



Functionality and Effectiveness of Marine Protected Areas in Southeastern Brazilian Waters for Demersal Elasmobranchs

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Ensuring the efficacy of Marine Protected Areas (MPAs) requires that adequate management strategies be implemented according to the MPA's objectives. Within the scope of species conservation, achieving MPA objectives demands understanding of the role played by MPAs for the target species. In 2014, Brazilian stakeholders and experts set the action plan for elasmobranchs' conservation, which intended to create new protected areas and expand the existing ones. Nevertheless, more than 65% of Brazilian elasmobranch species are threatened by anthropogenic pressures such as fisheries and habitat loss. In addition, their ecological aspects are not well studied, which might jeopardize the success of the proposed actions. To assess the functionality and effectiveness of two no-take MPAs for sixteen demersal species, the Wildlife Refuge of Alcatrazes (WRA) and the Tupinambás Ecological Station (TES), we evaluated the community structure, space-time variations in functional diversity and changes in fishery indicators. Community dynamics were driven by inshore intrusion and time persistent effects of a cold and nutrient-rich water mass, the South Atlantic Central Water, which increased the relative abundance of species, functional groups, and overall diversity. Spatially, the heterogeneity of benthic habitats, due to the action of stronger waves in specific parts of the MPAs, reflects a diverse community of benthic invertebrates, explaining differences in relative abundance and similarities in space use by the functional groups. Regarding effectiveness, the MPAs make up a key network with the surrounding protection areas to support the ecosystem maintenance on the central and northern coast of the São Paulo state. The establishment of the TES has positively influenced the community throughout the years while the recent creation of the WRA may have promoted some improvements in fisheries indicators for a threatened guitarfish. We propose different functions of the Alcatrazes archipelago for each species and suggest some measures to enhance not only elasmobranch conservation but also the MPAs' effectiveness.

Keywords: Alcatrazes archipelago, management strategies, habitat use, community structure, fishery indicators, elasmobranch conservation, functional diversity

INTRODUCTION

For decades, governments have been using Marine Protected Areas (MPAs) to manage use of ocean resources. MPAs can address socioenvironmental issues by supporting traditional fishing communities, avoiding fisheries depletion and marine habitat degradation, and maintaining ecological services (Halpern, 2003; Fox et al., 2012). They are usually employed as a tool for conservation of critical habitats and dependent organisms, accounting for different requirements through a species' life stages that can be safeguarded from anthropogenic disturbances (Claudet et al., 2010; Grüss et al., 2011; Wiegand et al., 2011; Knip et al., 2012; Rolim et al., 2019). Since the accomplishment of multiple objectives is challenging and success indicators, such as fishery sustainability, go beyond the MPA boundaries, coordination between MPA design and other management strategies (e.g., measures of control and restriction, networks of reserves, and adaptive management) are mandatory to achieve effectiveness (Fox et al., 2012; Lubchenco and Grorud-Colvert, 2015; Hilborn, 2016).

Previous works have highlighted the importance of adopting multiple strategies, especially when the MPA goals involve long-lived and mobile species like elasmobranchs (Chapman et al., 2005; Wiegand et al., 2011; Knip et al., 2012). For instance, Brazil is home to more than 14% of the worldwide biodiversity of sharks, skates and rays, driving experts and stakeholders to determine that conservation actions including MPAs are needed for the taxon (i.e., The action plan for elasmobranch conservation; ICMBio, 2016a). Currently, at least 65% of the species recorded in Brazilian waters are threatened or have insufficient data (ICMBio, 2016b; IUCN, 2021) and this lack of information might jeopardize the success of conservation and management actions (Gill et al., 2017; Giakoumi et al., 2018).

Among the strategic regions delimited by the action plan (ICMBio, 2016a) two marine reserves call attention: The Wildlife Refuge of Alcatrazes (WRA) and the Tupinambás Ecological Station (TES). They were established three decades apart seeking ecosystems preservation by restriction of human interference (Brazil, 1987, 2016). First, TES was created in 1987 to secure coastal and offshore rock formations, covering two coastal islands in northern São Paulo (i.e., Cabras and Palmas islands) and the islets, shallow flats and submerged pinnacles of the Alcatrazes archipelago. Later, in 2016, the WRA was implemented to shelter a greater area of the archipelago, especially the Alcatrazes island, becoming the largest marine reserve in south and southeastern Brazil. Both are no-take zones and although their delimitations overlap, they have different management plans. TES is the most restrictive, allowing only scientific and educational activities, while the WRA allows supervised visits to general public (ICMBio, 2017; Marconi et al., 2020).

At present, WRA and TES are part of a critical network for biodiversity maintenance that includes adjacent protected areas on the central and northern coasts of the São Paulo state (São Paulo, 2008). It is located at the middle continental shelf, which makes the Alcatrazes archipelago a unique

area that interfaces parallel and perpendicular gradients of granulometry and organic matter in relation to the coast (Mahiques et al., 1999, 2004, 2011). Furthermore, it is near temperate and subtropical transition zones, being markedly influenced by mesoscale physical processes that promote seasonal changes in water properties (Castro-Filho et al., 1987; Campos et al., 2000). From late spring through summer, the prevalence of north and northeast winds carries superficial waters offshore, composed by the Coastal and Tropical water masses. This process promotes bottom inshore intrusions of the South Atlantic Central Water (SACW), a colder water mass that stratifies the water column (Castro-Filho et al., 1987).

The archipelago is ecologically important, presenting greater values of species richness, abundance and biomass of fish assemblages compared to the fished areas inshore, as well as the other no-take areas in the region (Gibran and Moura, 2012; Morais et al., 2017; Rolim et al., 2019). These trends reflect a complex ecosystem primarily regulated by top-down effects, with higher heterogeneity of functional groups when compared to the previously mentioned areas (Rolim et al., 2019). The high abundance of larger individuals of fishery target species (e.g., Epinephelidae, Kyphosidae, Carangidae, and Scaridae) suggests a great spillover potential to adjacent zones (Rolim et al., 2019). However, for elasmobranchs, especially the demersal species, the relationship of local species with environmental features is unknown and available information is restricted to community studies that focus mainly in actinopterygians. Approximately seventeen elasmobranch species are reported in the area (Hoff, 2015; ICMBio, 2017; Rolim et al., 2019), which exhibit differences in feeding and reproductive strategies, and behavioral ecology (Lessa et al., 1986; Soares et al., 1992; Vögler et al., 2003; Vooren and Klippel, 2005; Aguiar and Valentin, 2010), highlighting the variety of roles that the WRA and TES MPAs may play according to habitat use by the species.

Obtaining knowledge on the ecology of these species is crucial since fishing pressure and habitat degradation on coastal and inner shelf regions have disturbed the ichthyofauna, resulting in population depletion, diversity loss, and ecosystem unbalancing (Imoto et al., 2016; Dias et al., 2017; Prado et al., 2019; Rolim et al., 2019; Trevizani et al., 2019). Thus, the present study aimed to assess the functionality and effectiveness of the two MPAs to assist the decision making process that involves the conservation of demersal elasmobranchs. Our findings are important not only to understand the local and regional dynamics, but also to enhance policies for species conservation, in order to underlie the MPAs' management. We hypothesize that those species use the archipelago for distinct purposes, which would reflect in different population structures. Differences in species distributions and in diversity metrics are also expected throughout space and time. Furthermore, we believe that variations in the relative abundance of functional groups as well as of their species, are related to the seasonal dynamics of the environment and to the heterogeneity of habitats. Finally, we expect that the size structure of a threatened guitarfish changes significantly due to the protection of a newer and larger MPA (i.e., the WRA).

MATERIALS AND METHODS

Ethics Statement

The animal study was reviewed and approved by the Ethics Committee of Animal Use of the Oceanographic Institute of the University of São Paulo (CEUA IO-USP) and by the Chico Mendes Institute for Biodiversity Conservation (ICMBio) under the survey permit SISBIO/55824.

Sampling

Biotic and abiotic data used in this study were obtained from five oceanographic expeditions performed by the following projects: Contributions to the Tupinambás Ecological Station Management Plan: oceanography and marine biodiversity (September/2011), Biotic Integrity of the Alcatrazes Archipelago Ecosystems (January/2014) and Geohabitat of the demersal ichthyofauna of the Alcatrazes region: an environmental assessment (September/2015, December/2018, and July/2019). Position of the oceanographic stations was defined according to the objectives of each project. Thus, they were set at different locations throughout the archipelago, except to 2019, when the 2018 stations were re-sampled (**Figure 1**). Sampling of sea water and sediments as well as capture of elasmobranchs were carried out at fifty oceanographic stations between 28 and 53 m depth.

Abiotic Data

The assessment of temperature and salinity data was performed through different methods. Both variables were directly assessed using a conductivity-temperature-depth probe (CTD) (2011 and 2015) and a multiparameter probe (2018). Samples of bottom water taken by Nansen bottles, in 2014 and 2019, were used to measure temperature and salinity values using reversing thermometers and a refractometer, respectively. The sediment mosaic of the MPA region was characterized from samples collected through a van Veen grab in 2011 (Palóczy et al., 2012) and 2019. The area was classified into five zones, calculated as buffers of 2.5, 5, 7.5, 10, and 12.5 km from the center of Alcatrazes island, according to the home ranges of the caught specimens (or nearest taxa, i.e., genus) (Cartamil et al., 2003; Collins et al., 2007; Farrugia et al., 2011; Tilley et al., 2013). These zones were intended to capture any potential changes in benthic ecology with distance from the Alcatrazes island. Species with relatively small home ranges might have home ranges at a finer scale than these zones, while more wide-ranging species would encompass multiple zones.

Biotic Data

Demersal elasmobranch specimens were collected through otter trawl nets (20–21 m in the foot rope, 40–60 mm mesh in the body as well as in the sleeves and 25–30 mm in the cod-end), which were operated from 10 to 20 min at a speed of two knots by the R/Vs Alpha Delphini (IO-USP) and Soloncy Moura (ICMBio). On board, specimens were accommodated in boxes with seawater and information was collected concerning their sex, total length (TL), disc width (DW), and total weight (TW). To ensure correct identification, pictures of each specimen were taken and identification to species level was conducted

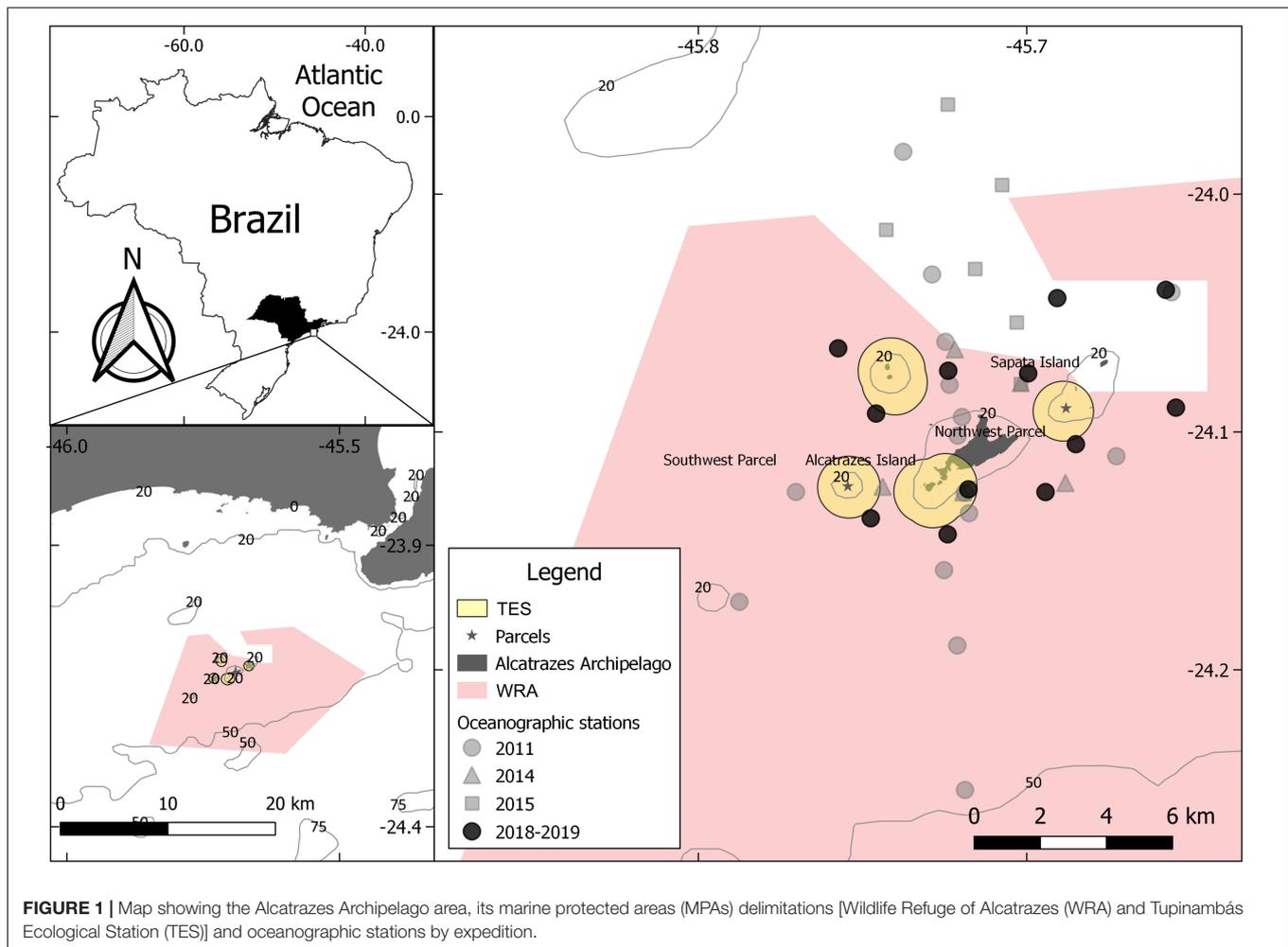
in accordance with Figueiredo (1977), Viana et al. (2016), and Gomes et al. (2019). After data collecting, all live elasmobranchs were released to the sea. The specimens that did not survive (i.e., less than 5% of the elasmobranch catches) were cooled and brought to the Oceanographic Institute (USP), being stored at the teaching collection. The non-elasmobranch species, such as the actinopterygians, were sacrificed through a solution of 400 mg L⁻¹ of eugenol (Fernandes et al., 2017), cooled and also brought to the Oceanographic Institute to be used as research material in studies of community ecology, reproductive biology and so on.

Hydrographic and Sedimentological Analyses

According to Rossi-Wongtschowski and Paes (1993), the community structure of actinopterygians and elasmobranchs of the northern coast of São Paulo was related to sediment distribution and to the SACW presence. Thus, granulometric and hydrographic analyses were performed, as well as the estimation of calcium carbonate concentrations (CaCO₃) of sediment.

In 2014, the refractometer did not operate correctly. Thus, based on the SACW properties, we fixed salinity values at 35.7 to water samples collected at depths where temperature was below 17°C, for this year only. For the whole dataset, values of temperature and salinity of each oceanographic expedition were combined in diagrams and potential densities with pressure equals zero (σ_θ) were calculated. We set diagrams with isopycnal curves through the oce package (Kelley et al., 2021) using $\sigma_\theta = 25.8$ (Stramma and England, 1999; Mémerly et al., 2000) as a threshold to identify the SACW presence. To define the sediment type of each oceanographic station, we combined available information about sedimentological parameters of the 2011 samples (Palóczy et al., 2012; Hoff et al., 2015) with data obtained in 2019. Sediment granulometry was determined by application of the sieve-pipette method (Suguio, 1973) to 50 g of the 2019 samples, followed by Folk and Ward (1957) classification. Further, concentrations of CaCO₃ were estimated through weight differences after digestion by 10% solution of hydrochloric acid. Gravimetric results were used to characterize the oceanographic stations in accordance with Larsonneur et al. (1982).

Three main factors determine the energy dynamic in the Alcatrazes island surroundings: its Y-shaped morphology, the abrupt change in the bathymetry and the predominance of incident waves from south and southeast. Together, they act as mitigating elements and reflect a more stable environment in the north and toward the coast, due to the indirect incidence of waves as well as energy loss by the decreasing bathymetry. Furthermore, regions are more energetic in the south, with waves varying slightly through the seasons and years (Takase et al., 2021). These factors rule the deposition process in the archipelago, forming sediment features that are sustained over time. Thus, the same characteristics of 2011 and 2019 samples were assumed for unsampled sediments of the other years. Both classifications were applied to the nearest oceanographic stations (**Supplementary Table 3**) with distances ranging from 0.38 to 3.17 km.



Ecological Analyses

A bibliographic survey was performed to gather information regarding the size at maturity, reproductive strategies, and food items of each species. They were used to classify specimens as juvenile or adult based on the size at first maturity and to identify functional groups through the reproductive and feeding guilds (**Supplementary Tables 1, 2**). Thus, species were classified into six groups by embryonic feeding method (trochophore, oviparous, or lecithotrophic) and by trophic category (hyperbenthivorous, infauna consumers, or piscivorous), according to Elliott et al. (2007). Due to spatial variations in terms of biological and ecological aspects we used information of specimens from the closest regions.

To estimate changes in diversity patterns over time, we calculated species richness, the Shannon-Wiener diversity (H') and the Pielou evenness (J') for each year (Begon et al., 2006). Due to differences in sampling effort among years, instead of comparing raw species counts, we estimated rarefaction curves and species richness through non-parametric estimators (Chao and Chiu, 2016). Those estimators take into account underestimations in richness due to low sampling effort and differences in detection probability of species, since some species

might have not been caught despite being present (Chao and Chiu, 2016). Quantities of juveniles and adults, sex ratios, and frequencies of TL/DW classes were counted for the most abundant species (>25 specimens caught). Deviations from 1:1 of sex ratios and contingency tables of species by life stages were evaluated by chi-square tests (χ^2). Distributions of TL/DW frequency classes between sexes were compared by two-sample Kolmogorov-Smirnov tests (Zar, 2009).

Next, to test our hypothesis that species use spatial areas differently, and thus elucidate the roles played by WRA and TES, we conducted a three-step analyses. First, for each oceanographic station, we estimated the Bray-Curtis dissimilarities of the functional group abundances and performed principal coordinate analysis (PCoA) (Borcard et al., 2011) using the “*cmdscale*” function in R. Then, the relationship of the two first ordination scores and buffers were modeled by smoothed splines fitted using the “*ordisurf*” function. This function uses generalized additive models (GAMs) to fit non-linear response surfaces of predictor variables to ordinations (Oksanen et al., 2020). Maps of species’ relative abundance by oceanographic expedition were set and compared to the PCoA results to identify spatial-temporal variations in the community composition.

Influences of abiotic features on the relative abundance of species and functional groups were evaluated through generalized linear models (GLMs). Before model fitting, the predictive variables temperature, salinity, depth, year, seasons, the SACW presence, buffers, sediment type, and classes of CaCO_3 concentrations were centralized and the collinearity of continuous and ordinal variables were estimated among pairs using the Spearman's correlation coefficient (Zuur et al., 2009, 2010). Since the SACW presence was correlated (>80%) with temperature, and sediment type was correlated (>0.80) with classes of CaCO_3 concentrations, only one of each pair of variables was included in each model. According to Larsson et al. (1982), sediments with CaCO_3 concentrations above 30% are substantially composed of biogenic sources (i.e., animal and vegetal debris), being classified as litho-bioclastic (from 30 to 50%), bio-lithoclastic (from 50 to 70%) and bioclastic (>70%). Therefore, for model fitting, the sediment variable was set as one of two categories: lithoclastic (up to 30% of CaCO_3) and biogenic sediments. Fixed effect models of the count of each species per trawl with the log of swept area (in meters per seconds) as offset term were set up according to prior information about which variables were likely to be relevant for each species (Oddone and Vooren, 2004; Vögler et al., 2008; Menni et al., 2010; Barbini et al., 2011; Palmeira, 2012; Schlaff et al., 2014). Models were fitted using “glm” and “glm.nb” functions with Poisson and Negative Binomial error distributions (Zuur et al., 2009). Alternative models were compared by the second order Akaike information criterion (AICc) with $\Delta\text{AICc} < 2$ as a threshold to evaluate them regarding their descriptive capacity (Burnham and Anderson, 2002). If more than one model was ranked as plausible, model averaging was applied and parameters estimates were weighted by the Akaike weights (W_i) (Burnham and Anderson, 2002). To evaluate the model fits, scaled residuals were analyzed through plots generated by the DHARMA package in R (Hartig and Lohse, 2020). DHARMA residuals are estimated as quantiles of one thousand simulated draws from the distribution used to calculate the likelihood corresponding to each observation. Deviations from the expected values of a uniform distribution as well as of variances in relation to predicted values were compared by qq-plots and residual plots, respectively.

Finally, the WRA effect was assessed through changes in size structure over time only for the most common species: the lesser guitarfish, *Zapteryx brevirostris* (Müller and Henle, 1841). None of the other species had a large enough sample size to calculate these size-based indicators. The TL data of *Z. brevirostris* were grouped in two periods (2011–2015 and 2018–2019) according to the MPA establishment in 2016 (Brazil, 2016). We set a linear model with interactions between season and time period ($TL \sim \text{period} \times \text{season}$) to test whether differences in mean TL are an effect of the MPA creation or due to sampling different seasons (Zar, 2009). Also, indicators of fishery sustainability for each period were estimated. Fishing mortality relative to natural mortality (F/M) and spawning potential ratios (SPR, defined as the spawning stock biomass relative to unfished SSB) are indicators of stock status. They measure how much higher is the mortality experienced by a fished population and how much lower is its potential fecundity

(Goodyear, 1993), respectively, compared to unfished conditions. The F/M indicator was calculated under two different methods with different assumptions about selectivity. First, in the mean length method, total mortality (Z) was estimated by the Beverton and Holt (1957) estimator assuming the same catchability of specimens over the minimum fully exploited size (L_c). The second method, length-based spawning potential ratio (LBSPR), assumes that catchability increases logistically with the length of specimens and estimates the logistic parameters as well as the average F/M and SPR that best fits the length-frequency data, assuming variability in length at age (Hordyk et al., 2015).

Life history parameters were required to estimate fishery indicators. However, most of them have not been calculated for Alcatrazes population, so we used values of populations from nearby regions. To estimate L_c and other parameters, such as the mean and variance of natural mortality (M), methods proposed by Babcock et al. (2013, 2018) were implemented (see **Supplementary Table 4** for details about parameters and indicators). Uncertainties of parameters' estimates were obtained by ten thousand Monte Carlo simulations. They were performed with bootstrapped samples of the observed length data and values of the life history parameters drawn from a multivariate normal distribution. Then, the 90% confidence interval (CI) of each indicator was set as the 5 and 95% quantiles of the simulated values (Babcock et al., 2018).

To evaluate whether a difference in mean length should be expected in the before vs. after MPA samples, the necessary time after the establishment of a MPA for the *Z. brevirostris* population to reach an unfished level of the mean length was assessed considering several selectivity assumptions. Life history values of a fished population (**Supplementary Table 4**) were used to calculate the numbers (Hilborn and Walters, 1992) and lengths at age (von Bertalanffy growth model, Beverton and Holt, 1957) assuming both natural and fishing mortalities before the WRA, and only natural mortality after its establishment. Then, we calculated the mean length of specimens larger than L_c , which is the mean length that is used for the Beverton-Holt estimator, in each year after the founding of the MPA.

All analyses were performed using the R environment (R Core Team, 2020) through the vegan (Oksanen et al., 2020), SpadeR (Chao et al., 2016), MASS (Ripley et al., 2021), MuMIn (Bartoń, 2020), DHARMA, mvtnorm (Genz et al., 2020), and LBSPR (Hordyk, 2019) packages.

RESULTS

Hydrographic and Sedimentological Features

Temperature and salinity diagrams (**Supplementary Figure 1**) showed that the influence of SACW has changed over the years and across the MPA area. The water mass was detected in all years except 2019, which was characterized by higher values of temperature/salinity and homogeneity in the water column with the majority of temperature records from 22.4 to 23.5°C. Despite the absence of σ_0 reference values in 2014, low temperatures (18°C<) were verified by reversing thermometers up to 25 m

above the bottom, indicating the presence of SACW. In terms of distribution through the area, the SACW was identified at all oceanographic stations until 2015. Although the 2018 campaign was conducted in summer, the SACW was only detected at oceanographic stations exposed to the open ocean (#08, #09, #10, #11, and #12) and in the area between the Sapata and Alcatrazes islands (#05). These variations in the water mass coverage indicate that the intrusion process was beginning, since the samples were collected at the onset of the season. Sediments of both MPAs were defined by fine grains (fine and very fine sand > 85%) and poor CaCO₃ composition (i.e., lithoclastic sediments). However, bio-lithoclastic and bioclastic sediments with large quantities of biogenic CaCO₃ (making up by 79% of sediment content) were assessed on patches of coarse and very coarse sand. The distribution of these patches was limited to nearby regions of the Alcatrazes island and especially to the island side that is exposed to open ocean (i.e., the south side). Hydrographic and sedimentological compiled data are presented in **Supplementary Table 3**.

Diversity and Community Structure

A total of 562 specimens were recorded, belonging to 16 species of seven families. Species richness across all years was estimated as 16.33–17, depending on the estimation method used, with CIs ranging from 16.02 to 27.05 species (**Table 1**). Two families, the Trygonorrhinidae and Arhynchobatidae, were the most common, accounting for almost 85% of the elasmobranchs sampled (**Supplementary Table 5**). Trygonorrhinidae was represented by just one species, *Z. brevirostris*, which was recorded in 86% of the oceanographic stations and showed the highest number of individuals caught ($n = 257$; **Supplementary Table 5**). Following *Z. brevirostris*, the Rio skate, *Rioraja agassizii* (Müller and Henle, 1841), made up around 15% of the total sample ($n = 81$; **Supplementary Table 5**) and despite its absence in 2015, the species was recorded in 60% of all oceanographic stations.

According to the estimates of diversity, evenness, and species richness, changes in demersal community composition were identified over the time. Overall, the number of observed species and specimens caught were lower (**Table 2**) in oceanographic expeditions of smaller sampling effort: the summer of 2014 (five trawls) and spring of 2015 (six trawls). However, rarefaction curves did not reach asymptotes (**Supplementary Figure 2**) and the 95% upper CI limits revealed the potential for greater values of estimated richness (**Supplementary Table 5**). Diversity and evenness of those oceanographic expeditions were quite similar with higher estimates of the other spring and summer expeditions (2011 and 2018, respectively), which were carried out with a sampling effort almost three times greater (**Table 2**). In this sense, a trend in diversity and evenness was observed, with estimates increasing through the seasons, from the lowest ones in the winter (2019' oceanographic expedition) to the highest during the summer (**Table 2**).

Altogether, lengths were measured for 554 and sexes for 549 specimens, of which 499 were from six species that had a samples size of at least 25 (**Supplementary Table 5**). Species showed significant differences in the distribution of life stage

TABLE 1 | Species richness estimates by non-parametric estimators.

Estimators	Estimate	SE	95% CI
Total			
Chao1 (Chao, 1984)	17.00	1.87	16.09–27.05
Chao1-bc	16.33	0.93	16.02–21.96
iChao1 (Chiu et al., 2014)	17.00	1.87	16.09–27.05
ACE (Chao and Lee, 1992)	16.95	1.48	16.11–24.38
2011			
Chao1 (Chao, 1984)	9.17	0.53	9.01–12.51
Chao1-bc	9.00	0.79	9.00–11.64
iChao1 (Chiu et al., 2014)	9.17	0.53	9.01–12.51
ACE (Chao and Lee, 1992)	9.84	1.41	9.09–17.14
2014			
Chao1 (Chao, 1984)	7.00	0.53	7.00–8.55
Chao1-bc	7.00	0.53	7.00–8.55
iChao1 (Chiu et al., 2014)	7.25	0.53	7.02–10.21
ACE (Chao and Lee, 1992)	7.43	0.97	7.03–13.00
2015			
Chao1 (Chao, 1984)	5.98	2.16	5.07–18.3
Chao1-bc	5.98	2.16	5.07–18.3
iChao1 (Chiu et al., 2014)	5.98	2.16	5.07–18.3
ACE (Chao and Lee, 1992)	7.09	3.51	5.22–25.21
2018			
Chao1 (Chao, 1984)	12.17	0.53	12.01–15.52
Chao1-bc	12.00	0.82	12.00–14.68
iChao1 (Chiu et al., 2014)	12.17	0.53	12.01–15.52
ACE (Chao and Lee, 1992)	12.43	0.89	12.03–17.36
2019			
Chao1 (Chao, 1984)	14.46	7.13	10.49–50.53
Chao1-bc	11.49	2.58	10.15–24.95
iChao1 (Chiu et al., 2014)	15.46	5.04	11.17–35.46
ACE (Chao and Lee, 1992)	12.06	2.78	10.28–25.16

Notations: standard error (SE), lower and upper limits of 95% confidence intervals (95% CI).

TABLE 2 | Relative abundance, number of species and ecological index estimates by oceanographic expedition of demersal elasmobranchs.

OEs	<i>n</i>	<i>N</i>	<i>H'</i>	<i>J'</i>
2011	9	98	0.79	0.77
2014	7	95	1.19	0.76
2015	5	58	0.74	0.73
2018	12	196	1.31	0.86
2019	10	101	0.79	0.65

Notations: oceanographic expeditions (OEs), observed number of species (*n*), relative abundance (*N*), Shannon-Wiener diversity (*H'*) and Pielou's evenness (*J'*) indexes.

classes ($\chi^2 = 105.6$, $df = 5$, $p < 0.05$). The community was mainly composed of adults for *Z. brevirostris*, *R. agassizii*, the zipper sand skate, *Psammobatis extenta* (Garman, 1913) and the groovebelly stingray, *Dasyatis hypostigma* Santos and Carvalho, 2004. However, for two species of the Arhynchobatidae family, the spotback skate, *Atlantoraja castelnaui* (Miranda Ribeiro, 1907) and the eyespot skate, *Atlantoraja cyclophora* (Regan, 1903), the number of juveniles were substantially higher (over

75% of each species abundance). Deviations in sex ratios from 1:1 were verified of both Arhynchobatidae species, with males outnumbered by females (0.33:1, $\chi^2_{A. castelnaui} = 25$, $df = 1$, $p < 0.05$; 0.4:1, $\chi^2_{A. cyclophora} = 18.37$, $df = 1$, $p < 0.05$). Concerning the species length ranges, no significant differences among sexes were found for either of these two species ($D_{A. castelnaui} = 0.26$, $p > 0.05$; $D_{A. cyclophora} = 0.26$, $p > 0.05$; **Figure 2**).

Conversely, for the other two skate populations, more than 70% of collected specimens were adults. Differences in sex ratios were also verified with more females of *R. agassizii* (0.57:1, $\chi^2 = 7.44$, $df = 1$, $p < 0.05$) and of *P. extenta* (0.54:1, $\chi^2 = 8.84$, $df = 1$, $p < 0.05$). For the latter, TL frequencies did not differ ($D = 0.20$, $p > 0.05$), however, females of *R. agassizii* exhibited larger sizes ($D = 0.43$, $p < 0.05$) prevailing in TL classes above 40 cm (**Figure 2**). The same pattern was observed for *Z. brevirostris* with more than 70% of the analyzed specimens as adults. The ratio between males and females was equal (0.88:1, $\chi^2 = 0.44$, $df = 1$, $p > 0.05$) and as for *R. agassizii*, females were larger than males ($D = 0.19$, $p < 0.05$). For *D. hypostigma*, there were no differences among sex ratios (0.75:1, $\chi^2 = 2.04$, $df = 1$, $p > 0.05$) and life stage classes were also similar (**Supplementary Table 5**). Although the majority of males showed smaller sizes (**Figure 2**), no significant differences were found in DW distributions by sex ($D = 0.38$, $p > 0.05$).

Habitat Functionality

The first two axis of the PCoA explained 55.6% of the data variance (PCoA1 = 32.4 and PCoA2 = 23.20), being correlated with distances from the Alcatrazes island (i.e., buffers) as shown by the contour lines (**Figure 3**). The slight differences in space use by the functional groups appeared to be more related to the species' trophic categories than to their reproductive modes. While the hyperbenthivorous and infauna consumers were common in regions of intermediate distances, the piscivorous species were mainly caught at the farthest oceanographic stations (i.e., those positively loaded on the PCoA1 and negatively loaded on the PCoA2). Regarding the reproductive guilds, such oceanographic stations were also the most different, being separated even from those of other lecithotrophic species (i.e., negatively loaded on the PCoA1). Fifteen individuals of two shark species, the angular angel shark, *Squatina guggenheim* Marini, 1936 and the dogfishes, *Squalus albicaudus* Viana et al., 2016 and *Squalus sp.* were classified as lecithotrophic and piscivore (**Supplementary Table 5**). They were caught at seven oceanographic stations that were characterized by low temperatures ($\mu = 18.1^\circ\text{C}$), presence of the SACW and predominance of finer grains without biogenic CaCO_3 .

Differences in relative abundances were observed through the archipelago (**Figure 4**). In general, the functional groups were present in all regions of the archipelago, however, the region that corresponds to the exposed side of the Alcatrazes island showed higher values of relative abundance and was more heterogeneous in terms of species composition than the northwest side. Some species were widely distributed while occurrence of the other ones was occasional and restricted to certain regions. *A. castelnaui* and *A. cyclophora* were abundant

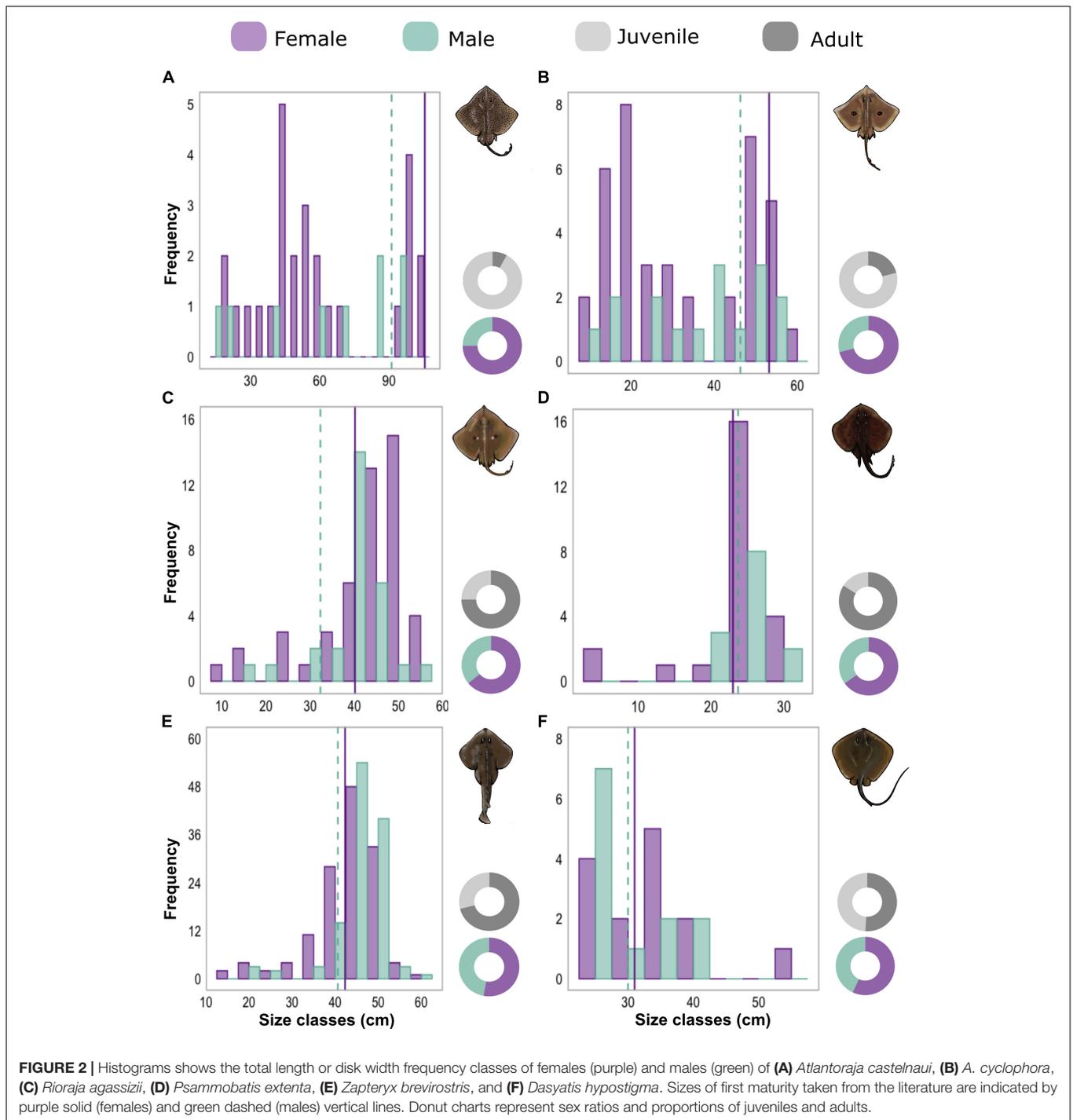
in the surroundings of the Alcatrazes island and were present through almost the entire sampling period. Similarly, *R. agassizii* and *Z. brevirostris* were ubiquitous in terms of space-time occurrence. However, in 2019 a pattern was identified with concentrations of the skate in the northeast and of the guitarfish in the northwest and south regions. Also, in 2019 large groups of *D. hypostigma* and solitary individuals of the bullnose eagle ray, *Myliobatis freminvillei* Lesueur, 1824 were observed in the northeast region. Still in the northeast, juveniles of *S. albicaudus* were recorded in 2018. Congeneric species, such as the cownose rays and the angel sharks, were not caught together in any of the trawls, indicating possible spatial segregation with the exposed region being mainly used by *Rhinoptera brasiliensis* Müller, 1836 and *S. guggenheim* and the northwest side by *Rhinoptera bonasus* (Mitchill, 1815) and *Squatina occulta* Vooren and Silva, 1991.

According to the most parsimonious models ($\Delta\text{AICc} < 2$), temperature and seasons were the predominant variables that explained shifts in abundance of the species and functional groups (**Table 3**). Except for the trophonemata-hyperbenthivorous (i.e., species that produce lipid-rich liquid through trophonemas to supplement embryo nutrient provision and feed on benthic invertebrates which live above the sediment, respectively), the relative abundance of all groups was inversely related to bottom water temperature (**Table 4**). Moreover, significant differences between summer and spring were found with higher abundances of oviparous-hyperbenthivorous (i.e., species of which embryos depend solely on the yolk-sac reserves, developing inside encapsulated eggs that were deployed in the environment) and lecithotrophic-infauna consumers (i.e., species of which embryos also feed mainly on the yolk-sac reserves, but develop inside the mother uterus and, in later life' stages, feed on benthic invertebrates which live in the sediment) in the former season.

Similar trends were exhibited by the species (**Table 5**). For example, the relative abundance of *A. castelnaui* changed seasonally, with higher values in the summer, the same trend seen for its group (i.e., oviparous-hyperbenthivorous). Increases in *A. cyclophora* as well as in the most representative species of lecithotrophic-infauna consumers, *Z. brevirostris*, were related to temperature decrease and, particularly for some skates, salinity had an inverse effect (e.g., *P. extenta*). Spatial variations were mainly explained by depth and differences among buffers. For the oviparous-hyperbenthivorous group, the number of specimens were higher at farther buffers and increased with depth (**Table 4**). Overall, the relative abundance of this group, and specifically of *A. castelnaui* (**Table 5**), appear to be lower in shallow regions. However, none of the skates varied in relative abundance among buffers and only *R. agassizii* showed significant differences with CaCO_3 content (**Table 5**). Its lower abundance in biogenic than in lithoclastic sediments might reflect the patterns of the functional group, since oceanographic stations with higher CaCO_3 concentrations were found in the vicinity of Alcatrazes island.

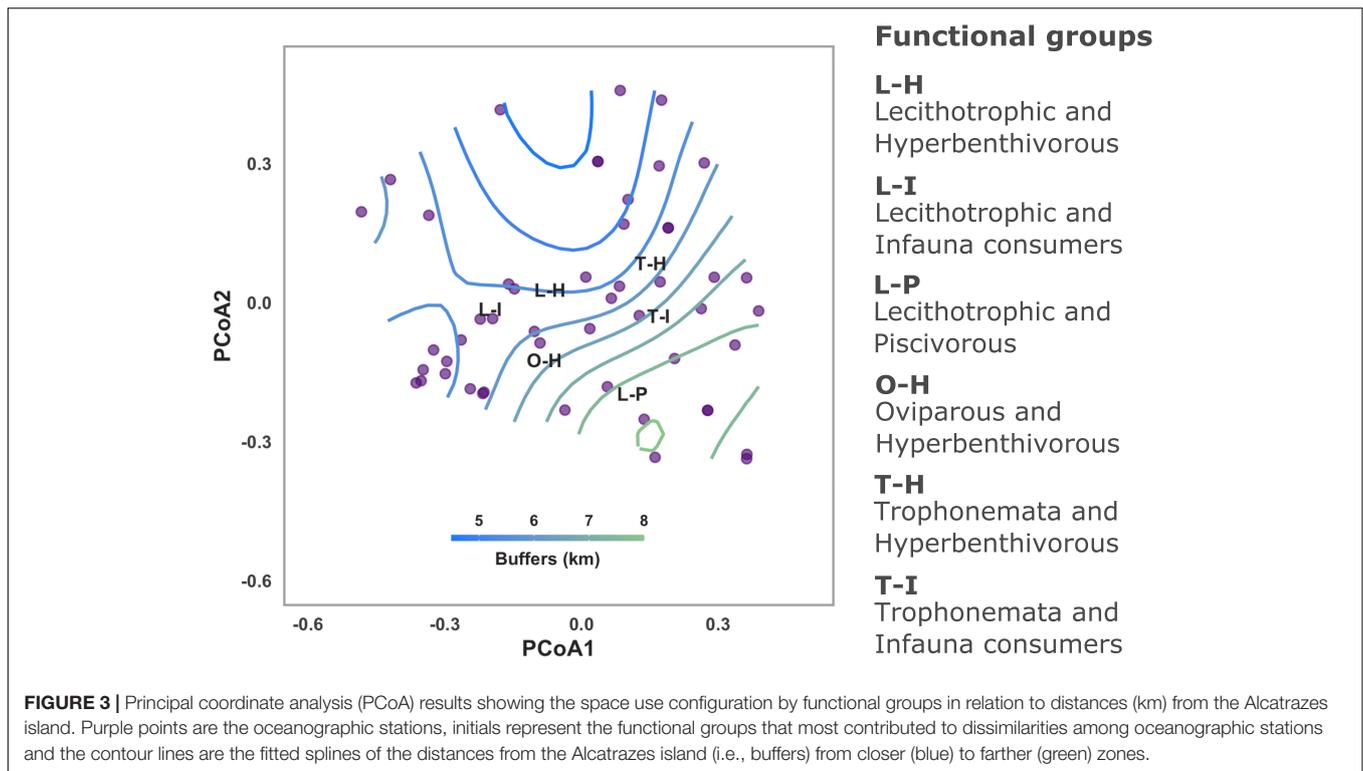
MPA Effectiveness for *Z. brevirostris*

No significant differences in mean lengths of *Z. brevirostris* were identified before and after the WRA MPA establishment when



season was included in the model ($\beta_{before + summer} = 44.89 \pm 1.33$; $\beta_{after + summer} = 45.14 \pm 0.77$, $t = -0.19$, $p = 0.85$). On the other hand, there was a significant effect of seasons, with higher mean TL in summer than in spring (Table 6). The number of specimens of sizes above L_c , meaning they were susceptible to fishery harvest, was 168 (before MPA: $n = 65$, after: $n = 103$) and the small increase in mean length implied a small decrease in the mean F/M for fish larger than L_c estimated by the

Beverton-Holt method although the effect was not significant judging by the overlapping CIs. According to LBSPR, which estimates F/M of fully selected (i.e., large) individuals, assuming a logistic selectivity curve, the mean estimated fishing mortalities increased and CIs of $(F/M)_{LBSPR}$ overlapped, being above the overfishing threshold (>1) (Supplementary Figure 3A). These numbers are not directly comparable because they correspond to fish of different sizes. Nevertheless, large values of either



metric can be taken as evidence of overfishing. The CIs of SPR also overlapped, although the mean increased slightly (current $SPR > 0.4$) (**Supplementary Figure 3B**). According to our simulation, if fishing was completely eliminated, the mean length of guitarfish larger than L_c would be expected to increase after the WRA establishment, reaching the unfished level in approximately 5 or 6 years depending on the assumed selectivity of the fishery (**Supplementary Figure 4**).

DISCUSSION

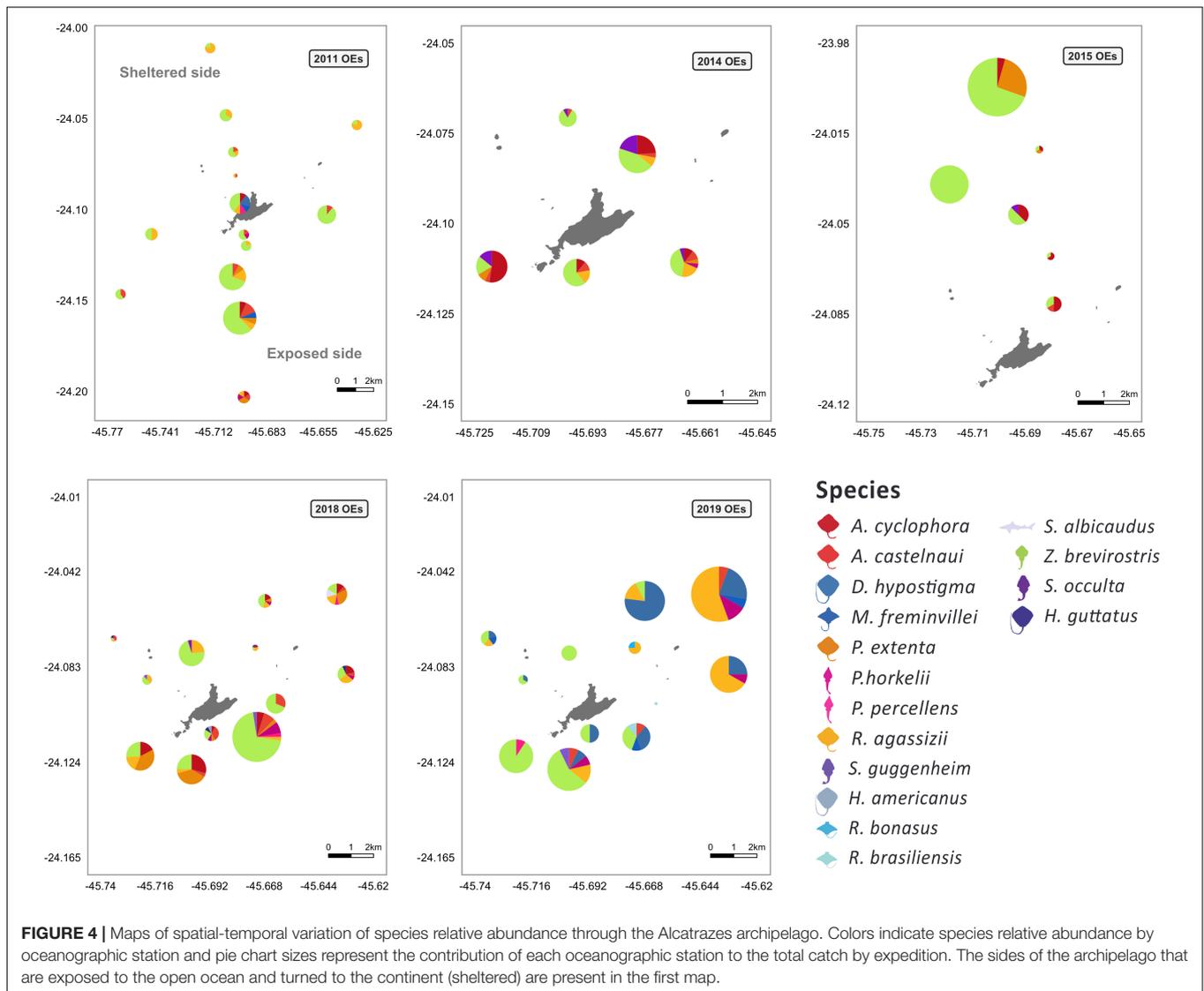
MPA's Functionality

Oceanographic Features Driving the Community Dynamics

Marine communities are usually characterized by a few predominant species that are continuously present and many other species that have relative low abundances and occasional occurrences associated with natural events (Magurran and Henderson, 2003). Our findings showed such patterns with shifts in the Alcatrazes elasmobranch fauna, and consequently in the MPA's functional diversity, being driven by thermohaline and chemical changes in the water column through the seasons. The inshore intrusion of the SACW is known for lowering water temperatures, raising primary production in the euphotic zone, and enriching the bottom by the input of particulate organic matter during spring and summer. Therefore, increases in diversity metrics were likely a response of the enhancement of feeding resources, given that the energy surplus advantages the benthic megafauna, and is also a consequence of the expansion

of the SACW's associated species (Pires-Vanin et al., 1993; Castro-Filho and de Miranda, 1998; Muto et al., 2000). On average, 60% of the species caught are temperate species that are probably related to the water mass (Menni and Stehmann, 2000; Menni et al., 2010). Higher abundances of functional groups in spring and summer (e.g., lecithotrophic-infauna consumers and oviparous-hyperbenthivorous) and their increase with a decrease in temperature, indicate the same association with the SACW. Even though variations could be explained by the input of individuals, the reproductive cycle of such species appears to be synchronized to periods of more suitable conditions. Reported peaks on mating, birth or egg-laying of *A. cyclophora*, *A. castelnaui*, *R. agassizii*, *Z. brevirostris*, the Brazilian guitarfish, *Pseudobatos horkelii* (Müller and Henle, 1841), and *S. occulta*, coincides with the timing of the SACW influence (Lessa et al., 1986; Ponz-Louro, 1995; Oddone and Vooren, 2005; Vooren and Klippel, 2005; Oddone et al., 2007, 2008; Colonello et al., 2011, 2012). This could enable energy recovery by females and access to food by the newborns.

On the other hand, when the SACW retreats to deeper zones (>100 m) in autumn and winter, the Tropical Water mass dominates the middle shelf, increasing the temperature and salinity of the water (Castro-Filho and de Miranda, 1998; Campos et al., 2000). Our results show that under the Tropical Water influence, the community became less diverse although some of the recorded species had never been caught before (e.g., *R. bonasus* and *R. brasiliensis*). The cownose rays are trophonemata species that display reproductive traits of high energetic demand to improve likelihood of offspring success (Rangel et al., 2020). Seasonal migrations to nursery areas



along the coast have been suggested, with parturition from late spring through summer (Rangel et al., 2018). Thus, the recorded specimens might have been caught while foraging for more energetic resources to improve reserves before mating or during gestation (e.g., Rangel et al., 2021). After stronger SACW events, the availability of potential food items, including higher level species of the benthic megafauna, are more abundant on the middle shelf, making Alcatrazes a productive foraging area (Pires-Vanin et al., 1993; De Léo and Pires-Vanin, 2006; Shimabukuro et al., 2016).

Spatially, while the northwest and northeast parts were predominantly characterized by finer grains and poor CaCO_3 content, the south (i.e., part exposed to the open ocean), could be distinguished in two regions: the eastern portion, that is similar to the first two, and the western, with presence of coarse sands and higher CaCO_3 concentrations. According to Takase et al. (2021), this region is highly influenced by energetic waves which explains the sediment configuration by the displacement

of finer grains to the east. Consequently, the heterogeneity of habitats in the exposed part resulted in a more diverse fauna in comparison to the northern area. Higher abundances of oviparous and hyperbenthivorous species at farther offshore and deeper locations might be related to the distribution of preys. For example, organisms of biogenic source such as mollusks, starfishes, and corals, are not part of the *R. agassizii* diet, which like *P. extenta*, feeds significantly on small crustaceans of the benthic macrofauna (Soares et al., 1992; Aguiar and Valentin, 2010; Bornatowski et al., 2014). Moreover, brachyuran and portunid crabs are main preys of *A. castelnaui* and *A. cyclophora*, respectively (Soares et al., 1992, 2008). Thus, great densities of the macrobenthos on the inner and outer shelf (Pires-Vanin, 2008) and presence of such crabs (e.g., *Persephona punctata*, *Libinia spinosa*, *Portunus spinimanus*, and *Callinectes sapidus*), which were found in trawls performed at deeper oceanographic stations, would have attracted the skates to those regions, consistent with our findings. Likewise, spatial differences between angel sharks

TABLE 3 | Best ranked models for the number of individuals of functional groups and species.

Models	k	AICc	Δ AICc	Wi
Lecithotrophic and Infauna consumers				
Seas + Temp	5	271.27	0	0.49
Temp	3	273.02	1.75	0.21
Oviparous and Hyperbenthivorous				
Seas + Temp + Buffers	9	243.78	0	0.29
Seas + Dep + Buffers	9	243.81	0.03	0.28
Seas + Temp	5	244.50	0.72	0.20
Seas	4	245.48	1.70	0.12
Trophonemata and Hyperbenthivorous				
Temp	3	95.92	0	0.62
Atlantoraja cyclophora				
Temp + Sal	4	121.89	0	0.62
Atlantoraja castelnaui*				
Seas + Dep + CaCO ₃	5	104.18	0	0.36
Seas + Dep	4	104.22	0.04	0.36
Seas + CaCO ₃	4	106.05	1.87	0.14
Rioraja agassizii				
CaCO ₃	3	177.14	0	0.61
Seas + CaCO ₃	5	178.66	1.52	0.28
Psammobatis extenta				
Sal + Dep	4	106.09	0	0.30
Sal	3	106.17	0.08	0.29
Sal + CaCO ₃	4	107.47	1.38	0.15
Zapteryx brevirostris				
Seas + Temp	5	269.24	0	0.46
Seas + Temp + CaCO ₃	6	270.71	1.47	0.22

Log of swept area was included as an offset in all models. Notations: k (number of parameters estimated), AICc (Akaike's second-order information criterion), Δ AICc (AICc - AICcmin), Wi (Akaike weight), seasons (Seas), bottom water temperature (Temp), bottom water salinity (Sal), depth (Dep), distance from the Alcatrazes island (Buffers) and CaCO₃ classes (CaCO₃).

*Poisson GLMs were fitted for *A. castelnaui*.

were probably related to the resource distribution. Abundance of infauna invertebrates (e.g., polychaetas), may be higher in the northwest part due to sediment composition and higher levels of organic matter (Hoff et al., 2015). Thus, whereas *S. guggenheim* are strictly piscivorous, eating demersal, and pelagic species (Vögler et al., 2003), the *S. occulta* diet, which consists of polychaetas and nematodes, relies on configurations of benthic habitats (Aguilar and Valentin, 2010; Domingos et al., 2021).

Groupings of mature males (i.e., calcified clasper) of *R. agassizii* and *Z. brevirostris*, in different parts of the archipelago, suggest formation of shoals for reproductive purposes (Paijmans et al., 2019). Although specific evidence of females' maturity stage has not been assessed, the majority of recorded specimens in 2019 were bigger than the published size of first maturity (Supplementary Table 1). Those results support the reproductive cycle defined by Oddone et al. (2007) and Colonello et al. (2011). Nevertheless, it is possible that the lesser guitarfishes of tropical waters perform two mating periods, since mature males were also recorded during summer oceanographic expeditions. Colonello et al. (2011) previously

TABLE 4 | Estimated parameters of variables from the best models that explain the number of individuals of functional groups.

Variables	β	SE	Z-value	P-value
Lecithotrophic and Infauna consumers				
Intercept	-7.07	0.20	34.92	<0.01
Temp	-0.28	0.13	2.21	0.03
Spring	-0.63	0.25	2.43	0.02
Winter	0.46	0.59	0.77	0.44
Oviparous and Hyperbenthivorous				
Intercept	-7.34	0.42	17.32	<0.01
Temp	-0.25	0.11	2.17	0.03
Buffer 5 km	0.64	0.34	1.86	0.06
Buffer 7.5 km	0.97	0.39	2.40	0.02
Buffer 10 km	1.23	0.41	2.90	<0.01
Buffer 12.5 km	1.51	0.51	2.91	<0.01
Spring	-1.11	0.28	3.90	<0.01
Winter	-0.64	0.66	0.96	0.34
Dep	0.05	0.02	2.61	<0.01
Trophonematas and Hyperbenthivorous*				
Intercept	-9.84	0.35	-28.16	<0.01
Temp	0.57	0.13	4.26	<0.01

Parameters with significant P-value (<0.05) were highlighted. Notations: estimated coefficients (β), standard error (SE), Z test (Z-value) and significance in Z test (P-value).

*Except for Trophonematas and Hyperbenthivorous parameters of other groups were weighted by the Akaike weight (Wi) of the best models in which variables were present.

highlighted the asynchrony of reproductive females when comparing populations from temperate regions and the northern São Paulo coast (Ponz-Louro, 1995). Catches of *D. hypostigma* and *M. freminvillei* at the same oceanographic stations may indicate formation of mixed-species shoals. Despite the fact that both species are hyperbenthivorous and the diet overlap could increase species competition, interspecific associations may also increase foraging efficiency (Paijmans et al., 2019). Stingrays perform foraging traits which expose the benthic fauna (Freitas et al., 2019), facilitating prey catchability.

Community Structure and Use of the MPA

Overall, dissimilarities regarding the population structures from other Brazilian regions may be related to geographical features, sexual segregation, and ontogenetic changes in habitat use (Schlaff et al., 2014). Despite the substantial presence of adults, most of them were individuals just over the reference size of first maturity. In almost all species, juveniles were present, but only *A. castelnaui* and *A. cyclophora* were dominated by them, which will be discussed later. The sex ratio favoring females was similar to what was found with populations of *A. castelnaui*, from the northern coast of São Paulo (Ponz-Louro, 1995) and of *R. agassizii*, along the southeastern Brazil (Oddone and Amorim, 2007). In contrast, the sex ratio of the northern state population of *P. extenta* did not deviate from 1 (Martins et al., 2005) which was not consistent with our findings of a female dominated sex ratio. Furthermore, Martins et al. (2005) found variations in habitat use through the species' life span. This does not seem to be our case as young juveniles, older juveniles, and adults were

TABLE 5 | Estimated parameters of variables from the best models that explain the number of individuals of elasmobranch species.

Variables	β	SE	Z-value	P-value
<i>Atlantoraja cyclophora</i>*				
Intercept	-9.95	0.41	-24.18	<0.01
Temp	-0.68	0.18	-3.88	<0.01
Sal	-3.16	0.90	-3.52	<0.01
<i>Atlantoraja castelnaui</i>				
Intercept	-8.85	0.27	31.79	<0.01
Spring	-0.82	0.37	2.19	0.03
Winter	-1.54	0.62	2.43	0.02
Dep	0.07	0.03	2.36	0.02
Bio sed	0.72	0.41	1.71	0.09
<i>Rioraja agassizii</i>				
Intercept	-8.00	0.26	30.24	<0.01
Bio sed	-1.01	0.45	2.20	0.03
Spring	-0.70	0.40	1.70	0.09
Winter	-0.08	0.43	0.17	0.86
<i>Psammobatis extenta</i>				
Intercept	-9.74	0.49	19.51	<0.01
Sal	-3.79	1.33	2.79	<0.01
Dep	0.09	0.06	1.61	0.11
Bio sed	0.84	0.85	0.96	0.34
<i>Zapteryx brevirostris</i>				
Intercept	-7.14	0.25	28.20	<0.01
Temp	-0.28	0.14	2.01	<0.05
Spring	-0.52	0.28	1.81	0.07
Winter	0.28	0.66	0.41	0.68
Bio sed	0.29	0.27	1.03	0.30

Parameters with significant P-value (< 0.05) were highlighted. Notations: estimated coefficients (β), standard error (SE), Z test (Z-value), significance in Z test (P-value) and class of sediment composed by biogenic sources (Bio sed).

*Except for *A. cyclophora* parameters of other groups were weighted by the Akaike weight (W_i) of the best models in which variables were present.

TABLE 6 | Effects of the Wildlife Refuge of Alcatrazes (WRA) establishment and seasons in mean total length (TL) of *Zapteryx brevirostris*.

Variables	β	SE	t-value	P-value
After WRA + Summer	45.14	0.77	58.75	<0.01
Before WRA	-0.25	1.33	-0.19	0.85
Spring	-3.28	1.31	-2.49	0.01
Winter	1.95	1.45	1.34	0.18

Parameters with significant P-value (<0.05) were highlighted. Summer was the only season in which specimens of *Z. brevirostris* were caught before and after the MPA establishment.

found in Alcatrazes. No significant deviations from 1 were found for *A. cyclophora* in southern and southeastern Brazil (Oddone and Vooren, 2004; Oddone and Amorim, 2007). The evaluated specimens of both studies came from different, and even deeper regions (over 100 m), inside of a wider area, which might have caused those disparities. For *Z. brevirostris* and *D. hypostigma*, our results exhibited equal rates between sexes, which agreed with results of the northern guitarfishes evaluated by Ponz-Louro (1995). But, for the last one, no information about population

structure was found, pointing out the necessity of efforts to broaden our understanding of the species.

Based on the structure results, evidence of reproductive availability and patterns found in the literature, we propose uses of the MPAs by each elasmobranch although further research regarding species movement ecology is essential to strengthen these conclusions (Supplementary Table 5). Like other insular regions in Brazil (Wetherbee et al., 2007; Aguiar et al., 2009), Alcatrazes is a nursery area specifically used for development by many species. Early life stages, such as neonates, young of the year and/or juveniles were found, supporting this hypothesis. Juveniles of angel sharks and stingrays (genus *Hypanus*) were found at deeper regions, whereas records of smaller specimens (e.g., *Hypanus americanus* (Hildebrand and Schroeder, 1928) and *S. albicaudus*), indicate that younger animals may use sheltered habitats (Aguiar et al., 2009; Farrugia et al., 2011), such as the shallow zones closer to rock formations and low energetic parts in the northeast. However, for two skates, *A. castelnaui* and *A. cyclophora*, the area works not only as nursery, but also as mating place, as indicated by the lower frequencies of adults and seasonal records of mature males. The possibility that records of mature specimens of the other species may have been related to migratory behavior hampers the definition that the area was used only for reproduction by them. Thus, as proposed for cownose rays, which are species of large home ranges and exhibit key areas for population maintenance along the coast (Collins et al., 2007; Rangel et al., 2018), we suppose that the MPAs may be a seasonal feeding ground for *M. freminvillei* and *D. hypostigma*.

Connection between the inner and outer shelf may play a critical role in the species' reproductive success, especially for *P. horkelii* and the chola guitarfish, *Pseudobatos percellens* (Walbaum, 1792). Seasonal migrations of *P. horkelii*, from deeper regions (>100 m) to give birth and mate in coastal zones, is well described by Lessa et al. (1986). This might have been the case of the adult females of both species that were caught in spring and summer. Even though movements of great distances were not reported for *P. percellens*, embryonic diapause, which is a reproductive trait associated with the migratory behavior of *P. horkelii*, was proposed for the former species (Rocha and Gadig, 2013). This may suggest that *P. percellens* also displays such behavior, being consistent with the absence of neonates in our records. Finally, for *R. agassizii*, *P. extenta*, and *Z. brevirostris*, all length classes were collected, indicating their resident status. Nevertheless, their presence may be intermittent, particularly for the skates that were absent in some oceanographic expeditions. According to Martins et al. (2005), abundance fluctuations of *P. extenta* was observed in the northern coast, being higher in periods when the species were not recorded in Alcatrazes (e.g., 2009' expedition).

WRA Effectiveness for *Z. brevirostris* and Further Challenges to Conservation of the Species

Magnitude differences between the methods and uncertainties in fisheries indicators for *Z. brevirostris* may be caused in part by the small sample size, requiring larger datasets to

obtain more precise and accurate results, especially for the LBSPR method. Despite the fact that our results did not find a significant positive effect of the WRA establishment, the decrease in mean $F/M_{(ML)}$ and increase in mean SPR may suggest some improvements in fisheries indicators. Our calculation of the expected time to show an improvement in mean length after MPA establishment suggests that under several possible selectivity patterns in the fishery, the WRA effect could be detectable within a few years of the MPA formation. However, further monitoring is needed to estimate the trends of the Alcatrazes population. The WRA is a novel MPA, for which the management plan was defined in 2017 (ICMBio, 2017), starting its initiatives 1 year before our last sampling campaign. Thus, our short-term evaluation and inconsistent sampling among seasons, might be the reason to the small changes we got in the mean length between periods. Furthermore, *Z. brevirostris* is a relative long-lived species that exhibits late maturity and low intrinsic rate of population growth (Caltabellotta, 2014; D'Alberto et al., 2019), which would increase the estimated times of recovery relative to more short lived species.

As previously mentioned, parts of the archipelago have been being protected by TES and even before its creation, by the Brazilian Navy, which used to perform tactical exercises, forbidding navigation in the surroundings (Hoff et al., 2015). At that time, the demersal fish community was represented by predominance of sole fishes (e.g., *Syacium micrurum*, *S. papillosum*, *Citharichthys macrops*, and *Symphurus jenynsi*) and poor diversity of elasmobranchs, with *Z. brevirostris* as the only one in the records (Paiva-Filho et al., 1989). Nowadays, the archipelago shows a well-structured community, with presence of higher-level predators (Rolim et al., 2019) and the apparent improvement of the *Z. brevirostris* population, since the great number of recorded specimens is comparable to other studies that were performed in wider areas along the coast (e.g., Marion et al., 2011; Caltabellotta et al., 2019). In this sense, our results provide a useful baseline for further evaluations of causal effects regarding the WRA. Some studies have pointed out the importance of tracking changes in ecological indicators of a MPA throughout time (Edgar et al., 2004, 2011) and between a control site (Villaseñor-Derbez et al., 2018). However, the historical safeguarding of the archipelago, the influence of physical processes (Castro-Filho et al., 1987), the higher complexity of ecological interactions (Rolim et al., 2019) and its great distance from coastal as well as other insular regions, increase the potential sources of variability (Edgar et al., 2014), making difficult the designation of control areas or comparisons with other MPAs.

The relevance of the MPAs for the local ichthyofauna is clear, especially the WRA, which broadened the protection, encompassing the Alcatrazes island and consequently, the essential habitats for elasmobranchs. Furthermore, both areas seem to play pivotal roles for endangered species, as more than 75% of the recorded elasmobranchs are in threatened categories (IUCN, 2021). Both MPAs together encompass an area of approximately 70,000 ha (ICMBio, 2017) which would

cover the home ranges of the caught species (see Section "Abiotic Data"). Nevertheless, ontogenetic differences in their requirements may not be provided, so that for some species the archipelago was used only at specific life stages (i.e., non-resident species). Such differences imply movements to specific habitats outside the MPAs boundaries, raising the threats over the species and consequently affecting the efficiency of the protected areas. Chapman et al. (2005) discovered that the lack of connectivity among adjacent habitats was exposing reef and nursery sharks to the fisheries, demanding additional management measures for species conservation, and some Alcatrazes species may experience similar threats.

Similarly, the intense anthropogenic pressure in the surrounding area may compromise such functionality and thus, the effectiveness of TES and WRA. Alcatrazes is placed between two disturbed areas on the São Paulo coast. To southwest, the Santos Port is the largest port in Latin America and the most important industrial hub in Brazil (Luiz-Silva et al., 2002), producing great concentrations of mercury and plastic pellets, that reach adjacent (e.g., Santos Bay) (Siqueira et al., 2005; Ribeiro, 2020) and even farther regions, such as the archipelago. To northwest and closer to Alcatrazes, the São Sebastião Port will be expanded over the Araçá Bay (Angelini et al., 2018), an important nursery place (Contente et al., 2020). Besides the local impacts, its expansion could also affect the vicinities, disturbing the fauna by the carriage of pollutants and increase in underwater noise (Slabbekoorn et al., 2010; Barletta et al., 2016).

In addition, despite fishery activities being concentrated on the inner and middle shelf (Imoto et al., 2016), including inside the less restrictive protected areas (Carneiro et al., 2013), exploration of deeper zones has been increasing in the past decades (Pincinato and Gasalla, 2019). According to Imoto et al. (2016), great amounts of demersal catches were obtained by industrial fleets in those regions, raising the threat over species that use the archipelago seasonally for feeding or for mating, while also using the surrounding fished area. Currently, fishing of threatened elasmobranchs is forbidden or only allowed for subsistence in Brazilian waters (i.e., species classified as VU) (MMA, 2014). Nevertheless, they are still caught as bycatch by fleets that are known to directly impact the demersal fauna, such as gillnets, and otter, double-ring, and pair trawlers. Those activities are controlled in the surroundings of TES and WRA by the management plans of other two protected areas (i.e., Marine Environment Protection Area of the North and Central Coast – APA Norte and APA Centro) (Forestry Foundation, 2019, 2020) and different legislations of federal and state level. Inside the APAs, input measures, such as the restriction of industrial (APA Centro) and even traditional (APA Norte) pair trawlers until the 23.6 m isobath as well as the specification of day periods to operation of beach seines (São Paulo, 2009, 2012), are applied. Nevertheless, the fishing zonation become less restrictive as distance from the coast increases and despite seasonal closures of catfish and shrimp fishing occur from January to March (SUDEPE, 1984) and March to May (IBAMA, 2008), respectively, gillnets remain allowed (IBAMA, 2007).

Thus, based upon the MPAs use by elasmobranchs and the potential connectivity with other protected areas, we recommend that besides the creation/expansion of marine reserves, fishing control measures should be implemented. Temporal closures in winter as well as extension of the pre-existing ones through all summer months, and limitation of effort (Cochrane and Garcia, 2009), could reduce the pressure on species that make reproductive migrations and/or require larger home ranges (e.g., guitarfishes, eagle, and cownoses stingrays). Moreover, economic incentives (i.e., referred to “Seguro Desemprego,” a category of social insurance in Brazil) (Brazil, 2003, 2009, 2015) could be provided to artisanal fishermen during the proposed temporal closures and to those who will not be able to fish or will have to change their techniques due to permanent spatial closures. Last, integrated evaluations of the effectiveness of conservation actions for benthic elasmobranchs and the Alcatrazes ecosystem must consider the associated areas, since they have provide essential services to the ecosystem’s maintenance (Rolim et al., 2019; Contente et al., 2020). If these measures are taken into account, a network with key habitats along the coast (e.g., nursery, reproduction and feeding places) could be developed, assisting the conservation of elasmobranch populations in the southeastern Brazil and consequently, enhancing the WRA and TES efficacy.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the Ethics Committee of Animal Use of the Oceanographic Institute of the University of São Paulo (CEUA IO-USP) and by the Chico Mendes Institute for Biodiversity Conservation (ICMBio) under the survey permit SISBIO/55824.

AUTHOR CONTRIBUTIONS

TK, JD, and EB conceptualized this study. TK, RG, and JD collected abiotic and biotic samples, with PP, identified functional groups. TK and RG performed the sedimentological analyses. TK, EB, and PP performed statistical analyses and results interpretation. TK prepared the original draft. EB, JD, PP, and RG reviewed the manuscript. All authors contributed

to the manuscript elaboration and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.694846/full#supplementary-material>

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