ORIGINAL RESEARCH

Drivers of reef fish assemblage structure in a mosaic of Brazilian marine habitats

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Abstract

Fishes are conspicuous and threatened components of reef ecosystems. Understanding the role of the variables that shape their assemblages is important to buffer species, fishery stocks, and habitats from anthropogenic threats. So, the influence of depth and topographic complexity on trophic guilds and body size of reef fishes was assessed by underwater visual censuses (UVCs) conducted in biogenic reefs, rocky reefs, and rhodolith beds interspersed with algae, invertebrates, and sand. The study area lies in the southern continental shelf of Espírito Santo state, Brazil, a region that has lacked thorough UVC surveys of biogenic reefs and rhodolith habitats. A total of 105 species belonging to 42 fish families were registered. Among the eight trophic guilds registered, mobile invertebrate feeders and herbivores were the most representative in terms of density and biomass. Biogenic and rocky reefs showed higher biomass, density and richness than rhodolith habitats due to greater topographic complexity, which promotes more food resources and shelter. The five habitats hosted distinct fish assemblages (guilds and taxonomic diversity) probably because of the varying ability of resources they provide. Nevertheless, all habitats were dominated by species of low trophic level. Large fish, especially macrocarnivores, were mostly found in the deepest zones. This pattern is associated with ecological preferences but could also be strengthened by overfishing on shallower sites, decreasing the abundance of top predators and influencing their depth distribution. Our results provide a baseline for future studies, presenting subsidies for the management of human activities and the conservation of marine ecosystems in southeastern Brazil.

Keywords Brazilian province · Rhodolith beds · Rocky reefs · Biogenic reefs · Underwater visual census (UVC) · Espírito Santo

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Introduction

Reef environments host the greatest biodiversity in the marine realm (Knowlton and Jackson 2017) but have been historically threatened by anthropogenic stressors such as global warming, pollution and overfishing (Hughes et al. 2017). Consequently, reefs have been suffering community structural changes and stock depletion (Friedlander and DeMartini 2002; Gardner et al. 2003; Guabiroba et al. 2020; Meira et al. 2023), and environmental services and goods they provide (e.g., fishing resources, tourism, and cultural values) have been widely affected (Woodhead et al. 2019). Notwithstanding, knowledge gaps and a low understanding of the ecological aspects of assemblages hinder the development of management strategies to mitigate these impacts.

With more than 6300 species (Parravicini et al. 2013), or about 40% of the marine ichthyofauna (Nelson et al. 2016), fishes are some of the most conspicuous organisms present in reefs. Their peak of diversity is situated in the Central Indo-Pacific (Kulbicki et al. 2013; Mora et al. 2003), and the South Atlantic presents an impoverished fauna resulting from a dearth of geotectonic events, long-term climatic trends and isolation from the Indo-Pacific through biogeographic barriers (Floeter et al. 2008). The center of diversity of the south-western Atlantic is the tropical-subtropical sub-province (11.5°S to 29.3°S), where the Brazilian state of Espírito Santo is found (Pinheiro et al. 2018).

Beyond biogeographical and broad scale factors, reef ichthyofauna is finely structured under the influence of local-scale variables (Darling et al. 2017). Among these, depth, topographic complexity and habitat type are the main factors of trophic, taxonomic, and body size structure (Alvarez-Filip et al. 2009; Maia et al. 2018; Cáceres et al. 2020). On the Brazilian coast and oceanic islands, reef fish assemblages (e.g., density, biomass, and individual size) are strongly driven by depth and complexity (Krajewski and Floeter 2011; Pinheiro et al. 2013; Anderson et al. 2023). These factors need to be considered in spatial planning strategies for the conservation of reef environments in front of anthropogenic-driven pressure. However, previous research on reef fish assemblages in the Espírito Santo state has mostly focused on tide pools (e.g., Macieira and Joyeux 2011; Pimentel et al. 2018) and rocky reefs (e.g., Floeter et al. 2007; Pinheiro et al. 2013; Simon et al. 2011, 2013), leaving extensive habitats unassessed (but see Mazzei et al. 2017 and Anderson et al. 2022a).

A number of fish and other marine organisms have their southern or northern geographic occurrence limit in or near Espírito Santo, a state that presents a variety of transitional ecosystems along its 400 km-long coast (a neritic ecotone; Pinheiro et al. 2018; Carvalho et al. 2020; Martins et al. 2022; Anderson et al. 2022b), and is a critical area for conservation in Brazil (Vila-Nova et al. 2014). To assess the ichthyofauna and its drivers, we conducted underwater visual censuses in five habitats of the southern continental shelf of Espírito Santo, including rhodolith beds. Such habitats are key benthic components in the southwestern Atlantic (Brasileiro et al. 2016; Amado-Filho et al. 2017), and their community and rhodolith-forming species have been studied locally (Amado-Filho et al. 2007; Villas-Bôas et al. 2015). Rhodolith ecosystems are responsible for the major production of $CaCO_3$ of the tropical south-western Atlantic, yet rhodolith-inhabiting ichthyofauna is understudied (Anderson et al. 2022b). The five habitats offer distinct substrate formation (Teixeira et al. 2013) and are exposed to different environmental (e.g., topographic complexity) and anthropogenic pressures (e.g., unregulated fishing and tourism) (Pinheiro et al. 2009; Teixeira et al. 2013). Thus we hypothesized that (1) the assemblage structure (guilds and taxonomic diversity) differs between habitats and (2) larger individuals and high-level

trophic guilds should be mainly associated with deeper sites. Addressing these topics could improve the knowledge of the locality's biodiversity and promote key subsidies for their conservation.

Methods

Study area

The study area covers the southern coast of the state of Espírito Santo, between latitudes 20°42′S and 21°09′S (Fig. 1). The weather is tropical with a mean annual temperature of 22 °C and a rainy season that extends from spring to summer (October to March). While tropical storms may impact fish assemblages (Ibarra-García et al. 2020; 2022), no such episode was recorded during the study period. The locality lies in an oceanographic transition region dominated by tropical waters brought by the Brazilian Current and influenced by summer upwelling events of cold and nutrient-rich waters (Aguiar et al. 2014; Schmid et al. 1995). The morphology of the continental shelf is complex and supports a diversity of coastal habitats. Nineteen sampling sites were assessed, encompassing a variety of habitats and depths (Fig. 1).

Data collection

We conducted underwater visual censuses (UVCs) through SCUBA diving to access the fish assemblages. The method consists of identifying, counting and estimating total length (in sizes classes 0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, and so on) of all individual fish sighted in a 40 m2 (20×2 m) transect. The diver, when unrolling the tape, registers the more mobile fishes that are generally larger than 10 cm and have demersal or pelagic habits. After swimming the 20 m, the diver returns to the initial point rolling the tape and registering the cryptic species that are usually smaller and have bentho-demersal habits.
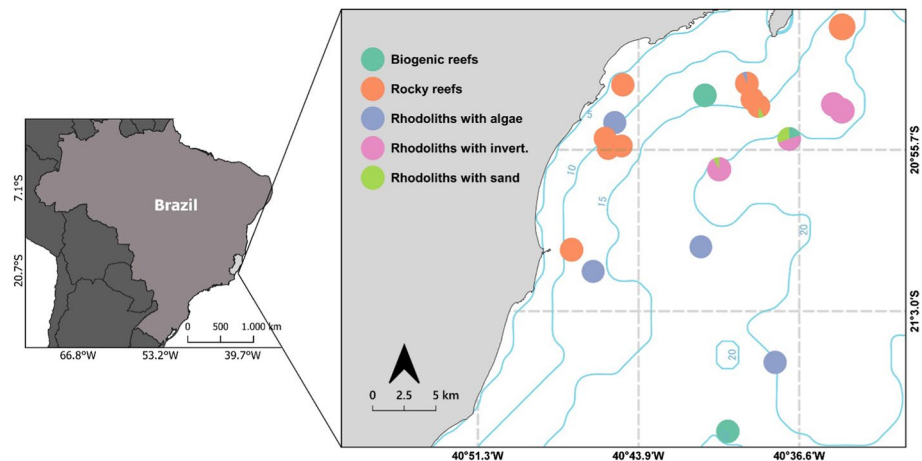

Fig. 1 Study area and sampled habitats. Isobaths at 5 m intervals

This is a well established method to survey the reef fish assemblage of Brazilian coastal sites due to high turbidity and low visibility (e.g., Floeter et al. 2007; Pinheiro et al. 2013; Simon et al. 2013; Morais et al. 2017).

During the austral summers of 2008/9 and 2009/10, we conducted 251 UVCs between 3 and 23 m depth (Table 1). Substrate structural complexity was classified in three categories following Pinheiro et al. (2013): high, represented by boulders and holes larger than 1 m of size and depth; intermediate, with boulders and holes smaller than 1 m of size and depth; and low, with few and small benthic organisms. The benthic composition was accessed through photoquadrat (35 × 20 cm) analysis using the software CPCe (Kohler and Gill 2006). In each of the 19 dive sites, we randomly distributed three transects of 20 m in which one photo was taken every two meters. Twenty points were randomly distributed in each photo and the corresponding biotic or abiotic category was registered (Fig. S1). The five habitats sampled were classified based on direct visual observations of divers and confirmed with data presented by Teixeira et al. (2013). These authors mapped habitats at a regional scale using traditional ecological knowledge (TEK) of local fishermen (from 19 fishing villages) and high-resolution benthic habitat mapping from side-scan sonar surveys covering about 130 km^2. Habitats were classified as biogenic reefs (BR), rocky reefs (RR), rhodoliths with algae (ROAL), rhodoliths with invertebrates (ROIN), and rhodoliths with sand (ROSA) based on their origins, either geological or biological, and the benthic organisms associated to the substrate (Fig. 1 and 2; Table 1). The discrepancy in the number of transects among habitats is due to logistical and diving limitations (Table 1).

Locally known by fishermen as 'cabeços', biogenic reefs are small round or cylindrical patch-reefs isolated in areas of unconsolidated sediment (Fig. 2a and b; Teixeira et al. 2013). Worldwide, this habitat is usually formed by hermatypic corals but reef building scleractinians show low abundance in the region (Simon et al. 2013; Aued et al. 2018). Instead, the living cover of these reefs is mainly composed of calcareous coralline algae, bryozoans, non-scleractinian corals, and other sessile or benthic invertebrates (Teixeira et al. 2013; Aued et al. 2018). The rocky reefs, mainly found on shores and around coastal islands, are granite-based and support a high-diversity benthic flora and fauna (Fig. 2c and d; Teixeira et al. 2013). They also cover a broader surface area than biogenic reefs.

Table 1 Number of UVC transects per habitat, depth and complexity level

	BR	RR	ROAL	ROIN	ROSA	Total
Total	17	163	28	38	5	251
Depth						
0–5 m	–	77	–	–	–	77
5–10 m	–	63	6	–	–	69
10–15 m	10	12	18	22	1	63
15–20 m	5	11	–	11	1	28
20–25 m	2	–	4	5	3	14
Complexity level						
Low (%)	–	41 (25%)	23 (82%)	17 (45%)	5 (100%)	86
Intermediate (%)	3 (18%)	78 (48%)	5 (18%)	21 (55%)	–	107
High (%)	14 (82%)	44 (27%)	–	–	–	58

BR biogenic reefs, *RR* rocky reefs, *ROAL* rhodoliths with algae, *ROIN* rhodoliths with invertebrates, *ROSA* rhodoliths with sand
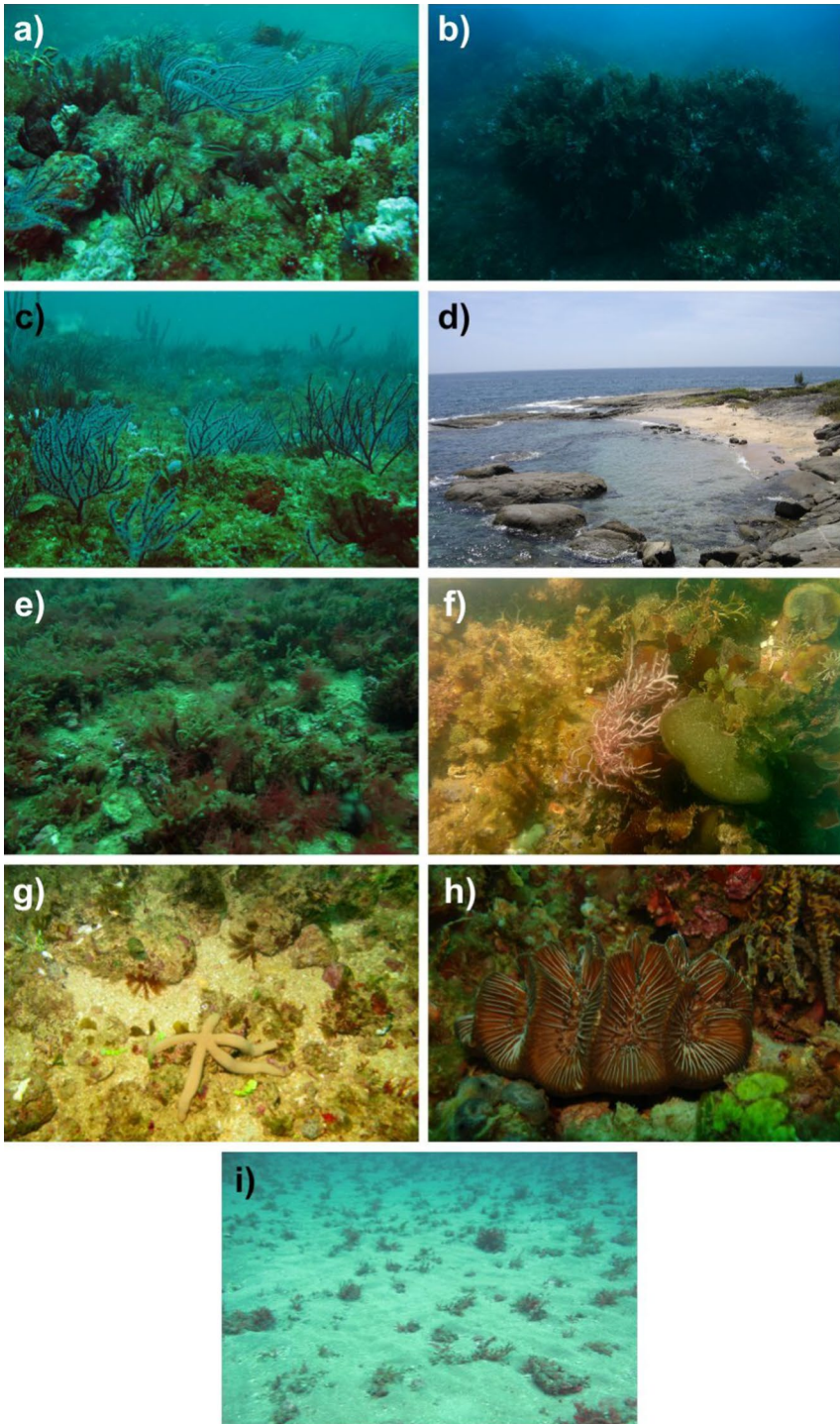
Fig. 2 Habitats sampled in the southern continental shelf of Espírito Santo. **a–b** biogenic reefs, **c–d** rocky reefs; **e–f** rhodoliths with algae, **g–h**, rhodoliths with invertebrates, **i** rhodoliths with sand

The other three habitats are made of rhodoliths, which are free-living nodules constituted mostly by non-geniculate coralline algae often accompanied by encrusting fauna such as bryozoans (Foster 2001). Rhodolith beds were classified and nominated according to the main organism or sediment associated with them. Thus, rhodoliths with algae (Fig. 2e and f) present a high density of fleshy macroalgae and turf that are subject to seasonal fluctuations in abundance and distribution (Teixeira et al. 2013); rhodoliths with invertebrates (Fig. 2g and h; Teixeira et al. 2013) are beds where crinoids, sponges, octocorallia, ascidians and other benthic organisms are highly represented; and rhodoliths with sand (Fig. 2i; Teixeira et al. 2013) are sandy areas securing smaller rhodolith patches.

Data analysis

Reef fish assemblage

Following Pinheiro et al. (2018), fish species were grouped into six trophic categories (Table S1): herbivores (HERB), macrocarnivores (MCAR), mobile invertebrate feeders (MINV), omnivores (OMN), planktivores (PLANK), and sessile invertebrate feeders (SINV). Species were further classified according to their status in international and domestic red lists (ICMBio, 2018; IUCN, 2023; Table S1) as not evaluated (NE), data deficient (DD), least concern (LC), near threatened (NT), and vulnerable (VU).

Individual weights were obtained through length–weight relationships. We use the equation $W = a \times TL^b$, where W is the calculated weight in grams; TL is the total length in centimeters, using the center of each size class; and a and b are the species-specific regression parameters available in the literature (details are available in Table S2). Biomass, as the sum of all individual weights, was computed for each transect. Fishery catches landed between April 2011 and March 2012, the type of association with human activities, and the commercial interest of each species are presented in Table S3.

Statistical analysis

The average fish density (number of individuals per 40 m^{-2}±SD), biomass (kg.40 m^{-2}±SD) and richness (number of species per 40 m^{-2}±SD) were compared among habitats (five levels: BR, RR, ROAL, ROIN, ROSA) through One-Way ANOVA based on permutations. This analysis was conducted with the *perm.oneway.anova* function of the R package *wPerm* (Weiss 2015) using 9999 permutations. To further address which pairs of habitats differed, pairwise comparison tests were run using the *pairwise.wilcox.test* function of the package *Stats* (R Core Team 2022). The same routine was used to compare assemblage metrics (fish density, biomass, and richness) among the three topographic complexity levels (low, intermediate, and high). Permutational multivariate analyses of variance (PERMANOVA; Anderson 2017) were used to investigate the influence of habitats on taxonomic and trophic assemblage structures with the *adonis* function of the R package *Vegan* (Oksanen et al. 2022). These analyses use Bray–Curtis distance matrices calculated from standardized (Hellinger method) density and biomass of species and trophic guilds, 9999 permutations, and type III sums of squares. Posterior to PERMANOVAs, a Principal Coordinate Analysis (PcoA) run with the *cdmscale* function of the R package *Stats* (R Core Team 2022) was used to visualize the relationships between trophic and taxonomic structures of the assemblage with the five habitats. An analysis of similarity percentage (SIMPER) for species biomass was used to detect the largest contributors to dissimilarity

among habitats running the function *simper* of the R package *Vegan* (Oksanen et al. 2022; with Bray–Curtis index and 9999 permutations). Following Cáceres et al. (2020), after a cutoff of 60% for the accumulated contribution of dissimilarity, species were further selected based on one qualitative (Ql_1) and two quantitative criteria (Qn_1, Qn_2). Ql_1 includes the species with the highest incidence in the dissimilarities among habitats; Qn_1, the species with the highest average contribution to the dissimilarity; and Qn_2 the species with the greater differences in biomass among habitats (Cáceres et al. 2020). PERMANOVAs, using the procedure detailed above, were used to analyze the influence of depth (five levels: 0–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m) and complexity (three levels: low, intermediate, and high) on trophic and body size structures of the assemblage. Bray–Curtis distance matrices were calculated from the standardized density of size classes and of trophic guilds. Redundancy analysis (RDA) was used to graphically visualize the influence of the independent variables (complexity and depth) on the dependent ones (size and guilds). RDA were performed with the *rda* function of the R package *Vegan* (Oksanen et al. 2022). All graphics were made with the functions *ggplot2* (Wickham 2016) and *plot* (R Core Team 2022).

Results

General aspects of the assemblage

During the visual surveys, 14,605 fishes belonging to 105 species and 42 families were recorded (see Table S1 for density; Table S2 for biomass). The most species-rich families were Haemulidae (8 species), Serranidae (7), Carangidae (6), Labridae (6) and Pomacentridae (6) (Table S1). Seven species are considered vulnerable or threatened globally (5 NT, 2 VU) and twelve nationally (7 NT, 5 VU; Table S1; ICMBio, 2018; IUCN, 2022). Only two individuals of a single elasmobranch species (*Bathytoshia centroura*) were sighted (Table S1). The average density, biomass and richness ($\pm$SD) per transect were 58.2 ± 95.9 ind.40 m^{-2}, 7.6 ± 23.4 kg.40 m^{-2} and 10.0 ± 5.7 sp.40 m^{-2}, respectively. Ten species occurred in more than half of transects done in a particular habitat (Table S1). Among these, *Diplectrum radiale* was detected in all ROSA transects, *Stegastes fuscus* in 71% of RR transects, and *Halichoeres poeyi* in over 65% in all habitats except ROSA (20%; Table S1). According to the SIMPER analysis, the most important species to the average dissimilarities among habitats were: *Haemulon aurolineatum*, *Acanthurus chirurgus*, *A. bahianus*, and *Halichoeres poyei*, based on Ql_1 criterion; *Haemulon aurolineatum*, *A. chirurgus*, *H. atlanticus*, and *Pagrus pagrus*, based on Qn_1 criterion; and *A. chirurgus*, *H. atlanticus*, *Priacanthus arenatus*, and *Sparisoma axillares*, based on Qn_2 criterion (Table S4). Only *P. pagrus* (487,387 kg), *Priacanthus arenatus* (8769 kg), and *H. atlanticus* (1030 kg) showed significant landings in Espírito Santo state (Table S3).

Mobile invertebrate feeders (35.5 ± 83.8 ind.40 m^{-2}), herbivores (11.9 ± 17.3 ind.40 m^{-2}) and planktivores (7.8 ± 29.6 ind.40 m^{-2}) were the main trophic categories in terms of density; the first two guilds also dominated the biomass (3.3 ± 17.0 and 3.3 ± 13.0 kg.40 m^{-2}) of the overall assemblage (Fig. 3). The habitats showed differences in density ($F = 4.62$, $p = 0.0088$), biomass ($F = 3.97$, $p = 0.0336$) and richness ($F = 20.82$, $p < 0.001$). These assemblage variables showed similar values in ROAL, ROIN and ROSA. However, values for rhodolith habitats were lower than those for reef habitats BR and RR (Fig. 4). Rocky and biogenic reefs showed similar density and richness (Fig. 4a and c),
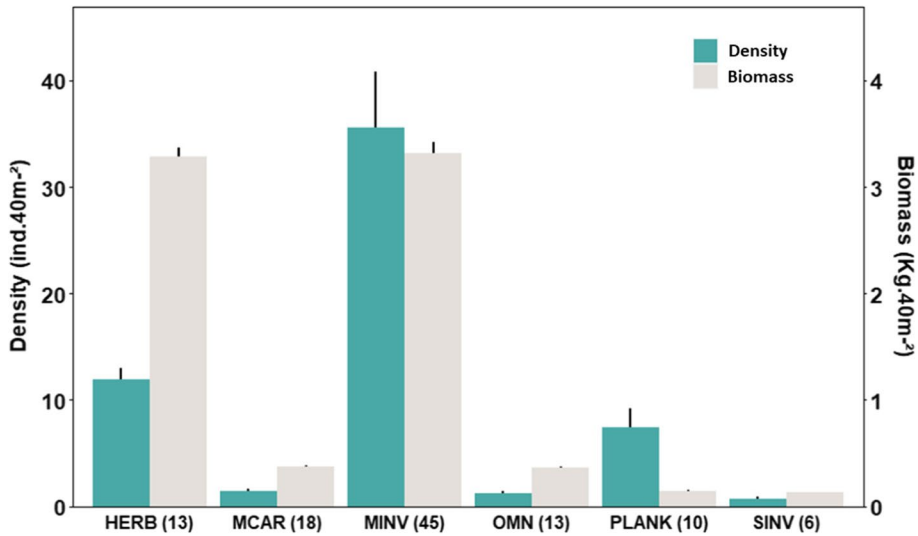
Fig. 3 Density and biomass (mean ± SE) of trophic guilds. The number of species of each trophic guild is given between brackets. *HERB* herbivores. *MCAR* macrocarnivores, *MINV* mobile invertebrate feeders, *OMNI* omnivores, *PLANK* planktivores, *SINV* sessile invertivores

but biomass was higher in biogenic reefs (Fig. 4b). Sites with greater topographic complexity presented higher fish density ($F = 15.11$, $p < 0.001$; Fig. S2a), biomass ($F = 18.39$, $p < 0.001$; Fig. S2b), and richness ($F = 47.83$, $p < 0.001$; Fig. S2c).

Mobile invertebrate feeders numerically prevailed in all habitats; the other trophic guilds displayed modest spatial patterns (Fig. 5a). Rocky reefs hosted the greatest proportion of herbivores, while the three types of rhodolith habitats displayed the greatest proportion of macrocarnivores (Fig. 5a). Herbivores, instead of mobile invertivores as in other habitats, accounted for over half the biomass on rocky reefs (Fig. 5b).

Influence of habitat and environmental factors on fish assemblages

Taxonomic and trophic structure varied among habitats (PERMANOVA for species density: *Pseudo-F* = 12.12, $R^2 = 0.16$, $p = 0.001$ and biomass: *Pseudo-F* = 11.68, $R^2 = 0.16$, $p = 0.001$; PERMANOVA for trophic guild density: *Pseudo-F* = 25.26, $R^2 = 0.29$, $p = 0.001$ and for trophic guild biomass: *Pseudo-F* = 24.40, $R^2 = 0.28$, $p = 0.001$). The HERB guild and a number of representative herbivores (i.e. *Stegastes variabilis*, *S. fuscus* and *Acanthurus bahianus*) were positively associated with rocky reefs (Fig. 6). In contrast, *Pagrus pagrus* and *Serranus baldwini*, two mobile invertebrate feeders, were associated with rhodoliths (Fig. 6a and b). However, as a guild, MINV showed an association to such substrates only through density.

The distribution of trophic guilds was better explained by depth (PERMANOVA for guild density: *Pseudo-F* = 28.13, $R^2 = 0.30$, $p = 0.001$) than complexity (PERMANOVA: *Pseudo-F* = 11.46, $R^2 = 0.06$, $p = 0.001$). Equivalent explanation levels for the distribution of size classes were reached using depth (PERMANOVA for size density: *Pseudo-F* = 6.67, $R^2 = 0.09$, $p = 0.001$) or complexity (PERMANOVA: *Pseudo-F* = 6.98, $R^2 = 0.05$,

$p = 0.001$). Macrocarnivores and mobile invertebrate feeders were positively associated with greater (15–25 m) and intermediate depths (10–15 m), respectively (Fig. 7a), where herbivores showed lower density. The largest fishes were found mainly in deeper sites and with greater topographic complexity (Fig. 7b), while species and individuals of small size showed the opposite pattern (Fig. 7b).

Discussion

Our study is the first ecological assessment of the ichthyofauna from a mosaic of habitats of the Espírito Santo southern continental shelf, in the central Brazilian coast. Among these habitats, rhodolith beds are extremely understudied by UVCs along the Brazilian Province (Anderson et al. 2022b). Here, despite presenting mean density, richness, and biomass lower than rocky and biogenic reefs, rhodolith habitats host unique and key components of the fish fauna. Moreover, agreeing with previous hypotheses, we found that while fish assemblages differ trophic- and taxonomically between habitats, all are dominated by guilds at lower trophic levels. In general, larger and macrocarnivorous fishes are relegated to deeper sites and more complex habitats.

Rocky and biogenic reefs show higher density, biomass and richness because they have greater topographic complexity than rhodolith beds. This feature provides shelter (García-Charton and Pérez-Ruzafa 2001; Willis and Anderson 2003; Cáceres et al. 2020) and increases food resources availability (Letourneur et al. 2003), attracting more fish and boosting the assemblage metrics. Complexity is often associated with the presence of massive and branching corals that are common reef builders in the Indo-Pacific and Caribbean realms where the majority of studies have been conducted to date (Alvarez-Filip et al. 2009; Graham et al. 2013). In our area, coral cover is low and complexity is almost exclusively provided by other invertebrates (e.g., octocorals and sponges; Fig. S1), crustose coralline algae, and boulders and holes on the reef surface. Despite this apparent simplicity, these reefs are equally susceptible to anthropogenic impacts affecting topographic complexity (e.g., trawling, mining and die-offs).

Rhodolith beds harbor species and trophic guilds of key ecological and commercial interest such as the mobile invertivores *Pagrus pagrus* and *Haemulon plumieri*, and the macrocarnivores *Pomatomus saltatrix* and *Caranx crysos*. The latter two species benefit from greater depth and exposure (Floeter et al. 2007, Carvalho-Filho 1999), which are characteristics of the rhodoliths sampled. Furthermore, the red porgy *Pagrus pagrus* is strongly associated with rhodolith habitats (Anderson et al. 2022a, b), particularly ROIN but also ROSA. There, it appears to control the density of macroalgae consumers (e.g., sea urchins, mollusks) and crustaceans (Goldman et al. 2016). Overfishing has caused critical depletions of its populations along the Brazilian southern coast (Haimovici et al. 2020). In Espírito Santo, it represented a significant fishery resource a decade ago (UFES 2011) and appears increasingly targeted in response to catch reduction of more valuable fishes, a historical phenomenon observed worldwide (e.g., Thurstan and Roberts 2010). Another threat to this and other species is that rhodolith beds and biodetritus placers are among the most targeted benthic habitats aiming at mining micronutrients- and phosphorus-rich marine carbonate (Paiva et al. 2023). For example, a single company collected about 73 tons of calcareous algae in Espírito Santo between 2002 and 2006 (Amado-Filho et al. 2017; Paiva et al. 2023). At present, dozens of active

processes (e.g., survey authorization, mining concession and geological reconnaissance)
involved in the exploration of the seabed in the area (ANM 2023).

Differences in assemblage structure (guilds and taxonomic diversity) are probably
associated with a varying ability of habitats to provide resources (Friedlander and Par-
rish 1998; Nagelkerken et al. 2001). For instance, herbivores represented over 50% of
the biomass in rocky reefs but contributed less than 5% in other habitats. The main
species responsible for RR biomass forage mainly on turf (*S. axillare*, *A. bahianus*, *A.
chirurgus,* and *Stegastes fuscus*; Ferreira et al. 2004), an abundant benthic component of
Brazilian reefs (Aued et al. 2018). Additionally, this habitat has high topographic com-
plexity, a feature that enhances herbivory by fish and the presence of scarids (Graham
and Nash 2013). Furthermore, sessile invertebrate feeders appeared in greater propor-
tions in rhodolith habitats, which support a high density of food sources such as ascid-
ians and sponges (Ferreira et al. 2004; Fig S2). However, all habitats were dominated by
species of low trophic level, particularly mobile invertebrate feeders such as the tomtate
grunt (*Haemulon aurolineatum*). This grunt often dominates assemblages on coastal
Brazilian reefs (Ferreira et al. 2004; present study) and, its daily migration between reef
and surrounding soft bottoms to feed (Alheit 1983; Nagelkerken et al. 2000; Pereira and
Ferreira 2013), probably explains its conspicuous presence in all habitats.

Macrocarnivores and larger fishes, such as *Pomatomus saltatrix* and *Caranx crysos*,
were associated to deeper zones, a pattern likely related to ecological preferences (Fran-
cini-Filho and Moura 2008) and to cross-shelf migration during ontogenetic develop-
ment (Moura et al. 2011; Gibran and Moura 2012). In Brazilian waters, similar pat-
terns have been detected, as elsewhere in Espírito Santo (Floeter et al. 2007), in Bahia
(Francini-Filho and Moura 2008), and in the oceanic island of Fernando de Noronha
(Krajewski and Floeter 2011). However, the distributional skew toward greater depths is
probably magnified by intense fishing of these highly targeted species (Letourner et al.
2003) in shallower waters due to easier and cheaper logistics.

Fishing exercises a top-down control on assemblages as it removes predators and is
more intense near shore closer to fishing communities (Pauly et al. 1998; Cinner et al.
2013). The depressed biomass and density of macrocarnivores allow lower-level trophic
guilds (e.g., mobile invertebrate feeders) to dominate and thus promote assemblage
homogenization (Friedlander and DeMartini 2002; Dulvy et al. 2004). In contrast to
Cáceres et al. (2020), who reported that groupers and snappers were some of the most
important species to dissimilarities among habitats of the Mesoamerican Barrier Reef
System, fishes of low trophic level and commercial interest are responsible for dis-
similarities in our area and top predators were rare in our censuses. However, remote
southwestern Atlantic sites and those with higher levels of protection and regulation
for fishing clearly show the presence of top predators (Morais et al. 2017; Guabiroba
et al. 2022a). For example, biomass of the black grouper (*Mycteroperca bonaci*) in
unprotected islands near the Arvoredo Reserve is half ours [~4.2 g.40 m^{-2} according to
Anderson et al. (2014) *vs*. 10.6 g.40 m^{-2}], but is twice ours (i.e. 23.6 gm^{-2}) in Arvore-
do's no-take areas, ~16-fold ours in the Abrolhos National Marine Park and ~24 fold
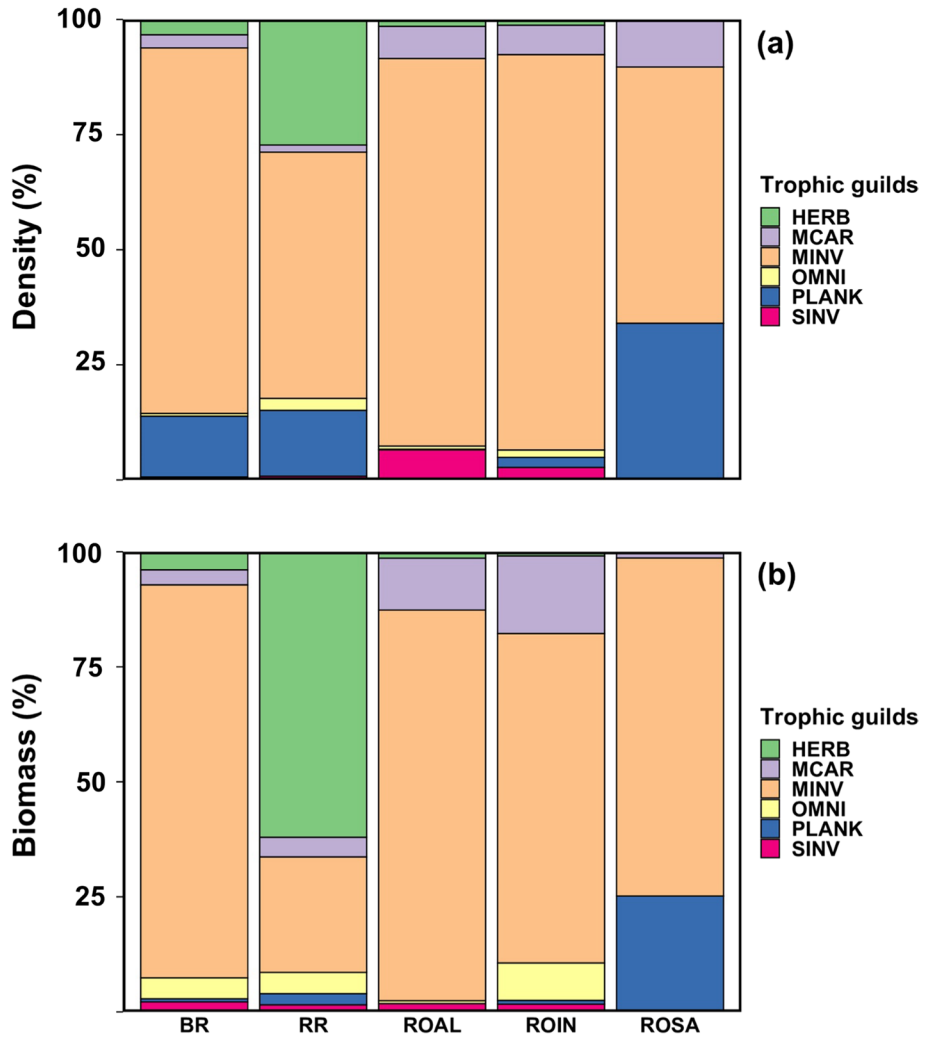ours in Abrolhos' no-entry areas (Guabiroba et al. 2022b).
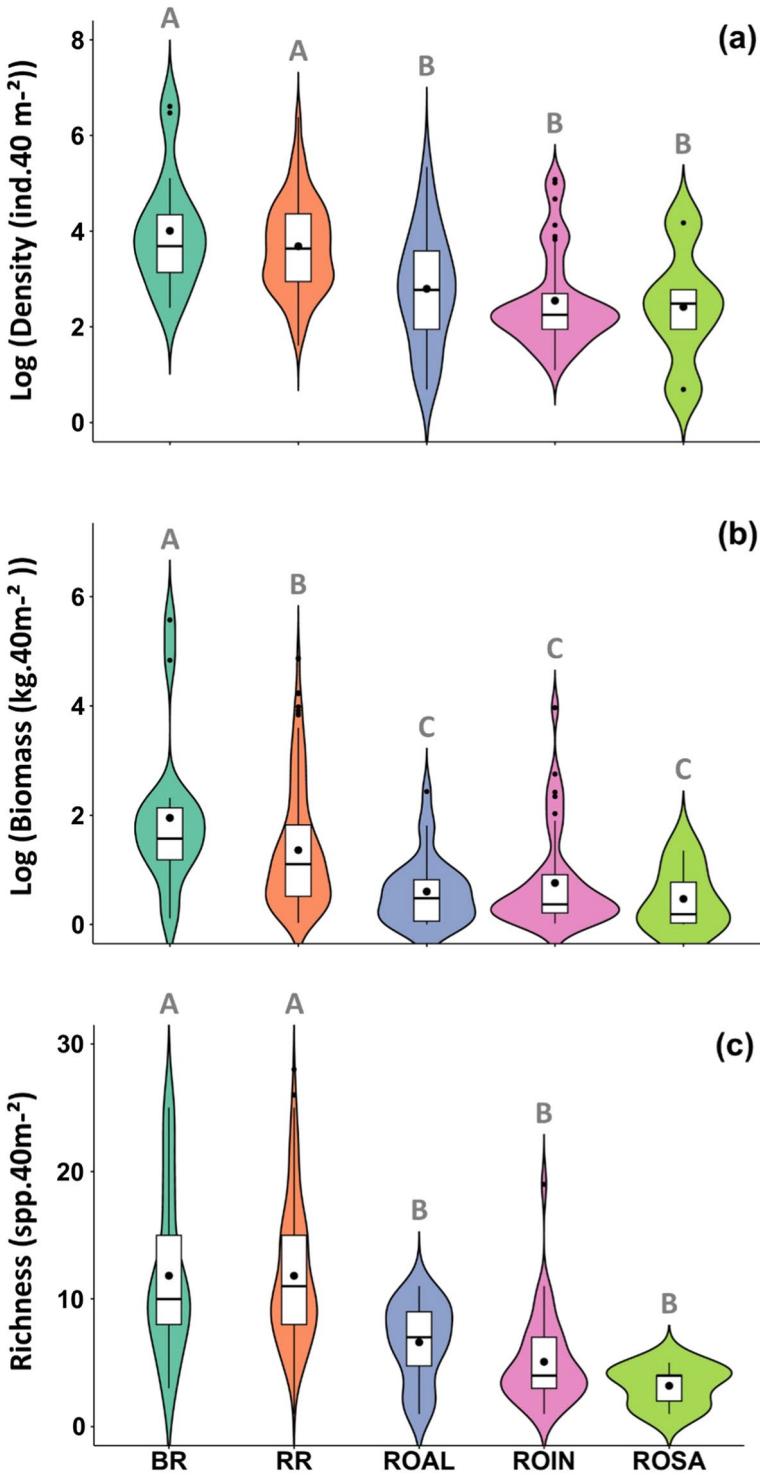
Fig. 5 Proportion of density (**a**) and biomass (**b**) of the five trophic guilds among the habitats. *BR* biogenic reefs, *RR* rocky reefs, *ROAL* rhodoliths with algae, *ROIN* rhodoliths with invertebrates, *ROSA* rhodoliths with sand

MPAs are efficient tools in maintaining greater biomass and fishes of larger size in comparison to sites without use restrictions (Mosquera et al. 2000; Halpern 2003), as in some cases in Brazil (e.g., Floeter et al. 2006; Rolim et al. 2019; Anderson et al. 2020). MPAs are also responsible for returning depleted assemblages to healthier levels (Murawski et al. 2000; Barrett et al. 2007; Waterhouse et al. 2020). Our study revealed assemblages with high overall richness, but depleted of top predators and dominated by low trophic level fishes. Thus, a MPA would be key for the conservation of Espírito Santo's southern reefs. The creation of a MPA encompassing a considerable part of the study area was officially requested by scientists, NGOs and local citizens about a decade ago. However, it was not
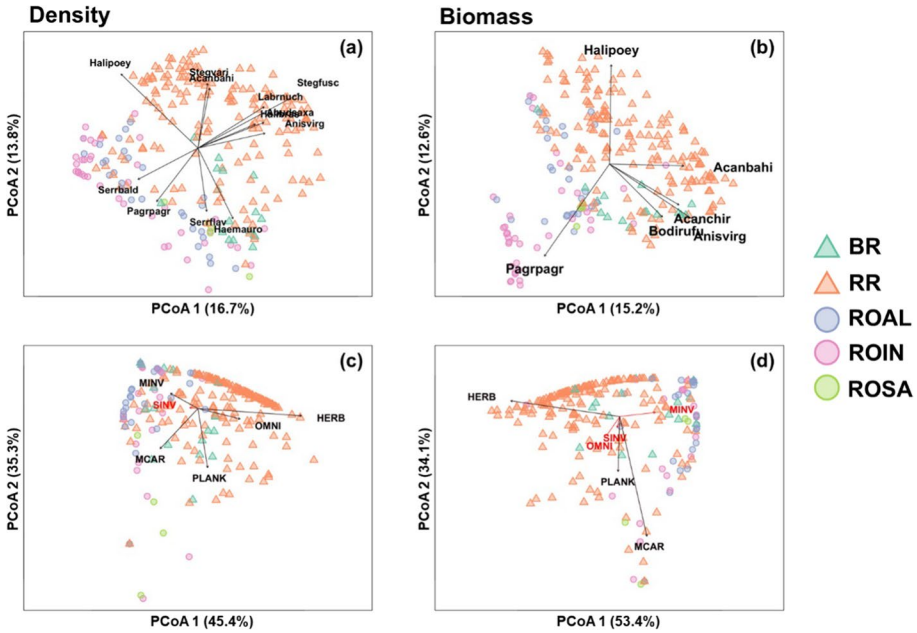
Fig. 6 Principal coordinate analysis (PCoA) performed on density (**a**, **c**) and biomass (**b**, **d**) of species (**a**, **b**) and trophic guilds (**c**, **d**). The plotted species are those with r^2 greater than or equal to 10%. Red letters indicate non-significative variables. Species codes: Abudsaxa—*Abudefduf saxatilis;* Anisvirg—*Anisotremus virginicus*; Acanbahi—*Acanthurus bahianus*; Acanchir—*Acanthurus chirurgus*; Bodirufu—*Bodianus rufus*; Halibras—*Halichoeres brasiliensis*; Halipoey—*Halichoeres poeyi*; Haemauro—*Haemulon aurolineatum*; Pagrpagr—*Pagrus pagrus*; Labrnuch—*Labrisomus nuchipinnis*; Serrbald—*Serranus baldwini*; Serrflav—*Serranus flaviventris*; Stegfusc—*Stegastes fuscus*; Stegvari—*Stegastes variabilis*

established and the sole significant advance that has been made since then is the designation of the area as being of 'extremely high' priority for conservation (MMA 2018; Paiva et al. 2023). Furthermore, information on the local impact of fisheries (in contrast to non-local, high-seas or remote zone fisheries) is sorely lacking despite artisanal and commercial fishing being key activities on the southern coast of Espírito Santo (Pinheiro et al. 2009; 2015). As such, the data discussed in this study represent an important baseline for the development of local conservation actions. They show that convergent surveys using different methodologies and techniques (UVCs, TEK, and high-resolution mapping) allow a fine-scaled understanding of fish assemblage structure over large swaths of habitats. Similar efforts using complementary methods (e.g., BRUVs, artisanal fishery landings) would provide information on fish recruitment patterns, fish reproductive aggregations and spatial distribution of fishery resources that is highly relevant to MPA proposal and establishment.
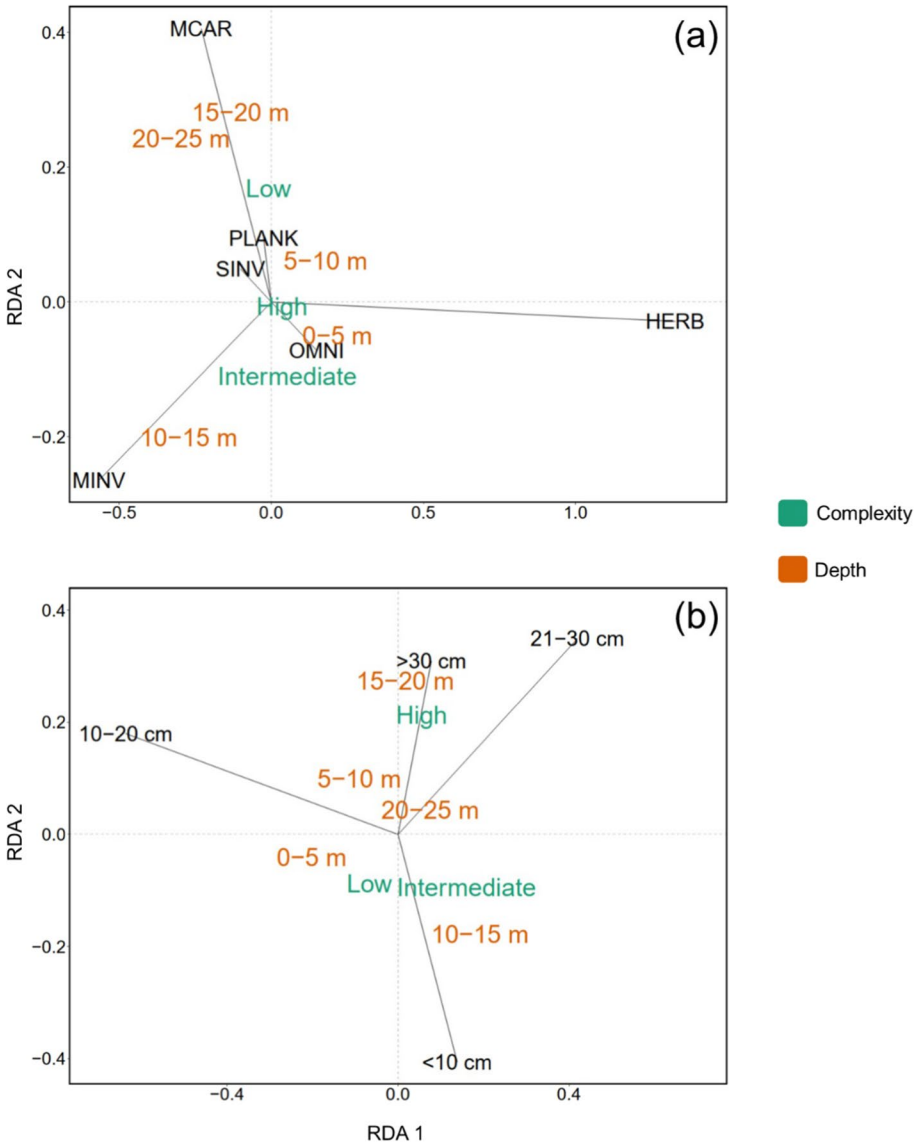
Fig. 7 Redundancy analysis (RDA) biplots showing the influence of complexity (green) and depth (orange) on trophic guild (**a**) and size classes density structure (**b**)

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Data availability Data will be made available on request.

Declarations

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