DOI: 10.1111/ifb.14441

REGULAR PAPER



Spatiotemporal variations in density and biomass of rocky reef fish in a biogeographic climatic transition zone: trends over 9 years, inside and outside the only nearshore no-take marine-protected area on the southern Brazilian coast

Antônio B. Anderson^{1,2}

| Jean-Christophe Joyeux² | Sergio R. Floeter¹

¹Marine Macroecology and Biogeography Laboratory, Department of Ecology and Zoology, Federal University of Santa Catarina, Florianópolis, Brazil

²Laboratory of Ichthyology, Department of Oceanography, Federal University of Espírito Santo, Vitória, Brazil

Correspondence

Antônio B. Anderson, Laboratory of Ichthyology, Department of Oceanography, Federal University of Espírito Santo, Vitória, ES 29075-910, Brazil. Email: aabbiologia@gmail.com

Sergio R. Floeter, Marine Macroecology and Biogeography Laboratory, Department of Ecology and Zoology, Federal University of Santa Catarina, Florianópolis, Brazil Email: sergio.floeter@ufsc.br

Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Numbers: SISBIOTA-Mar (CNPq 563276/2010-0; FAPESC 6308/2011-8), CNPq 475367/2006-5; Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina, Grant/Award Number: FAPESC 4302/2010-8; Fundação Estadual de Amparo à Pesquisa do Estado do Espírito Santo, Grant/ Award Number: PROFIX program N° 10/2018 -T.O.: 348/2018; Petrobras, Grant/Award Number: Projeto MAArE - Monitoramento Ambiental do Arvoredo e Entorno

Abstract

Accepted: 18 June 2020

Biogeographical transition zones are important areas to investigate evolutionary ecological questions, but long-term population monitoring is needed to better understand ecological processes that govern population variations in such edge environments. The southernmost Brazilian rocky reefs are the southern limit of distribution for 96% of the tropical ichthyofauna of the western Atlantic. The Arvoredo Marine Biological Reserve is the only nearshore no-take marine-protected area (MPA) located in this transition zone. The main aim was to investigate how the populations of rocky reef fish species vary in density and biomass in space and over time, inside and outside the Arvoredo MPA. This study presents results based on a 9 year (2008-2017) underwater visual census monitoring study to evaluate the density and biomass of key fish species. Variations in density and biomass were detected for most species. Factors and mechanisms that may have influenced spatial variation are habitat structural complexity and protection from fisheries. Temporal variations, otherwise, may have been influenced by species proximity to their distributional limit, in synergy with density-dependent mechanisms and stochastic winter temperature oscillations. The MPAs harbour higher density and biomass for most species. Nonetheless, a prominent temporal decline in the recruitment of Epinephelus marginatus calls into guestion the continuous effectiveness of the MPA.

KEYWORDS

Arc of Capricorn, long-term monitoring, MCMCglmm, southern Atlantic, time series

1 INTRODUCTION

Species and ecosystem distribution globally is driven by ecological variables such as latitude (temperature), altitude (topographic elevation), isolation (islands) and habitat area (Cox, 2001; Ferro and Morrone, 2014; MacArthur and Wilson, 2001; Nelson, 1978; Odum, 1953). Augustin de Candolle founded in 1820 the worldwide system of biogeographic regions based on the distribution of plants.

He defined 20 areas of endemism, claiming that each was characterized by plant species, whose distribution was limited by natural barriers such as oceans, deserts and temperature or by interspecific competition (de Candolle, 1820). The conceptual ecological framework for the study of the intersections among the biogeographic areas suggested by de Candolle was given by Odum in 1953. According to Odum (1953), "An ecotone is a transition between two or more communities; it is a junction zone or tension belt which may

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have considerable linear extent but is narrower than the adjoining community areas themselves."

Biogeographical transition zones (ecotones) have been a matter of controversy among scientists since the advent of the "Wallace line" (Ferro and Morrone, 2014; Wallace, 1860). Then, naturalists and scientist realized that biotas intergrade into one another as zones rather than merely lines on a map (Ferro and Morrone, 2014; Huxley, 1868; Mayr, 1944; Wallace, 1860). In the 20th century, this subject was still treated superficially by biogeographers (Darlington, 1957; Ferro and Morrone, 2014). For instance, Pielou (1992) stated that transition zones tend to present impoverished biotas because few elements from each region are found in the transition. Other studies, on the contrary, revealed that transition zones can be exceptionally speciesrich: the Mexican transition zone (Ferro and Morrone, 2014; Morrone. 2010). the south-eastern Australian coast (Malcolm et al., 2010), the southern African coast and the Bermuda archipelago (the northernmost tropical outpost in the western Atlantic) (Briggs and Bowen, 2013). Therefore, it has become a consensus among biogeographers and ecologists to consider transition zones as valuable tools to investigate evolutionary and ecological principles at spatial and temporal scales (Ferro and Morrone, 2014).

Southern Brazilian rocky reefs are the limit of distribution for 96% of tropical reef fishes which inhabit the tropical portion of the Brazilian coast (Anderson *et al.*, 2015). This peculiar region, a transitional climatic zone influenced by both warm tropical waters from the Brazil Current and cool waters from the South Atlantic Central Water, is regarded as the "Arc of Capricorn" (Anderson *et al.*, 2015). Recently, considerable effort has been made (Anderson *et al.*, 2015, 2017, 2019; Begossi *et al.*, 2012; Hackradt *et al.*, 2011), but most works have left a severe gap in regard to the temporal variations in marine populations. Moreover, the mechanisms responsible for temporal variation in reef fish density and biomass remain a matter of controversy and debate (Choat *et al.*, 1988; Doherty, 2002).

Strict or no-take marine-protected areas (MPAs) are regarded worldwide as an important tool to protect marine life biodiversity (Chung *et al.*, 2017; Mellin *et al.*, 2016). Effectively managed no-take MPAs reduce the impacts of overfishing, allowing the restoration of fish stocks and also promoting the "spillover effect" (Anderson *et al.*, 2014; Chung *et al.*, 2017). The spillover effect occurs when fish density per unit area inside the MPA exceeds the maximum carrying capacity, leading to the migration of fish towards adjacent areas (Chung *et al.*, 2017; Di Lorenzo *et al.*, 2016).

The Arvoredo Marine Biological Reserve (MBR) is a nearshore notake MPA located in the Arc of Capricorn biogeographic climatic ecotone (Anderson *et al.*, 2015). It is the only no-take MPA located between two biogeographic marine ecoregions: the tropical southwestern Atlantic (northern Brazilian coast) and warm temperate southwestern Atlantic (southern Brazilian coast to Uruguay and northern Argentina) (Horta et al., 2001; Spalding et al., 2007).

To understand the dynamics of rocky reef fish populations on the southern Brazilian coast, a long-term monitoring programme was created in 2006 to determine the variation in biomass and density of marine fish associated to rocky reefs inside and outside Arvoredo MPA. After 9 years of gathering data, answers to the following questions started to emerge: (a) Do rocky reef fish species populations present fluctuations (variations) in density or biomass in space and time? (b) Do trophic groups show different population signatures related to the impact of fisheries (*i.e.*, areas protected against fisheries vs. unprotected areas) in time? (c) Does recruitment vary in space and over time? (d) How is the size spectrum near the climatic threshold of a species distribution?

2 | MATERIALS AND METHODS

2.1 | Study area

The southern Brazilian rocky reef geomorphology is characterized, in its major portion, by steep granitic rocky reefs ending in sandy bottoms usually starting from 12 to 15 m in depth (Anderson *et al.*, 2014, 2015). These rocky reefs are regarded as the southernmost limit of distribution of tropical reef fish species that inhabit the tropical northern portion of the Brazilian coast (Anderson *et al.*, 2015; Floeter *et al.*, 2008).

The MPA in the Arvoredo marine reserve, established in 1990 and encompassing 17,800 ha, is the only nearshore, no-take and noentry Brazilian MPA (Anderson et al., 2014) totally closed to fishing, harvesting and human presence except for scientific research (Anderson *et al.*, 2014, 2015, 2019). The MPA encompasses three islands: Arvoredo (only the north portion of the major island), Deserta and Galé. Fishing, harvesting and human presence are strictly forbidden by law. It is also the only nearshore MPA in the south-southeast coast of Brazil, protecting fragments of the Atlantic rainforest and marine biodiversity (Anderson *et al.*, 2015; Hostim-Silva *et al.*, 2006).

The study was conducted on subtropical islands on the north and east sides of Florianópolis Island (27° 35′ 41.08″ S, 48° 32′ 38.96″ W), Santa Catarina State, southern Brazil, inside and outside Arvoredo MPA. The subtropical islands (sites) were selected based on the amount of data [underwater visual censuses (UVCs)] available since 2008 (≥20 samples per year per site) (Figure 1), Arvoredo Island and Xavier Island outside the MPA and Galé Island and Deserta Island inside the MPA (Figure 1).

Its ecological, oceanographic and geographic peculiarities qualify Arvoredo as one of the most important MPAs of the SW Atlantic and as a potential natural laboratory for climate change studies using species, populations and community variations as models (Anderson *et al.*, 2015; McLeod *et al.*, 2009).

2.2 | Density and biomass calculations

UVCs through scuba diving, based on 20×2 m (40 m²) strip transects, were used to record fish species during mornings in austral summers (*i.e.*, from December to March) (Floeter *et al.*, 2007) in the shallow parts (5–14 m deep) of the reefs. The procedure required a diver swimming 1 m above the substratum while unrolling a measuring tape and recording all species and binning total lengths into 5 cm categories (Floeter *et al.*, 2007).



FIGURE 1 (a) Map of studied sites. Santa Catarina State is represented in green. The dashed dark-green polygon represents the Arvoredo Marine Biological Reserve [marine-protected area (MPA): no-take zone (MPA)], circles with numbers represent sampled sites (islands). (b) Interpolated map of temperature with occurrence frequencies (%FO) < 16°C, during the austral winters (from June to August). Green circles show the sites where temperature sensors were deployed. (c) Enlarged view of the MPA

The present work is based on 9 years of UVCs conducted by the authors and access to the database of the Marine Macroecology and Biogeography Laboratory. In total, over 1000 UVCs from 2008 to 2017 were conducted, and then a cut-off of 20 UVCs per site per year was selected for analyses. The cut-off of 20 UVCs in space and time has been adopted considering the smallest number of replicates (UVCs) per site per year available in the database. In such cases, all replicates (UVCs) were used. Considering sites with a higher number of replicates, the UVCs conducted by more-experienced divers were sorted out, and then 20 UVCs were selected randomly. Note that there are no data for 2010.

From over 280 species detected from 2008 to 2017 (see Anderson et al., 2015, and Pinheiro et al., 2018), 16 species accounting for 70% of total biomass recorded in this study, representing all trophic groups and functional redundancy (e.g., representing all roles in the ecosystem functionality), and detected in all ontogenetic stages (e.g., recruits, sub-adults, adults and terminal-phase individuals) were selected as models: Abudefduf saxatilis (Linnaeus, 1758), Anisotremus virginicus (Linnaeus, 1758), Bodianus rufus (Linnaeus, 1758), Chaetodon striatus (Linnaeus, 1758), Chromis limbata (Valenciennes, 1833), Chromis multilineata (Guichenot, 1853), Diplodus argenteus (Valenciennes, 1830), Mycteroperca acutirostris (Valenciennes, 1828), Epinephelus marginatus (Lowe, 1834), Haemulon aurolineatum (Cuvier, 1830), Halichoeres poeyi (Steindachner, 1867), Pomacanthus paru (Bloch, 1787), Sparisoma axillare (Steindachner, 1878), Sparisoma frondosum (Agassiz, 1831), Stegastes fuscus (Cuvier, 1830) and Stegastes variabilis (Castelnau, 1855). The biomass of fishes was accessed using the following equation: $W = a \times TL^{b}$ (published weight-length relationships), where W is the total wet weight in grams, a and b are species-specific parameters of the relationship and TL is the total size in centimetres (Froese and Pauly, 2020).

Species were divided into seven trophic categories following Ferreira *et al.* (2004), Luiz *et al.* (2008) and Anderson *et al.* (2015) (Table 1).

2.3 | Species recruitment over time and populational structure

Among the models, six species presenting the highest density and biomass and higher number of recruits per area unit (40 m²) (*i.e.*, young individuals) (see Supporting Information Appendix S1) were selected to evaluate trends over time in recruitment based on mean density of young individuals and in populational structure based on mean density and biomass of individuals per size class: A. *saxatilis*, A. *virginicus*, *D. argenteus*, H. *aurolineatum*, E. *marginatus* and S. *fuscus*. In most species, small individuals less than 5 cm were categorized as recruits. In the larger species E. *marginatus*, individuals less than 10 cm were recognized as recruits. The same sampling method was applied to record small young individuals (recruits) (UVC: 20×2 m strip transects = 40 m^2).

2.4 | Data collection of topographic variables and temperature data

Underwater visual census (30×4 m strip transects = 120 m^2) was conducted to explore the topographic patterns of the sites (Anderson *et al.*, 2019). Eighteen transects were executed, totalling 2160 m² for

TABLE 1 Selected reef fish species arranged into seven trophic groups according to their feeding habits

Feeding habits	Trophic group	Code
Feeds on turfs, endolithic, and epilithic primary producers	Herbivores	HERB
Feeds on turfs, endolithic, and epilithic primary producers	Herbivores	HERB
Feeds on macroinvertebrates and fishes	Macrocarnivores	MCAR
Feeds on macroinvertebrates and fishes	Macrocarnivores	MCAR
Feeds on benthic mobile invertebrates such as mollusks, crustaceans and worms associated with hard or nearby unconsolidated substrate	Mobile invertebrate feeders	MINV
Feeds on benthic mobile invertebrates such as mollusks, crustaceans and worms associated with hard or nearby unconsolidated substrate	Mobile invertebrate feeders	MINV
Feeds on a variety of resources such as invertebrates, algae, and zooplankton	Omnivores	OMNI
Feeds on a variety of resources such as invertebrates and algae	Omnivores	OMNI
Feeds primarily on zooplankton	Planktivores	PLANK
Feeds primarily on zooplankton	Planktivores	PLANK
Feeds on sessile benthic invertebrates such as cnidarians, bryozoans, ascidians and sponges	Sessile invertebrate feeders	SINV
Feeds on algae, sponges, and ascidians	Sessile invertebrate feeders	SINV
Feeds on turfs and detritus	Territorial herbivores	THER
Feeds on turfs and detritus	Territorial herbivores	THER
	Feeding habitsFeeds on turfs, endolithic, and epilithic primary producersFeeds on turfs, endolithic, and epilithic primary producersFeeds on macroinvertebrates and fishesFeeds on macroinvertebrates and fishesFeeds on benthic mobile invertebrates such as mollusks, crustaceans and worms associated with hard or nearby unconsolidated substrateFeeds on benthic mobile invertebrates such as mollusks, crustaceans and worms associated with hard or nearby unconsolidated substrateFeeds on benthic mobile invertebrates such as mollusks, crustaceans and worms associated with hard or nearby unconsolidated substrateFeeds on a variety of resources such as invertebrates, algae, and zooplanktonFeeds on a variety of resources such as invertebrates and algaeFeeds primarily on zooplanktonFeeds on sessile benthic invertebrates such as cnidarians, bryozoans, ascidians and spongesFeeds on algae, sponges, and ascidiansFeeds on turfs and detritusFeeds on turfs and detritus	Feeding habitsTrophic groupFeeds on turfs, endolithic, and epilithic primary producersHerbivoresFeeds on turfs, endolithic, and epilithic primary producersHerbivoresFeeds on macroinvertebrates and fishesMacrocarnivoresFeeds on macroinvertebrates and fishesMacrocarnivoresFeeds on benthic mobile invertebrates such as mollusks, crustaceans and worms associated with hard or nearby unconsolidated substrateMobile invertebrate feedersFeeds on benthic mobile invertebrates such as mollusks, crustaceans and worms associated with hard or nearby unconsolidated substrateMobile invertebrate feedersFeeds on a variety of resources such as invertebrates, algae, and zooplanktonOmnivoresFeeds primarily on zooplanktonPlanktivoresFeeds on sessile benthic invertebrates such as cruidarians, bryozoans, ascidians and spongesSessile invertebrate feedersFeeds on turfs and detritusCervitorial herbivores

each site. The diver recorded environmental data every 5 m, totalling six environmental data sets per 30 m transect. Environmental variables included (a) complexity: number of small [radius (*r*) < 10 cm], medium (*r* = 10–50 cm) and large (*r* > 50 cm) rocks; (b) shelter availability: number of small [opening (*o*) < 10 cm]], medium (*o* = 10–50 cm) and large (*o*) > 50 cm holes; and (c) slope of the rocky reef: inclination of the reef using a plastic protractor (Anderson *et al.*, 2019). All samples were collected in the same sites and sampled areas as the UVCs conducted to evaluate rocky reef fish species densities and biomass.

Temperature data were collected using data loggers (HOBO Data Logger UA-002) deployed on the rocky reefs by divers during sampling expeditions in January 2013 and removed in January 2016, totalling 3 years of sampled temperature data (Faria-Junior & Lindner, 2019; Sarti & Segal, 2018). Each data logger was fixed on the bottom with epoxy resin. Fourteen data loggers were deployed: seven on the "shallow" (slope) stratum and seven on the "intermediate" (interface) (Figure 1).

El Niño and La Niña southern oscillations (ENSO) data were downloaded from the National Oceanic Atmospheric Administration (NOAA), Southern Oscillation Index, site available online (www.ncdc. noaa.gov/teleconnections/enso/indicators/soi). Data from 2008 to 2017 were extracted from NOAA's time series and then converted into a factor with five levels: WE (weak El Niño), ME (moderate El Niño), VSE (very strong El Niño), WL (weak La Niña) and ML (moderate La Niña) (see Supporting Information Appendix S3 for cut-off values).

2.5 | Data analyses

2.5.1 | Key species spatiotemporal variations

Count data are assumed to follow the Poisson distribution. Despite the fact that generalized linear mixed models furnish a versatile framework for modelling a wide range of data (Hadfield, 2010), for non-Gaussian response variables, the likelihood cannot be obtained in a closed form (Hadfield, 2010). In a Bayesian approach, the posterior distribution of the model can be interpreted as a relevant measure for the model evidence based on observed data (Hadfield, 2010). Therefore, Bayesian generalized mixed models (MCMCglmm) were chosen to analyse trends in reef fish species abundance and biomass based on their analytical efficiency in approximating posterior marginal probabilities, in comparison to conventional glmm approaches (Bisanzio *et al.*, 2011; Hadfield, 2010; Rue and Martino, 2007).

The efficiency of the models was evaluated using the deviance information criterion (Bisanzio *et al.*, 2011; Hadfield, 2010; Spiegelhalter *et al.*, 2003). To specify a Gaussian error structure in the models, density and biomass data were log₁₀ transformed. Diffuse priors were used; burn-in was set to 10,000 MCMC iterations followed by 100,000 iterations to sample posterior distributions with a thinning interval of 100 iterations (Chapman, 2013; Hadfield, 2010). For all models, spatiotemporal variations in density/biomass for species, trophic groups, recruits and population size structure were used as dependent variables; time (years), sites nested within zone (no-take and non-protected) and ENSO strength (WE, ME, VSE, WL, ML) were used as fixed effects; and site was used as a random effect once the censuses were performed haphazardly in each of the sampled sites. The R package MCMCglmm (Hadfield, 2010) was used to perform all MCMCglmm analyses.

2.5.2 | Key species spatial distribution patterns and abiotic affinities

To explore and highlight tendencies and patterns of species distribution and habitat use, redundancy analysis (RDA) was applied on

species "Hellinger" transformed biomass data (Clarke and Warwick, 1994; Legendre and Gallagher, 2001). This technique summarizes the linear relationships between components of response variables and a set of explanatory variables (Legendre and Legendre, 2012; Ter Braak, 1994). RDA extends multiple linear regression (MLR) by allowing regression of multiple response variables on multiple explanatory variables (Van Den Wollenberg, 1977). A matrix of the fitted values of all response variables generated through MLR is then subjected to a PCA (Legendre and Legendre, 2012; Ter Braak, 1994). This ordination statistical method is considered more accurate for small biogeographical gradients (Anderson et al., 2019; García-Charton et al., 2004; Legendre and Legendre, 2012; Ter Braak, 1994). RDA was carried out using the R package Vegan (Oksanen et al., 2007). Variance inflation factor (VIF) was also calculated to test the redundancy of environmental variables in the analysis. A large VIF implies that the variable is redundant with other variables in the data set (Oksanen et al., 2007). Statistical analyses were performed using the computing environment R (R Development Core Team. 2019).

3 | RESULTS

3.1 | Species and trophic groups' spatiotemporal variations

All 16 models, except *H. poeyi*, and most trophic groups presented significant spatial and temporal variations in density and biomass (Table 2; Figures 2 and 3). Total density presented significant spatiotemporal variation (Table 2, Supporting Information Appendix S5). Total biomass also presented significant variation in space and time, with higher biomass inside the no-take zone (Table 2, Supporting Information Appendix S5). The six species selected to evaluate trends in recruitment and in populational structure (*A. saxatilis, A. virginicus, D. argenteus, H. aurolineatum, E. marginatus* and *S. fuscus*) were dominant in terms of density and biomass (see Supporting Information Appendix S1 for density and biomass values).

3.2 | Species population structure and recruitment variations

The population structure of the six dominant species varied significantly, except for A. *saxatilis* (Table 2, see Supporting Information Appendix S2 for pMCMC values). Most species varied significantly in mean density of early-stage individuals except for A. *saxatilis* that did not show significant variations over time (Figure 4).

3.3 | El Niño and La Niña southern oscillations

From 2008 to 2017 the ENSO temperature oscillation varied in intensity, except in 2013 when it was similar to that in 2012 (Table 2, DURNAL OF **FISH** BIOLOGY

Supporting Information Appendix S3). Species density and biomass, trophic groups, recruitment and population structure did not show ENSO-correlated variation for any of the five levels (see Table 2 and Supporting Information Appendix S2 for pMCMC values).

4 | DISCUSSION

4.1 | Spatiotemporal trends in variation of key species

Some of the key species studied tend to present more homogeneous spatial distribution. This may indicate adaptability to stochastic seasonal temperature oscillations and an affinity to both cooler and warmer waters (e.g., A. saxatilis, D. argenteus and H. aurolineatum) (Figures 1 and 5). Such pattern could indicate a connection with an evolutionary process in which these species adapted more rapidly than the others to temperature oscillations (Donelson et al., 2011). Otherwise, population variation in time could be mainly influenced by densitydependent mechanisms with a decrease dependent upon the postsettlement survival rate of recruits or the predation of sub-adult and adults and with an increase resulting from the removal of predators by fisheries or a high level of larval production and recruitment (density-dependent facilitation-Allee effect) (Anderson, 1988; Begon et al., 2006; Carr. 1991; Carr and Hixon, 1995; Leirs et al., 1997). Moreover, deterministic mechanisms coupled with the evolutionary history (habitat affinity), habitat heterogeneity of rocky substrate availability (Anderson et al., 2019), cyclic seasonal temperature oscillations (Bernardes et al., 2018) and protection factor (e.g., E. marginatus and M. acutirostris) could also have influenced such patterns (Anderson et al., 2014, 2019; Ault and Johnson, 1998; García-Charton et al., 2004; García-Charton and Pérez-Ruzafa, 2001).

On the contrary, other species such as A. virginicus, H. poeyi, S. axillare and S. frondosum seem to be more sensitive to stochastic seasonal temperature intrusions (e.g., low temperatures < 16°C). Consequently, their spatial distributions tend to show higher density and biomass in warmer temperature areas (Figures 1 and 5). Annual variations seem to be governed by predation and higher mortality rates during harsh winters (Anderson, 1988; Begon et al., 2006; Carr, 1991; Carr and Hixon, 1995; Leirs et al., 1997) (Figures 2 and 3 and Supporting Information Appendix S4). According to Almada and Faria (2004), for many rocky reef species of teleost fishes whose populations are compressed against their distributional borders, fluctuations in abundance are frequent. For example, in extreme low temperatures during harsh winters, the metabolism of herbivorous parrotfishes is not high enough to provide energy for normal diurnal activities. The fish, numb by the cold, lie on the reef substrate, and most are preyed upon (Anderson & Floeter, per. obs.). Such coldinduced conditions may have roots in their evolutionary Caribbean past (Floeter et al., 2008; Rocha, 2003).

A clear pattern in regard to the effectiveness of Arvoredo MPA emerges from the analysis of biomass. Despite yearly variation (McCann *et al.*, 1998), biomass was significantly higher at the MPA for

El Niño/La Niña southern oscillatic	suc	SL	ME	ЯΕ	ML	Μ	I	WE	VSE	VSE	WL	SU	
Species	Population descriptor	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	Zone/year (pMCMC < 0.05)	Zone
Abudefduf saxatilis	Density	Î	\leftarrow	su	←	\rightarrow	~	\rightarrow	\leftarrow	←	\rightarrow	$MPA \neq NPZ/year \texttt{2008} \texttt{2009} \texttt{2011} \texttt{2012} \texttt{2013} \texttt{2014} \texttt{2015} \texttt{2016} \texttt{2017}$	su
	Biomass	Ŷ	\leftarrow	su	\rightarrow	<i>←</i>	<i>←</i>	\rightarrow	\leftarrow	\leftarrow	\rightarrow	$\textbf{MPA} \neq \textbf{NPZ/year. 2008, 2012, 2014, 2015, 2016}$	su
Anisotremus virginicus	Density	Î	\rightarrow	su	\rightarrow	<i>←</i>	\rightarrow	\rightarrow	<i>←</i>	~	\rightarrow	$MPA \neq NPZ/year\text{ 2008, 2009, 2011, 2012, 2013, 2014, 2015, 2016}$	su
	Biomass	Ŷ	\leftarrow	su	\rightarrow	<i>←</i>	<i>←</i>	\rightarrow	\leftarrow	\rightarrow	su	$MPA \neq NPZ/year\text{ 2008, 2009, 2011, 2012, 2013, 2014, 2015, 2016}$	su
Bodianus rufus	Density	su	su	su	su	su	su	su	su	su	su	$MPA \neq NPZ/year:~ns$	su
	Biomass	Ŷ	su	su	<i>←</i>	\rightarrow	<i>←</i>	<i>←</i>	\rightarrow	\rightarrow	su	$MPA \neq NPZ/year.2014,2015,2016$	su
Chaetodon striatus	Density	î	\rightarrow	su	us	~	\rightarrow	su	su	\rightarrow	su	$\textbf{MPA} \neq \textbf{NPZ/year: 2008, 2012}$	su
	Biomass	î	\rightarrow	su	us	~	\rightarrow	<i>←</i>	\rightarrow	\leftarrow	su	$\textbf{MPA} \neq \textbf{NPZ/year: 2008, 2012, 2016}$	su
Chromis limbata	Density	su	su	su	us	su	~	<i>←</i>	\leftarrow	\leftarrow	←	$MPA \neq NPZ/year\text{: 2013, 2014, 2015, 2016, 2017}$	su
	Biomass	su	su	su	us	su	~	<i>←</i>	\leftarrow	\leftarrow	\rightarrow	$MPA \neq NPZ/year\text{: } \texttt{2014}\text{, } \texttt{2015}\text{, } \texttt{2016}\text{, } \texttt{2017}$	su
Chromis multilineata	Density	î	\leftarrow	su	\rightarrow	su	~	\rightarrow	\rightarrow	su	su	$MPA \neq NPZ/year\text{: 2008, 2009, 2011, 2013, 2014, 2015}$	su
	Biomass	ţ	\leftarrow	su	us	us	~	\rightarrow	\rightarrow	su	su	$\textbf{MPA} \neq \textbf{NPZ/year: 2015}$	su
Diplodus argenteus	Density	î	\leftarrow	su	\rightarrow	~	~	\rightarrow	\rightarrow	\leftarrow	\rightarrow	$\textbf{MPA} \neq \textbf{NPZ/year: 2008, 2009, 2011, 2012, 2013, 2014, 2015, 2016, 2017}$	MPA
	Biomass	î	\leftarrow	su	\rightarrow	~	~	\rightarrow	\rightarrow	\leftarrow	\rightarrow	$\textbf{MPA} \neq \textbf{NPZ/year: 2008, 2011, 2012, 2014, 2015, 2016, 2017}$	MPA
Haemulon aurolineatum	Density	su	\rightarrow	su		\rightarrow	\rightarrow	<i>←</i>	\leftarrow	\rightarrow	←	$\textbf{MPA} \neq \textbf{NPZ/year: 2009, 2011, 2012, 2013, 2014, 2015, 2016, 2017}$	MPA
	Biomass	su	su	su	\rightarrow	\leftarrow	\leftarrow	\leftarrow		\leftarrow	\rightarrow	$\textbf{MPA} \neq \textbf{NPZ/year: 2011, 2012, 2014, 2016, 2017}$	MPA
Halichoeres poeyi	Density	su	su	su	su	su	su	su	su	su	su	MPA eq NPZ/year: ns	su
	Biomass	su	su	su	su	us	su	su	su	su	\rightarrow	MPA eq NPZ/year: ns	su
Mycteroperca acutirostris	Density	su	su	su	su	us	su	\rightarrow	\rightarrow	\leftarrow	\rightarrow	MPA eq NPZ/year: ns	MPA
	Biomass	su	su	su	su	us	su	\rightarrow	\leftarrow		\rightarrow	MPA eq NPZ/year: 2015	NPZ
Epinephelus Marginatus ($ullet$)	Density	su	\leftarrow	su	\rightarrow	\rightarrow	~	\rightarrow	\rightarrow	su	\rightarrow	$\textbf{MPA} \neq \textbf{NPZ/year: 2009, 2011, 2013, 2014, 2015, 2017}$	su
	Biomass	su	\leftarrow	su	←	su	\rightarrow	←	\rightarrow	\leftarrow	us	$\textbf{MPA} \neq \textbf{NPZ/year: 2009, 2011, 2013, 2014, 2015}$	MPA
Pomacanthus paru	Density	su	su	su	su	su	su	su	su	su	su	MPA eq NPZ/year: ns	su
	Biomass	su	su	su	su	us	su	su	su	\leftarrow	su	$\textbf{MPA} \neq \textbf{NPZ/year: 2016}$	MPA
Sparisoma axillare	Density	su	su	su	su	us	su	su	su	su	su	MPA eq NPZ/year: ns	su
	Biomass	su	su	su	su	su	su	←	su	←	su	MPA eq NPZ/year: ns	su
Sparisoma frondosum	Density	su	su	su	su	su	su	su	su	su	su	MPA eq NPZ/year: ns	su
	Biomass	su	su	su	su	su	~	<i>←</i>	su	su	su	$\textbf{MPA} \neq \textbf{NPZ/year. 2011, 2014}$	su
Stegastes fuscus	Density	Î	\rightarrow	su	←	←	\rightarrow	\rightarrow	←	\rightarrow	\rightarrow	$MPA \neq NPZ/year\text{ 2008}, 2009, 2011, 2012, 2013, 2015, 2016, 2017$	MPA
	Biomass	Î	\rightarrow	su	su	~	su	su	\rightarrow	\leftarrow	\rightarrow	$\textbf{MPA} \neq \textbf{NPZ/year: 2008, 2011, 2012, 2015, 2016}$	MPA
Stegastes variabilis	Density	su	su	su	su	su	su	su	su	su	\rightarrow	MPA eq NPZ/year: ns	MPA
	Biomass	su	su	su	su	su	su	su	su	su	\rightarrow	$\textbf{MPA} \neq \textbf{NPZ/year: 2009, 2012, 2016, 2017}$	ZdN

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El Niño/La Niña southern oscillatic	suc	SL	Β	ME	۶	ML	-	νE νE	/SE	/SE	٨L	IS	
Trophic levels	Population descriptor	2008	2009	2010	2011	2012	2013 2	014 2	015 2	016 2	2017	Zone/year (pMCMC < 0.05)	Zone
HERB	Density	su	\rightarrow	su	\rightarrow	su	su	←	ns	su	su	MPA eq NPZ/year: 2009, 2011, 2013, 2014	MPA
	Biomass	su	~	su	←	su	<i>←</i>	←	ns	su	\rightarrow	$MPA \neq NPZ/year\text{ 2009, 2011, 2012, 2013, 2014, 2015, 2017}$	MPA
MCAR	Density	su	su	su	su	ns	su	su	\rightarrow	su	su	MPA eq NPZ/year: 2011	su
	Biomass	su	su	su	ns	\rightarrow	\rightarrow	←	\rightarrow	su	su	MPA eq NPZ/year: 2009, 2013, 2015	MPA
MINV	Density	su	\rightarrow	su	←	su	\rightarrow	←	ns	su	su	MPA eq NPZ/year: 2009, 2011, 2012, 2013, 2014, 2015, 2017	MPA
	Biomass	Ţ	\leftarrow	su	\rightarrow	~	<i>~</i>	←	\rightarrow	←	su	$MPA \neq NPZ/year\text{ 2008, 2009, 2011, 2012, 2013, 2014, 2015, 2016}$	su
OMNI	Density	Ţ	\leftarrow	su	←	\rightarrow	<i>~</i>	\rightarrow	←	←	\rightarrow	$MPA \neq NPZ/year\text{ 2008, 2009, 2011, 2012, 2013, 2014, 2015, 2016, 2017}$	MPA
	Biomass	Î	\leftarrow	su	\rightarrow	<i>~</i>	<i>~</i>	\rightarrow	←	←	\rightarrow	$MPA \neq NPZ/year\text{ 2008}, 2009, 2011, 2012, 2013, 2014, 2015, 2016, 2017$	MPA
PLANK	Density	su	\leftarrow	su	\rightarrow	ns	~	\rightarrow	\rightarrow	su	\leftarrow	MPA eq NPZ/year: 2009, 2011, 2012, 2013, 2014, 2015, 2017	MPA
	Biomass	su	\leftarrow	su	\rightarrow	ns	~	\rightarrow	←	\rightarrow	\rightarrow	MPA eq NPZ/year: 2009, 2011, 2012, 2013, 2014, 2015, 2016, 2017	MPA
SINV	Density	su	\rightarrow	su	\rightarrow	ns	su	\rightarrow	su	su	su	${\sf MPA} eq {\sf NPZ/year:}$ 2009, 2011, 2012, 2014	MPA
	Biomass	Î	\leftarrow	su	\rightarrow	~	\rightarrow	←	\rightarrow	←	\rightarrow	MPA eq NPZ/year: 2009, 2011, 2012, 2013, 2014, 2015, 2016, 2017	MPA
THERB	Density	su	\rightarrow	su	\leftarrow	ns	\rightarrow	\rightarrow	su	su	su	MPA eq NPZ/year: 2009, 2012, 2013, 2014, 2015	us
	Biomass	su	\leftarrow	su	←	ns	~	~	\rightarrow	su	su	MPA eq NPZ/year: 2009, 2012, 2013, 2015	us
El Niño/La Niña southern oscillatic	suc	SL	ME	ЯΕ	۶	ML	-	VE /	/SE /	/SE	٨L	IS	
Species recruitment	Population descriptor	2008	2009	2010	2011	2012	2013 2	014 2	015 2	016 2	2017	Zone/year (pMCMC < 0.05)	Zone
A. saxatilis (individual ≤ 5 cm)	Density	su	su	su	su	su	su	su	su	su	su	MPA eq NPZ/year: 2008, 2011, 2012, 2015	MPA
A. virginicus (individual ≤ 5 cm)	Density	su	\rightarrow	su	\leftarrow	su	\rightarrow	su	\rightarrow	su	su	MPA eq NPZ/year: 2011	MPA
D. argenteus (individual ≤ 5 cm)	Density	su	\leftarrow	su	su	us	<i>←</i>	su	\rightarrow	su	←	MPA eq NPZ/year: 2011, 2017	MPA
H. aurolineatum (individual ≤ 5 cm)	Density	su	\rightarrow	SU	<i>←</i>	su	\rightarrow	<i>←</i>	←	\rightarrow	←	MPA ≠ NPZ/year: 2008, 2011, 2012, 2014, 2015, 2016, 2017	MPA
E. marginatus (●) (individual ≤ 10 cm)	Density	ţ	su	su	su	su	\rightarrow	su	\rightarrow	SU	su	MPA eq NPZ/year: 2011, 2015	MPA
S. fuscus (individual ≤ 5 cm)	Density	su	\rightarrow	su	su	su	\rightarrow	\rightarrow	←	\rightarrow	←	MPA eq NPZ/year: 2015	su
Species size class	Population descriptor	0-5	5-10	10-20	20-30 3	0-40 4	0-50	0 9		E		Size class/zone (pMCMC < 0.05)	Zone
A. saxatilis	Density	su	su	su	su	I	ı	ı				MPA eq NPZ/size class: ns	su
	Biomass	su	su	su	su	I	ı	I				MPA eq NPZ/size class: ns	us
A. virginicus	Density	su	su	<i>←</i>	\leftarrow	\rightarrow	su	I				MPA $ eq$ NPZ/size class: 10-20, 20-30, 30-40	MPA
	Biomass	su	su	<i>←</i>	\leftarrow	\rightarrow	su	I				MPA $ eq$ NPZ/size class: 10-20, 20-30, 30-40	MPA
D. argenteus	Density	su	su	\rightarrow	\leftarrow	\rightarrow	su	I				MPA $ eq$ NPZ/size class: 10-20, 20-30, 30-40	MPA
	Biomass	su	su	←	←	\rightarrow	su	ı				MPA eq NPZ/size class: 10–20, 20–30, 30–40	ZdN
												(Con	ntinues)

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H. aurolineatum	Density	su	su	\rightarrow	\leftarrow	\rightarrow	ı	ī				$\textbf{MPA} \neq \textbf{NPZ/size class: 10-20, 20-30, 30-40}$	MPA
	Biomass	us	su	←	\leftarrow	\rightarrow	ı	ī				$\textbf{MPA} \neq \textbf{NPZ/size class: 10-20, 20-30, 30-40}$	MPA
Epinephelus marginatus (●)	Density	us	su	←	\rightarrow	\rightarrow	su	su				$\textbf{MPA} \neq \textbf{NPZ/size class: 10-20, 20-30, \textbf{30-40}}$	MPA
	Biomass	us	su	←	\leftarrow	~	su	su				$\textbf{MPA} \neq \textbf{NPZ/size class: 10-20, 20-30, 30-40}$	MPA
S. fuscus	Density	us	~	←	ı	ı	ı	ī				$\textbf{MPA} \neq \textbf{NPZ/size class: 5-10, 10-20}$	MPA
	Biomass	us	~	\rightarrow	ı	ı	ı	ī				$\textbf{MPA} \neq \textbf{NPZ/size class: 5-10, 10-20}$	MPA
El Niño/La Niña southern oscillat	ions	SL	ME	ЯЕ	۲	ML	ı	WE	VSE	VSE	٨L	ns	
	Population descriptor	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	Zone/year (pMCMC < 0.05)	Zone
All species combined	Density	\leftarrow	su	su	su	us	su	su	su	su	su	$\text{MPA} \neq \text{NPZ/year: 2008, 2009, 2011, 2012, 2013, 2014, 2015, 2017}$	MPA
All species combined	Biomass	\leftarrow	su	su	su	us	su	su	su	su	su	$\text{MPA} \neq \text{NPZ/year: 2008, 2009, 2011, 2012, 2013, 2014, 2015, 2016, 2017}$	MPA
ote El Niño/La Niña couthern o	ecillation code	th evode	A Vears	indicate	the int	ensity of	the nhe	cuemou	tedt di	narticu	ar vea	r (NOAA 2019): WF (weak El Niño) ME (moderate El Niño) VSE (verv si	trong El

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or bioightarrow) pMCMC < 0.05. The arrow direction is up (1) pMCMC < 0.05 when the mean significantly increased compared endangered species The zone presenting higher density (higher typeface sites; not recorded); size classes in the lower part of the table. in bold t years à at the sampling are represented plankton; SINV: sessile invertebrate. of the species differences among zones The same principle applies in regard to maximum size omnivores; PLANK: Significant (beyond available between zones. HERB: herbivore; MCAR: macrocarnivore; MINV: mobile invertebrate; OMNI: not to the previous year; it is down (1) pMCMC < 0.05 when the mean decreased; ns: not significant. Niño), WL (weak La Niña) and ML (moderate La Niña). Arrows indicate significant differences: (inside the NPZ). difference significant biomass ns: nonŗ density significant; (higher between brackets in bold type if in regular typeface vears mass inside the MPA) and available. is presented (IUCN); (-) not values

all years, corroborating that MPAs influence positively, directly and indirectly, species inhabiting them (Strain *et al.*, 2019) (see Supporting Information Appendix S5).

4.2 | Trophic groups' spatiotemporal variations

Macrocarnivore (MCAR) biomass seems to vary in space according to fisheries restrictions in the MPA (Anderson et al., 2014, 2019; Maggs et al., 2013; Mellin et al., 2016; Palumbi, 2004). The effectiveness of the MPA is evident, especially in protecting the old, large and furtive mothers (i.e., long-living individuals which can reach 50 years) (Palumbi, 2004; Reñones et al., 2002) (Figures 2 and 3). Old and large individuals are responsible for most of the production of high-quality larval output and the repopulation of adjacent areas ("spillover") (Chung et al. 2017; Di Lorenzo et al., 2016; Maggs et al., 2013; Palumbi, 2004). In contrast, density variation in space seems to be more influenced by a recruitment rate (Figure 2) that has been decreasing over the past 9 years (Figure 4). Tidal pools are regarded as nursery habitat for grouper recruits on southern Brazilian rocky reefs (Andrade et al., 2003; Cunha et al., 2007). Nonetheless, anthropic pressure on these habitats acting synergically with densitydependent mechanisms may have influenced the decrease in recruitment rates of MCARs (Anderson, 1988; Begon et al., 2006; Carr. 1991: Carr and Hixon. 1995: Leirs et al., 1997).

Density and biomass of herbivorous fishes show discrete stability trends, which may be due to their low density and biomass in south Brazil (see Supporting Information Appendix S1). These species are also sensitive to lower temperatures (Choat *et al.*, 2012; Hoey, 2018) that occur frequently in sites outside the MPA (Figures 1 and 5). Both variables, protection from fisheries and temperature, conjoined, seem to govern their distributions (density) and growth rates (biomass) (Choat *et al.*, 2012; Hoey, 2018; Parravicini *et al.*, 2018). The numbness induced by cold may have important consequences, especially in regard to mortality. The time duration these fish remain numb is unknown (see Supporting Information Appendix S4). Such patterns may indicate that spatiotemporal variation is influenced by mortality mediated by climatic oscillations (Almada and Faria, 2004; Begon *et al.*, 2006; Doherty, 2002; Sale, 1978, 1980) (Table 2).

Despite their modest commercial interest (Begossi *et al.*, 2012; Martins *et al.*, 2013), mobile invertebrate (MINV) feeders' biomass is higher inside the MPA. Such a strong response from accessory species corroborates Mellin *et al.* (2016) regarding the overall indirect benefits promoted by MPAs on ecosystems (Babcock *et al.*, 2010; Mellin *et al.*, 2016) (Figure 3).

In addition to indirect benefits, the MPA environmental complexity (Anderson *et al.*, 2019; Hackradt *et al.*, 2011) may have influenced sessile-invertebrate (SINV) feeders' spatial distribution (Figures 3 and 5).

Omnivores (OMNI) not targeted by professional fisheries (Begossi et al., 2012; Gasparini et al., 2005; Martins et al., 2013) also seem to benefit from being in the MPA (Babcock et al., 2010; Mellin et al., 2016)

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FIGURE 2 Dominant species' densities and biomass variations over time. Green circles represent all sites' [no-take zone (marine-protected area, MPA) and non-protected zone (NPZ)] density variations per year. Red circles represent all sites' (MPA and NPZ) biomass variations per year. All sites: (**(a)** density individual/40 m² ± s.E., (**(a)**) biomass g/40 m² ± s.E., (**(b)**) no-take zone (MPA), (----) non-protected zone (NPZ) and (**(b)**) mean. Blue circles represent the density variations per year. Orange circles represent the biomass variations per year. The red line across each graph represents the mean from 2008 to 2017. Inside/outside MPA: (**(a)** density individual/40 m² ± s.E., (**(b)** biomass g/40 m² ± s.E. and (*****) pMCMC < 0.05. Asterisks represent significant variations (pMCMC < 0.05)

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(MPA





















2011 2012 2013 2014 2015 2016 2017



MINV

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ns

1000

600

200

(g)











2008 2009 2011 2012 2013 2014 2015 2016 2017

THER





3 2014 2015 2016 2017

HERB - Herbivores MCAR - Macrocarnivores MINV - Macroinvertebrate feeders OMNI - Omnivores PLANK - Planktivores SINV - Sesile invertebrate feeders THER - Territorial herbivores

FIGURE 3 Functional trophic groups' densities and biomass variations in space and time. Green circles represent all sites' [no-take zone (marine-protected area, MPA) and non-protected zone (NPZ)] density variations per year. Red circles represent all sites' (MPA and NPZ) biomass variations per year. All sites: (a) density individual/40 m² ± s.e. and (b) biomass g/40 m² ± s.e. Blue circles represent the density variations per year. Orange circles represent the biomass variations per year. The red line across each graph represents the mean from 2008 to 2017. Asterisks represent significant variations (b pMCMC < 0.05). Inside/outside MPA: (b) biomass g/40 m² ± s.e., (*) pMCMC < 0.05., (----) no-take zone (MPA), (----) non-protected zone (NPZ) and (----) mean

(Figures 3 and 5). In addition, OMNIs' spatial distribution seems to be linked with microhabitats where lower temperatures are more likely to occur (Figures 1 and 5). OMNIs' annual variations may also indicate influences driven by density-dependent mortality mediated by climatic oscillations, intraspecific competition for shelter and predation (Sale, 1978, 1980, 2013; Doherty, 2002; Almada and Faria, 2004).

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FIGURE 4 Recruitment of dominant species' mean densities and biomass variations in space and time. Green circles represent all sites' [no-take zone (marine-protected area, MPA) and non-protected zone (NPZ)] density variations per year. All sites: (**•**) density individual/40 m² ± s.E., (----) non-protected zone (NPZ) and (-----) mean. Blue circles represent the density variations per year. The red line across each graph represents the mean from 2008 to 2017. Asterisks represent significant variations (***** pMCMC < 0.05). Inside/outside MPA: (**•**) density individual/40 m² ± s.E.

Plankton (PLANK) feeders in this particular case have their spatial and temporal distributions influenced by the invasion and colonization of the rocky reefs of southern Brazil by the Azores chromis (*C. limbata*) (Anderson *et al.*, 2017, 2020) The increasing variation in annual density of PLANKs may have been directly influenced by this invasive species pattern of population growth (Allendorf and Lundquist, 2003; Anderson *et al.*, 2017; Neubert and Caswell, 2000) (Figure 3). As for other trophic groups, deterministic, stochastic and density-dependent mechanisms may have also an important influence on the distribution and structure of PLANK populations on southern Brazilian rocky reefs (Almada and Faria, 2004; Ash, 2018; Begon *et al.*, 2006; Doherty, 2002; Sale, 1980).

4.3 | Species populational structure spatial variations

The domination of species population structure by sub-adult individuals (*i.e.*, intermediary size classes) may evidence high mortality rates in the initial stages (Almada and Faria, 2004; Doherty, 2002; Sale, 1978, 1980) (see Table 1 and Supporting Information Appendix S1). Stochastic dispersal of larvae (Cocheret de La Morinière *et al.*, 2002), fear effect (Preisser and Bolnick, 2008) and predation (Forrester, 1990), conjoined with random cold-water intrusions, may explain such patterns. Moreover, juveniles grow faster after populations are reduced by predators, resulting in lower intraspecific competition (Carr and Hixon, 1995).

The protection factor of the MPA seems to have influenced positively the survival of large individuals of highly targeted groupers (>50 cm) inside their restriction area. This corroborates the effectiveness of the protection offered by the MPA on overexploited species described in previous works (Anderson *et al.*, 2014).

4.4 | Recruitment in space and time

Most species showed a decline in recruitment that may be attributed to anthropic pressure on adjacent nursery areas [*e.g.*, mangroves, tidal pools, rhodolith beds, open estuaries (Almada and Faria, 2004; Cunha *et al.*, 2007; Vila-Nova *et al.*, 2011)] (Figure 5). The recruitment decline of *E. marginatus* raises very important questions about the continuing effectiveness of Arvoredo MPA (Botsford *et al.*, 2009; Pujolar



FIGURE 5 Redundancy analysis (RDA) showing distribution of species according to their total biomass (2008–2017) and environmental variables. Blue circles with outer rings represent the non-protected zone (NPZ) located outside the marine-protected area (MPA), where fisheries are allowed. Green circles with outer rings represent the no-take zone (MPA) located inside the MPA, totally restricted to fisheries. The arrows represent environmental variables. Orange circles represent all 18 key species; their sizes are proportional to their total frequency of occurrence (%FO)

et al., 2013). Spillover (Chung *et al.* 2017; Di Lorenzo *et al.*, 2016; Harmelin-Vivien *et al.*, 2008) and connectivity among populations are crucial to maintain a genetically healthy population inside the MPA (Pujolar *et al.*, 2013; Saenz-Agudelo *et al.*, 2011). But, so far, the grouper population inside the MPA and the exportation of larvae and adults to adjacent areas seem to be subsidized by the large old females (*i.e.*, individuals > 50 cm) which can be found only inside the MPA (Anderson *et al.*, 2014, 2019).

When these large and productive mothers perish, and if the decline in recruitment rate perdures, it could doom the future of Arvoredo MBR. Protection and restoration of nursery habitats of the southern Brazilian coast are urgent to ensure the future of grouper populations and other rocky reef fish species (Halpern *et al.*, 2007; Lotze *et al.*, 2006; Sundblad *et al.*, 2013). Urgent policies and projects for conservation and restoration of nursery-adjacent habitats and optimized management programmes (*e.g.*, law enforcement against illegal fisheries) are necessary to secure the future of Arvoredo MPA and all species directly and indirectly favoured by its existence.

4.5 | El Niño and La Nina southern oscillations

This work collected only 3 years of *in situ* temperature data. The data set is considered to be robust once the dataloggers remained deployed for 48 months, interruptedly, and prominent temperature variation among seasons, in these latitudes, occurs only between summer and winter. Furthermore, the data set covered years with no El Niño or La Niña activity and a very strong El Niño period (see Supporting Information Appendix S3).

All species studied seem to be adapted to temperature variations caused by ENSOs, and no significant variation in density or biomass was correlated to ENSO strength. Cold-water intrusions actually occur frequently in Brazilian southern rocky reefs (Table 1) (Bernardes et al., 2018). Species such as A. virginicus, H. poeyi, P. paru, S. axillare and S. frondosum seem to have affinities to sites where lower temperatures (< 16°C) are less likely to occur (Figures 1 and 5), whereas others, such as A. saxatilis and D. argenteus, seem to be indifferent to low temperatures. Despite their differences regarding environmental affinities, the species mentioned earlier have been spotted in a state of cold-induced torpor sharing the same hole or crevice in several occasions when temperatures were below 14°C (A. B. Anderson, pers. obs.). El Niño and La Niña oscillations seem to exert a weaker influence than cold-water intrusions that may occur year-round as the Malvinas current strengthens (Bernardes et al., 2018).

5 | CONCLUSIONS

Rocky reef fish species populations present dynamic balanced fluctuations in density or biomass in spatiotemporal scale. These variations in spatial distribution appear to be governed by habitat structural complexity and protection from fisheries. When species were grouped in trophic groups, they also showed significantly different population signatures related to the impact of fisheries in space and time. Directly (*e.g.*, protecting species targeted by fisheries) or indirectly, the Arvoredo MPA seems to promote higher density and biomass for most species and trophic groups. Such findings are expected to actually reflect the MPA action onto all reef fish species in the system. The recruitment of the studied species also varies in space and over time. The decline in recruitment rates detected for the endangered grouper *E. marginatus* requires urgent management actions regarding the Arvoredo MPA and adjacent nursery habitats. When the size spectrum of studied species near their climatic threshold of distribution was considered, a dominance of sub-adult and young adult individuals was detected.

Longer time series (> 10 years) are necessary for a better understanding of reef fish populational variation patterns in space and time, especially when their populations are stressed against a climatic biogeographic distributional barrier. Long-term monitoring projects and programmes must be encouraged and fomented.

ACKNOWLEDGEMENTS

We thank FAPES (Fundação de Amparo à Pesquisa e Inovação do Espírito Santo, Brazil)/CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil) (PROFIX programme number 10/2018 - T.O.: 348/2018) for postdoctoral scholarship to Antônio Batista Anderson We also thank the anonymous reviewers and Wally Rich (Red Sea Research Center - King Abdullah University of Science and Technology), who contributed to the improvement of this paper. Thanks to the Marine Macroecology and Biogeography Laboratory (LBMM) staff for field support. Funding sources: SISBIOTA-Mar (PI: S.R.F., CNPg 563276/2010-0; FAPESC 6308/2011-8), Projeto Ilhas do Sul (PI: Sergio Ricardo Floeter, CNPg 475367/2006-5). Projeto MAArE - Monitoramento Ambiental do Arvoredo e Entorno (PI: Barbara Segal), CAPES scholarship to Antônio Batista Anderson and Projeto Biodiversidade Marinha do Estado de Santa Catarina (PI: Alberto Lindner FAPESC 4302/2010-8).

CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

A.B.A. contributed to original idea, data generation, data analysis, manuscript preparation and reviews; J.-C.J. contributed to manuscript preparation and reviews; and S.R.F. contributed to original idea, manuscript preparation, reviews and funding.

COMPLIANCE WITH ETHICAL STANDARDS

1. Were fishes collected as part of faunal surveys? No.

2. Were fishes killed during or at the end of your experiment (*e.g.*, for tissue sampling)? No.

3. Were surgical procedures performed? No.

4. Did the experimental conditions severely distress any fishes involved in your experiments? No.

5. Did any procedures (*e.g.*, predation studies, toxicity testing) cause lasting harm to sentient fishes? No.

6. Did any procedure involve sentient, un-anaesthetized animals that were subjected to chemical agents that induce neuromuscular blockade, such as muscle relaxants? No.

ORCID

Antônio B. Anderson b https://orcid.org/0000-0003-2502-7018 Sergio R. Floeter b https://orcid.org/0000-0002-3201-6504

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SUPPORTING INFORMATION

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How to cite this article: Anderson AB, Joyeux J-C, Floeter SR. Spatiotemporal variations in density and biomass of rocky reef fish in a biogeographic climatic transition zone: trends over 9 years, inside and outside the only nearshore no-take marineprotected area on the southern Brazilian coast. *J Fish Biol*. 2020;1–15. https://doi.org/10.1111/jfb.14441