



# Spatial structure and potential processes linking fish and benthic communities in a protected reef ecosystem in SE Brazil

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**ABSTRACT:** Top-down and bottom-up processes can mediate the structuring of biological communities. Several studies have provided separate support for those processes in pelagic and benthic compartments of reef systems but studies focusing on whole-reef processes are less common. Here, we sampled 3 'reef compartments' in the Alcatrazes Archipelago in Southeastern Brazil: benthic cover of colonial organisms, solitary organisms, and reef fish (i.e. pelagic) to identify the groups responsible for spatial community structure among reefs. A dynamic mosaic structure best defines the assemblages of each compartment, with substantial changes observed among sites over 2 consecutive years and at 2 depth strata, separated by a sharp thermocline. Changes in benthic cover of colonial organisms are largely due to the extent of the blooming of *Sargassum* canopies, algal turfs, and the zoanthid *Palythoa caribaeorum*. Solitary organisms show a consistent monotonic change in the abundance of sea urchins, ascidians, and snails. Fish assemblage structure differed among reefs; however, we observed that large invertivore fish tended to concentrate in warmer water above the thermocline and small fish of different feeding habits were found in deeper and colder water in all reefs. We observed a potential strong link between the reefscape and solitary organisms, with a negative relationship between the abundance of urchins and the cover of *Sargassum* spp. suggesting top-down control. A second link is indicated by a positive relationship between low-lying cover composed of articulated turf and *P. caribaeorum* and larger invertivorous fish, suggesting bottom-up control through the provision of favorable foraging grounds.

**KEY WORDS:** Rocky reefs · Community dynamics · Marine protected areas · Benthopelagic coupling · Herbivory

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## 1. INTRODUCTION

Several studies have focused on the processes that modulate biological assemblages at different spatial scales (Sale 1977, Mora et al. 2003, Mittelbach & Schemske 2015, Bender et al. 2017). On a local scale, biological interactions such as competition and predation, for example, can regulate populations (Cantor

et al. 2018). On a regional scale, temperature, light, water movement, and topography are important ecological factors that regulate and filter species that shape a community (Pérez & Picard 1967, Riedl 1971). All those factors act together and with different intensities to shape the seascape by limiting the distribution of species. Despite differences that act on local and regional scales, reef ecosystems have often been

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explored separately for pelagic (Pinheiro et al. 2018, Feng et al. 2022) and benthic (Aued et al. 2018, Ashton et al. 2022) compartments. However, there are important processes that take place at their interface or that act at different spatial scales. Thus, understanding how those different compartments interact and what factors influence the communities at different scales with each other is key to understanding the ecology of the whole reef.

Studies in temperate (Rosemond et al. 2001) and tropical (Aronson & Precht 2000, Smith et al. 2013) systems support the dichotomy between bottom-up and top-down processes, many of them at the benthic–pelagic interface, and show how their balance ultimately controls reef communities. For instance, microphytobenthos and macroalgae may regulate the abundance of herbivore populations, and the flow rate of suspended organic particles (Taylor et al. 2018), including kelp debris (Duggins et al. 1989), may affect standing stocks or growth rates of sessile filter-feeding populations. Still, from the bottom-up perspective, the complex physical structure of macroalgal canopies (Tait & Schiel 2011, Figueiredo et al. 2020), as well as other biogenic habitats such as mussel, oyster, and seagrass beds (Hulot et al. 2014), provide food and shelter for a large diversity of mobile invertebrate feeders. On the other hand, top-down processes often consider predation of key species because their effects can cascade down through a sequence of different trophic levels (Paine & Vadas 1969, Menge et al. 1994). For instance, a decline in shark populations may directly increase the abundance of meso-predators and indirectly cause a drastic decrease in basal prey such as bivalves (Myers et al. 2007). Over decades, the intensified activity of killer whales in the Aleutian Islands ultimately caused a decline in kelp-forest cover through a cascading effect involving the decline of sea otters and an increase in grazing sea urchin populations (Estes et al. 1998). In the absence of top predators or herbivorous species (e.g. sea urchins and parrotfishes), 2 commonplace benthic consumers were found to play important roles in temperate shallow-reef habitats (Paine & Vadas 1969, Steneck et al. 2002). Although often considered separate processes, bottom-up and top-down controls often exert simultaneous effects on reef communities. In an asymmetric way, Russ et al. (2021) observed that changes in benthic cover (a bottom-up driver) and fishing pressure (a top-down driver) combined led to a substantial shift in the composition of reef fish on islands in the Philippines.

Mechanisms controlling tropical reefs, frequently dominated by scleractinian corals, are generally more

complex owing to the high diversity of species and biological interactions (Cantor et al. 2018). Corals and macroalgae comprise the main foundational species in the tropics (Idjadi & Edmunds 2006, Wikström & Kautsky 2007) and interact in several different ways (McCook et al. 2001). Negative allelopathy is frequent and causes declines in reproductive output (Monteil et al. 2020), settlement rate (Fearon & Cameron 1996, Koh & Sweatman 2000, Vermeij et al. 2009), growth, and increased mortality (Tanner 1995) in neighboring competing species. In temperate and tropical reefs, drastic declines in sea urchin populations (Edmunds & Carpenter 2001) and herbivorous fish are often followed by excessive macroalgal growth over corals. On the other hand, spikes in urchin populations may lead to excessive removal of calcium carbonate and whole-reef erosion (Eakin 1996, Yeung et al. 2021). However, other potentially relevant processes connecting pelagic and benthic environments, particularly those involving species-specific interactions and cryptic functional groups in highly diversified tropical reefs, are poorly documented (Brandl et al. 2019). For instance, cryptobenthic fish (small species usually <5 cm) may play crucial roles during their larval stage as food sources for a variety of invertebrates and larger fish species and fuel the whole ecosystem (Goatley et al. 2017, Brandl et al. 2019).

Shallow reefs in the Southeastern Brazil Ecoregion (as defined in Spalding et al. 2007) share some characteristics with both tropical coral reefs and temperate rocky systems dominated by macroalgae of different functional groups (Aued et al. 2018). The processes affecting overall standing stocks of reef fishes and controlling benthic seascapes in this region remain largely unknown. Abundant fish species process large amounts of dominant algal turfs (Francini-Filho et al. 2010, Mendes et al. 2018); however, top-down-mediated transitions to early successional algal assemblages, other than localized effects within damselfish territories (Ferreira et al. 1998), have not been verified to date. Indeed, field manipulations teasing apart fish and sea urchin effects on benthic assemblages point to top-down control by the latter, favoring crustose coralline algae by reducing the cover of algal turfs (Cordreiro et al. 2020), contrary to the evidence supporting predominant fish effects in tropical reefs (Roff et al. 2015). Still, low-lying algal turfs tend to dominate shallow reefs over the region, with the seasonal development of *Sargassum* spp. canopies providing habitat complexity during the summer (Godoy & Coutinho 2002, Figueiredo et al. 2020). Algal turfs and canopies host highly diversified but contrasting assemblages of mobile fauna, with fronds of *Sargassum*

spp. and *Dichotomaria marginata* facilitating a suite of hard-bodied invertebrates (e.g. crustaceans, mollusks, and echinoderms) that are preferred prey for most common invertebrate-feeder fish species in the region (Figueiredo et al. 2020). Although there are few studies investigating the influence of certain benthic cover characteristics on the distribution of invertebrates and fish in the southwestern Atlantic (Calderon et al. 2007, Eggertsen et al. 2017, 2020, Luza et al. 2022), the interplay of processes operating at the interfaces of reef compartments and how they modulate reefscape remains an open question.

Here, we sampled the shallow reef ecosystem along the main island of the Alcatrazes Archipelago, São Paulo State, Brazil, to explore potential processes linking the main compartments of reef biological assemblages. The spatial structure of benthic cover of colonial organisms (i.e. clonal colonies that live connected to each other and cannot be easily isolated and counted as individuals), solitary organisms (i.e. organisms that live alone or in groups that can be counted), and reef fishes (i.e. part of the pelagic community) were assessed over 2 consecutive years by sampling 3 sites along the more sheltered northwest-facing coastline of the main island, separated by several hundred meters. We first determined what groups within each compartment showed consistent spatial structure and then made use of multiple regressions to infer possible relationships among them. Considering that reefscape in the region are generally dominated by macroalgal turfs and canopies (Aued et al. 2018) and that previous experimental work had not evidenced large-scale effects of benthic consumers (Cordeiro et al. 2020), we hypothesized general bottom-up control linking habitat-forming species (i.e. colonial organisms) to solitary organisms and reef fish, along with secondary top-down regulation of benthic macroalgae through grazing (Fig. 1). Given that the Alcatrazes Archipelago is a protected environment, the potential functional relationships reported in this study could be used as a reference for other healthy reefs in the region.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study was conducted in the Alcatrazes Archipelago, located in southeastern Brazil, 36 km from the mainland (Fig. 2), within a wide transition zone under the influence of the Brazilian Current (warm with low concentrations of nutrients), the Falklands Current,

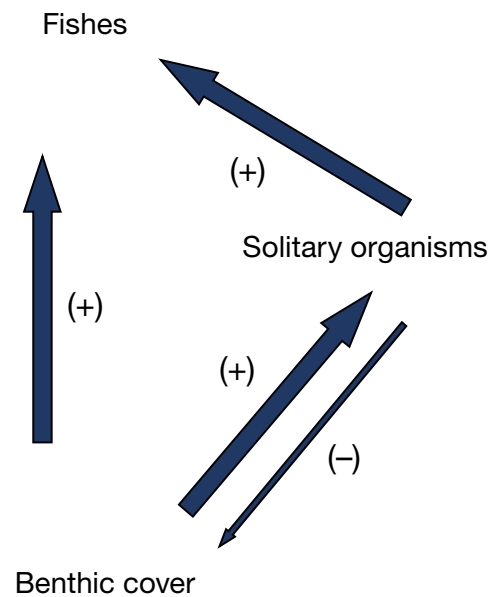


Fig. 1. A theoretical model of trophic hypotheses. General bottom-up control linking habitat-forming species (i.e. benthic cover of colonial organisms) to solitary organisms and fishes (indicated by the '+' sign), along with secondary top-down regulation of benthic macroalgae through grazing (indicated by the '-' sign)

and the South Atlantic Central Water (cold and nutrient-rich) (Ciotti et al. 2018). In the summer, intrusions of cold and nutrient-rich water from the Central South Atlantic contribute to the formation of the thermocline (see Ciotti et al. 2018), which occurs throughout the year but is less pronounced and at greater depths. In this part of the Brazilian coast, the climate is characterized by dry winters and hot rainy summers (Alvares et al. 2013, de Souza Rolim 2016). This archipelago is formed by the main island and 13 other rocky outcrops, and included within 2 no-take areas: the Refúgio da Vida Silvestre do Arquipélago de Alcatrazes, which covers a no-take area of 24.63 km<sup>2</sup> (Motta et al. 2021) (Government of Brazil 2016), and the Estação Ecológica Tupinambás (ESEC) (Government of Brazil 1987), restricted to reef habitats that presently sustain one of the largest concentrations of shallow-water reef fish biomass along the Brazilian Province (Morais et al. 2017).

### 2.2. Field sampling

Sampling took place during the austral summers of 2020 and 2021 over shallow reefs of positive slope (10°–45°) at 3 sites along the more sheltered northwest-facing coastline of the main island. Sampling

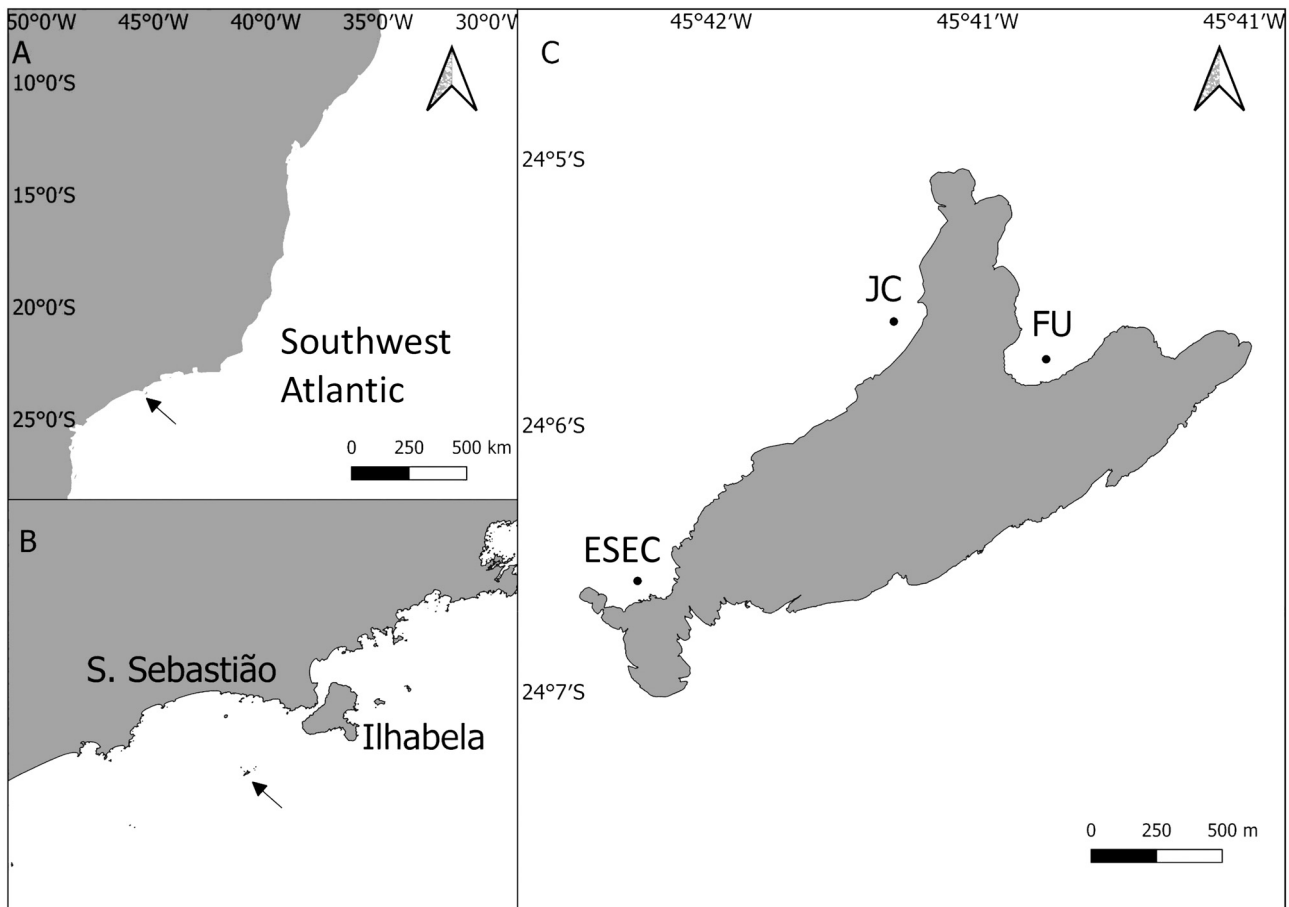


Fig. 2. Study area in the (a) Southwest Atlantic and (b) southeast coast of Brazil. The sites sampled in the Alcatrazes main Island are shown in (c). FU: Saco do Funil; JC: Jardim dos Corais; ESEC: Estação Ecológica Tupinambás

sites were Saco do Funil (FU), Jardim dos Corais (JC), and ESEC (Fig. 2), which are separated by at least 1600 m. Three specific protocols were used at each site to sample the benthic cover of colonial organisms, the abundance of solitary organisms, and both the abundance and body size of reef fish. For all 3 reef compartments, replicate sampling units were processed by SCUBA divers in a fully factorial design, encompassing both years, all 3 sites, and 2 depth strata (above and below the thermocline depth). Temperature measurements taken *in situ* during each sampling event were used to determine the depth of the thermocline, which averaged 8.5 m, ranging from 8 to 10 m. In summer, when this study was carried out, cold and nutrient-rich water intrusions of the South Atlantic Central Water contribute to the formation of the thermocline, which is very common in the region and provides a supply of nutrients to the reefs through upwelling (Ciotti et al. 2018). Among-site contrasts for the 3 components are emphasized in this study, as

they may indicate the underlying ecological processes generally controlling whole-reef communities.

### 2.2.1. Benthic cover and solitary organisms

Six 15 m replicate transects were haphazardly established and surveyed for all level combinations of factors 'year', 'site', and 'depth'. Benthic cover of colonial organisms was estimated using the point intercept method (Hill & Wilkinson 2004). This method involves each diver recording all observed benthic groups at specific points spaced 0.5 m apart along a 15 m belt transect while swimming ( $n = 6$  transects; Table S1 in the Supplement at [www.int-res.com/articles/suppl/m738p041\\_supp.pdf](http://www.int-res.com/articles/suppl/m738p041_supp.pdf)). All colonial organisms were classified into 20 groups (including macroalgae, soft and hard coral species), and subsequently grouped into 12 morpho-functional groups for statistical analyses (i.e. avoiding singletons; see Table 1). The extent

of bare rock and sand was also recorded. Solitary organisms were sampled in five 1 m<sup>2</sup> (1 × 1 m) quadrats along 6 belt transects of 15 m (Table S1). Each quadrat was spaced 3 m apart and placed on alternating sides along the same transects used for benthic cover sampling. All solitary organisms were classified into 26 groups and subsequently grouped into 10 groups for statistical analyses (see Table 1). Temperature and depth were recorded at the start and end of each transect using diving computers.

### 2.2.2. Reef fishes

For fish sampling, 15 underwater visual censuses were conducted for each combination of factors (i.e. both years, 3 sites, and 2 depth strata; Table S1). These censuses were conducted along 40 m<sup>2</sup> (20 × 2 m) random belt transects (Floeter et al. 2007). From the reef bottom to 2 m up in the water column, fish were identified, counted, and their size (total body length, in cm) was estimated. Transects were surveyed twice. Large and medium individuals with high mobility were recorded first, and bottom-dwelling, small (<10 cm), cryptobenthic and territorial individuals with low mobility were counted while swimming on the way back. Fish were pooled in size and trophic groups based on body size and diet categories. Size categories followed modal components of the whole fish sample: 0–14 cm, 15–23 cm, 24–35 cm, and >35 cm (Fig. S1). Diet categories followed those defined by Quimbayo et al. (2021): herbivores–detritivores (HD; feeding on turf and filamentous algae and/or detritus), herbivores (MA; grazing on large fleshy algae and/or seagrasses), sessile invertebrate feeders (e.g. preying on corals, sponges, sea squirts), mobile benthic invertebrate feeders (MI; e.g. crabs, mollusks), planktivores (PL; small organisms in the water column), piscivores (fish and cephalopods), and omnivores (OM; generalists feeding on both animals and macroalgae).

## 2.3. Statistical analyses

Analyses were divided into 2 stages. We first identified the main groups responsible for spatial contrasts and then determined whether such differences are temporally consistent. For those groups, we then searched for correlational evidence suggesting potential processes controlling whole-reef assemblages. All statistical procedures were performed using PRIMER v.6.1.13 software (Clarke & Gorley 2006) and

graphs were plotted using R v.4.0.2 (R Core Team 2022).

### 2.3.1. Spatial contrasts

We used linear mixed models, combining levels of the factors year (2020–2021), site (FU, JC, ESEC), and depth (above and below the thermocline) to test spatial contrasts and their temporal consistency. We considered year as a random factor. Separate permutational analyses of variance (PERMANOVAs) (Anderson 2001) were run for each biological component on either raw (solitary organisms) or square-root transformed data to reduce the influence of abundant and rare species (benthic cover, reef fishes) (Tichý et al. 2020). Unrestricted permutation or raw data (9999 times) and type III sums of squares were used. Pairwise testing followed omnibus analyses whenever factor site or its interactions with other factors were significant. Given that we aimed to identify groups accountable for the observed variations in spatial patterns among the assessed communities, rather than analyzing all recorded groups within these communities and because the triple interaction would hold a large number of pairwise comparisons (12) potentially indicating important spatial contrasts, a relatively high critical type I error rate was considered ( $\alpha = 0.10$ ). Similarity percentage (SIMPER) was then used to identify the groups responsible for among-site contrasts (>10% of whole dissimilarity in at least a single comparison).

### 2.3.2. Correlations

Based on relevant literature in other reef systems, we addressed trophic or other resource-based hypotheses that could determine the interplay among benthic foundational groups (i.e. benthic cover configuring seascapes), countable invertebrates (i.e. solitary organisms), and reef fish. Namely, we conceived that seascape features would influence reef fish assemblages directly, or indirectly through positive bottom-up control (e.g. facilitation; Fig. 1). Indirect impacts would mostly benefit carnivorous fish through the sustenance of abundant invertebrate populations. However, based on the potential effects of benthic grazers, trophic interactions could also result in both bottom and top-down control (Fig. 1).

Correlation matrices among groups within each reef component were tested to set the maximum number of non-collinear independent variables ( $r < |0.7|$ ). Step-

wise backward multiple regression was then used to identify benthic foundation groups explaining the variation in single countable invertebrates and reef fish groups and to identify countable invertebrate groups explaining the variation in reef fish groups. Positive and negative estimate parameters would indicate bottom-up and top-down control, respectively. In addition, we explored possible relationships between the Shannon's  $H'$  diversity indices of the 3 reef compartments.

### 3. RESULTS AND DISCUSSION

#### 3.1. Overall composition of reef compartments

The shallow reefscape at Alcatrazes resembles other coastal and insular reef habitats along the subtropical–warm temperate Southwestern Atlantic (Aued et al. 2018). Overall, we observed that 84% of the benthic cover was concentrated in 6 morpho-functional groups: the turf of articulated coralline algae was the most important (mean  $\pm$  SD:  $28 \pm 18.99\%$ ), followed by canopies of *Sargassum* spp. ( $22 \pm 25\%$ ), the zoanthid *Palythoa caribaeorum* ( $11 \pm 21\%$ ), filamentous algal turf ( $10 \pm 11\%$ ), the brain coral *Mussismilia hispida* ( $7 \pm 7\%$ ), and a heterogenous group (not described here) of erect macroalgae ( $6 \pm 7\%$ ; Table 1). Between 2011 and 2014, the same study area also showed a predominance of turf algae but low coverage of *Sargassum* spp. (Aued et al. 2018), possibly because the sampling period occurred at the end of the summer season, when most species of this furoid are already senescent (Széchy & Paula 2000). The relative cover of scleractinian corals, mostly brain corals and to a lower extent the ten-ray star coral *Madracis decactis* ( $0.8 \pm 2\%$ ), was slightly higher than at reef habitats along the Brazilian coast (Aued et al. 2018). However, with the exception of a few quadrants, hard corals were never dominant and most 3D structure is pro-

Table 1. Average abundance values and respective standard deviations for main groups covering the reef (%) and solitary organisms (ind.  $m^{-2}$ ). Rows in gray shading represent the same morpho-functional group

Compartments	Groups pooled	Mean	SD	%
<b>Cover</b>				
Bare rock	Barren ground	0.278	0.928	0.278
Corticated canopy	Other canopies	0.556	1.480	0.556
Cyanophyte canopy				
Filamentous canopy				
Foliose canopy				
<i>Sargassum</i> spp. canopy	<i>Sargassum</i> spp. canopy	21.71	25.478	21.71
<i>Madracis decactis</i>	<i>Madracis decactis</i>	0.787	2.272	0.787
<i>Mussismilia hispida</i>	<i>Mussismilia hispida</i>	6.713	6.886	6.713
Encrusting brown	Encrusting algae	6.157	5.964	6.157
Encrusting grey				
Encrusting pink				
Erect corticated	Other erect algae	6.435	6.556	6.435
Erect cyanophycean				
Erect filamentous				
Erect foliose				
Erect <i>Sargassum</i> spp.	Erect <i>Sargassum</i> spp.	6.019	10.506	6.019
Sand	Sand	3.519	9.036	3.519
Articulate turf	Articulated turf	27.685	18.986	27.685
Filamentous turf	Filamentous turf	9.537	11.401	9.537
<i>Palythoa caribaeorum</i>	<i>Palythoa caribaeorum</i>	10.602	20.611	10.602
<b>Solitary organisms</b>				
<i>Bunodosoma</i> sp.	Anemones	0.028	0.209	0.568
Other anemones				
<i>Anemonia sargassensis</i>				
Other ascidians	Ascidians	1.122	1.776	22.955
<i>Phallusia</i> sp.				
<i>Nodipecten</i> sp.	Bivalves	0.006	0.074	0.114
Other bivalves				
<i>Mithrax</i> sp.	Crabs	0.094	0.353	1.932
<i>Stenorhynchus</i> sp.				
<i>Isostichopus</i> sp.	Cucumbers	0.014	0.117	0.284
<i>Calcinus</i> sp.	Hermits	0.097	0.796	1.989
<i>Nudibranchs</i> sp.	Nudibranchs	0.006	0.074	0.114
<i>Echinaster</i> sp.	Seastars	0.047	0.249	0.966
<i>Narcissia</i> sp.				
<i>Astraea</i> sp.	Snails	0.300	1.084	6.136
<i>Leucozonia</i> sp.				
Other snails				
<i>Stramonita</i> sp.				
<i>Trachypollia</i> sp.				
<i>Arbacia</i> sp.	Urchins	3.175	5.066	64.943
<i>Astropyga</i> sp.				
<i>Diadema</i> sp.				
<i>Echinometra</i> sp.				
<i>Eucidaris</i> sp.				
<i>Lytechinus</i> sp.				
<i>Paracentrotus</i> sp.				

vided by the *Sargassum* spp. canopy, reaching a height of 30–40 cm (as in summertime, when this study was conducted). Barren grounds were relatively uncommon ( $0.3 \pm 0.9\%$ ), indicating that any physical disturbances or consumptive effects are overwhelmed by the development of algal turfs and even *P. caribaeorum* (Cruz et al. 2018, Reverter et al. 2022).

Solitary organisms mostly comprised sea urchins ( $3.17 \pm 5.07$  ind.  $m^{-2}$ , 65%), followed by ascidians ( $1.12 \pm 1.78$  ind.  $m^{-2}$ , 23%) and gastropod snails ( $0.30 \pm 1.08$  ind.  $m^{-2}$ , 6%), which together accounted for 95% of the whole sample (Table 1). The dominance of sea urchins, along with their rather clustered distribution (as indicated by a variance-to-mean ratio of 8.11), first indicates high potential consumptive effects at grazing fronts (as in Paine & Vadas 1969, Steneck et al. 2002, Ling et al. 2018).

Table 2. Results of PERMANOVA analyses using Bray-Curtis dissimilarities, testing the fixed effects of depth and site and the random temporal variation (between sampling years) on the abundance of main morpho-functional groups covering the reef, main solitary organisms, and reef-fish functional groups

Group	df	Pseudo- <i>F</i>	p (perm)
<b>Cover</b>			
Year	1	28.47	0.0001
Depth	1	1.73	0.2919
Site	2	3.81	0.3292
Year × depth	1	3.81	0.0004
Year × site	2	4.52	0.0022
Depth × site	2	1.10	0.4507
Year × depth × site	2	2.34	0.0173
Residual	60		
Total	71		
<b>Solitary organisms</b>			
Year	1	2.11	0.0608
Depth	1	4.53	0.036
Site	2	13.83	0.1735
Year × depth	1	1.48	0.1424
Year × site	2	2.03	0.0715
Depth × site	2	2.49	0.1408
Year × depth × site	2	1.88	0.0516
Residual	60		
Total	71		
<b>Fish</b>			
Year	1	12.81	0.0001
Depth	1	1.08	0.4167
Site	2	2.91	0.1643
Year × depth	1	4.69	0.0001
Year × site	2	4.50	0.0001
Depth × site	2	0.85	0.6012
Year × depth × site	2	1.51	0.0723
Residual	168		
Total	179		

We observed 94 reef fish species belonging to 36 families (Table S2), but only 9 species concentrated more than 80% of the whole fish abundance: *Haemulon aurolineatum* was the most important species (48%), followed by *Abudefduf saxatilis* (9%), *Stegastes fuscus* and *Coryphopterus glaucofraenum* (5% each), *Harengula clupeiola* (4%), *Decapterus macarellus* (3%), and *Holocentrus adscensionis*, *Coryphopterus* sp., *Diplodus argenteus* and *Parablennius pilicornis* (2% each; Table S2). Among the registered species, 5 are nationally threatened in the vulnerable category (ICMBio 2018): *Sparisoma frondosum*, *S. axillare*, *Scarus zelindae*, *Elacatinus figaro*, and *Epinephelus marginatus*, the latter also listed internationally as Threatened (Pollard et al. 2018). Small and medium MI feeders were the most abundant trophic group, comprising up to 56% of the whole sample, followed by small OM (13%), small PL (8%), and small HD (5%; Table S2). The outstanding abundance observed in the Alcatrazes Archipelago can be associated with the long history of enforcement, as the area has been patrolled and used for military practice since the 1980s and this has reduced the incidence of illegal fisheries of any kind — especially until 2008, and again from 2016 with the creation of the Refúgio da Vida Silvestre do Arquipélago de Alcatrazes. Interestingly, and as argued below, there are no clear indications of strong trophic processes linking fish trophic groups to benthic community structure that can account for the differences observed in the spatial patterns.

### 3.2. Spatial structure of reef communities in the Alcatrazes main island

A temporally dynamic, mosaic-like structure describes the communities of the 3 study components — benthic cover, solitary organisms, and reef fish groups — as indicated by the significant (or nearly significant) triple interaction of year × site × depth in all cases in the PERMANOVA (Table 2). Pairwise spatial comparisons following omnibus permutational analyses of variance evidenced important contrasts between sampling sites for both years and at the 2 depth strata for all components.

For the case of benthic cover and during 2020, the PERMANOVA, in pairwise comparisons, showed that the assemblages at FU differed from those at JC ( $t = 2.55$ ,  $p = 0.0152$ ) and ESEC ( $t = 2.41$ ,  $p = 0.0166$ ) in both the shallow and the deep stratum below the thermocline (FU vs. JC:  $t = 2.10$ ,  $p = 0.0071$ ; FU vs. ESEC:  $t = 2.02$ ,  $p = 0.0100$ ). In 2020, FU differed from the other sites at shallow depth because relative cover of

*Sargassum* spp. canopies was much reduced, ceding space for the persistence of the zoanthid *P. caribaeorum*, which was the most abundant morpho-functional group in this site. Conversely, at JC and ESEC, *Sargassum* spp. canopies and articulated turf made up the bulk of all cover (70–80%). Below the thermocline, FU still stood out, showing a more even contribution of cover groups. JC and ESEC, by contrast, were greatly dominated by *Sargassum* spp. canopies, which covered nearly 60% of the rocky surface. In 2021, the assemblages at JC were the ones contrasting with those at the other sites, both above (JC vs. FU:  $t = 2.12$ ,  $p = 0.0102$ ; JC vs. ESEC:  $t = 3.17$ ,  $p = 0.0020$ ) and below the thermocline (JC vs. FU:  $t = 1.87$ ,  $p = 0.0213$ ; JC vs. ESEC:  $t = 1.69$ ,  $p = 0.0541$ ; this latter at marginal significance under the usual standards, but still sufficient for our purposes of  $\alpha = 0.10$ , see Section 2.3.1). Similarity percentage (SIMPER) analyses indicated that *Sargassum* spp. canopies or

patches of erect algae combined (in 6 comparisons), turfs of articulated coralline algae (5), the zoanthid *P. caribaeorum* (4), and turfs of filamentous algae (1) were the organisms responsible for the largest contrasts between groups (contributions  $\geq 10\%$  of whole dissimilarity between groups; Table S3). The dynamics of algal canopies and turfs seem to play a major role in the structure of reefscapes (Fig. 3). In addition, in 2021, *Sargassum* spp. hardly reached canopy size across sites, remaining only as erect algae, to a reduced extent, and almost fully concentrated in the lower depth stratum. This can suggest that productivity and growth of *Sargassum* spp. are favored by higher levels of nutrients in the water during upwellings (Lapointe 1995). In the shallow reef, JC differed from the other sites, where turfs of articulated coralline algae were much more abundant (64%). The limited development of *Sargassum* spp. and turfs allowed *P. caribaeorum* to dominate at FU (33%) and ESEC

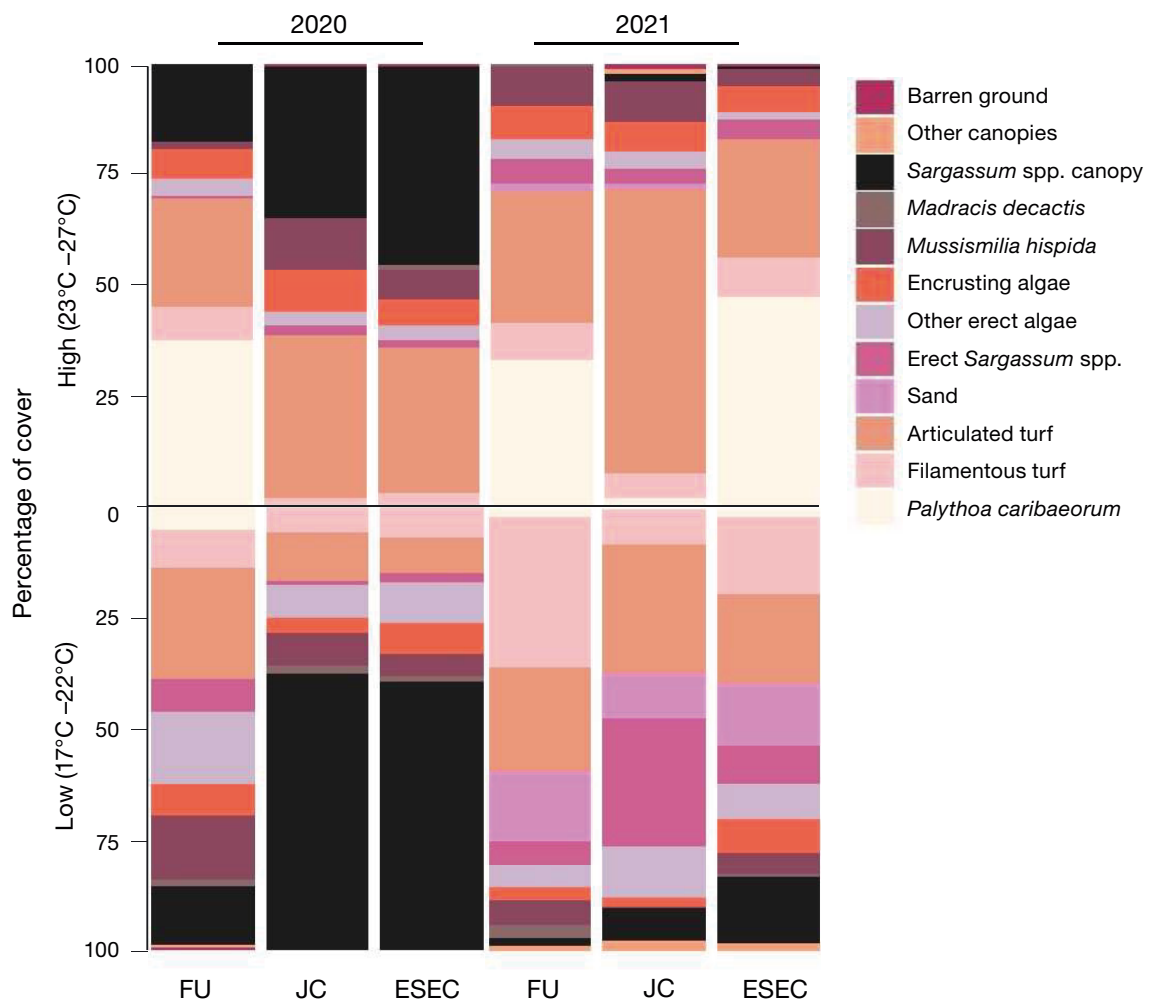


Fig. 3. Abundance of benthic cover recorded at sampling sites. FU: Saco do Funil; JC: Jardim dos Corais; ESEC: Estação Ecológica Tupinambás. High: above the thermocline; low: below the thermocline



(47%). In the deeper stratum, turfs of articulate coral-line algae were still more abundant at JC (although not as high as above the thermocline). This feature, together with a higher cover of erect *Sargassum* spp., made JC substantially different from FU and ESEC. These patterns suggest a competitive hierarchy, with *Sargassum* spp. ranking first, algal turfs second, and *P. caribaeorum* third, probably following an increasing growth rate gradient. In 2020, when conditions were apparently favorable to the development of canopies, *Sargassum* spp. may have restrained the growth of turfs, contradicting different studies suggesting that algal turfs are stronger competitors (O'Brien & Scheibling 2018, Gorman et al. 2020). In 2021, when *Sargassum* spp. blooming was restrained, algal turfs

became on average more abundant, and where they did not, *P. caribaeorum* prevailed.

The PERMANOVA in pairwise comparisons also evidenced a clear spatial structure of assemblages of solitary organisms. As for benthic cover, contrasts were year- and depth-specific; however, in this case, there is a more consistent monotonic pattern from FU to ESEC, with idiosyncratic differences largely attributable to the magnitude of contrasts (Fig. 4). Pairwise comparisons between any 2 sites were always significant ( $0.0019 \leq p \leq 0.0206$ ), except for FU vs. JC ( $t = 1.22$ ,  $p = 0.2122$ ) and JC vs. ESEC ( $t = 1.19$ ,  $p = 0.2138$ ) above the thermocline and JC vs. ESEC ( $t = 0.99$ ,  $p = 0.4615$ ) below the thermocline in 2020. The 3 groups contributing to the substantial dissimilarity

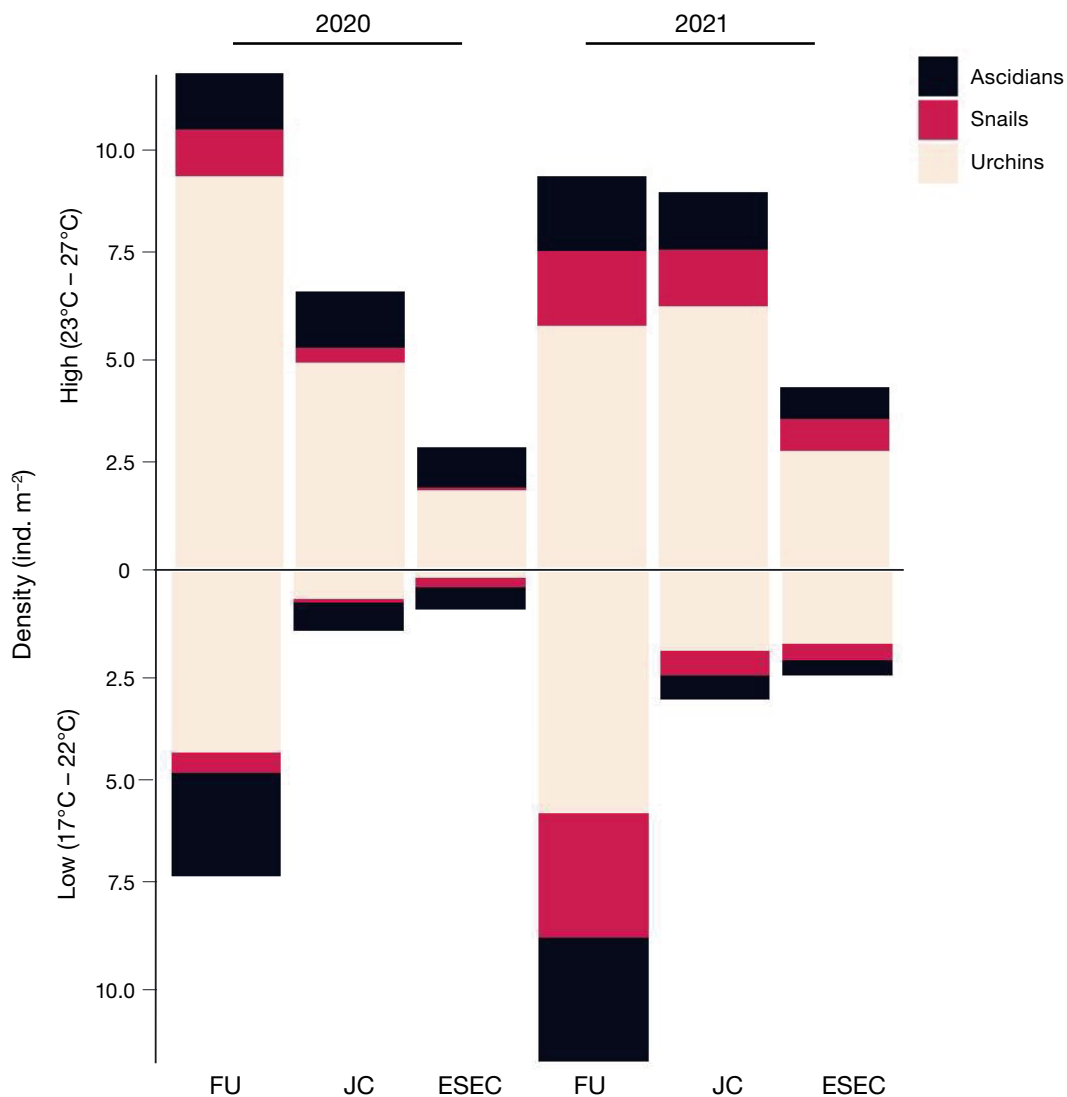


Fig. 4. Abundance of groups of solitary organisms responsible for the most dissimilarity between sample sites, as identified in SIMPER analyses. FU: Saco do Funil; JC: Jardim dos Corais; ESEC: Estação Ecológica Tupinambás. High: above the thermocline; low: below the thermocline

between groups according to the SIMPER analysis were sea urchins, ascidians, and gastropod snails (Table S4). The abundance of all 3 groups exhibited a decrease from FU to ESEC and from the shallow to deep stratum (Fig. 4), in this latter trend except for ascidians at FU (both years). It is challenging to advance any processes underlying such a striking pattern. One could speculate that current patterns, together with some retention at the more sheltered site (FU), might determine a gradient of larval supply and settlement rate (as in Breitbart et al. 1995, Silva et al. 2006, Mazzei et al. 2021) along the NE–SW axis of the island, but specific observational studies and experimental research should be conducted to test this possibility.

Fish spatial patterns also changed from year to year and depth. Pairwise comparisons following the omnibus PERMANOVA analysis among sites were generally significant ( $0.0001 \leq p \leq 0.0366$ ) except for 2020 JC vs. ESEC at both the shallow ( $t = 1.02$ ,  $p = 0.4194$ ) and the deep stratum ( $t = 1.13$ ,  $p = 0.2338$ ) and 2021 FU vs. ESEC at the shallow depth ( $t = 0.99$ ,  $p = 0.4611$ ). SIMPER analyses showed that the functional groups responsible for large dissimilarities were MI (0–14 cm), MI (15–23 cm), OM (0–14 cm), PL (0–14 cm), and HD (0–14 cm) (Table S5). For all those groups, spatial abundance trends at the shallow reef, across sites, were inconsistent between years (Fig. 5). Below the thermocline, however, all groups

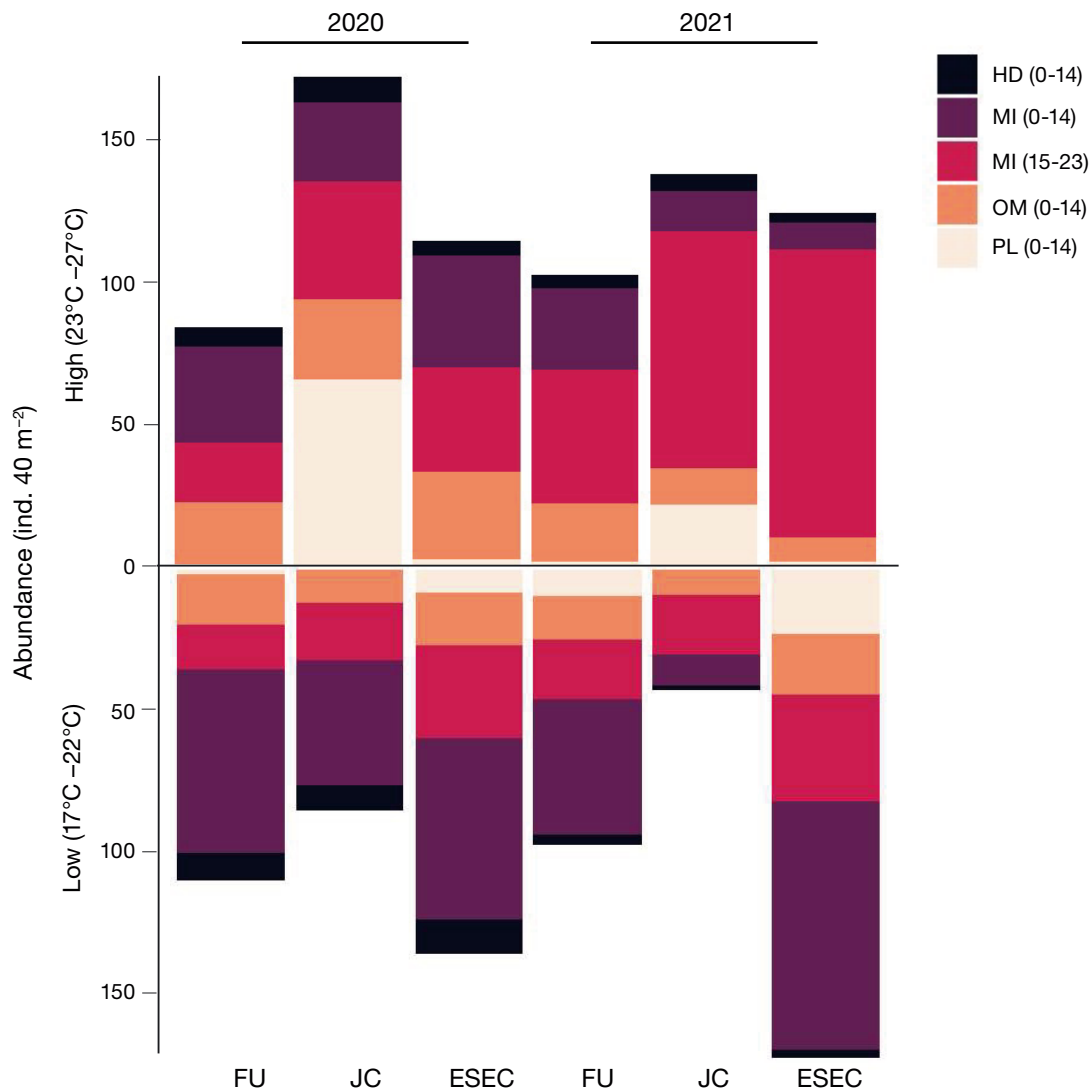


Fig. 5. Abundance of functional groups of fish responsible for the most dissimilarity between sample sites, as identified in SIMPER analyses. HD: herbivores–detritivores; MI: mobile benthic invertebrate feeders; OM: omnivores; PL: planktivores. Numbers after fish groups refer to size intervals: (0–14): between 0 and 14 cm; (15–34): between 15 and 23 cm. FU: Saco do Funil; JC: Jardim dos Corais; ESEC: Estação Ecológica Tupinambás. High: above the thermocline; low: below the thermocline

except MI (15–23 cm) tended to be more abundant at FU and ESEC than at JC. Regardless of feeding habit, smaller fish (0–14 cm) tended to be either evenly distributed (OM) or more abundant (MI, HD) below the thermocline, while larger fish (MI, 15–23 cm) were more abundant in the shallow reef. Space occupation may include suboptimal temperature conditions in the presence of conspecifics or heterospecifics, depending on the cost-effectiveness of the interaction (Nay et al. 2021). Hence, the observed trend can be explained by competitive interactions whereby larger fish may be displacing smaller fish to marginal habitats. However, smaller fish representative of benthic-dwelling groups (e.g. Pomacentridae, Gobiidae, and Blenniidae) would not be able to migrate to shallow parts of the reef because of substrate availability or mobility restrictions irrespective of sub-optimal temperature conditions.

### 3.3. Correlations suggesting ecological relationships between reef components

We did not observe any correlations between the Shannon's diversity indices observed at the 3 reef compartments (i.e. benthic cover, solitary organisms, and reef fish) (Fig. S2). Except for fish and some specific cases, we did not identify the organisms to the species level, so correlations were made considering the groups of each compartment, which can encompass many different species. On the other hand, we observed positive and negative relationships among certain groups (Table 3), indicating that trophic inter-

actions may underlie the spatial patterns observed in the area.

As there was high collinearity between the 3 solitary organisms (Table 4), we selected urchins for multiple regressions because they are known to be important herbivores on reefs (Estes & Palmisano 1974, Estes et al. 1998, Steneck et al. 2002). Along with several other studies showing their control over different macroalgae in both temperate (e.g. Steneck et al. 2002, Leung et al. 2014) and tropical (coral) reefs (Edmunds & Carpenter 2001, Idjadi et al. 2010), we observed a negative relationship between sea urchins and *Sargassum* spp. cover ( $r^2 = 0.43$ ,  $p = 0.02$ ; Fig. 6a), potentially indicating top-down control over *Sargassum* spp.

Canopies of *Sargassum* spp. are structurally complex habitats that shelter a great diversity of invertebrate prey (mostly hard-bodied groups; Figueiredo et al. 2020) and probably play an important role in whole-reef trophic dynamics. Despite their relative abundance in the study area ( $22 \pm 25\%$ ), canopies of *Sargassum* spp. still occupy a lower reef space compared to articulated turf ( $28 \pm 18.99\%$ ). Over the last decades, there has been a decrease in *Sargassum* spp. canopies in the SW Atlantic — arguably due to global warming and other anthropogenic stressors — which have been replaced by turf-forming algae (Gorman et al. 2020). Similar benthic species turnover has been observed in the Mediterranean Sea where canopy algae *Cystoseira* spp. has been replaced by turf-forming algae, known to be more tolerant to environmental disturbance (O'Brien & Scheibling 2018), and mussel beds due to anthropogenic stressors (Benedetti-Cecchi et al. 2001, Perkol-

Table 3. Stepwise backward multiple regression analyses testing the overall effects of morpho-functional benthic cover on the abundance of solitary organisms and fishes. Significance ( $p < 0.05$ ) of overall selected models and respective predictors are specified in **bold**. The cases where the predictors were not significant are indicated by dashes (–). The overall effects of benthic cover on the abundance of omnivorous, planktivorous, and detritivorous herbivorous fish of 0–14 cm, and the effects of the abundance of solitary organisms on fish abundance are not reported as no significant p-values were observed. ATC: articulated coralline turf; ZC: zoanthid cover; SC: *Sargassum* spp. canopy; ES: erect *Sargassum* spp.; FT: filamentous turf; MI: mobile-invertebrate feeders. Fish size classes follow trophic groups

	— Benthic cover on urchins —			— Benthic cover on reef fish —					
	Coeff.	<i>t</i>	<i>p</i>	Coeff.	MI (0–14 cm)		MI (15–23 cm)		
					<i>t</i>	<i>p</i>	Coeff.	<i>t</i>	<i>p</i>
Intercept	5.57	6.77	<b>&lt;0.001</b>	140.70	4.70	<b>0.003</b>	–	–	–
ATC	–	–	–	–1.85	–3.40	<b>0.014</b>	0.867	2.41	<b>0.043</b>
ZC	–	–	–	–1.46	–2.88	<b>0.028</b>	1.046	3.14	<b>0.014</b>
SC	–0.07	–3.74	<b>0.006</b>	–	–	–	–	–	–
ES	–	–	–	–	–	–	–	–	–
FT	–	–	–	–	–	–	–	–	–
	Mult. $r^2$	$F_{2,8}$	<i>p</i>	Mult. $r^2$	$F_{4,6}$	<i>p</i>	Mult. $r^2$	$F_{2,8}$	<i>p</i>
	0.557	7.28	<b>0.016</b>	0.556	4.12	0.061	0.581	7.93	<b>0.013</b>

Table 4. Correlation matrix of the 3 reef compartments to identify collinearity. ATC: articulated coralline turf; ZC: zoanthid cover; SC: *Sargassum* spp. canopy; ES: erect *Sargassum* spp.; FT: filamentous turf; URC: urchins; ASC: ascidians; SNA: snails; MI: mobile-invertebrate feeders; OM: omnivores; PL: planktivores; HD: herbivore–detritivores. Fish size classes follow trophic groups

	ATC	ZC	SC	ES	FT	<i>Sargassum</i> spp. (SC + ES)
<b>Benthic cover</b>						
ATC	–					ATC –0.559
ZC	–0.023	–				ZC –0.547
SC	–0.514	–0.439	–			FT –0.420
ES	0.033	–0.193	–0.375	–		
FT	–0.200	–0.057	–0.413	0.111	–	
	URC	ASC	SNA			
<b>Solitary organisms</b>						
URC	–					
ASC	<b>0.640</b>	–				
SNA	<b>0.870</b>	0.465	–			
	MI (0–14 cm)	MI (15–23 cm)	OM (0–14 cm)	PL (0–14 cm)	HD (0–14 cm)	
<b>Reef fish</b>						
MI (0–14 cm)	–					
MI (15–23 cm)	–0.507	–				
OM (0–14 cm)	0.442	–0.337	–			
PL (0–14 cm)	0.005	0.099	0.447	–		
HD (0–14 cm)	0.358	–0.287	0.251	0.1	–	

Finkel & Airoidi 2010). In tropical and temperate reefs, herbivory is one of the most important processes, which can either maintain its functioning through the control of macroalgae and consequent maintenance of corals (Scheffer et al. 2001, Lee 2006, Myhre & Acevedo-Gutiérrez 2007) or drastically

modify the landscape through overgrazing (Gagnon et al. 2004, Leung et al. 2014). Therefore, sea urchin populations and the extent of *Sargassum* spp. canopies should be carefully monitored and experimentally manipulated for a better understanding of this trophic link.

Articulated turf added to the zoanthid cover (i.e. components with a significant association in the multiple regression) showed a positive relationship with the abundance of 15–23 cm fish invertebrate feeders ( $r^2 = 0.44$ ,  $p = 0.02$ ; Fig. 6b). We suggest indirect bottom-up control, mediated by mobile invertebrates present in the turf (Figueiredo et al. 2020). The most abundant fish species in this study, *H. aurolineatum* (Table S2), and chiefly individuals larger than 15 cm (included in the 15–23 cm group of invertivores), prey largely on soft-bodied polychaetes (Pereira et al. 2015), which are especially abundant in algal turfs (Figueiredo et al. 2020). Large patches of low-lying turfs can thus be used as main foraging grounds by larger *H. aurolineatum* and

adult stages of other, less abundant fishes. However, the strong relationship found was largely due to 2 data points. For more robust results, experiments with a larger number of replicates are needed. Such a preference likely impacts the distribution of smaller invertebrate fish (0–14 cm), which are negatively ( $r^2 = 0.46$ ,

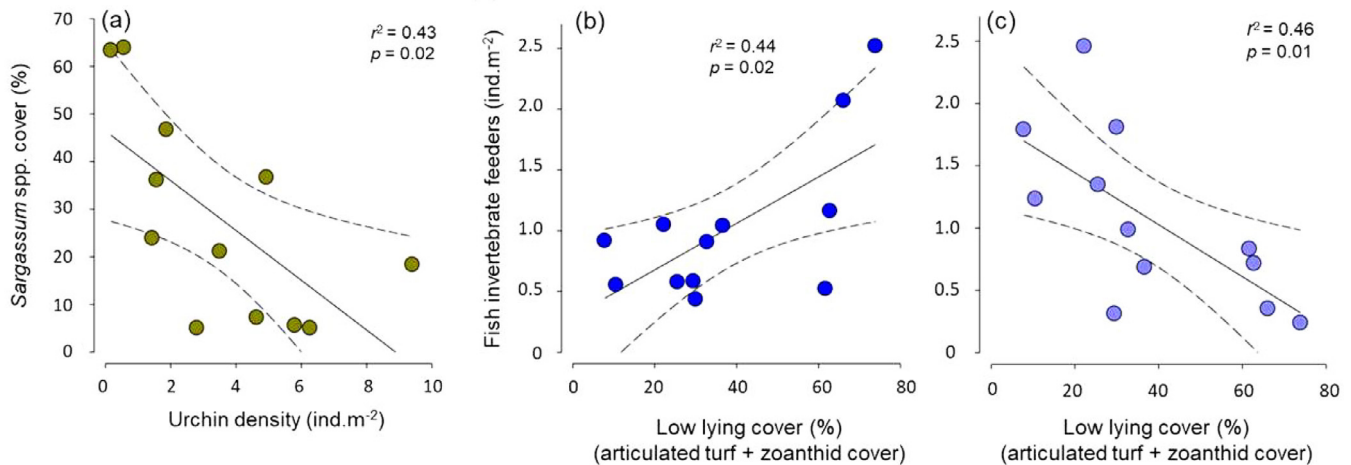


Fig. 6. Linear regressions between (a) sea urchins and benthic cover, and between low lying cover and (b) 15–23 cm fish invertebrate feeders and (c) 0–14 cm fishes invertebrate feeders. Each point represents the combination of year (2 years), sites (3 sites), and depth (2 classes). Dashed lines: 95% CIs

$p = 0.01$ ; Fig. 6c) associated with the low-lying cover made of turf algae and zoanths. Rather than controlling the extent of low-lying reef cover — which seems impossible given the occupancy rates of turf algae and zoanths and the foraging strategies and diet of small invertivores — smaller fish may be displaced to marginal habitat through interference competition.

#### 4. CONCLUSIONS

In this study, we report that reef communities in Alcatrazes are mainly dominated by turfs of articulated coralline algae, canopies of *Sargassum* spp., and patches of the zoanthid *Palythoa caribaeorum* and suggest that the relative abundance of those dominant groups is driven by complex spatial and temporal dynamics. Evidence of top-down control is, at present, restricted to the potential grazing effects of sea urchins on *Sargassum* spp. canopies. Indirect bottom-up effects explain concentrations of larger invertivores fish (15–23 cm) on foraging low-lying grounds of turfs and zoanths where prey abundance is high. Smaller invertivores followed the inverse trend, arguably reducing interference competition. We highlight the importance of long-term reef monitoring and experimental manipulations to further test those processes and to detect any drivers of phase shifts, such as overgrazing on *Sargassum* spp. meadows, which have been declining over the last few decades over the study region.

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