Recovery of grouper assemblages indicates effectiveness of a marine protected area in Southern Brazil

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ABSTRACT: Top predators have a strong influence on the structure and dynamics of marine ecosystems. These organisms have been largely used as indicators of the effectiveness of marine protected areas (MPAs). In Brazil, the impact of fisheries on reef species, such as groupers and sea basses, and the importance of local marine reserves in the maintenance of these fish communities are still poorly understood. Here we assessed the assemblage of groupers and sea basses (Epinephelidae and Serranidae) inside and outside the Arvoredo Marine Reserve (AR), a MPA in Santa Catarina State, southern Brazil. Density and biomass of 13 fish species (7 Epinephelidae and 6 Serranidae) were recorded. The most abundant groupers were *Epinephelus marginatus* and *Mycteroperca acutirostris*, while *Serranus flaviventris* and *S. balwini* were the most abundant sea basses. Grouper biomass was significantly higher inside the reserve, indicating the effectiveness of this MPA for target and threatened species, such as *E. marginatus*. In contrast, biomass of sea basses was higher outside the MPA, as a possible result of prey release effect. Despite the higher biomass of groupers inside AR, spearfishing records from the 1960s indicate that there is still a long way to a full recovery of the biomass of top predators, especially groupers and sharks. Thus, a more effective enforcement and longer-term protection are necessary to restore fish stocks and ecosystem health in these reefs.

KEY WORDS: Top predators · Reef fishes · Epinephelidae · Serranidae · Fisheries · Conservation · Rocky reef · Southwestern Atlantic

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INTRODUCTION

In marine ecosystems, the impact of fisheries and the extent of ecosystem recovery following major disturbances have been largely used as indicators to assess the effectiveness of marine protected areas (MPAs; Sale et al. 2005). Previous studies show that mean size and abundance of target fish species are relatively higher inside protected areas in comparison to unprotected areas (e.g. Roberts & Polunin 1991, Bohnsack 1998, Halpern & Warner 2002, Russ 2002, García-Charton et al. 2008, Kellner et al. 2010). However, the impact of fisheries on Brazilian reefs and the importance of local marine reserves in the

maintenance of fish communities are still poorly understood, as few studies have assessed the contribution of management strategies in protecting local reefs (but see Floeter et al. 2006, Francini-Filho & Moura 2008).

Top predators have a strong influence on the structure and function of marine communities, since they play critical roles in maintaining the structure and dynamics of food webs in these systems (Dulvy et al. 2004, Hutchings & Baum 2005, Baum & Worm 2009). Reductions in the biomass and abundance of top predators may trigger potentially irreversible cascade effects that destabilize food webs in the marine environment (Dulvy et al. 2004, Heithaus et al. 2008, Baum & Worm 2009). However, despite recognition by marine biologists of such damaging effects, numbers and biomass of top predators have been dwindling dramatically over the last century, with decreases of up to 90% in some regions (Heithaus et al. 2008). For this reason, biomass and abundance of marine fishes, as well as other indices associated to these variables (e.g. Large Fish Indicator, the Large Species Indicator, the biomass-weighted mean maximum length of fish species and the biomass-weighted mean maturation length of fish species of top predators targeted for fisheries), are considered important to assess the effectiveness of MPAs, as well as to evaluate the design, regulation and enforcement of these areas (Spedicato et al. 2005, García-Charton et al. 2008, Fung et. al. 2013).

Groupers (Epinephelidae) and sea basses (Serranidae) include a number of top and mesopredator species susceptible to overfishing. The vulnerability of epinephelids and serranids is usually explained by their long life cycles, typically characterized by slow growth rates, sex change and formation of spawning aggregations in some species (Sadovy & Colin 2012). Therefore, a number of groupers are currently placed within 'threatened' categories of international conservation indicators, such as the IUCN (International Union for Conservation of Nature) Red List of Threatened Species (Craig et al. 2011, Bender et al. 2012, 2013, IUCN 2014, Sadovy de Mitcheson et al. 2013).

In an attempt to better protect sharks, groupers and other threatened marine species, the Aichi Biodiversity Targets for 2020 proposed the establishment of a global and effective MPA management system (i.e. Target 11; CBD 2010). Although Brazil is one of the countries committed to achieve the proposed goals, few studies have assessed the effectiveness of Brazilian MPAs (e.g. Floeter et al. 2006, Francini-Filho &

Moura 2008, Gerhardinger et al. 2011). As a consequence, the effects of existing local MPAs are still largely unknown. Further information on the effectiveness of Brazilian MPAs is critically important, especially since most apex predator species, including large sharks and groupers, have declined along the Brazilian coast in the last few decades (Ferreira et al. 2004, Floeter et al. 2006). For example, in Santa Catarina State, the southernmost limit of the distribution of many tropical reef fishes in the Western Atlantic (Hostim-Silva et al. 2006, Floeter et al. 2008, Barneche et al. 2009), most top predators seem to have disappeared likely as a result of overfishing along the coast (Souza 2000). Reef fishes that were once secondary top predators (e.g. groupers and sea basses) now play the role of apex predators in these marine ecosystems, and their populations have clearly declined, along with reef sharks, from overfishing (Souza 2000).

In the present study, we assessed the assemblage structure of groupers and sea basses inside and outside the Arvoredo Biological Marine Reserve, a coastal MPA in Brazil. Both groupers and sea basses are representative of predatory species; however, while sea basses are usually smaller and less targeted by fishers, grouper species generally attain larger sizes and are heavily targeted (Bender et al. 2013, Sadovy de Mitcheson et al. 2013, A. B. Anderson pers. obs.). More specifically, we compared density and biomass of groupers and sea basses between protected sites, where fisheries are restricted by federal law, and unprotected areas, where fisheries are allowed.

MATERIALS AND METHODS

Study area

The study was conducted on subtropical reefs in the vicinity of Florianópolis, Santa Catarina State, southern Brazil (27° 35′ 41.08″ S; 48° 32′ 38.96″ W). Coastal and insular reefs in this region present similar geomorphology, characterized by steep granitic rocky reefs that end in sandy bottoms, generally 12 to 15 m deep (Basei et al. 1992, Hostim-Silva et al. 2006, Tomazzoli & Lima 2006).

Sampling was conducted at a total of 8 sites (3 protected and 5 unprotected), grouped into 3 sectors: Sector 1 — unprotected northwest coast (CO): (1) Cape Araçá (Porto Belo City), (2) Cape Sepultura (Bombinhas City); Sector 2 — Arvoredo Biological Reserve (AR): (1) Arvoredo Island, (2) Galé Island and (3)

Deserta Island; Sector 3—unprotected southern islands (UI): (1) Arvoredo Island, (2) Aranhas Island and (3) Xavier Island (Fig. 1). The 3 protected reefs within Sector 2 are inside the Arvoredo Marine Biological Reserve (AR), about 11 km off northern Florianópolis. AR has been designated a no-take marine protected area since 1990 and encompasses 17800 ha. In 2000, AR officially became a no-entry area, where harvesting and human presence are strictly forbidden by law (researchers and managers excepted). Arvoredo Island is located at the border of the MPA, containing both protected and unprotected portions (see Fig. 1). On the unprotected side of the island, activities such as SCUBA diving and angling are allowed. CO sites are characterized by high levels of anthropogenic disturbances, such as recreational fisheries, small vessel traffic, freshwater discharge and sewage disposal. UI sites are also affected by recreational fisheries and boat traffic, but at lower levels.

The entire study was conducted during the austral summer of 2011, between February (sites at UI and CO, see below) and March and April (sites within AR). During the study, water temperature ranged from 22 to 28°C and underwater visibility ranged from 4 to 15 m at all study sites.
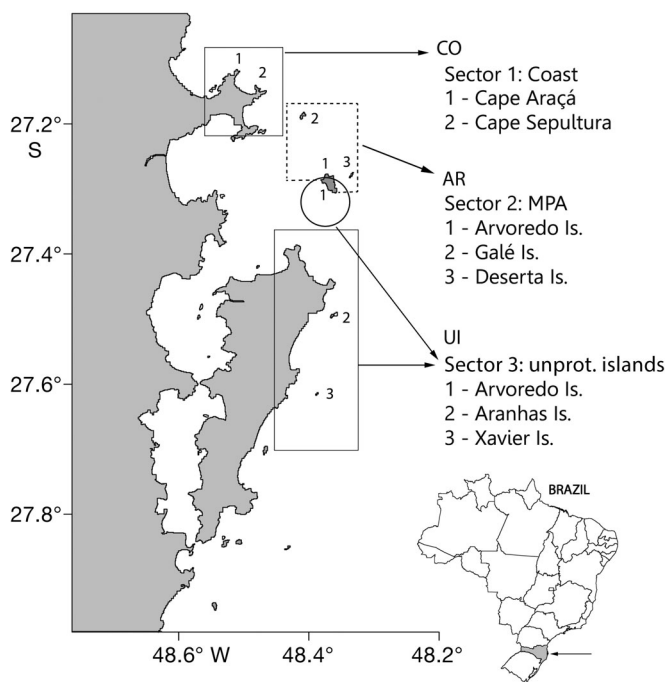

Fig. 1. Study area near Florianópolis, southern Brazil. The dashed polygon represents the limits of the MPA of Arvoredo Marine Biological Reserve. The numbers indicate the study sites within each sector

Data collection

Underwater visual census (30 × 4 m strip transects = 120 m^2) was used to quantify density and biomass of grouper and sea bass populations and to explore topographic patterns at the sites. A scuba diver swam 1 m above substratum along each transect, while unrolling a measuring tape, recording all grouper and sea bass (Epinephelidae and Serranidae) individuals found and classifying them into species and 5 cm total length (TL) categories. Fish TL was used to estimate biomass for each species at each study site using published weight–length relationships, according to the following equation: $W = a \times TL^b$, in which 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 cm (Froese & Pauly 2013).

At each study site, 2 depth strata were sampled: slope and interface. Slope (S) was considered the area between the water surface and half of the total depth (TD). Thus, if TD = 6 m, S = 0 to 3 m. Interface (I) corresponded to the transition zone between the rocky reef and the non-consolidated substratum—typically sandy bottom in this case. Maximum TD varied from 5 m at Cape Sepultura to 23 m at Xavier Island. For each depth stratum, 9 transects were surveyed, totalling 18 transects (2160 m^2) sampled per site. All transects were conducted in the morning.

Data analysis

One-way ANOVA was used to evaluate differences in average total (i.e. groupers and basses altogether) density and biomass across the 8 study sites. We also used ANOVA to test for differences in average biomass across protection status (sectors AR, UI, CO) for groupers and basses separately. In both tests, when significant differences were found, Tukey HSD post hoc test was used to verify sources of variation. Before both analyses, assumptions of normality and homoscedasticity were assessed with the Kolmogorov-Smirnov/Lilliefors and Bartlett's tests (Underwood 1981, Snedecor & Cochran 1989, Zar 1999).

Permutational Multivariate Analysis of Variance based on the Bray-Curtis dissimilarity matrix (PERMANOVA, Anderson 2001) was used to test for differences in assemblage structure, both in terms of density and biomass. PERMANOVAs (9999 permutations) were performed following a design with 3 factors: (1) protection status represented by Sector (Se): fixed, with 3 levels and unbalanced (AR, UI and CO);

(2) Site [Si(Se)]: random and nested within Sector, with 8 levels and unbalanced (3 AR sites, 3 UI sites and 2 CO sites; see Fig. 1); and (3) Depth Stratum (St): fixed and orthogonal, with 2 levels (slope and interface).

RESULTS

A total of 6 bass species (non-targeted), and 7 grouper species (targeted) were recorded across the 8 study sites. *Epinephelus marginatus* and *Mycteroperca acutirostris* were the dominant groupers in terms of biomass and density, while *Serranus flaviventris* and *S. baldwini* were the dominant sea basses in both density and biomass across the 8 study sites (detected in 6 and 4 study sites, respectively). Among the 8 study sites, 2 islands presented higher species richness of sea basses and groupers: Deserta Island (AR) and Xavier Island (UI), with 9 and 10 species detected, respectively (Table 1).

Mean grouper biomass was, on average, higher inside the reserve ($F = 126.2$, $p < 0.001$, Figs. 2 & 3). These differences mostly resulted from the higher number of larger fish (TL > 30 cm) inside AR (Table A1). Also, large individuals of species targeted by fisheries, such as *M. microlepis*, *M. bonaci*, *M. interstitialis* and *E. morio*, were found exclusively within AR.

Two species of sea basses presented higher biomass among small species: *S. flaviventris* and *Diplectrum radiale*. Mean biomass of sea bass was not significantly higher inside AR (Fig. 3). *S. baldwini* was mostly associated with rodolith beds in Deserta and Aranhas Islands and was the only species with a considerably higher biomass inside AR. *S. flaviventris* and *D. radiale* were detected mostly in shallow areas (maximum 5 m deep) at the interface.

Differences in the distribution of fish biomass (Fig. 4) among sites were related to 'Protection Sector' ($p = 0.024$), but not to 'depth strata' ($p = 0.075$) (PERMANOVA, 9999 permutations). Differences in density revealed virtually the same patterns (Table 2).

DISCUSSION

To the best of our knowledge, this is the first study to assess the effectiveness of the Arvoredo Marine Biological Reserve (AR) in protecting the heavily targeted piscivorous fishes. The overall higher biomass of groupers inside AR in comparison to unprotected sites suggests that the protected area is highly important to sustain populations of large predatory fishes,

Table 1. Mean density (D) and biomass (B, grams) of Epinephelidae and Serranidae per 120 m² at 3 protected (within the Arvoredo Reserve) and 5 unprotected sites (UI and CO) in Southern Brazil. IUCN categories: EN = Endangered, NT = Near-Threatened, VU = Vulnerable, LC = Least Concern; (–) zero occurrence; nc = not classified

| Species	Arvoredo Reserve (no-take zone; AR)						Unprotected islands (UI)						Unprotected coast (CO)						IUCN
	Deserta Is.		Galé Is.		Arvoredo Is.		Arvoredo Is.		Aranhas Is.		Xavier Is.		C. Sepultura		C. Araçá			
	D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B		
EPINEPHELIDAE																		
Epinephelus marginatus	5.4	1918.3	5.7	2789.0	1.7	772.3	1.4	277.3	3.8	564.0	3.4	564.8	0.7	174.8	0.4	43.6	EN
E. morio	0.1	11.9	–	–	0.1	70.6	–	–	–	–	–	–	–	–	–	–	NT
Hyporthodus niveatus	–	–	0.1	8.6	–	–	–	–	0.1	0.1	–	–	–	–	0.1	1.0	VU
Mycteroperca acutirostris	1.0	485.0	1.4	305.2	2.4	2281.4	2.1	797.2	1.0	245.7	1.1	204.4	0.6	126.5	2.8	479.6	LC
M. bonaci	0.2	212.2	–	–	–	–	0.1	32.1	–	–	0.1	5.5	0.1	11.2	–	–	NT
M. interstitialis	0.2	57.1	–	–	–	–	0.1	36.4	–	–	0.1	1.0	–	–	–	–	VU
M. microlepis	0.1	52.4	–	–	–	–	–	–	–	–	–	–	0.1	10.1	–	–	LC
SERRANIDAE																		
Diplectrum formosum	0.1	6.3	–	–	–	–	–	–	0.1	6.3	0.1	6.3	–	–	–	–	nc
D. radiale	–	–	–	–	–	–	–	–	–	–	0.1	8.2	–	–	3.0	31.5	nc
Dules auriga	–	–	–	–	–	–	–	–	–	–	0.1	1.7	–	–	–	–	nc
Serranus atrobranchus	–	–	0.1	0.9	–	–	–	–	0.4	7.2	0.2	2.9	–	–	–	–	nc
S. baldwini	1.1	5.9	–	–	–	–	0.2	1.2	0.4	2.1	0.1	0.2	–	–	–	–	nc
S. flaviventris	0.1	1.2	0.4	12.5	–	–	0.1	1.2	–	–	0.1	0.1	0.8	22.3	1.9	91.5	nc
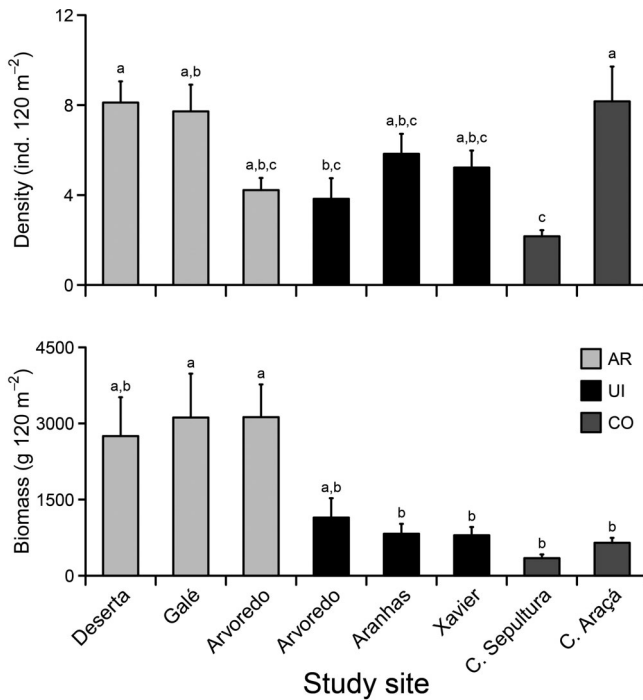
Fig. 2. Density (top) and biomass (bottom) (mean + SE) of groupers (Epinephelidae) and sea basses (Serranidae) at 8 reefs: 3 protected sites in the Arvoredo Marine Reserve (AR) and 5 unprotected sites: 3 islands (UI) and 2 coastal sites (CO). Different letters above bars indicate significant differences (Tukey HSD, p < 0.05)
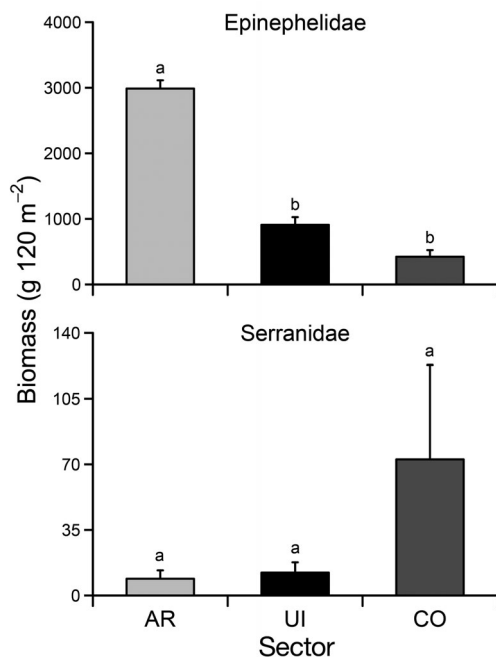

Fig. 3. Biomass (mean + SE) of Epinephelidae (top) and Serranidae (bottom) species at 8 reefs: 3 protected sites in the Arvoredo Marine Reserve (AR) and 5 unprotected sites: 3 islands (UI) and 2 coastal sites (CO). Different letters above bars indicate significant differences (Tukey HSD, p < 0.05)

as observed in other rocky reefs (Hackradt et al. 2014). These predators are widely considered important for maintaining the structure and dynamics of marine food webs (Dulvy et al. 2004, Heithaus et al. 2008, Baum & Worm 2009).

Among the 7 species of groupers recorded in the present study, 3 are considered threatened according to the IUCN Red List of Threatened Species (Bender et al. 2012, IUCN 2014) (Table 1). Indeed, large reproductive individuals of *Epinephelus marginatus* were found exclusively inside AR, suggesting that the reserve acts as a refuge for species heavily targeted by fisheries in the region, particularly since no other no-take MPA exists near Florianópolis.

In addition to the higher richness of grouper species inside AR, grouper individuals were usually larger in protected sites, which may have direct implications for the impact of these fishes in the ecosystem. Body size and mass directly shape the biology of fishes in a number of ways, as fishes of different sizes and ontogenetic stages may have different energetic and diet requirements (Eggleston et al. 1998, Barneche et al. 2014), microhabitat utilization and home ranges (Dahlgren & Eggleston 2001). As a consequence, individuals of different sizes may play different roles in the marine ecosystem, either by targeting different prey or by focusing their activities in distinct reef zones. The removal of larger specimens of a given species from the ecosystem may change the structure and dynamics of the assemblage. Furthermore, larger fish make a disproportionately higher contribution to the production of eggs and gametes, and their larvae usually present higher survivorship in comparison to those produced by smaller individuals (Birkeland & Dayton 2005). The reduction in fish size may thus have direct and negative impact on the reproductive potential, with severe and detrimental consequences to the maintenance and growth of the population.

At unprotected sites, density and biomass of large groupers were reduced, whereas density and biomass of sea basses were increased (though the difference was not significant; ANOVA, $F = 2.69$, $p = 0.16$) (Tables 1 & A1, Fig. 3). This process, termed 'prey release effect' (Dulvy et al. 2004), is usually observed in reefs with overexploitation of top predatory species, such as sharks and large groupers, in which populations of smaller piscivorous fishes, such as sea basses, increase in abundance. This pattern seems to be the case for the present study, considering the observed differences in environmental characteristics across the 8 study sites and the contrasts in bass and grouper as-

Table 2. Multivariate PERMANOVA evaluating combined densities of Epine-phelidae and Serranidae species as a function of protection status (Se), site (Si) and depth stratum (St). **Bold** indicates significant (p < 0.05) results. p (perm): p-value of permutational analysis; Unique perms: number of unique permutations

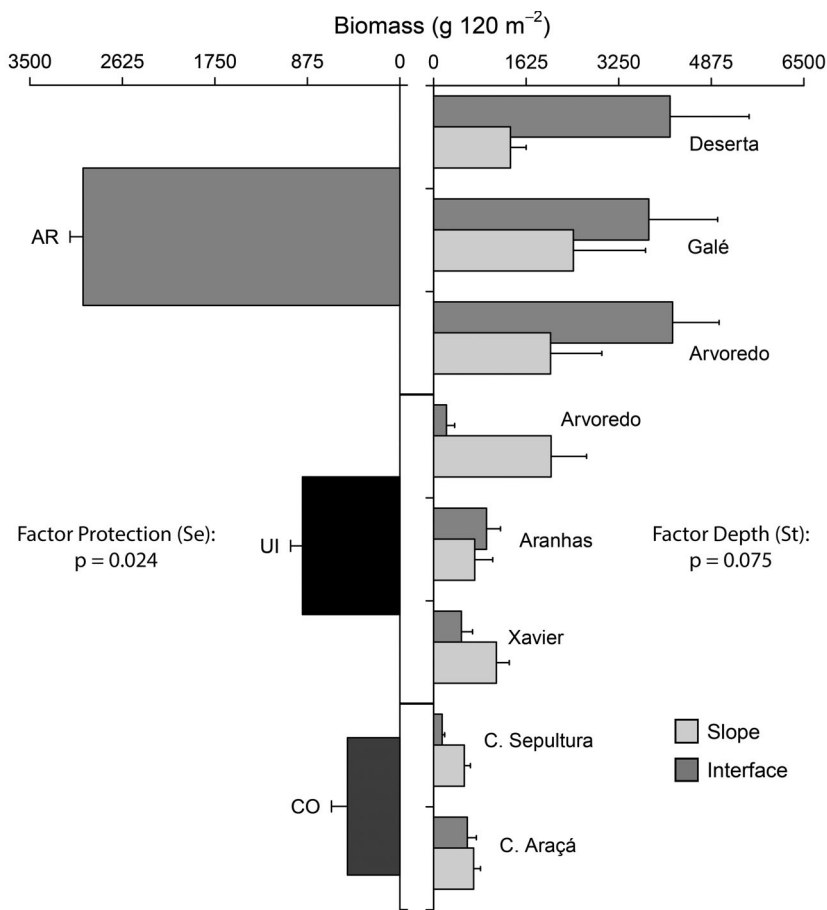| Source	df	SS	MS	Pseudo-F	p (perm)	Unique perms
Se	2	41040	20520	2.8761	**0.0495**	280
St	1	3242.5	3242.5	2.2727	0.1108	9953
Si(Se)	5	35673	7134.5	7.056	**0.0001**	9899
St×Se	2	10326	5163.2	3.619	**0.0268**	9944
St×Si(Se)	5	7133.5	1426.7	1.411	0.0962	9907
Res	128	1.2942×10^{-5}	1011.1			
Total	143	2.2642×10^{-5}				

Fig. 4. Multivariate PERMANOVAs comparing biomass (mean + SE) distributions of Epinephelidae and Serranidae among 8 reefs, considering protection sector (left) and depth stratum (right) as factors. See 'Materials and methods' for full description of study sites and sampling strategy

semblages apparently related to reef protection status. The reduced pressure of bigger predatory species in unprotected reefs around Florianópolis is thus a probable cause for the increased population of sea basses in fish assemblage at local reefs.

Despite AR effectiveness in contributing to a higher biomass of groupers within the reserve, our results still raise questions concerning its management, considering the MPA's age (over 20 yr), high protection status (no entry), and large area. In the early 1960s, for example, 2 local fishers during a 3 h spearfishing trip at Galé Island (currently within the MPA) caught 5 grey nurse shark *Carcharias taurus* and 3 Atlantic goliath grouper *Epinephelus itajara* (Fig. A1). This type of catch was not uncommon based on the considerable number of reports and photographs of similar activities around Florianópolis between 1940 and 1960 with equally high biomasses in fish caught within a few hours (e.g. Souza 2000). In contrast, during the 60 h of SCUBA dives in the present study, not a single individual of *C. taurus* or *E. itajara* was observed. Furthermore, in more than 300 h of monitoring the studied fish communities over the last 5 yr, neither of these species has been sighted (A. B. Anderson, D. R. Barneche & S. R. Floeter pers. obs.). This difference in predatory fish biomass between AR in the present study and reefs off Florianópolis during the 1960s suggests that the effectiveness of the reserve has not reached its real potential, despite the current larger grouper biomass in AR in comparison to unprotected reefs.

Previous works on the inference of MPA's effectiveness based on groupers sizes, biomass and abundance found that time/age of the MPA could be crucial to restore grouper biomass due to their long life spans and reproductive behaviours (García-Charton et al. 2008, Sadovy & Colin 2012, Fung at al. 2013). The time needed for a marine reserve to become effective (i.e. the time taken to restore populations of target species and ecosystem biodiversity) is critical for the formulation of marine management strategies (Halpern 2003, Lotze et al. 2006, Claudet et al. 2008). This subject, however, is quite controversial, as some studies have found significant increases in

fish density and species richness after only 3 yr of protection (e.g. Halpern & Warner 2002, Russ et al. 2005, Claudet et al. 2006), while in others this recovery took decades (e.g. Micheli et al. 2004, Russ & Alcala 2004, Fung et al. 2013).

A possible reason for the lower than expected biomass of predatory fishes at AR, given its establishment time and protection status, includes the practice of illegal fishing, which has been taking place since the reserve's designation. As observed over the last few years, an increase of AR enforcement, associated with the application of management strategies focusing on environmental education of local communities, is expected to improve the effectiveness of this protected area. However, as in most MPAs around the world, a considerable lag time may exist for educating the public about the importance of protecting these reefs and their associated biota (c.f. Godoy et al. 2006, Gerhardinger et al. 2009, 2011).

CONCLUSIONS

The present study suggests that the Arvoredo Marine Biological Reserve may have critical importance as a refuge for reef species heavily targeted for fisheries (such as groupers) in southern Brazil. However, despite recent efforts in research on the conservation and management of the Brazilian coast, the current protection of less than 1% of the coastline (regarded as no-take areas) and the poor enforcement of the existing no-take/no-entry zones are far from ideal (Gerhardinger et al. 2011). Therefore, the establishment of more protected marine areas that encompass the nursery areas on the Brazilian coast, along with proper enforcement, is critical to the protection of endangered and vulnerable marine species. The removal of key species, such as top predators, has direct and detrimental implications on the size of fish stocks and on the dynamics and structure of the ecosystem. Thus, protecting the reef ecosystem also depends on protecting these species from exploitation.

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Appendix.

Table A1. Frequency of occurrence (FO) and mean number of individuals in 4 size classes (5–10, 11–20, 21–30, >31 cm total length) of 2 fish species (*Epinephelus marginatus* and *Mycteroperca acutirostris*) at reefs around Florianópolis, southern Brazil. Study sites included 3 protected sites in the Arvoredo Marine Reserve (AR) and 5 unprotected sites: 3 islands (UI) and 2 coastal sites (CO). For each site, FO was calculated dividing the absolute frequency of individuals in a size class by the total number of transects (n = 18)

Study sites	5–10 cm		11–20 cm		21–30 cm		>31 cm	
	FO (%)	Mean no. (±SE)	FO (%)	Mean no. (±SE)	FO (%)	Mean no. (±SE)	FO (%)	Mean no. (±SE)
Epinephelus marginatus								
Galé Island (AR)	38.89	0.5 ± 0.19	88.89	2.61 ± 0.49	61.11	1.33 ± 0.34	66.67	1.22 ± 0.35
Deserta Island (AR)	38.89	0.5 ± 0.17	94.44	2.33 ± 0.34	83.33	1.56 ± 0.25	61.11	1.06 ± 0.34
Arvoredo Island (AR)	5.56	0.06 ± 0.06	38.89	0.67 ± 0.24	27.78	0.28 ± 0.11	44.44	0.72 ± 0.23
Aranhas Island (UI)	33.33	0.61 ± 0.22	77.78	2.17 ± 0.42	44.44	0.78 ± 0.25	22.22	0.28 ± 0.14
Xavier Island (UI)	66.67	0.94 ± 0.21	72.22	1.39 ± 0.29	44.44	0.72 ± 0.23	27.78	0.33 ± 0.14
Arvoredo Island (UI)	27.78	0.28 ± 0.11	55.56	0.72 ± 0.19	22.22	0.33 ± 0.18	11.11	0.11 ± 0.08
Cape Araçá (CO)	0	0	16.67	0.22 ± 0.13	16.67	0.17 ± 0.09	0	0
Cape Sepultura (CO)	0	0	22.22	0.28 ± 0.14	33.33	0.33 ± 0.11	5.56	0.06 ± 0.06
Mycteroperca acutirostris								
Galé Island (AR)	0	0	55.56	0.83 ± 0.22	33.33	0.44 ± 0.17	16.67	0.17 ± 0.09
Deserta Island (AR)	0	0	27.78	0.33 ± 0.14	27.78	0.28 ± 0.11	22.22	0.39 ± 0.2
Arvoredo Island (AR)	0	0	16.67	0.22 ± 0.13	22.22	0.28 ± 0.14	66.67	1.94 ± 0.44
Aranhas Island (UI)	5.56	0.11 ± 0.11	38.89	0.5 ± 0.17	22.22	0.22 ± 0.1	16.67	0.17 ± 0.09
Xavier Island (UI)	0	0	38.89	0.61 ± 0.2	27.78	0.33 ± 0.14	11.11	0.11 ± 0.08
Arvoredo Island (UI)	11.11	0.17 ± 0.12	33.33	0.67 ± 0.28	22.22	0.39 ± 0.2	33.33	0.83 ± 0.39
Cape Araçá (CO)	5.56	0.11 ± 0.11	61.11	1.39 ± 0.5	66.67	1.22 ± 0.31	11.11	0.11 ± 0.08
Cape Sepultura (CO)	11.11	0.11 ± 0.08	27.78	0.28 ± 0.11	5.56	0.06 ± 0.06	11.11	0.11 ± 0.08

Fig. A1. Catch of 2 spearfishermen during 3 h of activities at Galé Island, southern Brazil, in 1960: 3 goliath groupers *Epinephelus itajara* (left) and 5 sand tiger sharks *Carcharias taurus* (right) (extracted from Souza 2000)