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Habitat use of five key species of reef fish in rocky reef systems of southern Brazil: evidences of MPA effectiveness

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Abstract

Species functional behaviors amidst the food web, such as feeding ecology in ecosystems, are directly connected to their habitat preferences and use. In reef ecosystems, groupers and sea bass are considered key species, as top-down controllers, regulating the trophic levels on which they feed. Moreover, they are a diversified group of actinopterygian fishes, ranging from 7 to 250 cm of total length and inhabiting many types of reef habitats, from shallow waters up to 200 m deep. Due to the exceptional ecological and commercial importance of groupers and sea bass to the rocky reef systems of southwestern Atlantic and considering the small amount of information on their behavior and habitat use available for this particular region, three questions have emerged. First, how are the species spatially distributed considering the topography complexity of their environment? Second, do large Epinephelids and small Serranids have the same use of the water column, when foraging (e.g., position related to the substrate)? Third, do marine protected areas influence the distributional patterns of both families? To answer these questions, we assessed the spatial distribution and habitat use of two dominant species of groupers (*Epinephelus marginatus*, *Mycteroperca acutirostris*) and three species of sea bass (*Diplectrum radiale* and *Serranus flaviventris* and *S. baldwini*), using underwater visual census at Santa Catarina State, southern Brazil, during the austral summers of 2010 and 2011. All of the five sympatric species studied are directly associated with specific topographic characteristics that may be related to shelter as well as to reproduction and feeding. Except for *M. acutirostris*, which was mainly recorded foraging in the water column, all the remaining species are benthic dwellers. Significant evidences of effectiveness advocate that Arvoredo Marine Biological Reserve has critical importance as a refuge for heavily targeted reef species in southern Brazil, such as *E. marginatus* and *M. acutirostris*. The establishment of more protected marine areas that encompass the nursery areas near AR, along with proper enforcement, is critical to the protection of endangered and vulnerable marine species. The present work has contributed to the knowledge of habitat use and partitioning of some key reef fishes, especially target species, which is critical to effective conservation measures, including the design and management of MPAs.

Keywords Groupers · Sea bass · Arvoredo Biological Marine Reserve · Top predators · MPA management

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Introduction

One of the many challenges in studies of biodiversity is to understand the role that environmental variables play affecting the behavior and distribution of morphologically similar species that are frequently present in natural communities (Connell 1980; Schmitt and Coyer 1982; Schoener 1974; Wagner et al. 2012). Moreover, understanding the factors that enable the long-term presence and co-occurrence of potential competitors, as closely related species, also challenge marine ecologists (Connell 1980; Schmitt and Coyer 1982; Schoener 1974; Wagner et al. 2012). Rocky reefs extensively occur between Espírito Santo and Santa Catarina States (Floeter et al. 2001), but in spite of their biological importance, ecological studies focusing on rocky shore fish assemblages are still relatively scarce (Anderson 2017; Anderson et al. 2015; Gibran and Moura 2012; Neves et al. 2016).

Epinephelidae (groupers) and Serranidae (sea bass) fishes are examples of closely related taxa also considered as key organisms of reef systems, due to their ecological role in regulating community structure as top predators (Almany 2004; Almany and Webster 2004; Anderson et al. 2014; Craig et al. 2011; Sadovy de Mitcheson et al. 2013, Sadovy et al. 1994). Besides their ecological relevance, some species are also considered commercially important for artisanal and speargun fisheries (Anderson et al. 2014; Figueiredo and Menezes 1980; Medeiros et al. 1997; Freitas et al. 2011).

Groupers and sea bass are diversified groups of actinopterygian fishes ranging from 7 cm (e.g., lantern bass, *Serranus baldwini*) to 250 cm (e.g., goliath grouper, *Epinephelus itajara*) in total length, and they typically inhabit sandy, coral, and rocky bottoms in both shallow waters and waters of depths up to 200 m, living in caves, crevices, and depressions inside soft bottoms and on ledges (Anderson et al. 2014; Craig et al. 2011; Gibran 2007). They can also be substrate-associated, displaying territoriality and dominant behavior (Gibran 2007; Kline et al. 2011). These taxa include complex, long-living species, with organized social structures and complex sexual behaviors (Anderson et al. 2014; Craig et al. 2011). Some species are clearly more susceptible to overfishing based on their reproductive characteristics, such as sex change, or aggregation spawning behavior (Anderson et al. 2014; Carter et al. 1994; Freitas et al. 2011; Olsen and LaPlace 1979; Sadovy et al. 1994). Despite their prominent influence on the trophic structure, and thus, function of reef systems, they have dramatically declined in size structure and numbers of individuals since the end of the past century due to overfishing, with some species having a population reduction of up to 90% in some regions of the world (Sadovy de Mitcheson et al. 2013).

Due to the exceptional ecological and commercial importance of groupers and sea bass to the rocky reef systems of the southwestern Atlantic (Anderson et al. 2014; Gibran 2007), and considering the small amount of information on their behavior and habitat use available for this particular region (Anderson et al. 2014; Gibran 2007), three questions have emerged. First, how are the species spatially distributed considering the topography complexity of their environment? Second, do large epinephelids and small serranids have the same use of the water column, when foraging (e.g., position related to the substrate)? Third, do marine protected areas influence the distributional patterns of both families? Herein, we evaluated habitat use of two species of groupers (*Epinephelus marginatus* and *Mycteroperca acutirostris*) and three species of bass (*Diplectrum radiale* and *Serranus flaviventris* and *S. baldwini*) in a marine reserve in southern Brazil (Arvoredo Biological Marine Reserve). The knowledge on habitat use and behavior of reef fishes, especially target species, is critical to effective conservation measures, including the design and management of marine protected areas (MPAs) (Anderson et al. 2014; García-Charton et al. 2008; Spedicato et al. 2005).

Materials and Methods

Study area

Field work was carried out in the coast of Santa Catarina State, southern Brazil (25° 57′ 41″ S and 29° 23′ 55″ W), an area which represents ~ 7% of the Brazilian coastline (Anderson et al. 2015; Diehl and Horn Filho 1996) (Fig. 1). Such portion of Brazilian coastline is considered the southernmost limit for most tropical reef fish species in the southwestern Atlantic (Anderson 2017; Anderson et al. 2015, 2017). In Brazil, rocky reefs extensively occur between Espírito Santo and Santa Catarina States (Floeter et al. 2001). The geomorphology of these coastal rocky bottoms is characterized mainly by Precambrian basaltic and granitic rocks (Anderson et al. 2015; Basei et al. 1992).

Sampling was conducted inside the no-take zone of Arvoredo Marine Biological Reserve (AR) and around it. Arvoredo MPA is located about 11 km off northern Florianópolis (Fig. 1). Arvoredo has been designated a no-take marine protected area since 1990 and encompasses 17,800 ha. In 2000, AR officially became a no-entry area, where harvesting and human presence are strictly forbidden by law (researchers and managers exempted) (Anderson et al. 2014).

To evaluate MPA effectiveness, a beyond BACI approach (Underwood 1997) was used by establishing the contrast between the protected area and two unprotected ones. In each area, three sectors were randomly located except at Sector 1 which held only two sampling sites due to poor water visibility conditions: Sector 1, unprotected sites located at the coast encompassing, Cape Araçá and Cape Sepultura; Sector 2,

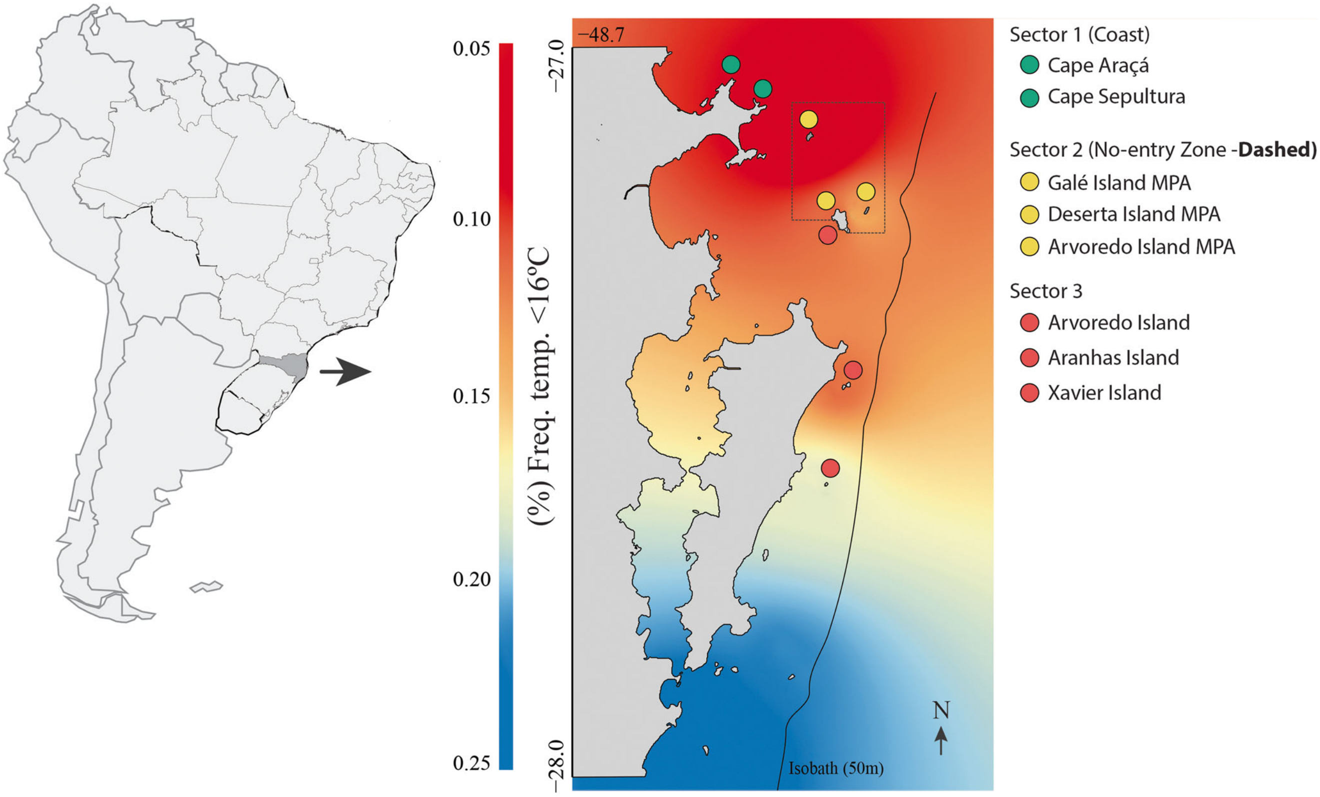

Fig. 1 Study area. The dashed polygon represents the limits of the MPA of Arvoredo Marine Biological Reserve. The colored points indicate the study sites for each sector (from north to south, respectively). Sector 1—northwest coastal portion: (green points) Cape Araçá (Porto Belo City) and Cape Sepultura (Bombinhas City); Sector 2—no-entry zone: (yellow points) Galé, Deserta, and Arvoredo Islands; Sector 3—southern insular portion: (red points) Arvoredo, Aranhas, and Xavier Islands. Temperature colours indicate the frequency of occurrence of temperatures below 16 C

protected sites including Arvoredo (no-entry portion), Deserta, and Galé Islands; and Sector 3, unprotected sites represented by Aranhas, Xavier, and no-protected portion of Arvoredo Islands (Fig. 1). In total, we sampled eight sites and all data were recorded during the austral summers of 2010 and 2011.

Fish counts and habitat characterization

Data on habitat use, fish abundance, and individual sizes were assessed by an underwater visual census technique using SCUBA diving within strip transects, a nondestructive and effective methodology (Floeter et al. 2007). The density and biomass of species were used to evaluate the patterns of habitat use.

Two distinct depth strata (i.e., slopes and interfaces) were considered: (1) slopes, rocky complex habitats along the distance from water surface to half of total reef depth (TD); and (2) interfaces, which correspond to the transition zone between rocky (slope) to soft (mostly sandy) bottoms (Anderson 2017; Anderson et al. 2015).

A total of 144 transects were conducted covering a total area of 17.280 m^2. In each site, 18 transects of 30 m in length by 4 m in width (120 m^2 of sampled area) were conducted, totaling 2.160 m^2 for all of three sectors (Fig. 1). Transect dimensions were selected considering species ecology, shelter availability, and water transparency (Anderson et al. 2014). Water transparency during sampling ranged from 4 to 12 m, and minimum reef depth reached during the study was 2.5 m at Cape Sepultura and the deepest was 23 m at Xavier Island.

Fish individuals were counted while the diver unrolled the tape measure along the length of transects then categorized within size classes of 5-cm interval. The biomass was estimated by weight-length relationship for each species (Froese and Pauly 2017). The spatial distribution [e.g., distance of each fish from the bottom (including if it was sheltered), and position in the water column] was also recorded together with the body size of each fish individual. While rolling back the tape measure, the diver also recorded environmental data at every 5 m. Environmental variables included (1) rugosity [topographic diversity recorded following a visual scale in which 1 was one type topography (e.g., rocky reefs slope) of relief and 5 was the most complex topography (e.g., intersection among rocky reefs, sandy bottoms, and rodolith beds)]; (2) rocky reef slope (in grades); (3) number of small (radius = $r < 10$ cm), medium ($r = 10$–50 cm) and large rocky boulders ($r > 50$ cm); and (4) number of small (opening = $o < 10$ cm), medium ($o = 10$–50 cm), and large holes/shelters ($o > 50$ cm) (Anderson 2017).

Water temperature was measured with data loggers (HOBO® Data Logger UA-002) installed on the rocky reefs of Galé, Deserta, Arvoredo, and Xavier Islands by divers during sampling expeditions from 2012 to 2016. Each data logger was fixed on the bottom with epoxy resin. Eight data loggers were installed: four on the "shallow" (slope) stratum and four on the "intermediate" (interface).

Data analysis

To assess and define the rocky reef topographic similarities among sites, we calculated the Bray-Curtis similarity on environmental "Hellinger"-transformed data (Clarke and Warwick 1994; Legendre and Gallagher 2001). The results were subjected to the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster analysis. A cophenetic correlation test was performed to verify how faithfully the dendrogram preserved the pairwise distances between the original data (Sokal and Rohlf 1962). A similarity profile test (SIMPROF) was performed to test the significance of the cluster branches (SIMPROF, $p < 0.05$) (Legendre and Legendre 2012). A generalized linear model (GLM/ "Poisson") was used to test differences in species biomass distributions among sites (Faraway 2016). Redundancy analysis (RDA) was applied on species biomass "Hellinger" transformed data (Clarke and Warwick 1994; Legendre and Gallagher 2001), to explore and highlight tendencies and patterns of species distribution and habitat use (spatial distribution of species). Such technique summarizes linear relationships between components of response variables with a set of explanatory variables (Legendre and Legendre 2012; ter Braak 1994). The RDA analysis extends multiple linear regression (MLR) by allowing regression of multiple response variables on multiple explanatory variables. A matrix of the fitted values of all response variables generated through MLR is then subject to principal component analysis (PCA) (Legendre and Legendre 2012; ter Braak 1994). Such a statistical method is considered more accurate for small biogeographical gradients (García-Charton and Pérez-Ruzafa 2001; Legendre and Birks 2012; Legendre and Legendre 2012; ter Braak 1994). Redundancy analysis was carried out using the R package Vegan (Oksanen et al. 2007, 2010). Statistical analyses were performed using the computing environment R (R Development Core Team 2017).

Results

Habitat structure and its use by the studied fishes

Fourteen species of Serranids were detected during this work. Seven species of sea bass (Serranidae): *Diplectrum formosum* and *D. radiale*; *Dules Auriga*; *Serranus atrobranchus*, *S. baldwini*, and *S. flaviventris*; and *Paranthias furcifer*, none of them included in the IUCN red list of endangered species. Seven species of highly targeted groupers (Epinephelidae): *Epinephelus marginatus* (EN-IUCN) and *E. morio* (NT-IUCN); *Hyporthodus niveatus* (VU-IUCN); *Mycteroperca acutirostris* (LC-IUCN), *M. bonaci* (NT-IUCN), *M. intertitialis* (VU-IUCN), and *M. microlepis* (LC-IUCN) (Anderson et al. 2014). Five dominant species were selected considering their densities and biomass (in decreasing order): *E. marginatus*, *M. acutirostris*, *D. radiale*, *S. flaviventris*, and *S. baldwini*.

The topography of Arvoredo Island, as well as that of Aranhas, Galé, and Deserta Islands, are mostly characterized by small rocks (blocks $r < 10$ cm), medium rocks (blocks $r < 50$ cm), and large rocks (blocks $r > 50$ cm) which provides correspondingly habitat complexity, rugosity (habitat diversity), and shelter availability. Among all the studied sites, Arvoredo Island has the largest reef area. Large rodolith beds, consisting of nodules of marine benthic coralline algae, formed by numerous small round calcareous structures, are mostly found in Arvoredo, Deserta, and Galé Islands (Anderson et al. 2014). The topography of Aranhas Island is further characterized by the presence of two small granitic islands of similar size. Most of the reef area of the smaller western island is characterized by very large boulders which increases the inclination of the reef area (slope). The rocky bottom of Xavier Island is similar to that of Arvoredo Island MPA; otherwise, the biomass of fish inhabiting the islands outside the MPA is significantly smaller (GLM $p < 0.05$), reiteratively evidencing the effectiveness of Arvoredo MPA. Sites at Cape Araçá and Cape Sepultura showed low structural complexity, with a short vertical rocky reef area (maximum depth of 5 m). Cape Araça's bottom consists mostly of small granitic and basaltic rocks that form a large number of small holes for shelter. The shallow bottom of Cape Sepultura is mostly sandy. Otherwise, the abrupt changes in topographic structure of the reef (e.g., from slope to sandy bottom) confers modest complexity to these particular sites (Fig. 3a).

Despite the environmental characteristics of each site [e.g., large rodolith beds in Arvoredo MPA and Galé MPA, higher topographic complexity in Deserta MPA, lower minimum temperatures during austral summers in Aranhas and Xavier Islands ($\% < 16$ °C), etc.] (Fig. 1), significant topographic similarities among sites were highlighted in the cluster (Fig. 2). Otherwise, the densities and biomass of large targeted Epinephelidae were directly influenced by the MPA no-entry zone effectiveness. For example, the dusky grouper *E. marginatus* (EN-IUCN) presented the respective biomass: 50.20 kg of total mean biomass Galé MPA, 34.52 kg in Deserta MPA, 13.90 kg in Arvoredo MPA, 4.99 kg in Arvoredo Island, 10.15 in Aranhas Island, 10.16 in Xavier Island, 3.14 kg in Cape Araçá, and 0.78 kg in Cape Sepultura (Fig. 2, Table 1).

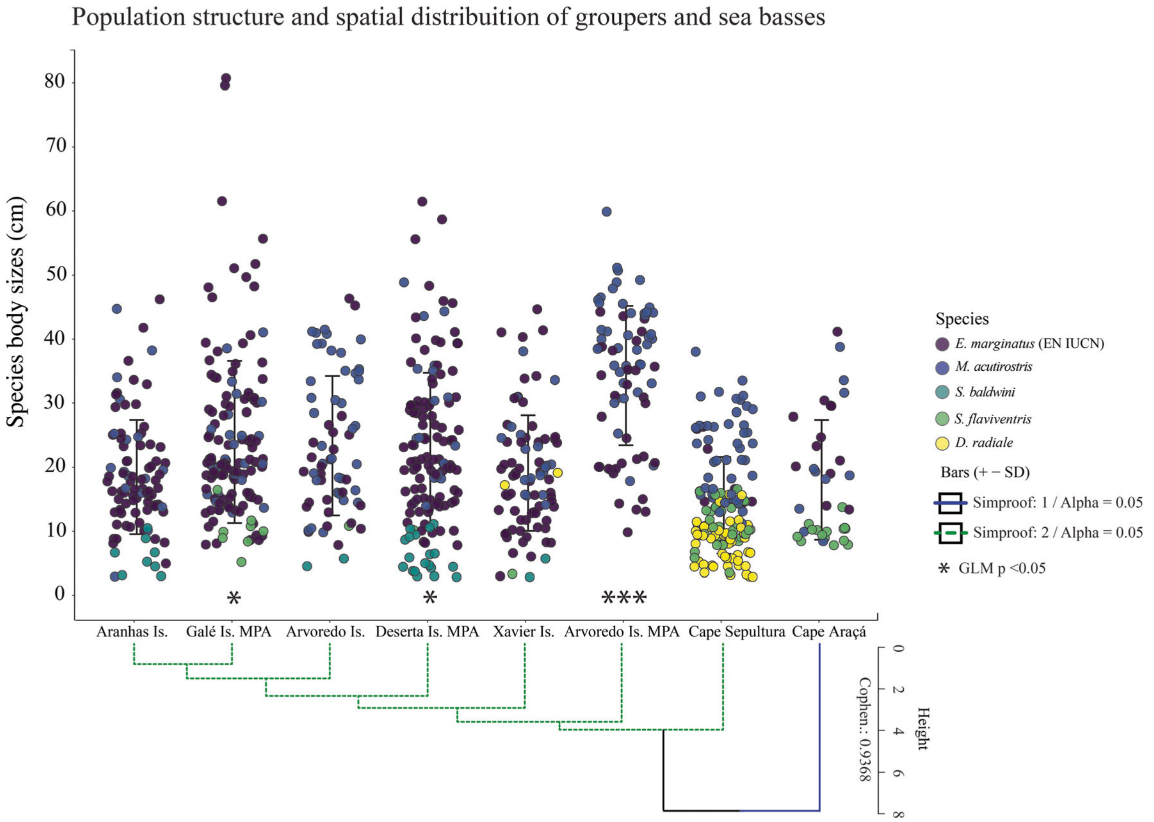

Fig. 2 Population structure and spatial distributions of species among sites. The points show species sizes and distributions among sites. Asterisks represent significant differences among sites, considering species biomass (GLM $p < 0.05$). Graphical dendrogram representation of the UPGMA cluster analysis applied to Bray-Curtis similarity among sites calculated on Hellinger-transformed environmental data. Blue and dashed green branches indicate significantly similar groups based on the similarity profile (SIMPROF) test ($p < 0.05$) which suggests the structure is not random. Cophenetic correlation (0.93) measures how the original dissimilarity structure is preserved by the dendrogram

The RDA emphasized tendencies of distribution of species according to their densities and environmental variables (Legendre and Legendre 2012; ter Braak 1986; ter Braak 1994). Targeted species, such as dusky grouper *E. marginatus* (Endangered-IUCN), showed a pattern of distribution positioned near “Small rocks”, which can be explained by the large number of small/juvenile individuals (< 30 cm TL) recorded herein (Figs. 2 and 3a). The lantern bass *Serranus baldwini* was mostly associated with rodolith beds, at Deserta Island. It is the only Serranidae species with an important density biomass inside the no-entry zone. The twinspot bass *S. flaviventris* and the pond perch *D. radiale* were mostly detected at Cape Araçá and Cape Sepultura in shallow areas having a maximum depth of 5 m and at reef interfaces with sandy bottom (Fig. 3a). Temperature seemed not to affect the distributions of the species.

Individuals of *E. marginatus* were recorded inside, or close to their shelters, and the few individuals positioned in the water column were never found vertically higher than 1 m. Most *M. acutirostris* individuals were recorded in the water column at 1 m above the substrate. Individuals of *S. baldwini* were recorded on rodolith beds mostly at Deserta and Galé Islands. Individuals of *S. flaviventris* were mostly recorded at sites located along the coast at Cape Araçá and Cape Sepultura, exclusively inhabiting the interfaces. Most *D. radiale* individuals were exclusively associated with soft substrate and never recorded in the water column (Fig. 3b).

Discussion

Our findings on habitat use by the Epinephelidae (*E. marginatus* and *M. acutirostris*) and Serranidae (*S. baldwini*, *S. flaviventris*, and *D. radiale*) show that these species are all directly associated with the structural topography of the environment and habitat conditions (Figs. 2, 3) (Gibran 2007).

Most individuals of *E. marginatus* (EN-IUCN) recorded herein were juveniles < 30 cm TL ($n = 293$ individuals; 72.16%) and were positioned mainly inside or close to their shelters, with a few individuals positioned in the water column, but never vertically higher than 1 m above the bottom. Such habitat association tends to be closely related to the necessity for shelter, which seems to be an important factor

Table 1 Species frequency of occurrence (FO%) and mean (± standard error, SE) abundance by sites for each of the four size classes (5–10, 10–20, 20–30, > 30 cm of total length, TL) considered in this study. Large Epinephelidae individuals (> 30 cm TL) remained rare outside the MPA

Species	FO%	Galé Island MPA							
	5–10	Mean ± SE	10–20	Mean ± SE	20–30	Mean ± SE	> 30	Mean ± SE	Dens./site
E. marginatus	8.82	3 ± 1.73	46.08	15.66 ± 2.08	23.53	8 ± 1.42	21.57	7.33 ± 1.06	102
M. acutirostris	0.00	0 ± 0	57.69	5 ± 1.12	30.77	2.66 ± 0.88	11.54	1 ± 0.57	26
D. radiale	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
S. flaviventris	100.00	2.66 ± 1.02	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	8
S. baldwini	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
		Deserta Island MPA							
	5–10	Mean ± SE	10–20	Mean ± SE	20–30	Mean ± SE	> 30	Mean ± SE	Dens./site
E. marginatus	9.18	3 ± 1.73	42.86	14 ± 1.87	28.57	9.33 ± 1.53	19.39	6.33 ± 0.13	98
M. acutirostris	0.00	0 ± 0	33.33	2 ± 0.81	27.78	1.66 ± 0.68	38.89	2.66 ± 0.54	18
D. radiale	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
S. flaviventris	100.00	0.33 ± 0.57	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	1
S. baldwini	100.00	6.33 ± 0.8	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	19
		Arvoredo Island MPA							
	5–10	Mean ± SE	10–20	Mean ± SE	20–30	Mean ± SE	> 30	Mean ± SE	Dens./site
E. marginatus	3.23	0.33 ± 0.57	38.71	4 ± 1.15	16.13	1.66 ± 0.93	41.93	4.33 ± 0.32	31
M. acutirostris	0.00	0 ± 0	9.09	1.33 ± 0.76	11.36	1.66 ± 0.93	79.55	12.66 ± 0.65	44
D. radiale	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
S. flaviventris	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
S. baldwini	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
		Arvoredo Island							
	5–10	Mean ± SE	10–20	Mean ± SE	20–30	Mean ± SE	> 30	Mean ± SE	Dens./site
E. marginatus	19.23	1.66 ± 1.29	50.00	4.33 ± 0.8	23.08	2 ± 0.7	7.69	0.66 ± 0.81	26
M. acutirostris	8.11	1 ± 1	32.43	4 ± 0.5	18.92	2.33 ± 0.57	40.54	5 ± 1.18	37
D. radiale	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
S. flaviventris	100.00	0.33 ± 0.57	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	1
S. baldwini	100.00	0.66 ± 0.81	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	2
		Aranhas Island							
	5–10	Mean ± SE	10–20	Mean ± SE	20–30	Mean ± SE	> 30	Mean ± SE	Dens./site
E. marginatus	15.94	3.66 ± 1.39	56.52	13 ± 1.88	20.29	4.66 ± 0.93	7.25	1.66 ± 0.51	69
M. acutirostris	11.11	0.66 ± 0.4	50.00	3 ± 0.88	22.22	1.33 ± 0.76	16.67	1 ± 0	18
D. radiale	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
S. flaviventris	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
S. baldwini	100.00	2.66 ± 0.73	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	8
		Xavier Island							
	5–10	Mean ± SE	10–20	Mean ± SE	20–30	Mean ± SE	> 30	Mean ± SE	Dens./site
E. marginatus	27.87	5.66 ± 1.78	40.98	8.33 ± 1.47	21.31	4.33 ± 1.42	9.84	2 ± 0.4	61
M. acutirostris	0.00	0 ± 0	57.89	3.66 ± 0.75	31.58	2 ± 1.08	10.53	0.66 ± 0.4	19
D. radiale	0.00	0 ± 0	100.00	0.66 ± 0.4	0.00	0 ± 0	0.00	0 ± 0	2
S. flaviventris	100.00	0.33 ± 0.57	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	1
S. baldwini	100.00	0.66 ± 0.4	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	2
		Cape Araçá							
	5–10	Mean ± SE	10–20	Mean ± SE	20–30	Mean ± SE	> 30	Mean ± SE	Dens./site
E. marginatus	0.00	0 ± 0	57.14	1.33 ± 1.15	42.86	1 ± 1	0.00	0 ± 0	7
M. acutirostris	3.92	0.66 ± 0.81	49.02	8.33 ± 1.3	43.14	7.33 ± 1.07	3.92	0.66 ± 0.81	51
D. radiale	92.59	16.66 ± 1	7.41	1.33 ± 0.57	0.00	0 ± 0	0.00	0 ± 0	54
S. flaviventris	58.82	6.66 ± 1.61	41.18	4.66 ± 2.16	0.00	0 ± 0	0.00	0 ± 0	34

Table 1 (continued)

Species	FO%	Galé Island MPA							
	5–10	Mean ± SE	10–20	Mean ± SE	20–30	Mean ± SE	> 30	Mean ± SE	Dens./site
S. baldwini	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
		Cape Sepultura							
	5–10	Mean ± SE	10–20	Mean ± SE	20–30	Mean ± SE	> 30	Mean ± SE	Dens./site
E. marginatus	0.00	0 ± 0	41.67	1.66 ± 0.51	50.00	2 ± 0.4	8.33	0.33 ± 0.57	12
M. acutirostris	27.27	1 ± 1	45.45	1.66 ± 0.51	9.10	0.33 ± 0.57	18.18	0.66 ± 0.81	11
D. radiale	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0
S. flaviventris	100.00	5 ± 2.01	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	15
S. baldwini	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0.00	0 ± 0	0

in determining their occurrence (Derbal and Kara 1995; Gibran 2007; La Mesa et al. 2002; Parrish 1987; Smith 1961) (Figs. 2, 3a). Juveniles of *E. marginatus* avoid foraging distant from their shelters (Gibran 2007). During this initial ontogenetic stage, when individuals are more versatile in their feeding habits than adults (consuming a myriad of small marine invertebrate species, mostly small crabs), but also more vulnerable to predation, topographic variables providing shelter seem more limiting than food resources (Gibran 2007; Machado et al. 2003; Sluka et al. 1994, 1996; Sluka and Sullivan 1998).

Individuals of *M. acutirostris* (fast-swimming epinephelids) are more opportunistic and versatile predators than *E. marginatus* due to ecomorphological attributes such as body and caudal fin shape (e.g., slender body with truncated tail) (Gibran 2007). They feed both on benthic crustaceans and small schooling fishes (Bonaldo et al. 2004; Gibran 2007; Sazima 1986). Accordingly, *M. acutirostris* individuals were recorded in the water column positioned mostly at 1 m above the substrate (Fig. 3b), a phenomenon which corroborates the hypothesis that they are not conditioned to shelter availability, but rather to food resources in complete contrast to *E. marginatus* individuals which surprise their prey mostly near the bottom and never far from their shelters (Bonaldo et al. 2004; Gibran 2007; Sazima 1986) (Fig. 3b). Another important aspect regarding *M. acutirostris* predation strategies compared to those of *E. marginatus* is the versatile ability of rapidly changing color patterns (in less than 10 s) to match the environment (camouflage) (Anderson, A. B. pers. obs; Fig. 4). Considering the limited underwater visibility of the water (< 12 m) in these reefs most of the year, it could be considered as another morphological attribute to consider when analyzing the success of *M. acutirostris* against their prey as compared to other studied species (Fig. 4).

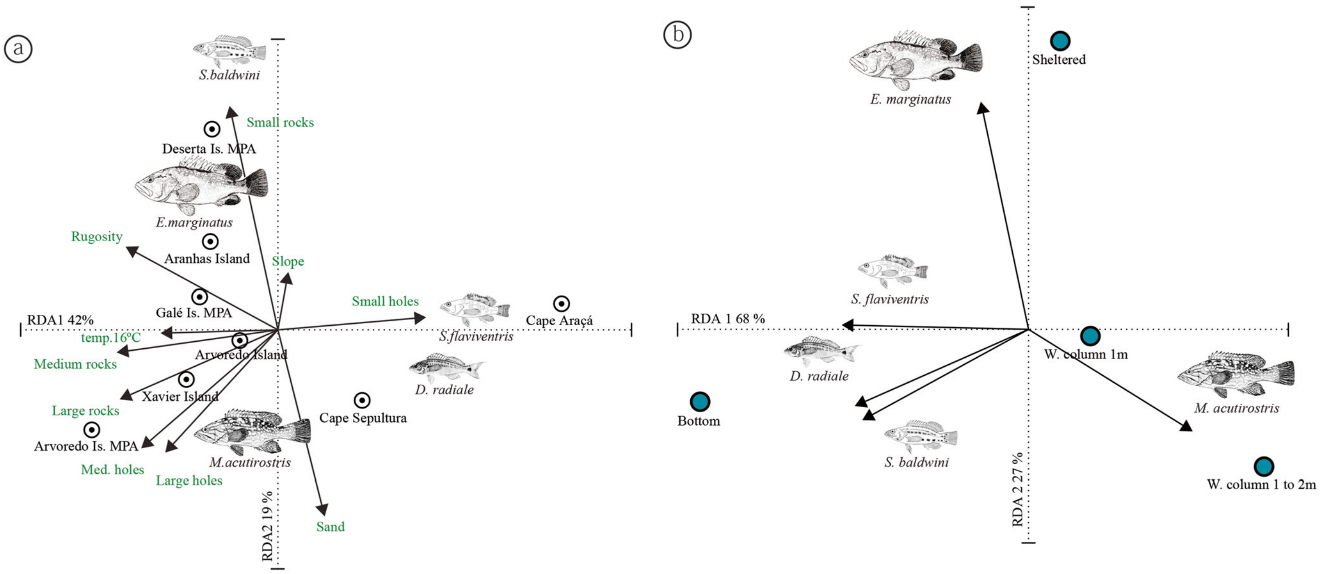

Fig. 3 Redundancy analyses (RDA): **a** species distribution of among sites (circles with black dots), according to their biomass and environmental variables (black arrows); **b** blue circles show the distribution of species according to their position in the water column (1 m, 2 m over the bottom), and habitat use on the substrate, either sheltered or on the bottom

Fig. 4 Three different cryptic patterns of *M. acutirostris* while foraging on different types and colors of substrate: **a** near red algae; **b** near green algae and sand interface; **c**, **d** near white bluish sand bottom. Images taken at Arvoredo Island MPA from 2011 to 2012 by Anderson, A. B

The relatively smaller species of the Serranidae family are mostly associated with soft, low-complexity bottoms, such as gravel or mud, or rodolith beds (Gibran 2007; Gibran and Moura 2012; Petersen and Fischer 1986). These three serranid species all presented a similar pattern of habitat use; most individuals were recorded at the interface between the rocky reefs and the soft bottoms (Figs. 2, 3a,b). However, while *S. flaviventris* and *D. radiale* individuals were mainly recorded over the soft coastal bottoms with small holes at Cape Araçá and Cape Sepultura, *S. baldwini* was more associated with rocky areas outside sheltered sectors. This spatial segregation between these two species was also reported by Gibran and Moura (2012). Most individuals of *D. radiale* are exclusively associated with unconsolidated substrate, as observed herein (Gibran 2007).

Coastal sites are usually characterized by high levels of anthropogenic activities, including recreational fishing and spearfishing, small vessel boat traffic, freshwater runoff, and sewage disposal, besides shallower waters, which may explain the low occurrence of large Epinephelidae species in these sites (Fig. 2, Table 1) (see Gibran and Moura 2012). Otherwise, lower density of *S. flaviventris* and *D. radiale* at insular sites may be caused by their habitat preferences or/and by the large number of groupers (sea bass predators) recorded in these sites (Sluka et al. 1996).

Arvoredo MPA evidences of effectiveness and management

The present study corroborates that Arvoredo Marine Biological Reserve has a critical importance as a refuge for heavily targeted reef species such as groupers in southern Brazil (Anderson et al. 2014). However, the productivity of AR in terms of density and biomass of groupers and sea bass can be considered low, when considering the size (17,800 ha) and age (nearly 30 years since implementation) of this particular MPA (Anderson et al. 2014).

When compared to other effective and highly productive MPAs worldwide (Aburto-Oropeza et al. 2011; García-Charton et al. 2008), AR seem to have severe management problems (Anderson et al. 2014). The recent decline on recruitment of several species (including groupers and sea bass) residing at AR points towards the degradation of nursery areas on its vicinity (e.g., mangroves and tide pools) (Anderson 2017; Harmelin and Harmelin-Vivien 1999; Machado et al. 2003). The design of new or the enlargement of already existing MPAs should include the habitat for the whole life cycle of emblematic fish species (Cheminée et al. 2017). Therefore, the establishment of more protected marine areas that encompass the nursery areas near AR, along with proper enforcement (Giakoumi et al. 2017), is critical to the protection of endangered and vulnerable marine species.

In the past decade, several monitoring programs have been implemented and conducted synergically with ICMBio (Instituto Chico Mendes, Brazil), the governmental institution responsible for the management of AR. Enforcements dedicated to eradicate illegal fisheries and restore nursery areas have been increased over the years and results are beginning to emerge. Systematic annual monitoring campaigns have been conducted inside and around AR MPA since 2002 and local scientists are optimistic regarding the future of this particular MPA (Anderson 2017).

Conclusion

Topographic variables describing structural habitat, as shelter availability and reef complexity (i.e., rugosity and topographic heterogeneity), tend to directly influence rocky reef fishes' distribution and habitat use, such as the Epinephelidae and Serranidae fishes studied herein. Therefore, the present study has contributed to the knowledge of habitat use and, thus, spatial partitioning of some key target species. Such information may be a valuable tool to improve the knowledge of managers of existing MPAs along the Brazilian coast, and also contribute to the design of future MPAs which are going to be implemented in a near future (Anderson et al. 2014; García-Charton et al. 2004; Spedicato et al. 2005).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities.

References

Aburto-Oropeza O, Erisman B, Galland GR, Mascareñas-Osorio I, Sala E, Ezcurra E (2011) Large recovery of fish biomass in a no-take marine reserve. PLoS One 6:e23601

Almany GR (2004) Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology 85:2872–2880. https://doi.org/10.1890/03-3166

Almany GR, Webster MS (2004) Odd species out as predators reduce diversity of coral-reef fishes. Ecology 85:2933–2937. https://doi.org/10.1890/03-3150

Anderson AB (2017) Peixes tropicais no seu limite de distribuição: dinâmica temporal da ictiofauna recifal no Sul do Brasil. Ph.D. thesis. Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brasil-202 p

Anderson A, Bonaldo R, Barneche D, Hackradt C, Félix-Hackradt F, García-Chartón J, Floeter S (2014) Recovery of grouper assemblages indicates effectiveness of a marine protected area in southern Brazil. Mar Ecol Prog Ser 514:207–215

Anderson AB, Carvalho-Filho A, Morais RA, Nunes LT, Quimbayo JP, Floeter SR (2015) Brazilian tropical fishes in their southern limit of distribution: checklist of Santa Catarina's rocky reef ichthyofauna, remarks and new records. 2015:11. https://doi.org/10.15560/11.4.1688

Anderson AB, Salas EM, Rocha LA, Floeter SR (2017) The recent colonization of south Brazil by the Azores chromis *Chromis limbata*. J Fish Biol 91:558–573. https://doi.org/10.1111/jfb.13363

Basei MA, Siga O Jr, Machiavelli A, Mancini F (1992) Evolução tectônica dos terrenos entre os Cinturões Ribeira e Dom Feliciano (PR-SC). Rev Bras Geosci 22:216–221

Bonaldo RM, Krajewski JP, Sazima I (2004) Does the association of young fishes with jellyfishes protect from predation? A report on a failure case due to damage to the jellyfish. Neotropical Ichthyology 2:103–105

Carter J, Marrow GJ, Pryor V (1994) Aspects of the ecology and reproduction of Nassau grouper (*Epinephelus striatus*) off the coast of Belize, Central America

Cheminée A et al (2017) Shallow rocky nursery habitat for fish: spatial variability of juvenile fishes among this poorly protected essential habitat. Mar Pollut Bull 119:245–254. https://doi.org/10.1016/j.marpolbul.2017.03.051

Clarke K, Warwick R (1994) An approach to statistical analysis and interpretation. In: Change in Marine Communities, vol 2, pp 117–143

Connell JH (1980) Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131–138. https://doi.org/10.2307/3544421

Craig MT, Sadovy de Mitcheson Y, Heemstra PC (2011) Groupers of the world. Published by NISC, Grahamstown 402p

Derbal F, Kara M (1995) Habitat et comportement du mérou *Epinephelus marginatus* dans la région d'Annaba (Algérie). Cah Biol Mar 36:29–32

Diehl FL, Horn Filho N (1996) Compartimentação geológico-geomorfológica da zona litorânea e planície costeira do Estado de Santa Catarina Notas Técnicas 9:39–50

Faraway JJ (2016) Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models, vol 124. CRC press, Boca Raton

Figueiredo J, Menezes N (1980) Manual de peixes do sudeste do Brasil IV. Teleostei, Museu de Zoologia da Universidade de São Paulo

Floeter SR, Guimarães RZP, Rocha LA, Ferreira CEL, Rangel CA, Gasparini JL (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. Glob Ecol Biogeogr 10:423–431. https://doi.org/10.1046/j.1466-822X.2001.00245.x

Floeter SR, Krohling W, Gasparini JL, Ferreira CEL, Zalmon IR (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. Environ Biol Fish 78:147–160. https://doi.org/10.1007/s10641-006-9084-6

Freitas MO, Leão de Moura R, Bastos Francini-Filho R, Viviana Minte-Vera C (2011) Spawning patterns of commercially important reef fish (Lutjanidae and Serranidae) in the tropical western South Atlantica. 75:12. https://doi.org/10.3989/scimar.2011.75n1135

Froese R, Pauly D (2017) Fishbase. http://www.fishbase.org. Accessed 08/21/2017

García-Charton JA, Pérez-Ruzafa Á (2001) Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. Mar Biol 138:917–934. https://doi.org/10.1007/s002270000524

García-Charton JA, Pérez-Ruzafa Á, Sánchez-Jerez P, Bayle-Sempere JT, Reñones O, Moreno D (2004) Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. Mar Biol 144:161–182. https://doi.org/10.1007/s00227-003-1170-0

García-Charton JA et al (2008) Effectiveness of European Atlanto-Mediterranean MPAs: do they accomplish the expected effects on populations, communities and ecosystems? J Nat Conserv 16:193–221. https://doi.org/10.1016/j.jnc.2008.09.007

Giakoumi S, Scianna C, Plass-Johnson J, Micheli F, Grorud-Colvert K, Thiriet P., Claudet J, Di Carlo G, Di Franco A, Gaines S, García-Charton JA, Lubchenco J, Reimer J Guidetti P (2017) Marine protected areas in the crowded mediterranean sea: assessing ecological effects of full and partial protection. Sci Rep 7:8940. https://doi.org/10.1038/s41598-017-08850-w

Gibran FZ (2007) Activity, habitat use, feeding behavior, and diet of four sympatric species of Serranidae (Actinopterygii: Perciformes) in southeastern Brazil. Neotrop Ichthyol 5:387–398

Gibran FZ, Moura RL (2012) The structure of rocky reef fish assemblages across a nearshore to coastal islands' gradient in southeastern Brazil. Neotrop Ichthyol 10:369–382

Harmelin J-G, Harmelin-Vivien M (1999) A review on habitat, diet and growth of the dusky grouper *Epinephelus marginatus* (Lowe, 1834). Marine Life 9:11–20

Kline RJ, Khan IA, Holt GJ (2011) Behavior, color change and time for sexual inversion in the protogynous grouper (*Epinephelus adscensionis*). PLoS One 6:e19576

La Mesa G, Louisy P, Vacchi M (2002) Assessment of microhabitat preferences in juvenile dusky grouper (*Epinephelus marginatus*) by visual sampling. Mar Biol 140:175–185. https://doi.org/10.1007/s002270100682

Legendre P, Birks HJB (2012) From classical to canonical ordination. In: Birks HJB, Lotter AF, Juggins S, Smol JP (eds) Tracking environmental change using lake sediments: data handling and numerical techniques. Springer Netherlands, Dordrecht, pp 201–248. https://doi.org/10.1007/978-94-007-2745-8_8

Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280. https://doi.org/10.1007/s004420100716

Legendre P, Legendre LF (2012) Numerical ecology, vol 24, 2nd English edn. Elsevier, Amsterdam

Machado LF, Bertoncini ÁA, Hostim-Silva M, Barreiros JP (2003) Habitat use by the juvenile dusky grouper *Epinephelus marginatus* and its relative abundance, in Santa Catarina, Brazil. Aqua J Ichthyol Aquat Biol 6:133–138

Medeiros R, Polette M, Vizinho S, Macedo C, Borges J (1997) Diagnóstico sócio-econômico e cultural nas comunidades pesqueiras artesanais do litoral centro-norte do estado de Santa Catarina Notas técnicas da FACIMAR 1:33–42

Neves LM, Teixeira-Neves TP, Pereira-Filho GH, Araújo FG (2016) The farther the better: effects of multiple environmental variables on reef fish assemblages along a distance gradient from river influences. PLoS One 11:e0166679

Oksanen J, Kindt R, Legendre P, O'Hara B, Stevens MHH, Oksanen MJ, Suggests M (2007) The vegan package. Community ecology package 10:631–637

Oksanen J et al. (2010) Vegan: community ecology package. R package, version 1.18–2/r1135

Olsen DA, LaPlace J (1979) A study of a Virgin Islands grouper fishery based on a breeding aggregation

Parrish JD (1987) The trophic biology of snappers and groupers. In: Tropical snappers and groupers: Biology and fisheries management, pp 405–463

Petersen CW, Fischer EA (1986) Mating system of the hermaphroditic coral-reef fish, *Serranus baldwini*. Behav Ecol Sociobiol 19:171–178. https://doi.org/10.1007/bf00300857

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Sadovy de Mitcheson Y et al (2013) Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. Fish Fish 14:119–136. https://doi.org/10.1111/j.1467-2979.2011.00455.x

Sadovy Y, Colin PL, Domeier ML (1994) Aggregation and spawning in the tiger grouper, *Mycteroperca tigris* (Pisces: Serranidae). Copeia 1994:511–516. https://doi.org/10.2307/1447001

Sazima I (1986) Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. J Fish Biol 29:53–65

Schmitt RJ, Coyer JA (1982) The foraging ecology of sympatric marine fish in the genus Embiotoca (Embiotocidae): importance of foraging behavior in prey size selection. Oecologia 55:369–378. https://doi.org/10.1007/bf00376925

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39

Sluka RD, Sullivan KM (1998) The influence of spear fishing on species composition and size of groupers on patch reefs in the upper Florida Keys. Fish Bull 96:388–392

Sluka R, Chiappone M, Sullivan K (1994) Comparison of juvenile grouper populations in southern Florida and the central Bahamas. Bull Mar Sci 54:871–880

Sluka R, Chiappone M, Sullivan K, Wright R (1996) Habitat preferences of groupers in the Exuma Cays Bahamas. J Sci 4:8–14

Smith CL (1961) Synopsis of biological data on groupers (*Epinephelus* and allied genera) of the western North Atlantic, vol 23. Fisheries Division, Biology Branch, Food and Agriculture Organization of the United Nations

Sokal RR, Rohlf FJ (1962) The comparison of dendrograms by objective methods. Taxon 11:33–40. https://doi.org/10.2307/1217208

Spedicato M, Carbonara P, Lembo G (2005) Insight into the homing behaviour of the dusky grouper (*Epinephelus marginatus* Lowe, 1834) around the island of Ustica, Italy. In: Proceedings of the Fifth Conference on Fish Telemetry held in Europe, Aquatic telemetry: advances and applications, pp 103–109

ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179. https://doi.org/10.2307/1938672

ter Braak CJF (1994) Canonical community ordination. Part I: basic theory and linear methods. Écoscience 1:127–140. https://doi.org/10.1080/11956860.1994.11682237

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge

Wagner CE, Harmon LJ, Seehausen O (2012) Ecological opportunity and sexual selection together predict adaptive radiation. Nature 487:366–369 http://www.nature.com/nature/journal/v487/n7407/abs/nature11144.html#supplementary-information