spatial patterns and predict impacts on fish assemblage metrics, thus providing valuable information for management. Here, we investigated reef fish micro-scale spatial distribution around Alcatrazes Island in the subtropical region of the Southwest Atlantic, Brazil. Multivariate Regression Trees were fitted to explore the effects of structural heterogeneity, wave power, depth, water temperature, and benthic cover on the structure of reef fish assemblages, addressing composition, richness, density, biomass, trophic groups, mobility, and conservation status. Our results suggest that depth, turf, and coral cover were the main predictors of fish assemblages in rocky reefs at Alcatrazes Island, revealing five distinct fish assemblages with different habitat preferences. These results provide additional insights into the relationship between reef fishes and their environment, providing empirical evidence for decision-makers to implement spatially based management policies, especially to prioritize zones for conservation along the island.

Keywords Reef fish · Environmental variables · Rocky reef · Benthic cover · Southwestern Atlantic

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Introduction

Reef fish assemblages respond to changes in environmental conditions with fluctuations in richness and abundance at different spatial and temporal scales (Parravicini et al. 2013). The dynamics of community structure in marine environments at the local level are influenced by population relationships to biotic and habitat characteristics. In reef systems, biochemical and physical factors with the potential to shape biological assemblages include water temperature (Floeter et al. 2001; Bellwood et al. 2005), wave exposure (Friedlander et al. 2003; Maia et al. 2018), depth gradient (Teixeira-Neves et al. 2015; Pereira et al. 2018; Matheus et al. 2019), and nutrient production (Williams et al. 2015). Such environmental features shape the geomorphology, which influences sessile benthic communities by affecting reef organism recruitment and settlement (Carleton and Sammarco 1987; Mallela 2018), thus influencing key structural features of fish habitats (Sale 2013; Teixeira-Neves et al. 2015; Russ et al. 2021). For instance, increasing reef structural complexity has been described as beneficial to species richness by providing more space in quantity and types of shelters (e.g., Friedlander et al. 2003; Darling et al. 2017). Therefore, the spatial context can influence the structure of reef fish assemblages, with relevant mechanisms involved directly related to the scale of analysis.

Identifying the variables influencing the spatial distribution of reef fishes is important to understand the forces that shape assemblage structure, providing data to guide management strategies such as spatial planning (Haupt et al. 2017). Variations in local environmental conditions can influence feeding, metabolism, growth rates, pelagic larvae duration, and even species survival (O'Connor et al. 2007). However, in many sites, disentangling the importance of environmental variables in the structure of fish communities has been challenging when they occur synergistically with sources of anthropogenic impacts such as fishing and tourism (Richards et al. 2012). To reduce the potential bias, studying sites with minimal human interference at the local level, such as effective and well-enforced no-take marine protected areas (MPAs), can be ideal.

Studies investigating spatial patterns of the ichthyofauna based on environmental predictors have been conducted at large (i.e., > 50 km; Bender et al. 2013; Endo et al. 2019; Quimbayo et al. 2019) and small spatial scales (Friedlander and Parrish 1998; Arias-González et al. 2006; Brokovich et al. 2006; Cvitanovic and Hoey 2010; Agudo-Adriani et al. 2019), with most studies focusing on tropical reefs. However, patterns of variation in reef fish assemblages over micro-spatial scales (i.e., from meters to < 2 km) in subtropical reefs remain less explored (García-Charton et al. 2004; Teixeira-Neves et al. 2015; Neves et al. 2016; Ferrari et al. 2018; Nanami 2022; Barreto et al. 2024).

In this study, we investigated the spatial distribution of reef fish assemblages at Alcatrazes island, a subtropical coastal island off Brazil, Southwestern Atlantic. More specifically, we explored the potential effects of structural heterogeneity, wave power, depth, water temperature, and benthic cover on reef fish assemblages' structure, composition, richness, density, biomass, trophic groups, mobility, and conservation status.

Material and methods

Study area

Alcatrazes is the largest island of the Alcatrazes Archipelago, formed by six islands located 33 km away from the coast of the São Paulo state, Southeastern Brazil (Southwestern Atlantic; Fig. 1). Alcatrazes Island encompasses two no-take MPAs: the Tupinambás Ecological Station (ESEC–IUCN Category Ia), created in 1987, and the Alcatrazes Archipelago Wildlife Refuge (REVIS–IUCN Category III), established in 2016. The Archipelago features rich terrestrial and marine biodiversity with several terrestrial endemic and threatened species (ICMBio 2017). Regarding oceanographic conditions, the region is influenced by three water masses transported by the Brazil Current, one of which, the South Atlantic Coastal Water, is associated with coastal upwelling (Castro et al. 2008). The upwelling occurs mainly in the austral summer, changing the physicochemical parameters with consequences for biological processes in the region (Pires-Vanin et al. 1993).

The sublittoral rocky bottom is characterized by its range of structural features, from flat plateaus of large and uniform rock walls (exhibiting little to no structural complexity), to large boulders up to 15 m in diameter, spaced a few meters apart, and featuring numerous

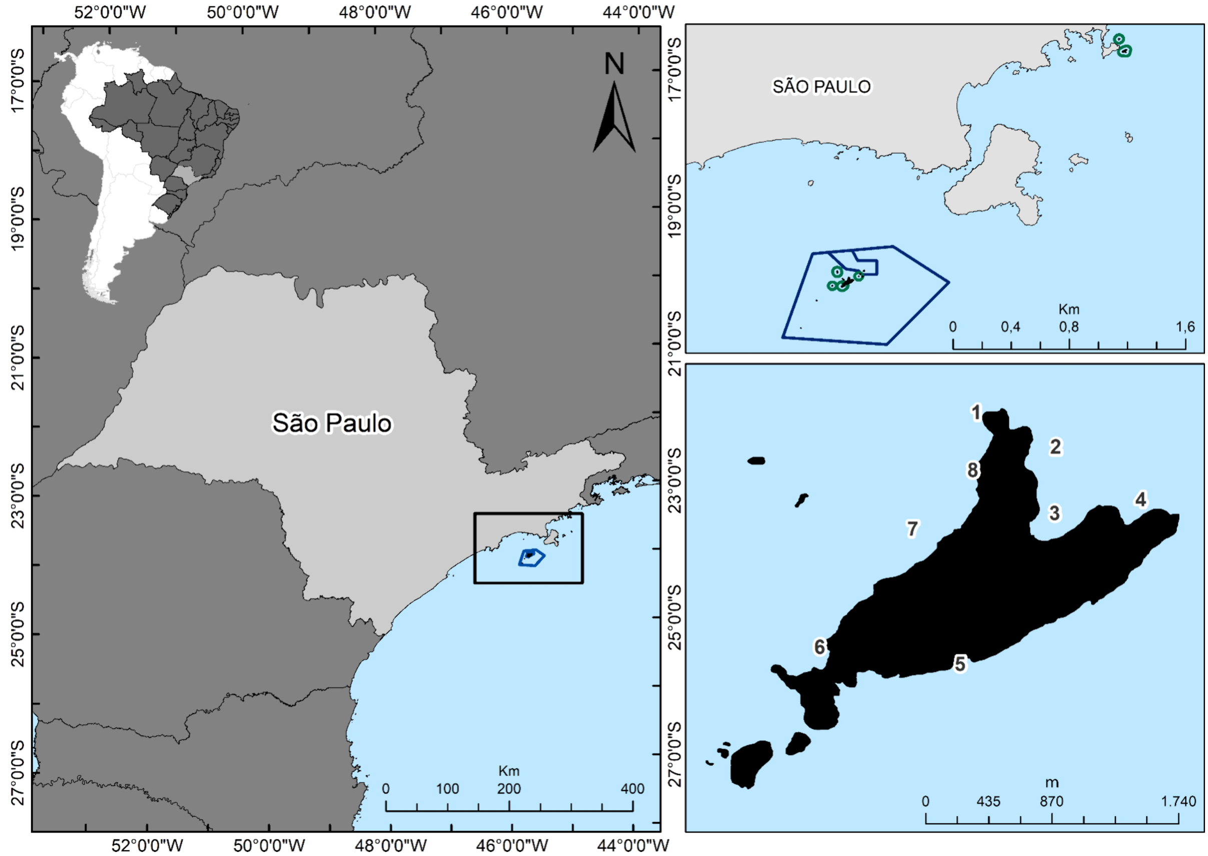

Fig. 1 The study area is located within the Wildlife Refuge of the Alcatrazes Archipelago (blue polygon), on the north coast of the State of São Paulo. The green circles represent the Tupinambás Ecological Station, a no-take marine protected area created in 1986, covering areas of the Alcatrazes Archipelago (south sector 1) and Palmas and Cabras Islands (north sector 2). The detailed map shows Alcatrazes Island with the eight sample sites. 1 Matacões, 2 Raia, 3 Baba de Boi, 4 Tartaruga, 5 Paredão, 6 Oratório, 7 Geladeira, and 8 Jardim dos Corais

crevices and holes. The leeward side of the island, with less hydrodynamic energy, harbors the richest benthic sessile cover, while encrusting calcareous algae dominate the windward sites, susceptible to waves and currents, with lower habitat complexity and lower benthic cover richness (Gibran and Moura 2012).

Data collection

The present study was authorized by the Brazilian Ministry of Environment through the Brazilian System of Information and Authorization in Biodiversity (SISBIO No. 46206–8) and approved by the Federal University of São Paulo Ethics Committee (CEUA No. 1015170420).

Reef fish assemblages

Data on reef fish abundance was collected around Alcatrazes Island in October 2018 (during the South Hemisphere Spring season), through 218 stationary visual censuses using scuba diving (adapted from Minte-Vera et al. 2008) at eight reef sites (Baba de Boi $n=27$; Geladeira $n=35$, Jardim dos Corais $n=34$; Matacões $n=30$; Paredão $n=26$; Raia $n=25$; Saco do Oratório $n=30$; Tartaruga, $n=11$). All sites, separated by at least 300 m, were differentiated and selected during the monitoring of the archipelago based on the range of habitats found, primarily influenced by topography and benthic composition. Therefore, the main aim of this study was to investigate the variations in fish assemblages across these distinct sites to inform management decisions.

The abundance of every fish species and individual body size were estimated within an observer-centered cylinder with 4-m radius for 5 min. Individuals with total length (TL) smaller than 10 cm were counted within a nested cylinder with a 2-m radius in two size classes (≤ 2 cm and 2–10 cm), while individuals > 10 cm TL were counted within a 4-m radius in four size classes (10–20; 20–30; 30–40; and > 40 cm). Stationary visual census has been historically used as a method for monitoring this no-take MPA (Motta et al. 2021; Rolim et al. 2024), as well as other marine reserves in Brazil (e.g., Moura and Francini-Filho 2005; Freitas et al. 2019). They are particularly useful for large reefs with high structural heterogeneity with diverse and abundant fish populations (Bohnsack and Bannerot 1986; Minte-Vera et al. 2008). Sampling was conducted between 9 a.m. and 5 p.m. BRT (GMT–3) to avoid bias due to changes in fish activity between day and night periods (Hobson 1965; Amaral et al. 2023). The minimum horizontal transparency of the seawater during data collection was 5 (i.e., larger than the sample unit radius).

Environmental variables

Structural features of the reef were examined to assign a broad structural complexity score for each fish sampling, following Wilson et al. (2007). The scores were 1 for the lowest, 2 for intermediate, and 3 for the highest structural complexity. Flat substrates with low potential to provide shelter for the reef biota receive scores of 1, whereas those with rocks, holes, and crevices with homogenous sizes receive scores of 2. Reefs with high complexity with many rocks, holes, and crevices of different sizes were assigned score 3. The standard deviation of structural complexity was calculated based on the scores averaged across all sampling units at each site (eight levels). This average served as a measure of heterogeneity, with higher heterogeneity values indicating sites with greater variation in structural complexity.

Data on wave power was gathered from Takase et al. (2021). These authors investigated the level of exposure to wave power distribution around Alcatrazes Island by applying a numerical model from a 14-year time series (2005–2018) extracted from the Global Wave Watch III model. Wave power was estimated through the relation that considers the synergistic effect between wave height and period (Takase et al. 2021). Data on wave power were extracted during springs (average for years 2005–2018) for each site (eight levels), the same season we sampled reef fish assemblages in 2018.

Depth and water temperature were collected in each sampling unit, i.e., census (218 levels) through a dive computer (Puck Pro Model–Mares®) with precision levels of ± 0.2 m and ± 2 °C, respectively. During data collection, depths ranged from 2 to 24 m and the water temperature ranged from 20 to 25 °C.

The characterization of the benthic cover was conducted through 10 photoquadrats of 70 × 70 cm distributed randomly in each sampling site. Each photoquadrat was composed of a mosaic of 15 digital images. The percentage cover was estimated using the software photoQuad (Trygonis and Sini 2012). In this software, twenty randomly located points were generated per digital image, thus totaling 300 points per photoquadrat. The organisms or colonies immediately below each point were classified into 12 major benthic categories: sand, bare rock, crustose coralline algae (CCA), frondose algae, coral, tunicate, soft coral (Zoantharia), cenocytic algae, Octocorallia, Echinodermata, Porifera, bivalve, Hydrozoa, and turf algae. Subsequently, the average of the percentage cover of each benthic category was calculated by site ($n = 8$). The dominant broad benthic categories (> 5%) were selected for the analysis, resulting in turf, frondose algae, soft corals (i.e., *Carijoa riisei* and *Palythoa caribaeorum*), and corals (i.e., *Madracis decactis* and *Mussismilia hispida*).

Data analysis

Fish species were categorized according to Pinheiro et al. (2018) in trophic groups as herbivores (HERB), macrocarnivores (MCAR), mobile invertebrate feeders (MINV), sessile invertebrate feeders (SINV), omnivores (OMNI), and planktivores (PLANK), as well as in mobility as highly mobile or migratory (HMO), roving (ROV), and sedentary or territorial (SED). The species were also assigned a conservation status based on the International Union for the Conservation of Nature Red List and the Brazilian Red List, as either Least Concern (LC), Near Threatened (NT), or Vulnerable (VU) (IUCN 2023). Fish biomass was estimated using length–weight relationships available in FishBase (Froese and Pauly 2020).

The calculations were done using the midpoint values for each length category (i.e., individuals in the 10–20 cm class were calculated as measuring 15 cm). When coefficient values were not available for a species, we used coefficients of the closest related species or genus. For each species, the relative abundance and relative biomass were calculated by dividing its number of individuals and total biomass by the corresponding totals for all species in the community. Mean density and biomass were then determined by dividing the species-specific abundance and biomass by the census area, yielding data in individuals and grams per square meter.

Multivariate regression trees (MRT) were fitted for the fish census data ($n = 218$ levels) using the R package *mvpart* to explore the influence of environmental variables (standard deviation of structural heterogeneity, wave power, depth, water temperature, and benthic cover) on the spatial distribution of reef fishes considering species as taxonomic level. The MRT allows recursive partitioning of quantitative or categorical environmental variables, determining the formation of clusters. The calculation occurs from repeated divisions of different sample groups, producing "nodes" as homogenous as possible concerning the response variable. Homogeneity is measured by finding the best division that minimizes the sums of squares over the multivariate average within each node (De'Ath 2002). The best tree was selected by choosing the highest cross-validation value and lowest value of the relative cross-validated error (De'Ath 2002). For analysis purposes, each category of benthic organism was added as an independent variable in the MRT.

Hellinger's pre-transformation was used on the species matrix, where the abundance values of each fish species are divided by the total abundance of the site. To explore patterns in an assemblage's segregation according to environmental variables, a non-metric multidimensional scaling (nMDS) over Euclidian dissimilarity matrices was calculated. This procedure allowed us to corroborate the explanatory potential of the outputs from the tree generated by the MRT. Differences in richness and biomass between assemblages revealed by the MRT were tested using the Kruskal–Wallis test and the post hoc Dunn test.

Boosted regression trees (BRT) were fitted for the census data (218 levels) using the R package *gbm* (Greenwell et al. 2019) to understand the drivers of the abundance of the most important fish species that contributed to splitting assemblages revealed by the MRT. Boosted regression tree (BRT) models are a modeling approach whereby a succession of regression trees is developed using machine learning models. To avoid model overfitting and attain the highest accuracy, as indicated by the lowest values of cross-validation deviance and standard error, optimal BRT models were selected by examining all possible combinations of values for bag fraction (0.5 and 0.75), learning rate (0.001, 0.005, 0.01, and 0.05), and tree complexity (1 to 5). BRT procedures were conducted following the protocol described by Elith et al. (2008). All analyses were conducted in the R software version 3.0.3 (R Core Team 2011).

Results

Fish assemblage structure and conservation aspects

We recorded a total of 14,524 individuals of 75 species, 49 genera, and 31 families at Alcatrazes Island. The ten most abundant fish species accounted for 88.9% of total fish abundance and for 69.5% of biomass (Table 1). The most common species, *Haemulon aurolineatum*, was found in 88.7% of censuses, representing 60.9% of the total abundance and 17.8% of the sampled biomass (Table 1). Haemulidae was the family with the largest abundance, followed by Pomacentridae, Holocentridae, Kyphosidae, Labridae, and the others (Fig. 2A). The most speciose families were Labridae with 12 species, Pomacentridae with seven species, followed by Carangidae and Haemulidae with six species each. The average richness per sampling was 8.3 ± 3.6 ($\pm$ s.d.) with a maximum of 19 species. The average abundance of specimens per sampling was 65.7 ± 57.7, ranging from 0 to 377 fishes. The average biomass per census was 112.5 ± 125.5 g/m^2, ranging from 0 to 804 g/m^2.

Regarding trophic groups, most fish sampled were mobile invertebrate feeders, accounting for 74.3% of all individuals counted and for 46.5% of total biomass (Fig. 2B), followed by omnivores (11.3% of biomass), herbivores (10.5%), planktivores (1.4%), sessile invertebrate feeders (1.4%), and macrocarnivores (1.1%). Mobile invertebrate feeders were the most speciose group, with 26 species, followed by macrocarnivores ($n = 18$; Fig. 2B).

Seven fish species recorded in Alcatrazes Island are listed in the Brazilian Red List of Threatened Species

Table 1 Ten most abundant reef fishes from Alcatrazes Island, Brazil. Trophic groups: herbivores (HERB), macrocarnivores (MCAR), mobile invertebrate feeders (MINV), sessile invertebrate feeders (SINV), omnivores (OMNI), and planktivores (PLANK). The full table with all species sampled is provided in Table S1

Family	Species	Trophic category	Average density (fish/m^2)	Relative frequency (%)	Relative abundance (%)	Relative Biomass (%)
Haemulidae	*Haemulon aurolineatum*	MINV	1.50	88.7	60.9	17.8
Pomacentridae	*Abudefduf saxatilis*	OMNI	0.54	40.3	8.5	7.9
Pomacentridae	*Stegastes fuscus*	HERB	0.28	51.6	4.5	1.9
Holocentridae	*Holocentrus adscensionis*	MINV	0.07	65.6	3.4	7.2
Kyphosidae	*Kyphosus* spp.	HERB	0.11	38.9	3.2	15.2
Haemulidae	*Anisotremus virginicus*	MINV	0.07	59.7	2.9	11.7
Sparidae	*Diplodus argenteus*	OMNI	0.09	40.3	1.6	1.6
Acanthuridae	*Acanthurus chirurgus*	HERB	0.11	23.1	1.4	4.1
Haemulidae	*Haemulon atlanticus*	MINV	0.66	9.5	1.3	0.4
Ephippidae	*Chaetodipterus faber*	MINV	0.09	16.3	1.2	1.7

as Vulnerable. Three threatened species were macrocarnivores of the Epinephelidae family (i.e., *Epinephelus marginatus*, *Mycteroperca bonaci*, and *Epinephelus morio*), where *Epinephelus marginatus* was the most abundant of the three species. Three species were herbivores of the Labridae family (*Sparisoma axillare*, *Sparisoma frondosum*, and *Scarus zelindae*). One species was a mobile invertebrate feeder, *Elacatinus figaro*. Threatened species represented 1.64% of total fish abundance and 8.26% of fish biomass.

Influence of environmental variables on the spatial distribution of reef fish

The most parsimonious MRT model, presenting greater explanatory power, lower error, and low number of nodes, was selected, resulting in five distinct assemblages (Supplementary Fig. 1; Fig. 3A,B). The MRT model selected explained 18.9% of data variability, with a cross-validated relative error (CVRE) of 0.88.

Three explanatory variables (depth, coral cover, and turf) were identified as the most important factors influencing the spatial distribution of reef fish assemblages. The nMDS ordination shows a clear overlap among three reef fish assemblages (Fig. 3C).

Assemblage A represented 79 censuses (Fig. 3B; Table 2), being dominated by the mobile invertebrate feeder *Haemulon aurolineatum* (33.2 ± 34.2 ind. census^{-1}), but the discriminating species was the omnivore *Diplodus argenteus* (2.8 ± 3.3 ind. census^{-1}). In this assemblage, areas of intermediate depth (6.45 m and 10.75 m) were grouped into five sites with coral coverage of less than 4.16% (Fig. 3A, B).

Assemblage B (8 censuses) was represented by the mobile invertebrate feeder *Coryphopterus glaucofraenum* (7 ± 4 ind. census^{-1}), but the discriminating species was the herbivore *Stegastes fuscus* (2.25 ± 1.83 ind. census^{-1}) which was related to greater coral cover (≥ 4.16%) at depths greater than 10.75 m and grouped into samples from two sites.

Assemblage C (27 censuses) was most represented by *Haemulon aurolineatum* (63.2 ± 56.8 ind. census^{-1}). This assemblage was driven by a higher coral cover (≥ 4.16%) and intermediate depths (≥ 6.45 to < 10.75 m). Here, samples from three sites were grouped (Fig. 3A).

The two remaining assemblages, D and E, featured the omnivore *Abudefduf saxatilis* and the herbivore *Kyphosus* spp. as discriminator species, the first species contributing with greater abundance and the second with greater biomass.

Assemblage D (six censuses) was most represented by the omnivore *Abudefduf saxatilis* (27.8 ± 10.5 ind. census^{-1}), at depths shallower than 6.45 m, and higher turf cover (≥ 82.84%). Here, samples were found only in one site, the most windward location, called “Paredão” (Fig. 3A, B).

Assemblage E (98 censuses) was dominated by *Haemulon aurolineatum* (50.3 ± 58.8 ind. census^{-1}), followed by *Abudefduf saxatilis* (15.3 ± 12.8 ind. census^{-1}). It was characteristic for shallower reefs (< 6.45 m) and turf cover lower than 82.84%. Here, samples from shallower reefs of seven sites were grouped.

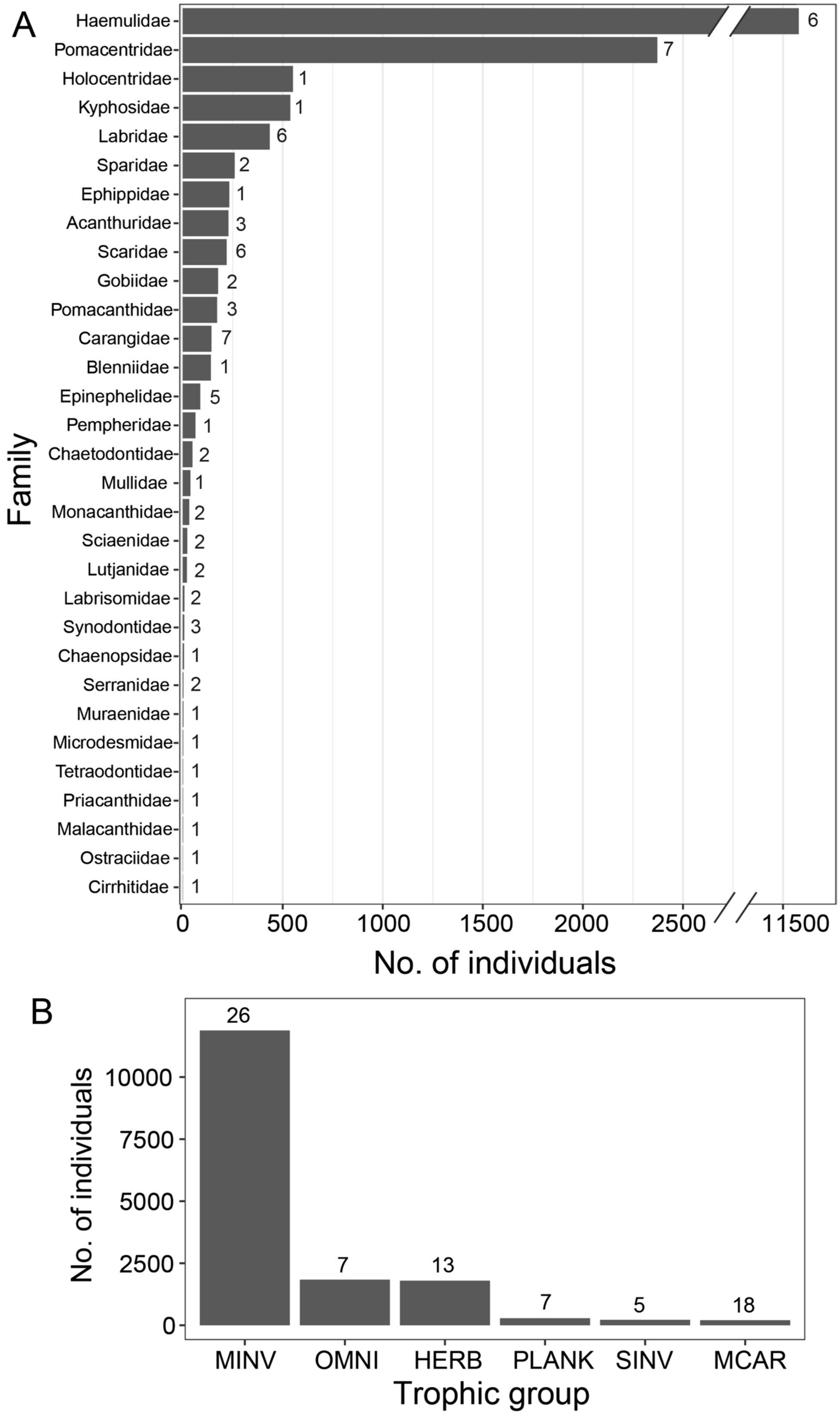

Fig. 2 Abundance by family (**A**) and trophic group (**B**). Numbers associated with each bar indicate total species richness within each fish family or trophic group. Trophic groups: mobile invertebrate feeders (MINV), omnivores (OMNI), herbivores (HERB), planktivores (PLANK), sessile invertebrate feeders (SINV), and macrocarnivores (MCAR)

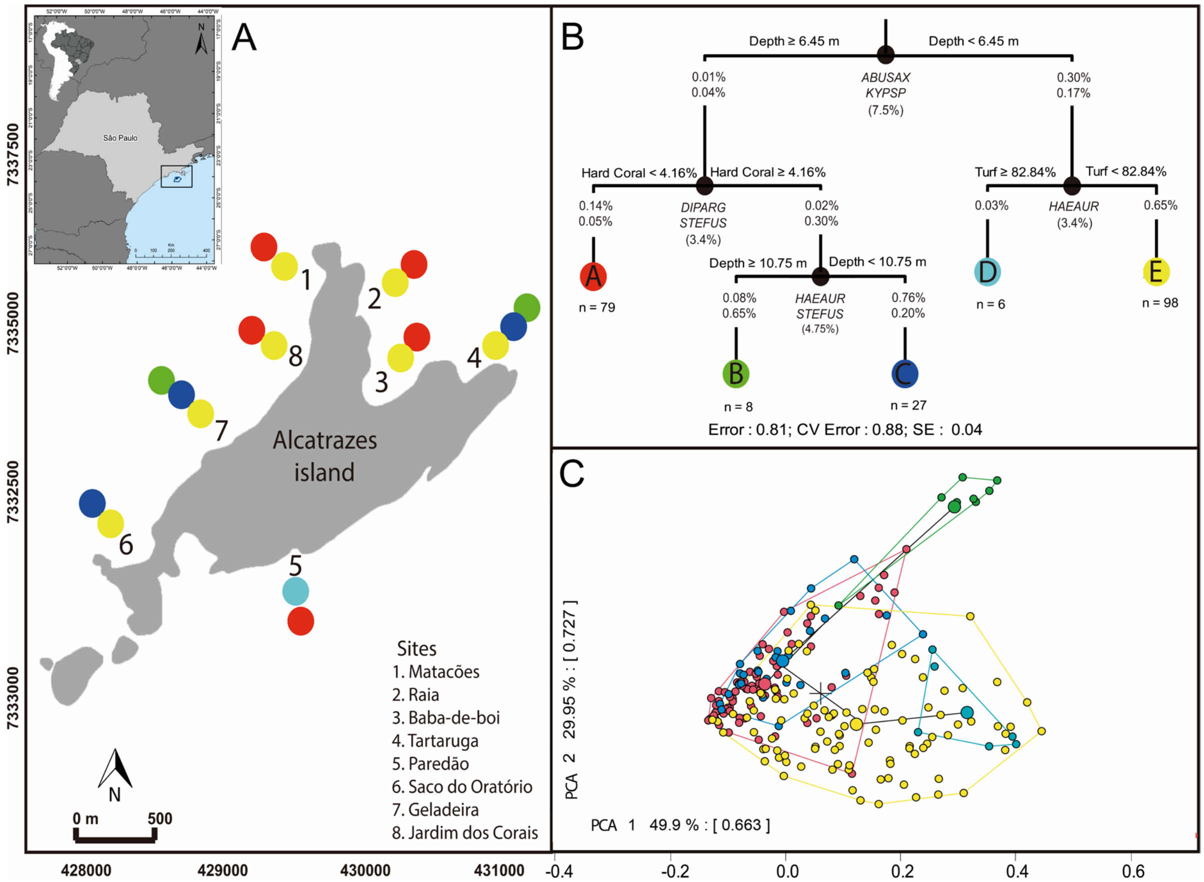

Fig. 3 **A** Sampled sites (numbers) around Alcatrazes Island and fish assemblages (colored circles) revealed by the multivariate regression tree (MRT). **B** MRT showing reef fish assemblages on Alcatrazes Island according to environmental variables: depth, hard coral cover, and turf. The variables are divided by the nodes (black circles), and the discriminating fish species responsible for the node and their relative contribution from the division to the total explained variance of the model are given at the bottom. Discriminant species: *ABUSAX*, *Abudefduf saxatilis*; *KYPSP*, *Kyphosus* spp.; *DIPARG*, *Diplodus argenteus*; *HAEAUR*, *Haemulon aurolineatum*; and *STEFUS*, *Stegastes fuscus*. "*N*" is the number of corresponding censuses for each assemblage distinguished by the MRT (colored circles labeled A, B, C, D, and E). **C** Principal components analysis (PCA) of five assemblages revealed by the MRT, illustrated through different colors

Table 2 Description (richness and biomass density) of each assemblage revealed by the multiple regression tree model, in terms of number of censuses in each assemblage (*N*), as well as minimum (Min), mean, standard deviation (Std Dev), median, and maximum (Max) values

Assemblages		A	B	C	D	E
N		79	8	27	6	98
Richness	Min	1	1	5	3	2
	Mean	6.94	3.88	9.15	7.67	9.91
	Std Dev	2.90	2.75	3.02	2.66	3.48
	Median	7	3	8	9	10
	Max	14	9	15	10	19
Biomass (g/m^2)	Min	0.00	0.01	0.42	1.25	0.27
	Mean	2.49	0.35	2.14	2.83	3.52
	Std Dev	2.67	0.37	1.16	2.33	2.51
	Median	1.60	0.23	1.94	1.53	2.91
	Max	16.00	1.02	4.75	6.84	12.26

Concerning assemblages' richness, the assemblages C and E presented the higher values, but were not significantly different from assemblage D (Fig. 4A, Table 2). The lowest richness values were registered in assemblages A and B (Fig. 4A, Table 2), but not significantly different from D. In terms of biomass (g/m^2), assemblage B presented significantly lower values (Fig. 4B, Table 2). Assemblages A, C, and D were not significantly different and assemblage E presented the highest biomass values, although not differing from assemblage D (Fig. 4B, Table 2).

The composition of trophic groups varied among assemblages, indicating a higher density of mobile invertebrate feeders in the deeper assemblages A, B, and C. The assemblages D and E, located in shallower areas, had a higher omnivore density, particularly D, which is exclusive to the reef area more exposed to wave action (Fig. 5). Despite showing similar density, the biomass of sessile invertebrate feeders and macrocarnivores was higher in deeper assemblages, while shallower assemblages displayed higher biomass of herbivores and omnivores (Fig. 5).

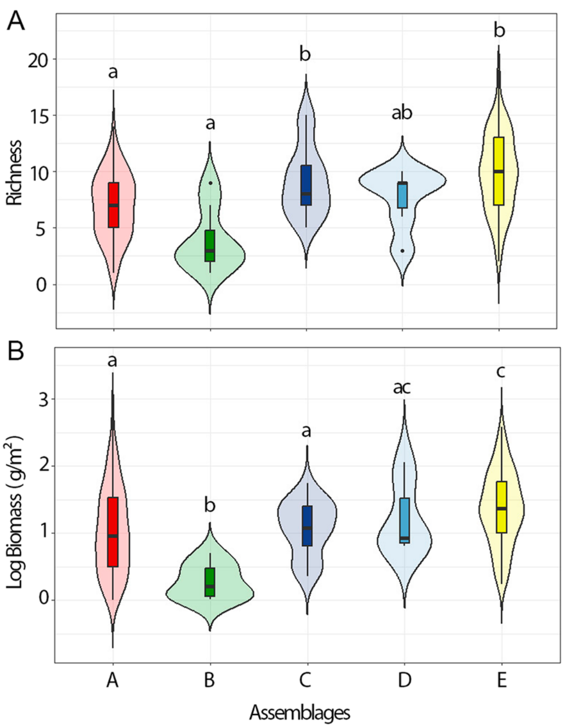

Fig. 4 **A** Reef fish richness (number of species) by census. **B** Total biomass (g/m^2) of the sampled censuses in each of the five assemblages revealed by the MRT model. The violin shape represents the distribution of data, the boxplot within the violins represents first and third quartiles of the data, vertical lines are the 95% inferior and superior limits, and the dots are the outliers. Letters above assemblages represent differences between groups detected by a Dunn test ($P < 0.05$)

Regarding mobility, assemblages were dominated by roving species. Only assemblage B featured a higher density of sedentary or territorial species (78%), composed mainly by *Coryphopterus glaucofraenum* and *Stegastes fuscus*, but most of the biomass was of roving species (85%; Fig. 5; Supplementary Table 1).

Within the assemblages, according to the Brazilian Red List of Threatened Species, assemblage B comprised a higher density of Vulnerable species, represented mainly by *Elacatinus figaro* and *Epinephelus marginatus*. Assemblage E featured greater biomass of the Vulnerable species *Mycteroperca bonaci* and *Sparisoma frondosum*. Regarding biomass, the assemblages B and E comprised a higher amount of Vulnerable and Near Threatened species, representing 11% and 15% of biomass, respectively.

The BRT models corroborated patterns observed in the MRT and add more insights on the main environmental drivers shaping the spatial distribution of the most abundant species of reef fishes (Fig. 6). Depth was the most important predictor for *Abudefduf saxatilis* and *Kyphosus* spp., which were most abundant at depths < 6.45 m. *Stegastes fuscus* was more abundant at low turf cover and at depths between ≥ 6.45 and < 10.75 m. Higher abundances of *Haemulon aurolineatum* were mostly correlated with high coral cover and low turf, with the opposite being observed for *Diplodus argenteus* (Fig. 6).

Discussion

Our results revealed that the combination of depth, turf, and coral cover is an important predictor of fish assemblages at a micro-scale in the subtropical reefs of Alcatrazes Island, in the Southwestern Atlantic Ocean. The analysis revealed five distinctive fish assemblages with different habitat preferences around the island.

Fish assemblages' structure in a regional context

The reef fish fauna recorded in Alcatrazes Island, comprising 75 species, represents approximately 10% of the total reef fish fauna found in the

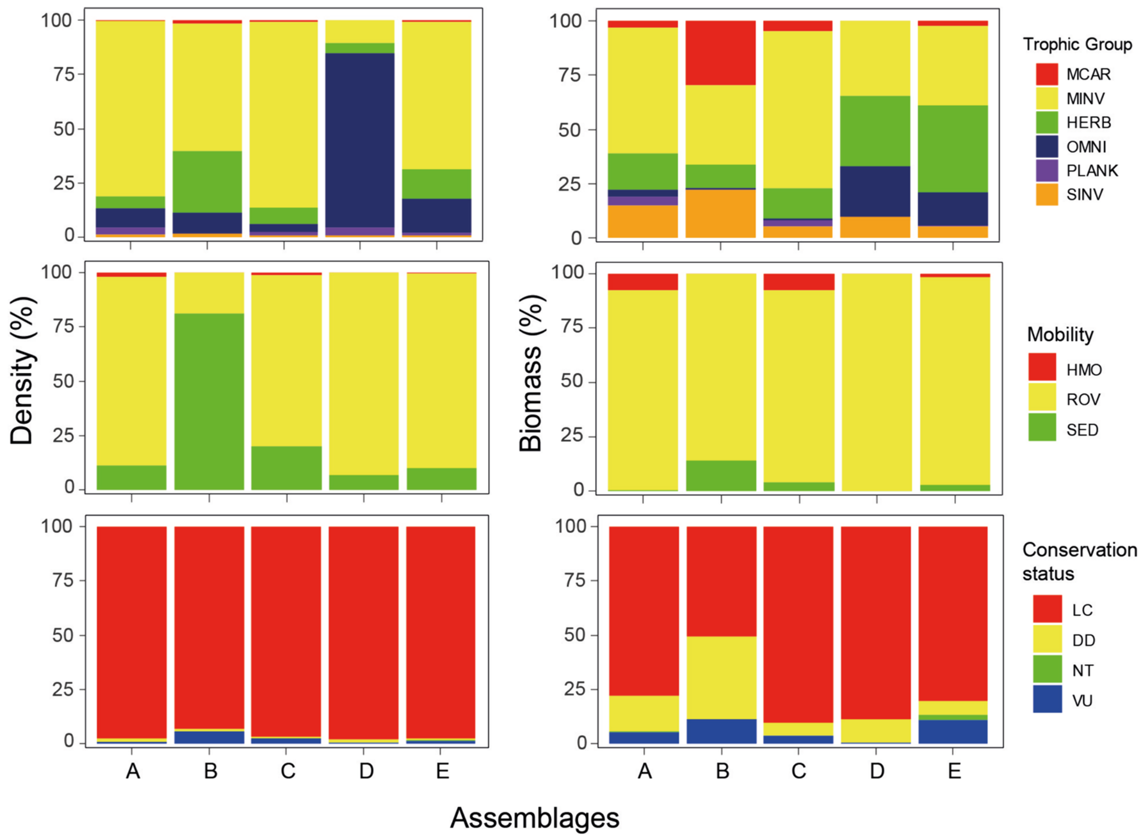

Fig. 5 Relative percentage (%) of density (left column) and biomass (right column) of reef fishes in the five assemblages revealed by the MRT—letters A, B, C, D, and E at the bottom of the figure. The *y*-axis of each subplot ranges from 0 to 100% in terms of relative percentage. Trophic groups: MCAR, macrocarnivores; MINV, mobile invertebrate feeder; HERB, herbivore; OMNI, omnivores; PLANK, planktivore; and SINV, sessile invertebrate feeder. Mobility HMO, highly mobile or migratory; ROV, roving; and SED, sedentary or territorial. Conservation status: LC, Least Concern; NT, Near Threatened; and VU, Vulnerable

Brazilian province (733 species) and 18% of resident reef fishes (73 out of 405 species) according to Pinheiro et al. (2018). This region encompasses the east-southeast subprovince, characterized by a transition from biogenic reefs to rocky reefs (Floeter et al. 2001; Pinheiro et al. 2018). It serves as an area of convergence for species from both environments (Floeter et al. 2001; Pinheiro et al. 2018). Indeed, the species list compiled in this study includes representatives from tropical waters, such as haemulids and labrids, and temperate waters, i.e., serranids and scarids (Supplementary Table 1, Floeter et al. 2001; Pinheiro et al. 2018).

The overall reef fish richness and trophic group composition in Alcatrazes Island resembled those of reefs in nearby coastal islands, as indicated by studies conducted by Souza et al. (2018) and Rolim et al. (2019), but were higher than those observed in sites closer to shore (Gibran and Moura 2012). This discrepancy underscores the importance of geographical factors, such as distance from the coast, in shaping reef fish assemblages in the region (Teixeira-Neves et al. 2015; Silva et al. 2021). Furthermore, coastal sites experience greater pressure from both legal and illegal human activities, including fishing (Imoto et al. 2016) and pollution (von Glasow et al. 2013) especially near megacities, due to their accessibility, highlighting the influence of sociocultural aspects on reef fish dynamics (Mora et al. 2011). The interplay between geographical and social characteristics likely contributes to this cross-shelf gradient in reef fish richness.

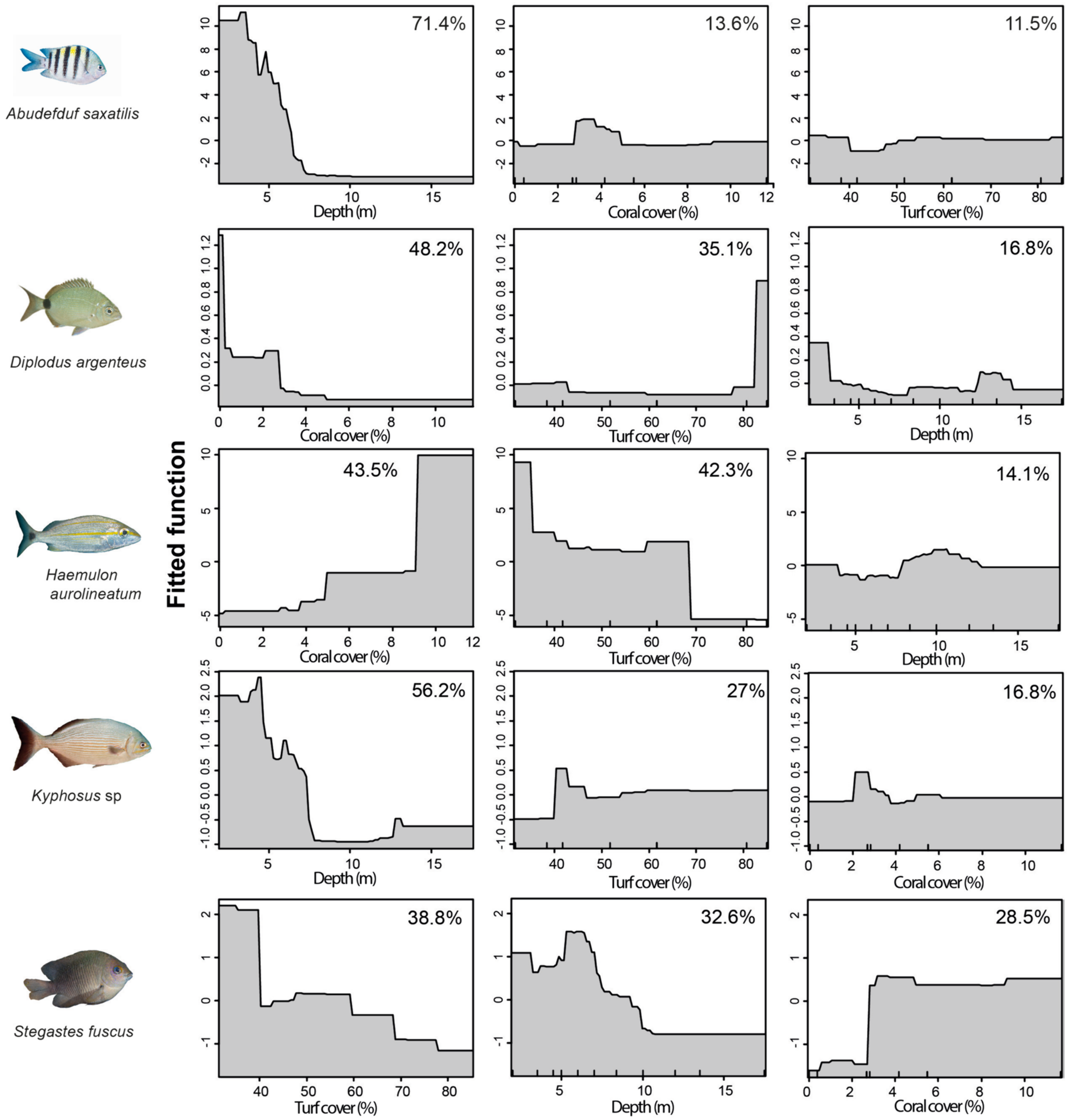

Fig. 6 Partial dependence plots revealed by the boosted regression trees using the three main predictors (depth, hard coral cover, and turf cover) and abundance of reef fish species characteristic for the assemblage revealed by the MRT

Predictors of spatial patterns in rocky reef fish assemblages

In the present study, depth was an important predictor for total biomass, in which the lowest values were registered in the deepest assemblage (> 10.75 m), as well as for some species, such as *Abudefduf saxatilis* and *Kyphosus* spp., whose abundances decreased with depth. Depth has been demonstrated as an important environmental variable affecting the structure of reef fish assemblages at a local level (Francini-Filho and Moura 2008; Pereira-Filho et al. 2011; Gibran and

Moura 2012; Pereira et al. 2018; Silva et al. 2021). Depth may influence reef fish assemblages by altering physical variables (e.g., wave exposure, temperature, luminosity, and salinity) and by modifying benthic assemblages' composition and structural complexity (García-Charton et al. 2004; Luiz et al. 2015; Ferrari et al. 2018). At Alcatrazes Island, deeper reefs usually present lower complexity and lower temperatures (Gibran and Moura 2012), which may limit the abundance of species with a preference for more complex shallow warm waters.

Intermediate depths seem to favor the territorialist species *Stegastes fuscus*, probably by providing light and exposure in ideal conditions for their food to grow, which is mainly composed of red filamentous algae (Ferreira et al. 1998). Turf cover was also an important predictor for the species, with higher abundances associated with less turf. This is not expected, since turfs are composed of multiple species of algae, usually including filamentous algae (Ferreira et al. 1998). As turf in the present study was not analyzed carefully, the composition of the algae species may change across habitats and depths along the reef. This topic needs further investigation concerning the different compositions of the turf in the Alcatrazes Island to properly investigate the relationship with *Stegastes fuscus* abundance.

Wave exposure is known to influence reef fish vertical distribution. More exposed reefs usually harbor lower richness and abundance of species (Luiz et al. 2015). In Alcatrazes Island, only one reef sampled was on the windward side exposed to a higher wave power, and the assemblage D occurred exclusively at this site, being predicted by shallow depths and higher turf cover. Despite the more extreme wave conditions, this assemblage did not show significant differences in species richness and biomass compared to leeward sites, yet it constituted a distinct assemblage specialized for such an environment. Assemblage D was characterized by a higher density of the omnivore species *Abudefduf saxatilis*, followed by *Diplodus argenteus* and *Anisotremus virginicus*. Such species have a diversified diet and do not present a well-established distribution pattern in the rocky shore habitats (Luiz et al. 2008; Anderson et al. 2015). With increased levels of exposure, the composition of benthic assemblages is also influenced, leading to the selection of species more resistant to challenging conditions (Matheus et al. 2019). Consequently, it is expected that higher abundances of fish species with less specialized resource demands will be recorded in such environments.

Regardless of the combination of predicted environmental variables, *Haemulon aurolineatum* was the most abundant species associated with higher coral cover (≥4.16%). In tropical coral reefs, the species is associated with middle-depth sites and intermediate to higher levels of coral cover (Francini-Filho and Moura 2008). However, at Alcatrazes Island, depth appears to not be a predictor of this species' occurrence, which was more related to benthic cover. *Haemulon aurolineatum* is dominant in subtropical rocky shores of the Western Atlantic, inhabiting reef slopes, reef-sand interfaces, and sandy bottoms, across a range of depths, and usually corresponding to more than 50% of fish species abundance (Luiz et al. 2008; Daros et al. 2012; Anderson et al. 2020). Juveniles of this species form large schools with more than 100 individuals and are associated with the reef at all life stages (Quimbayo et al. 2021). The preference for areas with high coral cover is likely related to foraging activities, with juveniles (< 10 cm) exploring food resources suspended in the water column above the reef, mostly copepods and amphipods, while adults (> 15 cm) primarily forage in the sand around the reef, usually feeding on polychaetes and crabs (Pereira and Ferreira 2013; Pereira et al. 2015). This close association with reef environments elucidates the positive effect of coral cover on the abundance of *Haemulon aurolineatum* at Alcatrazes Island, without a corresponding depth effect. The absence of a depth effect suggests that the species' foraging behavior is predominantly influenced by the availability of resources within reef habitats.

Turf algae, representing a multitude of short turf-forming species of macroalgae belonging to the orders Corallinales, Ceramiales, and other green and reef filamentous algae, is the dominant group of benthic organisms in most subtropical reefs (Aued et al. 2018). These communities play key roles in the ecology and trophodynamics of reef systems, occupying substantial areas of the reef from shallow habitats to the interface with soft bottoms in deeper reefs. At Alcatrazes Island, the distribution of *D. argenteus* was related to turf cover, a pattern observed in other subtropical rocky shores of the Brazilian province (Teixeira-Neves et al. 2015). Turf is usually not related to increased structural reef complexity, but it does support a diverse and abundant associated macrofauna that lives in the turf matrix and detritus, being an important resource for invertivore and herbivore species (Ferreira et al. 2004; Liuzzi and Gappa 2008).

The MRT model accounted for 18.9% of the variability in the data, and supplementary analytical approaches (PCA and BRT) supported the differentiation of reef fish assemblages and the significance of environmental variables in predicting reef fish fauna composition. We propose that variables beyond those we investigated may serve as predictors of reef fish assemblages on rocky shores, such as biotic factors like primary productivity in the water column. The abundance of plankton can significantly impact the distribution and abundance of reef fish species. According to the Resource Availability Theory, fluctuations in resource availability can influence the intensity of resource competition, potentially leading to evolutionary changes in life-history traits (Endara and Coley, 2011). Plankton constitute a crucial food source during the juvenile stages of certain reef fish species, such as *Haemulon* spp. and *Kyphosus* spp., which undergo ontogenetic shifts in their diet. While younger individuals predominantly consume planktonic items in the water column, adult *Haemulon* spp. favor invertebrates associated with reefs, and *Kyphosus* spp. specialize as herbivores (Silvano and Güth 2006; Pereira et al. 2015).

In addition, assemblages may vary temporally, influenced by seasonal wave exposure and water masses waters that cause a seasonal thermocline in the region. Further investigation is encouraged to verify if the spatial variation changes temporally (i.e., spatiotemporal patterns). Temporal changes in fish abundance can be relevant, for instance, after recruitment pulses (Lewis 1997), or under the influence of seasonal upwelling (Cordeiro et al. 2016), or communities may even remain spatially consistent over time (Anderson and Millar 2004; Sánchez-Caballero et al. 2019).

Anthropogenic drivers have been increasingly described as predictors of patterns in biodiversity. For instance, fishing has changed fish assemblages in subtropical Brazilian reefs by reducing the density of macrocarnivores and herbivores (Anderson et al. 2014; Bender et al. 2014). Sites with increased protection levels and distant from the coast or in remote areas contain higher species richness and biomass (Quimbayo et al. 2019; Fonseca et al. 2021). Alcatrazes Island was used by the Brazilian Navy for over two decades for military training, which has possibly decreased the occurrence of fishing activities in the region, but with insufficient enforcement. Since 2015, the MPAs of Alcatrazes Archipelago have increased enforcement levels compared to most Brazilian MPAs. Outcomes of the protection were a high reef fish abundance compared to other coastal sites (Morais et al. 2017; Motta et al. 2021) and an increase in body size and abundance of fisheries target species of groupers and jacks compared to nearby fished areas (Rolim et al. 2019; Motta et al. 2021). The enhancement in management effectiveness (Giglio et al. 2019) and enforcement in marine reserves of the Alcatrazes Archipelago are expected to increase the conservation effects for reef communities. Since 2018, part of the Alcatrazes Archipelago is open for a guided visitation through diving and, more recently, boating through a strict code of conduct (Marconi et al. 2020; Giglio et al. 2022). Systematic monitoring was implemented to evaluate the potential effects of human presence on rocky reef biota. Such data has been used in the adaptive management of public use in Alcatrazes Wildlife Refuge (Giglio et al. 2022). The continuation of the monitoring is essential to inform adaptive management on possible shifts in reef fish assemblages from local and regional anthropogenic activities. In addition, effective management of partially protected MPAs surrounding the Alcatrazes Archipelago is important to ensure its effectiveness since fish biomass inside marine reserves declines with increasing human impacts outside of reserves (Cinner et al. 2018).

At the same site, two or more assemblages were structured by depth and environmental characteristics. Assemblages in shallow reefs were more homogenous, composed of assemblage D and E, while at depths greater than 6.45 m, assemblages A and C were the most common. Interestingly, on reefs located in the no-entry area inside the Tupinambás Ecological Station ("Saco do Oratório" and "Paredão") and border sites ("Geladeira" and "Tartaruga"), reef fish assemblages were structured differently. These sites harbor the highest coral cover at Alcatrazes Island and a higher density and biomass of threatened and sedentary species. Such findings highlight the importance and suitability of the spatial zonation of use in Alcatrazes Island MPAs because the assemblages with distinct and important attributes are in the most protected area and at its border.

Conclusion

Depth, coral cover, and turf cover were important predictors of the spatial distribution of resident fish assemblages in subtropical rocky reefs of the Alcatrazes Island. Our results showed that two or more distinct fish assemblages can be identified in the same site in rocky reefs, varying according to local attributes. The outcomes of our study provide baseline data that can be useful for conservation use through spatial management approaches, considering local reef fish assemblage variation at local scales shaped by an assembly of processes, which is particularly important to improve the effectiveness of management strategies.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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