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The impact of functional selectivity by fisheries on the fish fauna of Abrolhos Bank

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ABSTRACT

Functional diversity (FD) is one of the aspects of biodiversity that can best represent eventual changes in the environment. Marine Protected Areas (MPAs) can be used to minimize the potential impacts of fishing on fish stocks. The objective of this study was to evaluate the role of the MPA network in the Abrolhos Bank (Brazil) in relation to the FD of fish fauna. Underwater visual censuses were carried out in no-take, partially protected and unprotected zones. We used FD metrics to assess the MPA network in terms of FD in each zone. The functional hypervolume of the target fish species was calculated. From fishers' information, we determined the Use Value of the main target species and proposed a Fisheries Functional Vulnerability Index (FFVI), which can indicate management priorities for the species at a local level. The results showed that MPAs maintained higher FD, especially in no-take areas. Two no-take sites showed significant functional divergence values, while one no-take site and one partially protected site showed greater functional richness than unprotected sites. A total of 23 target species accounted for 56% of the functional hypervolume. The FFVI indicated the most vulnerable species. The results indicate that functional metrics may be more informative for assessing the impact of fisheries. In addition, the findings reinforce the need to incorporate the local knowledge of resource users, as recommended by international institutions.

Keywords: Fishery management, Functional diversity, Functional hypervolume, Marine protected areas, Small-scale fisheries

INTRODUCTION

Commercial marine fisheries are fundamental to generating employment, income and food security for a significant portion of the world's population, especially in low- and middle-income countries (The World Bank, 2012; FAO, 2022a). Although management measures are in place in several locations around the world, the increasing share of stocks has shown unsustainable levels of capture (FAO, 2022b), and there is uncertainty about the recovery of some stocks (Britten et al., 2021). In low- and middle-income countries with

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tropical coral reefs, the situation may be even more uncertain, given the chronic lack of effective fisheries management policies in these areas, including lower quality of life and fragile institutions (Cinner, 2011; Mills et al., 2011).

Coral reef locations are remarkably relevant to the survival of millions of people and are a valuable source of food resources, protection from storms and erosion, and key ecosystem services such as recreation and tourism (de Groot et al., 2012; Costanza et al., 2014). However, previous studies have indicated an increasing trend of degradation of these environments (Pratchett et al., 2014; Eddy et al., 2021) and potential negative impacts on the productivity of fisheries (Rogers et al., 2017).

In view of the increasing threats to marine and coastal environments, no-take reserves (NTRs) are one of the potential strategies to minimize the degradation and loss of marine biodiversity and assist in the management of fisheries (Topor et al., 2019; Di Lorenzo et al., 2020; Allard et al., 2022). Previous studies have shown that NTRs may have better biological indicators (such as richness, density, biomass and abundance) than control areas (Lester et al., 2009; Allard et al., 2022). Similar results have also been found when comparing NTRs with partially protected marine areas (PPMAs; Lester and Halpern, 2008). However, PPMAs can also show satisfactory results (Tyler et al., 2011; Zupan et al., 2018; Hall et al., 2021). These studies show that the potential of NTRs and PPMAs as tools for the conservation and management of fisheries resources (Rowley, 1994; Weigel et al., 2014) is context-dependent. However, this becomes less clear when functional diversity (FD) metrics are taken into account. For example, Coleman et al. (2015) found that taxonomic (species diversity and richness) and trait-based (functional richness and dispersion) diversity metrics showed no differences with the level of protection (NTRs vs. PPMAs). On the other hand, these same authors suggested that FD metrics can be more sensitive and indicate in advance positive signals of biological indicators for target species within NTRs (Coleman et al., 2015). This feature of FD metrics has led to debates about their relevance and calls for their applicability in fisheries science (Barnett et al., 2019) and marine conservation (Stuart-Smith et al., 2015).

Recent studies have incorporated the FD perspective to assess the effectiveness of Marine Protected Areas (MPA; Cáceres et al., 2020; Carvalho et al., 2021; Davies et al., 2022). This approach has gained increasing relevance in ecology and more recently in fisheries (Koutsidi et al., 2016; Barnett et al., 2019; Mbaru, et al., 2020; Carvalho et al., 2021; Green et al., 2022; Rolim et al., 2022). With increasing applicability, several metrics have emerged that propose to assess different aspects of FD (Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010; Schleuter et al., 2010; Mouillot et al., 2013; Blonder et al., 2014). Regardless of the metric used, some studies have shown the impact of fishing on fish FD (Koutsidi et al., 2016; Mbaru, et al., 2020; Carvalho et al., 2021; Rolim et al., 2022) and the potential consequences of selective removal of species from the environment (Martins et al., 2012). However, to our knowledge, there are still no studies that estimate the magnitude of the impact of fishing on the functional space of fish, considering different management strategies from a regional perspective. That is, given that each species occupies a functional space (or functional niche; Mason et al., 2005), what is the functional volume targeted by fishing, considering the range of species in a region?

In recent decades, there has been a growing call for incorporating local/traditional knowledge of resource users into conservation initiatives (e.g., Berkes et al., 2000; Ban et al., 2018). Growing demand for fisheries resources, coupled with fragile fisheries management policies in low- and middle-income countries, has led to a growing incentive to incorporate the ecological/local knowledge of fishers into fisheries research, conservation and management strategies (e.g., Alati et al., 2020; Colloca et al., 2020; Leduc et al., 2021). This is in line with calls from international institutions and forums for more inclusive and democratic participation of different social actors in the management and governance of environmental and fisheries policies (Haggan et al., 2007; Cowie et al., 2020; FAO, 2022a). In addition, the United Nations (UN) has proposed the Decade of Ocean Science for Sustainable Development (2021-2030), in which civil society participation is fundamental to achieving the proposed objectives (Unesco-IOC, 2021).

In the south of the state of Bahia (Brazil) there is a network of MPAs with different management strategies. The largest reef complex in the South Atlantic—the Abrolhos Bank—is located in this region and is an important fishing area for the communities that live there. In this context, this study aimed to: (i) calculate FD indices for the different MPA sites, hypothesizing that sites with greater fishing restrictions (NTRs) have higher values; (ii) calculate the target functional hypervolume of the fishery; and (iii) propose a Fisheries Functional Vulnerability Index (FFVI). This index seeks to incorporate the value of each species from the perspective of fishers, in addition to combining functional metrics with the respective extinction risks of each species.

METHODS

Study area

The Abrolhos Bank is an extension of the continental shelf with a heterogeneity of habitats, such as rhodolith beds, seagrass and macroalgae, mangroves and unconsolidated sediments (Amado-Filho et al., 2012; Moura et al., 2011, 2013, 2021). In this region, there are a number of MPAs: (i) the Abrolhos National Marine Park (ANMP, 913 km²), created in 1983, an area with total restriction to any extractive activity, consisting of two discontinuous parts—the Timbebas Reef (110 km²), closer to the coast and with low enforcement, and the Abrolhos Archipelago (803 km²), farther from the coast and with active surveillance—(Francini-Filho and Moura, 2008a); (ii) the Corumbau Marine Extractive Reserve (MERCor, 895 km²), created in 2000; and (iii) the Cassurubá Marine Extractive Reserve (MERCas, 1007 km²), created in 2009. Both extractive reserves are MPAs with some fishing restrictions (including, for MERCor, the use of gillnets, bottom and/or midwater trawling and underwater fishing within the MPA; and for MERCas, limitations on the size and number of nets per vessel, mesh size, prohibition of fishing with a motorized boat within 500 m of the coastline in certain locations within the MPA, among others), that is, they are PPMAs, with limited enforcement capacity and co-management by beneficiaries (Moura et al., 2009; Nobre et al., 2017) and the federal agency (Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio), and can be used exclusively by traditional fishing communities in the region (Figure 1).

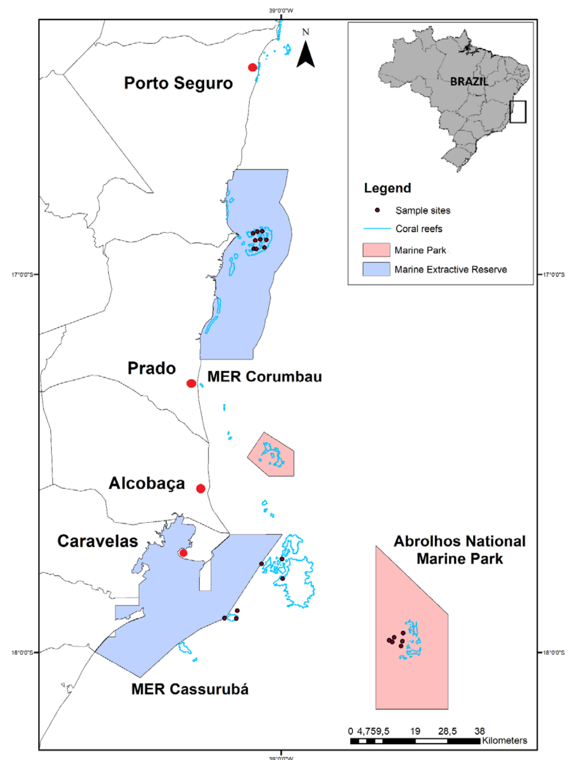

Figure 1. Study area showing the municipalities where landings were monitored, fishers were interviewed and marine protected areas were studied. Small red circles are the sampling sites of the Underwater Visual Census.

Fishing is one of the main economic activities developed in the region, and in terms of fish landings, this area has the highest fishing productivity of the Brazilian east coast (Cordell, 2006). Multiple fishing gears are used by the traditional fishing communities, such as hand line, gill net, spearfishing and shrimp trawling (Moura et al., 2013; Santos Neto et al., 2016; Previero and Gasalla, 2018). However, shrimp trawl fisheries were not considered in this study.

Data from interviews with fishers and fisheries landings

Fishers were interviewed at fish markets, households and ports in the municipalities of Caravelas (April-June/2015), Porto Seguro (February-March/2016), Alcobaça (September/2016) and Prado (March-April/2017). The interviews were conducted with the prior consent of the participants. Each fisher was asked which fish species they usually caught in general. Based on their responses, a free list of the species cited was created. Free listing is an approach to identifying items in a cultural domain and can be used to collect data quickly and easily (Quinlan, 2005). It involves listing things in a domain (in this case, fish) in any order that comes to mind. Data collection on landed species was carried out during the same time period mentioned above in public places commonly used for landing, storage and marketing of fish. Species caught were recorded to the lowest taxonomic level.

Caravelas is the closest site to both ANMP and MERCas. Fishers from this municipality usually have smaller vessels, which limits them to fishing areas closer to the coast. On the other hand, fishers from the municipalities of Porto Seguro, Prado and Alcobaça have larger vessels and can operate further away (Previero and Gasalla, 2018; Zapelini et al., 2019). For a better definition of the vessels operating in the Abrolhos Bank region, see Bueno and Schiavetti (2019). Although Prado and Alcobaça are close to MERCor, the landings of vessels from these municipalities did not include fish from MERCor, as they are not beneficiaries of this MPA.

This study was approved by the Ethics Committee of the Universidade Estadual de Santa Cruz (CEP/UESC, N° 37893014.5.0000.5526) and by the System of Authorization and Information on Biodiversity (SISBIO 43528-1/43528-2).

Fish sampling (Underwater Visual Census - UVC)

Reel fish composition and abundance were assessed at the ANMP and MERCor MPAs. We did not assess MERCas because there is no reef habitat within its boundaries. We applied a beyond-ACI design following Underwood (1992) to evaluate the effect of protection on fish assemblages. Three zones were selected from each site: two unprotected zones (UP1 and UP2) and one protected zone, corresponding to the no-take zone (NTZ1). For ANMP, an additional NTZ (called NTZ2) was sampled due to the different types of habitat within the marine park. In each zone, three randomly selected sectors separated by hundreds of meters were sampled to cover the maximum natural variability observed in the habitats. In each sector, 12 fish censuses were conducted. UVC was conducted in a strip transect line 20 m long and 2 m wide on each side. The visual census in each transect was carried out for all fish species. Fish were identified individually, and their size was estimated within size classes at 2 cm intervals.

Functional traits

To assess the functional diversity (FD) of the sampled fish assemblages, we defined seven functional traits, categorical and continuous (Table 1): trophic group (TG); maximum body size; maximum depth; environment; body shape; length to maturity (L50); and trophic level (TL), following Halpern and Floeter (2008) and Froese and Pauly (2019). Many previous studies used continuous and categorical traits (Dumay et al., 2004; Micheli and Halpern, 2005; Halpern and Floeter, 2008; Martins et al., 2012; Törnroos and Bonsdorff 2012; Villéger et al., 2017; Ladds et al., 2018). When trait data were missing for a given species, a corresponding value from a congener was used instead. Even after this procedure, it was not possible to obtain the L50 value for some species. We then followed the factorial analysis method for mixed data (FAMD) proposed by Audigier et al. (2013) using the missMDA package (Husson and Josse, 2019). The FAMD imputes missing values in a mixed data set (categorical and continuous variables) using the principal component method.

Table 1. Categorical functional traits selected and their description.

Trophic group	Full name	Description	Functional relevance
DPLA	Diurnal planktivores	Fish that primarily eat macro- and micro-zooplankton during the day	
EXCV	Excavator/eroders	Roving herbivores similar to scrapers but which leave deeper bite scars and remove greater quantities of substrata with each bite	
MALG	Macroalgae browser	Roving herbivore that tend to bite or "crop" algae, leaving the basal portions intact	
MCAR	Macrocarnivores	Fish that eat mobile benthic organisms and fish	
MINV	Mobile benthic invertivores/cleaners	Fish that primarily eat crabs, molluscs and other benthic mobile invertebrates	
NPLA	Nocturnal planktivores	Fish that primarily eat macro- and micro-zooplankton during the night	
OMNI	General omnivores	Fish that eat a variety of organisms, including animal and plant material in similar quantities	Energy fixation/rate of transfer [1]
PISC	Strict piscivores	Fish that only eat other fish	Regulating food web dynamics and nutrient balances [2]
SAND	Sand invertivores	Fish that primarily eat benthic invertebrates in sandy areas adjacent to reefs	
SCRP	Scrapers	Roving herbivores that remove pieces of the substratum together with algae, leaving distinctive but relatively shallow bite scars	
SINV	Coral/colonial sessile invertivores	Fish that eat sessile benthic invertebrates	
SPON	Spongivore/herb	Fish that primarily eat sponges, but also some algae	
THER	Territorial algae/detritus	Fish that eat farmed turf-algae within their territories	
TURF	Turf grazing	Roving herbivores that feed removing only algae and associated epiphytic material	
Maximum body size			
SMALL		0-10 cm	Regulating food web dynamics and nutrient balances [2]; Predator-prey interactions [3]; Fish's ability to swim [4]
MEDSMALL		10-25 cm	
MED		25-50 cm	
LARGE		>50 cm	
Maximum depth			
VSHALL		0-10 m	
SHALL		10-25 m	Nutrient cycling and transfer; trophic dynamics [2,3]
MID		25-50 m	
DEEP		50-100 m	
VDEEP		>100 m	
Environment			
BENTHOPELAGIC		Living and feeding near the bottom, in the midwater or near the surface	
DEMERSAL		Sinking to or lying on the bottom; living on or near the bottom and feeding on benthic organisms	Regulating food web dynamics and nutrient balances; nutrient cycling and transfer; trophic dynamics [2,4]
ESTUARINE		Living mainly in the lower part of rivers or estuaries; coastlines where marine and fresh water meet and mix; waters often brackish	
PELAGIC		Living or occurring in the open sea	
REEF-ASSOCIATED		Living and feeding on or near coral reefs	

continued

Trophic group	Full name	Description	Functional relevance
Body shape			
FLAT		Laterally compressed benthic fish	Locomotion, maneuverability, food acquisition [4,5]
EEL-LIKE		Fish that resemble the Anguillidae family	
NORMAL		Spindle-shaped; used in reference to the body shape of a fish that is cylindrical or nearly so and tapers towards the ends	
ELONGATED		Drawn out or extended in length relative to some other criterion (usually body depth)	
SHORT/DEEP		Dorso-ventrally flattened	

[1] Törnroos and Bonsdorff, (2012); [2] Holmlund and Hammer, (1999); [3] Halpern and Floeter, (2008); [4] Villéger et al., (2017); [5] Claverie and Wainwright (2014)

Data analysis

To evaluate FD metrics in relation to the different MPA management regimes (ANMP/MERCor) and their different protection levels (UP/NTZ), we used the FD package (Laliberté and Legendre, 2010) to calculate the following functional metrics: functional richness (Fric, represents the amount of functional space occupied by the assemblage); functional evenness (FEve, describes the evenness of abundance distribution in a functional trait space); functional divergence (FDiv, represents how abundance is distributed along a functional trait axis, within the area occupied by the assemblage); and functional dispersion (FDis, represents the mean distance in multidimensional trait space from an individual species to the centroid of all species). For more details on the metrics, see Villéger et al. (2008) and Laliberté and Legendre (2010). These indices provide us with information on FD at the site level, that is, for each MPA (ANMP / MERCor) and protection level (NTZ / UP).

A test was performed to check if the observed (real) values of the FD indices of each site were significant or if the observed value could be obtained after random permutations. A procedure was developed to randomize the abundance of each species between sites. Considering the A matrix, the columns represent the species (sp1, sp2, sp3, …, spn) and the rows represent the sites. The matrix cells represent the abundance of each species in each site. If a species was not present at a particular site, its abundance is set to zero. For each column (species), randomization was performed between the rows (sites). The randomization procedure was performed 1000 times for each index and site, and the P-value was estimated based on the null hypothesis that there were no differences between the observed and simulated indices for each site. The P-value represents the proportion of simulated values of the indices that are higher or lower than the observed values. Therefore, considering a two-sided test with a 5% risk (of rejecting the null hypothesis), if $P < 0.025$ or $P > 0.975$, the observed indices will be higher or lower than the values expected by chance, respectively. To estimate the P-value, the values observed for the indices were included in the set of simulated values. In this way, a conservative P-value was obtained (Ruxton and Neuhäuser, 2013).

To calculate the deviation of the observed indices in the distribution of the simulated index values, the standardized effect size (SES) for each index and site was calculated as follows: SES = (Iobs - Isim) / SDsim; in which Iobs is the value observed for the index, Isim is the mean value of the simulated index and SDsim is the associated standard deviation (Gotelli and McCabe, 2002; Villéger et al., 2010).

To assess the extent of the functional space that may be targeted by fisheries, we considered other studies in the region. Published data on fish species (presence/absence) in the reefs of the Abrolhos Bank region were considered (Kikuchi et al., 2003; Moura and Francini-Filho, 2005; Francini-Filho and Moura, 2008a, 2008b; Simon et al., 2016; Mazzei et al., 2017). This was done to include any species that were not observed in the UVC (this research), but were recorded elsewhere. This allowed for a more complete perspective of the diversity of the fish pool in the region.

First, considering the regional species pool, we wanted to check the degree of resource use by fisheries from the perspective of FD. That is, what is the volume of functional space targeted by fishing, considering the regional species pool (considering the entire Abrolhos Bank region)? To answer this question, we used the concept of hypervolume proposed by Blonder et al. (2014). This proposal is derived from the Hutchinsonian hypervolume concept (Hutchinson, 1957) to quantify the species niche. In this approach, a set of n variables (in this case, functional traits) represent biologically important and independent axes, and the hypervolume is defined by a set of points in n-dimensional space. This approach makes it possible to check the n-dimensional volume of fish assemblages separately. In addition, it makes it possible to assess the intersection between two data sets (e.g., regional pool of Abrolhos Bank and species targeted by fisheries). In this way, it is possible to assess the overlap between two hypervolumes (see Blonder et al., 2014). This approach is best suited for continuous variables, but can also be used for data with categorical variables. In this case, the data can first be ordinated to a smaller number of dimensions using other approaches (e.g., the Gower distance; Gower, 1971). Thus, we used the Gower metric to calculate the distance between species and then we used a PCoA analysis (ape package; Paradis and Schliep, 2019) to reduce dimensionality. The distance matrix between species can also have negative values, in which case they cannot be represented in a Euclidean space. The correction method described by Cailliez (1983) was applied. To facilitate the interpretation of the results, we used the first three axes of the PCoA for the hypervolume calculation. For this analysis, data on presence/absence were used (fish observed in scientific research - UVC; fish observed in fishing - landing record; and fish observed in both data sets).

Lastly, we verified the functional rarity of the species at the local (sites) and regional (Abrolhos Bank region) scales. For the local scale, we calculated the Functional Distinctiveness (Di) of the species, considering the presence of species in each MPA and protection level separately, and the species present in the fishing landing. For the regional scale, we calculated the Functional Uniqueness (Ui) of the species. Together, these metrics provide an overview of the functional rarity of the regional species pool (Grenié et al., 2017). To calculate these two indices, data on presence/absence were used. Di is related to the unusual traits of a species compared with traits of other species in the assemblage. Di is scaled between ‘0’, if the focal species is identical to all other species, and ‘1’ when the focal species is most dissimilar to the other species. Di then relates to functional redundancy in an assemblage: the larger the index value, the more distant (less redundant) the species (or an individual) is from the mean functional position of the assemblage in the functional space, which is the centroid. Ui is the functional distance from a focal species to its nearest neighbor in a set of assemblages. It quantifies how isolated a species is in the functional space without considering abundance: the higher the index value, the more distant a species is from its nearest neighbor in the functional space. These indices provide information on functional rarity at the species level at local and regional scales. The funrar package was used to calculate both indices (Grenié et al., 2017). To assess possible functional redundancy between species, we used the concept of Functional Entities (FE; Mouillot et al., 2014). FE refers to the unique combinations of the seven functional traits (see 2.4. Functional traits above), and the greater the redundancy, the greater the number of species belonging to the same FE. The number of FE was verified for the regional species pool. The mFD package was used for this analysis (Magneville et al., 2023).

From the free list of species caught and based on information from the interviews with the fishers, the Use Value (UV) was calculated for each species mentioned. The UV can be used to identify the most important species from the perspective of the fishing community. The calculation of this index was based on Phillips et al. (1994) with the adaptation suggested by Rossato et al. (1999), as follows: $UV = \Sigma U / n$; in which UV is the index of the use value of the species; U is the number of citations per species; and n is the number of respondents. UV ranges from 0 to 1: frequently cited species tend to have a value of 1, while less frequently cited species tend to have a value of 0. For this analysis, only species cited by fishers were considered.

The combination of Ui and UV values makes up the Fisheries Functional Vulnerability Index (FFVI). The FFVI is based on the metric that was recently proposed by Pimiento et al. (2020), which combines functional metrics with their respective risk of extinction. The FFVI combines the uniqueness of an individual species with its risk of extinction. The risk of extinction of fish for the local level (Brazil) was assessed based on the Red Book of Brazilian fauna in danger of extinction and its latest update, carried out by the Ministry of the Environment in Ordinance N° 148 (ICMBio, 2018a, 2018b; MMA, 2022). However, previous studies have already indicated signs of overexploitation of species, especially in the family Lutjanidae (Klippel et al., 2005, Frédou et al., 2009; Zapelini et al., 2019). Thus, the most conservative threat status for the species was considered, as they are not included in the latest update of the MMA (2022) and there is no evidence of improvement in their status.

In this way, FFVI was calculated as follows: FFVI = UVRI + URI

in which:

$$UVRI = \ln(1 + (UV * ER))$$

and

$$URI = \ln(1 + (Ui * ER))$$

ER is the classification of the extinction risk of the species at the local level and follows the classification already used in other studies (Isaac et al., 2007; Pimiento et al., 2020): LC (Least Concern) = 0; NT (Near Threatened) = 1; VU (Vulnerable) = 2; EN (Endangered) = 3; and CR (Critically Endangered) = 4; UVRI: Use Value-Risk Index; URI: Uniqueness Risk Index.

In this way, target species were classified according to their importance for fishing and their functional uniqueness. The index was applied at the local level because there is an incompatibility in threat levels depending on the scale of analysis, local or global (Rodríguez et al., 2000; Gärdenfors, 2001; Bender et al., 2012). Thus, local scale assessments are more appropriate for the finer geographic scale, making research and conservation efforts more effective (Rodríguez et al., 2000). In addition, as the UV used in the FFVI is based on information from local fishers, it is only appropriate to use the index for the local extinction risk level.

All statistical analyses were conducted using R software v. 3.6.3 (R Core Team, 2020).

RESULTS

A total of 201 fishers were interviewed (Alcobaça = 50; Caravelas = 50; Porto Seguro = 52; Prado = 49) and 64 fish species were cited, with Ocyurus chrysurus (n = 99; yellowtail snapper, Lutjanidae), Mycteroperca bonaci (n = 96; black grouper, Serranidae), Lutjanus jocu (n = 59; dog snapper, Lutjanidae) and Epinephelus morio (n = 51; red grouper, Serranidae) being the most frequently mentioned (Supplementary Material: Table S1).

Considering the entire dataset (UVC + fishing landings + other studies), we observed 215 species recorded in the region. Of these, 147 (68.4%) species were recorded in studies using UVC (this study + published data), of which 74 were recorded in the sampling sites of this study (Table S2), 45 (20.9%) were recorded exclusively in fishing and 23 (10.7 %) were present in both sets of data (UVC of this study + fishing landings). These species were associated with reef environments, with TL (mean±sd) = 3.66 ±0.64 and trophic group belonging to macrocarnivores (n = 7), mobile benthic invertivores (n = 6) or piscivores (n = 5). Most (n = 13) were large species (LARGE) and lived in habitats that were 50 to 100 m deep (DEEP; n = 13) or deeper (VDEEP; n = 8; Table S3). Most importantly, these species together represented more than 56% of the functional hypervolume. In other words, these target species occupied niches and performed different ecological functions within the functional hypervolume.

The FD indices for the sites are shown in Table 2. All sites showed some degree of functional redundancy; thus, the FE number was below the species richness (Tables 2 and S3). The FRic values at the ANMP_NTZ2 and MERCor_UP2 sites were statistically significant (Figures S1, S2, S3 and S4); that is, the functional space filled by the species present at these sites was greater than would be expected by chance. The FDiv values were significantly higher at the ANMP_NTZ1 and MERCor_NTZ1 sites; that is, divergence was high when the most abundant species had extreme functional trait values. Taken together, these results suggest that MPAs can maintain a more functionally diverse set of species, contributing to the resilience of these environments (specially in no-take sites).

Table 2. Functional diversity indices of fish assemblages in unprotected sites, Abrolhos National Marine Park and Corumbau Marine Extractive Reserve at different levels of protection.

Site	N_spp	FE	FRic	SES.FRic	FEve	SES.FEve	FDiv	SES.FDiv	FDis	SES.FDis
UP1	48	46	0.76	2.00	0.43	-0.24	0.93	0.67	0.33	0.95
UP2	43	41	0.62	0.14	0.51	1.17	0.86	-1.41	0.33	0.92
ANMP_NTZ1	30	29	0.60	-0.17	0.56	2.05	0.98	1.91*	0.33	0.66
ANMP_NTZ2	51	49	0.80	2.62*	0.40	-0.76	0.92	0.16	0.28	-1.31
MERCor_UP1	36	34	0.65	0.52	0.44	-0.03	0.95	1.13	0.33	0.58
MERCor_UP2	44	42	0.90	3.93*	0.45	0.05	0.88	-0.96	0.29	-0.77
MERCor_NTZ1	39	37	0.61	-0.04	0.41	-0.57	0.97	1.54*	0.33	0.75

ANMP: Abrolhos National Marine Park; MERCor: Corumbau Marine Extractive Reserve; NTZ: no-take zone; UP: unprotected zone; N_spp: species number, FE: Functional entities, FRic: functional richness, FEve: functional evenness, FDiv: functional divergence, FDis: functional dispersion. SES: standardized effect size for each index. Statistical significance: *$P < 0.025$.

The first three axes of the PCoA represent the hypervolume of each dataset; there were "holes" and overlaps (Figure 2). Species caught by fisheries accounted for more than 72% of the functional hypervolume of the regional pool (Table 3). This indicates that functional attributes are more sensitive indicators of the impact of fisheries on functional structure than the number of species (richness) alone.

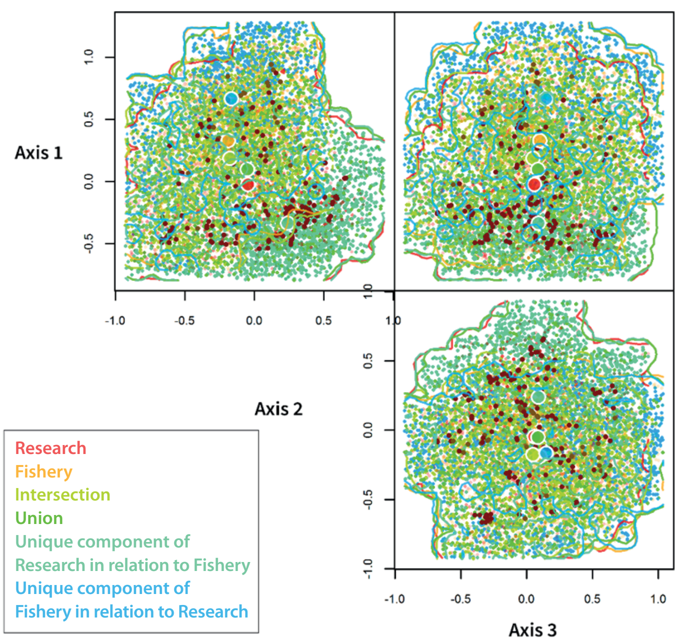

Figure 2. First three axes of the PCoA for the functional hypervolume of species registered at Abrolhos Bank, Bahia. Research (red): species recorded in scientific research (Underwater Visual Census); Fishery (orange): species observed in fishing landings; Intersection (light green): species observed in both scientific research and fishing landings; Union (dark green): total set of species (regional pool); Unique Component of Research in relation to Fishery (light blue): species observed only in the Research dataset; Unique Component of Fishery in relation to Research (dark blue): species observed only in the Fishery dataset. The large dots indicate the center point of the corresponding polygon for each color. The darkest points observed in the figure are red, but have a brownish tint due to overlap with the other colors.

Table 3. Hypervolume of fish species datasets recorded at Abrolhos Bank, Bahia, Brazil. Research: species recorded in scientific research (underwater visual census); Fishery: species observed in fishing landings; Intersection: species observed in both scientific research and fishing landings; Union: total set of species (regional pool); Unique Component of Research in relation to Fishery: species observed only in the Research dataset; Unique Component of Fishery in relation to Research: species observed only in the Fishery dataset.

Object of class Hypervolume	Dimensionality	Volume	%
Research	3	3.21	84.5
Fishery	3	2.74	72.1
Intersection (Research and Fishery)	3	2.15	56.6
Union (Research and Fishery)	3	3.80	100
Unique component of Research in relation to Fishery	3	1.06	27.9
Unique component of Fishery in relation to Research	3	0.59	15.5

Among the species recorded in UVC (this study + published data), those with the highest Di values were *Muraena pavonina* (whitespot moray, Muraenidae), *Ophichthus ophis* (spotted snake eel, Ophichthidae) and *Ginglymostoma cirratum* (nurse shark, Ginglymostomatidae). In Fishery, the species *Paralichthys* sp. (Paralichthyidae), *Isopisthus parvipinnis* (bigtooth corvina, Sciaenidae) and *Notarius grandicassis* (Thomas sea catfish, Ariidae) showed the highest Di. These species are not from reef environments, but they have very distinct functional traits. Of the species recorded in the unprotected sites, *Anisotremus moricandi* (brownstriped grunt, Haemulidae), *Coryphopterus glaucofraenum* (bridled goby, Gobiidae), and *Lutjanus alexandrei* (Lutjanidae)—all from UP1—and *C. glaucofraenum*, *Stegastes variabilis* (cocoa damselfish, Pomacentridae) and *Chloroscombrus chrysurus* (Atlantic bumper, Carangidae)—all from UP2—showed the highest Di. In the ANMP, *Malacoctenus delalandii* (Brazilian blenny, Labrisomidae), *S. variabilis* and O. chrysurus—from NTZ1—and *Synodus foetens* (inshore lizardfish, Synodontidae), *S. variabilis* and *Narcine brasiliensis* (Brazilian electric ray, Narcinidae)—from NTZ2—had the highest Di. In the MERCor, *C. glaucofraenum*, *Microspathodon chrysurus* (yellowtail damselfish, Pomacentridae) and *S. variabilis*—fromUP1—, *M. pavonina*, *A. moricandi* and *C. glaucofraenum*—from UP2—and *C. glaucofraenum*, *M. chrysurus* and *M. delalandii*—from NTZ1—showed the highest Di (Table S4).

At the regional level (Abrolhos Bank region), the species with the highest Ui values were *Centropyge aurantonotus* (0.315; flameback angelfish, Pomacanthidae), *N. grandicassis* (0.311), *Chaetodipterus faber* (0.301; Atlantic spadefish, Ephippidae), *Myrichthys ocellatus* (0.299; goldspotted eel, Ophichthidae) and *Chilomycterus spinosus* (0.295; Diodontidae). Of these species, only *N. grandicassis* appears in the fisheries dataset. On the other hand, target species of greater relevance for fisheries obtained low to medium values, e.g., *Scarus trispinosus* (0.157; greenback parrotfish, Labridae), *M. bonaci* (0.022), *O. chrysurus* (0.012), *Lutjanus synagris* (0.019; lane snapper, Lutjanidae), *L. jocu* (0.020) and *Scomberomorus cavalla* (0.009; king mackerel, Scombridae), indicating that they are less isolated in functional space (Table S5).

The FFVI varies according to the conservation status of the species (Table S6). The UVRI component indicates that *M. bonaci*, *E. morio* and *O. chrysurus* were the most relevant target species for fishers. On the other hand, *S. trispinosus*, *Rhomboplites aurorubens* and *Sparisoma amplum* (reef parrotfish, Labridae) appeared to be the most vulnerable species according to the URI component. It is important to highlight that fishing for *S. trispinosus* is prohibited; its capture is only allowed within the limits of sustainable use conservation units (such as MERs) that have a local management plan for fishing activity: a document that establishes guidelines, measures and recommendations for the conservation and recovery of species. However, the combination of these two components (FFVI) indicated that *M. bonaci*, *S. trispinosus*, *E. morio* and *O. chrysurus* were the most vulnerable species, both from fishers' perspective and based on their extinction risk category (Figure 3).

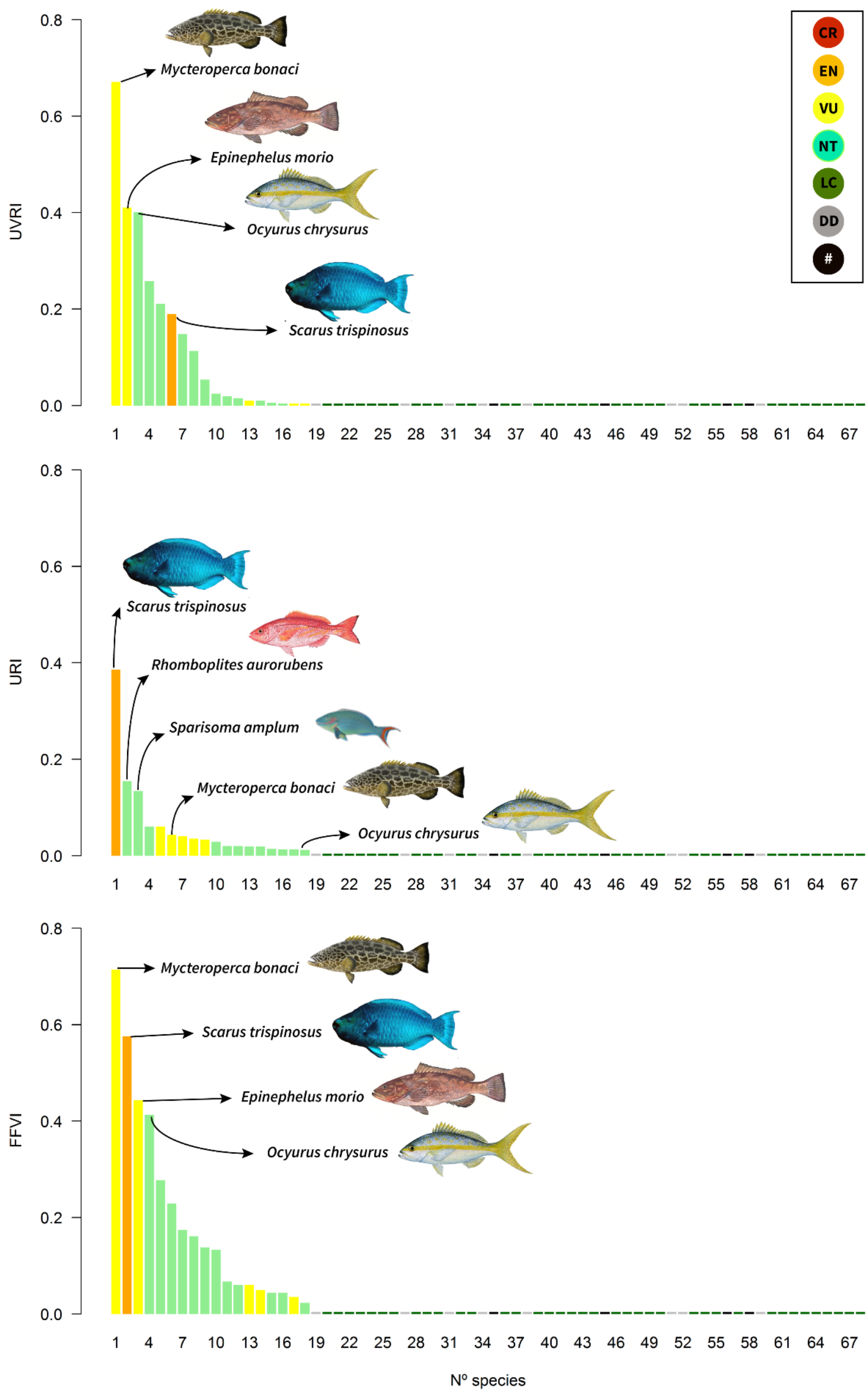

Figure 3. Components of the index of vulnerability to fishing for species registered at Abrolhos Bank, Bahia. A - UVRI: Use Value-Risk Index; B - URI: Uniqueness-Risk Index; C - Fisheries Functional Vulnerability Index (FFVI) (risk of extinction based on the Red Book of Brazilian fauna in danger of extinction). ICMBio: Instituto Chico Mendes de Conservação da Biodiversidade; CR: critically endangered; DD: data deficient; EN: endangered; LC: least concern; NT: near threatened; VU: vulnerable; #: absent in the ICMBio (2018a, 2018b) and MMA (2022) databases.

DISCUSSION

Our results suggest that MPAs can be relevant tools for the conservation of functionally distinct species targeted by fishing, especially in no-take areas. Functional metrics proved to be more informative about the potential impacts of fishing on target species. This is because species that occurred exclusively in the fisheries dataset (n = 45) represented around 21% of the regional species set, but these species have functional traits that add up to more than 72% of the functional hypervolume. In this sense, FFVI can be an adequate parameter to indicate fishing pressure together with the uniqueness of the species.

The no-take zones (ANMP_NTZ1 and MERCor_NTZ1) showed the highest values for FDiv. A high FDiv value is associated with (i) a greater number of species occurring at the extremities of the functional trait variation and (ii) a high degree of niche differentiation occupied by the species, resulting in less competition for resources. In addition, more efficient use of resources can lead to improved ecosystem functionality (Mason et al., 2005; Topor et al., 2019). Greenback parrotfish, which are the main targets of spearfishing in the Abrolhos Bank (Francini-Filho and Moura, 2008a, 2008b; Freitas et al., 2019; Giglio et al. 2020) and therefore listed as threatened in the IUCN red list (Padovani-Ferreira et al., 2012), showed higher abundance in both NTZs. Thus, the highest FDiv values found at these two sites only confirm that they are relevant areas for the management and conservation of this and other endangered species (Freitas et al., 2019; Roos et al. 2020) and the ecosystem functions they perform.

Significantly higher FRic values were found at ANMP_NTZ2 and MERCor_UP2. Although fishing is allowed at MERCor_UP2, it is done following gear and fishing restrictions, so it is not surprising that the highest FRic was found there. Moreover, ANMP is located about 70 km from the coast and is a well-enforced MPA, which may have contributed to this result. Previous studies have shown that features such as enforcement and distance from the coast contribute to better MPA performance (Edgar et al., 2014; Di Franco et al., 2016). However, these studies did not consider the functional component as presented here. The positive relationship between species richness and functional richness has been observed in other studies (Micheli and Halpern, 2005). However, the congruence between high functional diversity and MPAs is not always true. A study developed with the network of MPAs in the Mediterranean found that MPAs were spatially congruent with fish species diversity (richness), but did not show congruence with areas of high functional diversity (Mouillot et al., 2011). On a global scale, areas of high reef fish functional diversity were found to be concentrated in temperate latitudes, in contrast to patterns of species richness that peak in tropical regions (Stuart-Smith et al., 2013). Nevertheless, a recent study has shown that habitat representativeness within MPAs is the fundamental key to their effectiveness in protecting ecosystem functions within coral reef areas (Hernández-Andreu et al., 2024). Considering our results and these other studies, it is suggested that, in Abrolhos, no-take sites may adequately protect different aspects of biodiversity (i.e., fish functional diversity) and habitats, allowing for more niches, species and ecological functions. Thus, future assessments of MPA effectiveness should include not only traditional metrics (such as richness and abundance), but also functional metrics.

All sites showed some redundancy between species, with *Scarus zelindae* and *Sparisoma frondosum* belonging to the same FE, as well as *Halichoeres brasiliensis* and *H. poeyi*. However, it is known that the number and identity of the traits included in analyses determine the results of the DF metrics (Legras et al., 2019; Streit and Bellwood, 2023), and this must be taken into account when interpreting these results. In the case of labrids (*S. zelindae* and *S. frondosum*), the genus Sparisoma has greater feeding plasticity, which influences its greater distribution along the Brazilian coast (Ferreira et al., 2004). On the other hand, *S. zelindae* is one of the least abundant parrotfish species, being more common in offshore reefs (Hoey et al. 2018; Roos et al. 2019). A previous study demonstrated the occurrence of high complementarity and low redundancy in functional space among herbivores (Brandl and Bellwood, 2014). Therefore, functional redundancy between the two species must be considered with caution. In the case of *Halichoeres brasiliensis* and *H. poeyi*, both may have different microhabitat preferences in their foraging and diet (Nunes et al., 2013). In this way, species redundancy may simply be a methodological artifact influenced by the selection of functional traits. Thus, the presence of two (or more) species in a single FE does not indicate that one of them is "expendable," but rather that both are necessary to ensure greater resilience of the ecosystem to disturbance (Rosenfeld, 2002).

Taken together, these results suggest that MPAs can act as buffer zones for different forms of disturbance (in this case, fishing). This is relevant given that the current Brazilian MPA system does not meet global conservation goals (Vilar and Joyeux, 2021) and may face additional disruptions in connectivity between MPAs in a climate change scenario (Lima et al., 2021). This is a highly relevant issue when considering the achievement of Target 11 of the Convention on Biological Diversity (CBD), which highlights the importance of MPAs and recommends increasing protected areas that are ecologically representative and spatially integrated into networks (CBD, 2018).

At Abrolhos Bank, the species targeted by fishing represent 72% of the functional hypervolume of the regional species pool. Most of these species have large body sizes, a well-established characteristic in terms of fishing preferences. It is known that size-biased exploration can lead to truncation of stocks, in addition to the removal of BOFFFs (big, old, fat, fecund females; Hixon et al., 2014; Follana-Berná et al., 2021). However, in Abrolhos, three of the most targeted species (*E. morio*, *M. bonaci* and *S. trispinosus*) are protogynous hermaphrodites (females that turn into males). Protogynous fish are also susceptible to overfishing (Harris and Collins, 2000), and previous studies indicate that there is a distortion in the sex ratio of these three species, possibly indicating that males are overfished (Freitas et al., 2018, 2019). Furthermore, among the top three target species, there are two top predators and one herbivorous species, revealing a fishing down marine food web syndrome in Abrolhos Bank fisheries (Pauly et al., 1998), which is widely observed in the northeastern Brazilian coastal fishery (Freire and Pauly, 2010).

Parrotfish play a key functional role in reef environments by controlling algal growth and promoting the bioerosion necessary for the settlement of new coral recruits (Bellwood and Choat, 1990; Mumby et al., 2006). Larger herbivores, such as *S. trispinosus* and *S. amplum*, have broader functional roles with respect to space use, as they feed at larger scales than smaller species (Nash et al., 2013) and may contribute differently to reef dynamics as they grow, exploring different food resources throughout their development (Leitão et al., 2023). However, a previous study of Scarus spinus in Australia found that this species has a highly specialized diet (Nicholson and Clements, 2022). Therefore, more refined studies are needed to deepen the knowledge of the diet of parrotfish along the Brazilian coast (but see Francini-Filho et al., 2008). *Sparisoma amplum* is recognized as an excavating species, as well as the most specialized parrotfish coral predator in Brazil (Francini-Filho et al., 2008), and is a target of commercial and recreational fishing, especially spearfishing (Francini-Filho and Moura, 2008b; Giglio et al., 2020). The most recent list of threatened species did not include this species (MMA, 2022), although it appeared in the previous list as "near threatened" (NT; ICMBio, 2018a). Although *S. amplum* does not have the same relevance, from the perspective of fishing, as in other regions of the Brazilian Northeast (Roos et al., 2019), this species is included in the Recovery Plan for endangered Brazilian parrotfish (Freitas, 2016). In this way, it is necessary to establish risk criteria that are consistent with reality, considering that there is no evidence that the species is in better condition since the assessment carried out in 2018.

The functional hypervolume of the target species supports the results of a previous study suggesting that fishing may reduce the overall functional diversity of the regional pool (Martins et al., 2012). The decrease in functional hypervolume can have serious consequences for ecosystem functioning. Species with extreme values of functional traits can use different niches and collectively exploit a greater diversity of resources, maximizing multifunctionality

(Gross et al., 2017). Although fishing activity in Abrolhos is predominantly small- and medium-scale, there is evidence that this activity has a relevant impact on ecosystems (Jennings et al., 1999; Lokrantz et al., 2009; Guillemot et al., 2014; Rolim et al., 2022). Unfortunately, there are no official data on fishing effort in the study region. However, the trend observed at the regional and global level is towards increased fishing effort (Salas et al., 2007; McCluskey and Lewison, 2008; Watson and Pauly, 2013). This raises concerns about potential changes in the abundance of commercially important species with different life histories, especially considering the increasing tendency of fishing activity to focus on an increasing range of species that play different roles in the ecosystem (Trindade-Santos et al., 2020).

Notably, 23 reef species present in the fishing landings represent more than 56% of the functional hypervolume. Previous studies have shown comparable results, e.g., Mbaru et al. (2019) found that the target functional space for fishing was 17-50%, while Carvalho et al. (2021) obtained values of 5-70% depending on the fishing gear analyzed. Both studies used different methods than those used in the present study. However, all studies (including this one) indicate that fishing selectively removes few species with specific traits from the environment. This points to the importance of implementing management measures to reduce fishing effort on a group of species of eco-functional importance. For example, *S. trispinosus* was not among the species with the highest Ui index value. However, this species is the only one that was categorized as ”excavator/eroders” (EXCV; Halpern and Floeter, 2008), which highlights its functional role as one of the main removers of large amounts of substrate (coral), depending on its body size (Francini-Filho et al., 2008). In Brazil, a recent decision has sought to reduce the pressure on certain species under high threat levels, such as *S. trispinosus* (TCU, 2022). This decision overturns a previous Ordinance that allowed the capture of the species under certain conditions (e.g., fishing in free-diving, during the day, by professional fishers, and using a speargun; Brasil, 2018). However, this decision only covers species in the “Endangered” and “Critically Endangered” categories and does not address species classified as “Vulnerable,” such as *E. morio*, *M. bonaci*, *Lutjanus cyanopterus* (cubera snapper, Lutjanidae), among others. Furthermore, there are currently no targeted measures for *O. chrysurus*, for instance, a species that may already be showing signs of overfishing (Klippel et al., 2005; Frédou et al., 2009).

To date, approaches available in the literature on fish vulnerability to fishing are based on expert opinion (Cheung et al., 2005, 2007) or require a large amount of biological data (e.g., Dulvy et al., 2004). These approaches are difficult to apply in data-poor tropical systems such as Brazil and other countries with reef fishing. Furthermore, they do not incorporate the perspective of resource users: fishers themselves. The proposed index (FFVI) encompasses both the value placed on a species by fishers (use value) and scientific information (risk of extinction and functional traits). In this way, the FFVI responds to the call by international institutions to incorporate local/indigenous/traditional knowledge (Fischer et al., 2014; Unesco, 2017; Yap and Watene, 2019). It is imperative to open wider windows of participation for the small-scale sector in discussions on conservation and management strategies for fisheries resources. Today, there is a (growing) literature on how fishers participate in the most diverse areas of fish biology and ecology and fisheries management (e.g., Neis et al., 1999; Silvano and Begossi, 2012; Leduc et al., 2021).

The FFVI index can be broken down into components related to: (i) the use value of each species from the perspective of resource users and (ii) the functional isolation of this resource (species) in the functional trait space, that is, its functional distinction. Use value is the most direct indicator of fishing pressure on a species, as it indicates the potential for exploitation based on commercial value. It was originally proposed by Phillips and Gentry (1993a, 1993b) as a means of measuring user knowledge of a particular plant. In this study, the index was adapted to indicate the species of greatest importance to fishers. It is well known that more targeted species have greater value added due to market pressures (Cinner and McClanahan, 2006). From this perspective, the species most targeted by fishers have greater use value.

The functional component tells us which ecological processes can be affected by overfishing in a particular functional group. Fishing pressure can remove specific groups of species (and their respective unique traits), harming the environment (Koutsidi et al., 2016; Mbaru et al., 2020; Carvalho et al., 2021). In this way, taken together, the two components represent a factor that measures fishing pressure on functional rarity. Importantly, both components are uncorrelated (Pearson correlation: t = -1.31; df = 39; p-value = 0.20; cor = -0.20). In other words, species with greater use value are not necessarily those with greater functional isolation. The species with the greatest commercial interest share intermediate values in the functional distinction index (Ui). In this way, the set of functional attributes shared by species with higher UV is being removed from the environment.

This study showed that NTZs generally maintain greater FD than areas open to fishing, suggesting that sites where the management regime provides greater control or total restriction of fishing activities may preserve greater functional richness. The use of functional metrics indicated that fishing removes a relatively small number of species from the environment, but these species represent more than 70% of the functional volume of the regional species pool in the Abrolhos Bank. In this context, more coherent management measures need to be applied, considering that the current list of threatened fish species does not include a number of species that show no evidence of improvement since the previous assessment (eg., Sp. amplum and O. chrysurus; Queiroz Véras et al., 2023; Frédou et al., 2009). Lastly, the FFVI showed the species most vulnerable to fishing, considering two components: the use value of a species from the perspective of fishers and its respective level of vulnerability. Therefore, this index can be a reliable indicator of fishing pressure in other parts of the world, especially in low- and middle-income countries in data-poor contexts.

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AUTHOR CONTRIBUTIONS

A.S., C.H.W., C.Z., F.C.F-H.: Conceptualization.

C.H.W., C.Z., F.C.F-H.: Investigation.

C.Z.: Writing – original draft; Formal Analysis;

A.S., C.H.W., C.Z., F.C.F-H.: Methodology; Writing – review & editing.

A.S.: Supervision; Project Administration; Funding Acquisition.

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