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Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover

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Abstract Patterns of community structure in the marine environment are strongly influenced by population relationships to biotic and physical gradients. The aim of this work is to explore the relationships of tropical rocky reef fish assemblages to wave exposure and benthic coverage in a gradient of distance from the coast. The study was conducted on the Guarapari Islands, southeastern Brazilian coast. Fish were sampled by underwater visual census (166 transects) and benthic cover was estimated with quadrats (223 replicates). Two main kinds of habitats were found to be derived from the close interrelation between exposure and benthic coverage: (1) exposed areas subjected to major hydrodynamic forcing, and (2) sheltered or moderately exposed areas. The first group is associated with mid-water schooling species like planktivorous labrids and *Chromis*, piscivorous *Caranx*, as well as gregarious omnivores like *Abudefduf* and *Diplodus*. In terms of benthic composition, macroalgae and encrusting calcareous algae prevail in this high-energy habitat. The second group is characterized by site-attached and reef associated species like territorial pomacentrids, invertebrate feeders such as *Halichoeres poeyi* and *Chaetodon striatus*, and small cryptobenthic fishes (e.g. blenniids and labrisomids). Turf algae, zoanthids and massive corals dominate this environment. Environmental plasticity is also common with some genera showing high abundances in all habitats (e.g. *Holocentrus*, *Haemulon*, *Acanthurus*). Examples of the coupling of food availability and fish abundance were found. Planktivores, territorial herbivores, macroalgae browsers and spongivores were positively related with the abundance of their preferred food items along the exposure gradient. Within-family analyses of Pomacentridae and Labridae showed that niche partitioning is likely occurring and seems to be mediated by swimming 'ability' and associated feeding performance.

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Introduction

Patterns of community structure in the marine environment are strongly influenced by population relationships to biotic and physical gradients. Some important factors known to influence the distribution and abundance of reef fishes are: exposure (i.e. wave-induced water motion—McGehee 1994; Bellwood and Wainwright 2001), depth (Williams 1991; Friedlander and Parrish 1998; Russ 2003), topographic complexity (i.e. rugosity—Luckhurst and Luckhurst 1978; Roberts and Ormond 1987; Friedlander and Parrish 1998; Öhman and Rajassuriya 1998), and benthic composition (e.g. Bouchon-Navarro and Bouchon 1989; Munday 2002). These factors may occur synergistically on reef systems mediating the availability of (1) shelter, which is thought to influence the impact of predation (Jones et al. 1991; Hixon and Beets 1993; Caley and St. John 1996; Beukers and Jones 1997) and (2) food resources, like the positive relationships of coral-feeding chaetodontids and live coral cover (Bell and Galzin 1984; Bouchon-Navarro and Bouchon 1989) or planktivorous fish and zooplankton abundance related to water visibility and motion (Hammer et al. 1988; Hobson 1991). Fishes and benthic organisms preferentially occupy specific areas of the reef (e.g. Sebens and Johnson 1991; McGehee 1994; Fulton et al. 2001; Dutra et al. 2005). The interplay of hydrodynamics and inherent physiological capabilities of the fishes like swimming ability and associated feeding performance enable certain species or functional groups to explore particular niches, ultimately shaping fish communities (McGehee 1994; Bellwood and Wainwright 2001; Bellwood et al. 2002; Wainwright et al. 2002).

Reef-fish communities are found throughout the tropical and subtropical Brazilian coastline, from below the Amazon River mouth at Manuel Luiz Reefs (0°52′ S) to Santa Catarina State (27°30′ S) (Floeter et al. 2001; Ferreira et al. 2004). In the southeastern coast no truly coral reefs are found and rocky shores represent the main habitat for reef fishes and reef-associated biota. This region is seasonally affected by upwelling phenomena with cold (<18°C) and nutrient-rich waters (Castro and Miranda 1998; Ekau and Knoppers 1999). The Guarapari Islands are an insular complex at the southern coast of Espírito Santo State, southeastern Brazil (Fig. 1). They are located at a tropical-subtropical transition zone (20° S), and could be considered as 'marginal reef sites' (*sensu* Perry and Larcombe 2002) in the western Atlantic. These islands have the richest reef-fish fauna ever recorded in a single area on the southwestern Atlantic (Floeter and Gasparini 2000; Floeter et al. 2001; Gasparini and Floeter unpublished data). However, no quantitative data on fish or benthic community is available for this region. The geographical position of the islands presenting a gradient of distance from mainland provides an excellent opportunity for testing the effects of different wave exposure regimes in benthic and fish communities at a marginal reef site. Most studies to date are based on tropical well-developed reefs (Ebeling and Hixon 1991; Williams 1991) and the results might not be readily applicable to subtropical communities in rocky reefs.

The aim of this work is to explore the relationships of tropical rocky reef fish assemblages to wave exposure and benthic coverage. Specifically, we intend to describe the spatial variation in fish assemblages across a gradient of exposure related to distance from mainland, and to investigate how fish community structure is related to benthic composition and food availability.

Methods

Study sites

The study was carried out in Vila Velha–Guarapari region, southeastern Brazil (Fig. 1). Two small coastal archipelagoes, named Itatiaia (20°21′ S, 40°17′ W) and Três Ilhas (20°37′ S, 40°23′ W), and a single island, named Escalvada (20°40′ S, 44°24′ W) were investigated. These sites are subjected to distinct wave exposure due to morphological characteristics. Both water transparency and flow are much higher at Escalvada Is.
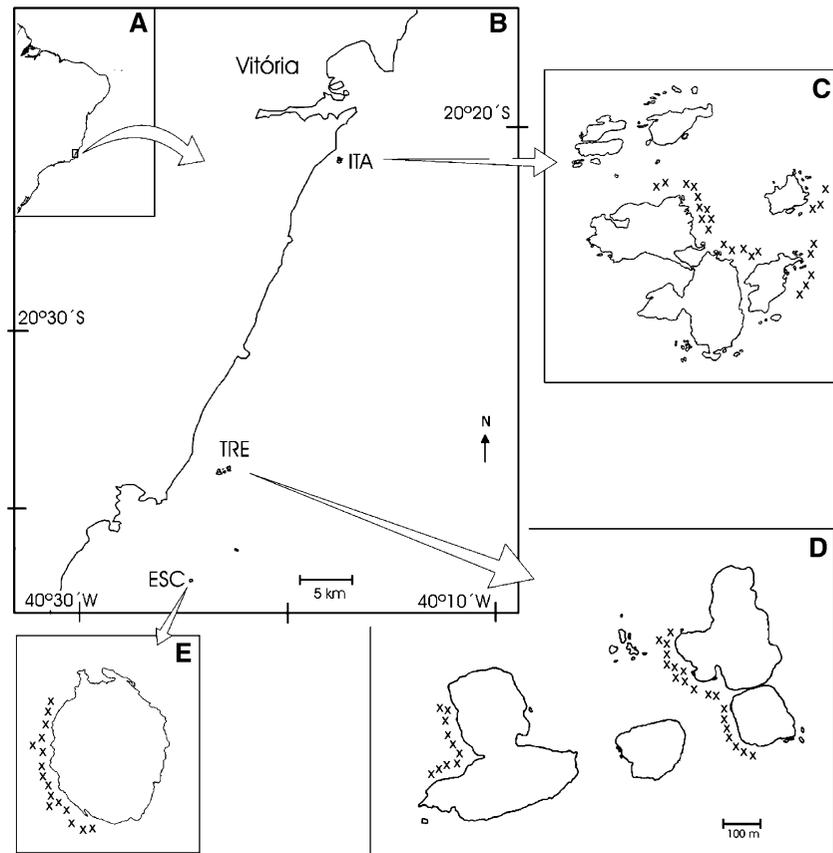
(ESC), which is an isolated island lying 10 km from the coast. The other two sites are archipelagoes with restricted water flow at sheltered areas of the islands (see Fig. 1). The Itatiaia Archipelago (ITA) is formed by several islets, located 0.5 km from the coast. This site is the most sheltered from prevailing winds and marine currents, due to its complex morphology and proximity to mainland. The Três Ilhas Archipelago (TRE), distant 3.5 km from the coast is formed by five small islands and has an intermediate wave exposure in relation to the others. Relatively sheltered locations in the three areas were chosen for sampling (Fig. 1). During the sampling period water horizontal transparency (visibility) was 6–15 m at ESC, 4–7 m at TRE and 3–5 m at ITA and surface water temperature varied from 19°C to 22°C (Austral summer). The three sites consist of rocky formations with a prolific benthic cover of seaweeds, octocorals, zoanthids, sponges and corals. Rocky shores and submerged rocky reefs are separated by extensive sandy bottoms.

Reef fish community structure

Fish surveys were conducted from January to April 2001 by three of us (SRF, JLG and CELF). A pilot study was conducted in order to calibrate differences among divers regarding total number of fish per transect. No significant differences were observed among divers (ANOVA $p < 0.883$, $F = 0.124$). Replicated visual transects using SCUBA diving were performed in each site. Transects were 20 m long and 2 m wide (40 m^2) in order to accommodate to the lowest visibility at the study sites. This procedure kept the sample units within a defined habitat, as well as improving the sampling of cryptic species when compared with wider transects. During the surveys, the observer unrolled a 20 m tape-measure from a point chosen randomly and the tape was unwound. All the fishes were counted along the transect, except the cryptic species that were counted by carefully scanning the substrate (and also looking beneath the rocks and crevices) when

the diver turned back and started wounding the tape. This approach ensured that the species more likely to swim away due to the observer are the first ones to be counted. This method allows good density estimation for all species (Aburto-Oropeza and Balart 2001, CELF unpublished). No significant temporal differences in fish abundance were observed during the 4-month period of sampling effort (ANOVA $p < 0.189$, $F = 0.160$), thus the data collected ($N = 166$ transects) along this study could be confidently used in the analyses without further consideration of temporal aspects.

Fishes were grouped into major trophic categories following Ferreira et al. (2004) (Table 1), and also through direct behavioral observations and stomach content analysis (Floeter unpublished data).

Benthic cover

Percent cover of benthic organisms (grouped in functional categories; e.g. turf algae, massive corals, octocorals, zoanthids) was obtained through randomly placed 50×50 cm quadrats in all depths and all types of substrate sampled for fishes. Each quadrat presented 30 intercept points, and the organism below each intercept point was recorded. Replicates ($N = 223$ quadrats) were distributed along the depth contour of the sites.

Statistical analyses

Fish abundance and percent cover of benthos were compared among different levels of hydro-dynamic exposure (i.e. distance of the studied sites from the coast) using one-way analysis of variance (ANOVA). When necessary, data were log-transformed to stabilize variances (Underwood 1997). Additional Student–Newman–Keuls (SNK) multiple comparisons of means test were performed as a post-hoc test (Zar 1999). The fish and benthos distribution and relationships among them was analyzed through a Canonical Correspondence Analysis (CCA). This ordination is considered to be a powerful multivariate technique that is useful to extract synthetic environmental gradients from ecological data (ter Braak and Verdonschat 1995).

Results

Fish community structure

A total of 12,774 individuals of 99 teleost fish species belonging to 37 families were recorded throughout the study, 93 taxa were positively identified to species level (Table 1). Elasmobranchs were not censused. The ten most abundant fishes in the three sites accounted for approximately 83 to 89% of all fishes censused during this study. Considering all study sites collectively, the ten most abundant fishes in decreasing order were *Holocentrus adscensionis*, *Halichoeres poeyi*, *Acanthurus bahianus*, *Haemulon aurolineatum*, *Diplodus argenteus*, *Stegastes fuscus*, *Chaetodon striatus*, *Chromis multilineata*, *Haemulon plumieri*, and *Malacoctenus* sp.n. (Table 1). The mean species richness per census (±SE) was 14.49 ± 0.36 species, with a minimum of 3 and a maximum of 25 species. The mean number of individuals per census (±SE) was 77.14 ± 3.06, with a minimum of 16 and a maximum of 272 fishes.

Considering all sites, the great majority of fishes counted were mobile invertebrate feeders summing up 57.82% (31 species), followed by roving herbivores with 16.66% (11 species), omnivores with 9.33% (9 species), territorial herbivores with 5.43% (3 species), sessile invertebrate feeders with 3.74% (5 species), planktivores with 3.48% (8 species), carnivores with 1.93% (16 species), and piscivores with 1.64% (6 species).

Fish and benthos in relation to the exposure gradient

Distinct fish assemblages were found in the three studied sites, with only four of the ten most abundant fishes shared among the three sites. The sheltered site (ITA) and the moderately exposed one (TRE) shared nine species among the top 10, whilst six different species appear at the most exposed site (ESC). ESC was the richest site with 75 species throughout the study, followed by TRE with 68 species and ITA with 47. Mean fish density (±SE) followed the same pattern (Table 2). The mean species richness per census showed an inverse pattern, although not statistically significant.

Table 1 Total composition of visual census in the three studied sites: Density per 40 m^2 (mean ± SE) per species and percent of total observed

Family/Name	Trophic group	ITA		TRE		ESC	
		Density	%	Density	%	Density	%
Acanthuridae							
Acanthurus bahianus	Rov. Herbiv.	**10.23** ± 1.36	15.42	**9.00** ± 0.97	12.35	**8.80** ± 1.76	9.62
A. chirurgus	Rov. Herbiv.	0.15 ± 0.08	0.23	0.35 ± 0.10	0.47	**1.42** ± 0.34	1.55
A. coeruleus	Rov. Herbiv.	0.18 ± 0.09	0.27	0.22 ± 0.05	0.31	0.29 ± 0.16	0.32
Aulostomidae							
Aulostomus strigosus	Piscivore	–	–	–	–	0.42 ± 0.09	0.46
Blenniidae							
Parablennius spp.	Omnivore	1.10 ± 0.21	1.66	0.68 ± 0.12	0.93	0.38 ± 0.10	0.42
Bothidae							
Bothus lunatus	Carnivore	–	–	–	–	0.04 ± 0.03	0.04
Carangidae							
Caranx crysos	Piscivore	0.03 ± 0.17	0.04	–	–	**3.60** ± 9.21	3.94
Chaetodontidae							
Chaetodon sedentarius	Sessile Invert.	0.21 ± 0.08	0.31	0.01 ± 0.01	0.02	0.25 ± 0.09	0.03
C. striatus	Sessile Invert.	**2.28** ± 0.32	3.44	**2.63** ± 0.26	3.60	1.29 ± 0.17	1.41
Chaenopsidae							
Emblemariopsis signifera	Mob. Invert.	–	–	–	–	0.11 ± 0.05	0.12
Dactylopteridae							
Dactylopterus volitans	Mob. Invert.	–	–	–	–	0.02 ± 0.02	0.02
Cirrhitidae							
Amblycirrhitus pinos	Mob. Invert.	–	–	0.03 ± 0.02	0.04	0.42 ± 0.10	0.46
Diodontidae							
Diodon hystrix	Mob. Invert.	–	–	–	–	0.02 ± 0.02	0.02
Gobiidae							
Coryphopterus glaucofraenum	Planktivore	0.10 ± 0.05	0.15	0.65 ± 0.14	0.90	0.09 ± 0.05	0.10
Elacatinus figaro	Mob. Invert.	–	–	0.03 ± 0.02	0.04	0.56 ± 0.32	0.62
Grammatidae							
Gramma brasiliensis	Mob. Invert./Plankt.	0.03 ± 0.03	0.04	0.26 ± 0.07	0.36	0.25 ± 0.11	0.28
Haemulidae							
Anisotremus moricandi	Mob. Invert.	0.10 ± 0.05	0.15	0.06 ± 0.03	0.08	0.09 ± 0.05	0.10
A. surinamensis	Mob. Invert.	0.03 ± 0.03	0.04	–	–	–	–
A. virginicus	Mob. Invert.	**2.15** ± 0.73	3.25	0.97 ± 0.20	1.33	0.27 ± 0.10	0.30
Haemulon aurolineatum	Mob. Invert./Plankt.	**3.33** ± 1.64	5.02	**9.78** ± 1.79	13.42	**9.67** ± 2.73	10.57
H. plumieri	Mob. Invert./Plankt.	1.15 ± 0.39	1.74	**3.53** ± 1.35	4.84	1.00 ± 0.73	1.09
H. steindachneri	Mob. Invert./Plankt.	**3.03** ± 0.98	4.56	**1.57** ± 0.72	2.15	0.05 ± 0.04	0.01
Orthopristis ruber	Mob. Invert.	0.18 ± 0.07	0.27	0.13 ± 0.06	0.17	–	–
Holocentridae							
Holocentrus adscensionis	Mob. Invert.	12.41 ± 1.78	18.71	**12.08** ± 1.71	16.59	**16.80** ± 3.26	18.37
Myripristis jacobus	Planktivore	–	–	0.03 ± 0.03	0.04	1.13 ± 0.33	1.23
Kyphosidae							
Kyphosus spp.	Rov. Herbiv.	–	–	–	–	1.09 ± 0.66	1.19
Labridae							
Bodianus pulchellus	Mob. Invert.	–	–	–	–	0.07 ± 0.04	0.08
Bodianus rufus	Mob. Invert.	0.21 ± 0.14	0.31	0.14 ± 0.05	0.19	1.11 ± 0.32	1.21
Clepticus brasiliensis	Planktivore	–	–	–	–	0.64 ± 0.20	0.70
Doratonotus megalepis	Mob. Invert.	0.03 ± 0.03	0.04	0.03 ± 0.02	0.04	–	–
Halichoeres brasiliensis	Mob. Invert.	0.23 ± 0.08	0.35	0.54 ± 0.10	0.74	1.16 ± 0.25	1.27
H. dimidiatus	Mob. Invert.	–	–	–	–	0.09 ± 0.04	0.10
H. penrosei	Mob. Invert.	0.13 ± 0.08	0.19	0.06 ± 0.03	0.08	0.18 ± 0.07	0.20
H. poeyi	Mob. Invert.	**13.36** ± 1.43	20.14	**16.19** ± 1.07	22.23	**3.73** ± 0.54	4.07
Thalassoma noronhanum	Planktivore	–	–	–	–	0.27 ± 0.13	0.30
Labrisomidae							
Labrisomus kalisherae	Carnivore	0.10 ± 0.06	0.15	0.04 ± 0.02	0.06	–	–

Table 1 continued

Family/Name	Trophic group	ITA		TRE		ESC	
		Density	%	Density	%	Density	%
Labrisomus spp.	Carnivore	0.95 ± 0.14	1.43	0.43 ± 0.08	0.59	0.18 ± 0.05	0.20
Malacoctenus delalandii	Mob. Invert.	–	–	0.01 ± 0.01	0.02	–	–
Malacoctenus sp.n.	Mob. Invert.	**2.18** ± 0.26	3.29	**1.71** ± 0.20	2.35	**1.42** ± 0.30	1.55
Lutjanidae							
Lutjanus jocu	Carnivore	–	–	0.01 ± 0.01	0.02	–	–
Ocyurus chrysurus	Carnivore	–	–	0.18 ± 0.06	0.25	0.02 ± 0.02	0.02
Monacanthidae							
Aluterus scriptus	Omnivore	–	–	–	–	0.02 ± 0.02	0.02
Cantherhines pullus	Omnivore	0.26 ± 0.08	0.39	0.44 ± 0.08	0.61	0.84 ± 0.12	0.91
Mullidae							
Mulloidichthys martinicus	Mob. Invert.	–	–	–	–	0.07 ± 0.05	0.08
Pseudupeneus maculatus	Mob. Invert.	**2.33** ± 0.33	3.52	**1.65** ± 0.23	2.27	0.87 ± 0.16	0.95
Muraenidae							
Gymnothorax moringa	Carnivore	0.08 ± 0.04	0.12	0.01 ± 0.01	0.02	0.07 ± 0.04	0.08
G. vicinus	Carnivore	–	–	0.01 ± 0.01	0.02	0.04 ± 0.03	0.04
Ogcocephalidae							
Ogcocephalus vespertilio	Carnivore	–	–	–	–	0.04 ± 0.03	0.04
Ophichthidae							
Myrichthys ocellatus	Mob. Invert.	–	–	0.01 ± 0.01	0.01	–	–
Ostraciidae							
Acanthostracion polygonius	Omnivore	–	–	–	–	0.07 ± 0.04	0.08
A. quadricornis	Omnivore	–	–	–	–	0.02 ± 0.02	0.02
Pomacanthidae							
Holacanthus ciliaris	Sessile Invert.	0.05 ± 0.05	0.08	0.11 ± 0.04	0.15	0.20 ± 0.07	0.22
H. tricolor	Sessile Invert.	–	–	0.06 ± 0.03	0.08	0.69 ± 0.11	0.76
Pomacanthus arcuatus	Omnivore	–	–	–	–	0.01 ± 0.02	0.02
P. paru	Omnivore	0.03 ± 0.03	0.04	0.07 ± 0.03	0.10	0.31 ± 0.08	0.34
Pomacentridae							
Abudefduf saxatilis	Omnivore	0.26 ± 0.17	0.39	1.28 ± 0.33	1.75	**3.44** ± 1.08	3.76
Chromis flavicauda	Planktivore	–	–	–	–	0.02 ± 0.02	0.02
C. jubauna	Planktivore	–	–	0.01 ± 0.01	0.02	–	–
C. multilineata	Planktivore	0.13 ± 0.05	0.19	0.76 ± 0.27	1.05	**5.24** ± 1.53	5.72
Stegastes fuscus	Ter. Herbiv.	**5.00** ± 0.90	7.54	**2.68** ± 0.52	3.68	0.29 ± 0.10	0.32
S. pictus	Ter. Herbiv.	0.03 ± 0.03	0.04	0.28 ± 0.07	0.38	**2.95** ± 0.59	3.22
S. variabilis	Ter. Herbiv.	0.26 ± 0.09	0.39	0.46 ± 0.09	0.63	0.09 ± 0.06	0.10
Priacanthidae							
Heteropriacanthus cruentatus	Mob. Invert.	–	–	0.01 ± 0.01	0.02	–	–
Scaridae							
Cryptotomus roseus	Rov. Herbiv.	0.03 ± 0.03	0.04	–	–	0.53 ± 0.37	0.58
Scarus zelindae	Rov. Herbiv.	–	–	0.01 ± 0.01	0.02	–	–
Sparisoma tuiupiranga	Rov. Herbiv.	–	–	–	–	0.05 ± 0.03	0.06
S. axillare	Rov. Herbiv.	0.67 ± 0.23	1.00	0.18 ± 0.07	0.25	0.33 ± 0.10	0.36
S. frondosum	Rov. Herbiv.	0.28 ± 0.12	0.43	0.39 ± 0.10	0.53	0.24 ± 0.09	0.26
S. radians	Rov. Herbiv.	0.08 ± 0.06	0.12	0.11 ± 0.06	0.15	0.09 ± 0.05	0.10
Sparisoma spp. (juv.)	Rov. Herbiv.	2.08 ± 0.41	3.13	0.50 ± 0.12	0.69	0.47 ± 0.28	0.52
Sciaenidae							
Odontoscion dentex	Carnivore	–	–	0.58 ± 0.26	0.80	0.11 ± 0.06	0.12
Pareques acuminatus	Mob. Invert.	0.51 ± 0.15	0.77	0.19 ± 0.05	0.27	0.47 ± 0.24	0.52
Scorpaenidae							
Scorpaena brasiliensis	Carnivore	–	–	0.01 ± 0.01	0.02	–	–
S. plumieri	Carnivore	0.03 ± 0.03	0.04	0.11 ± 0.04	0.15	0.18 ± 0.06	0.20
Serranidae							
Alphestes afer	Carnivore	–	–	0.07 ± 0.04	0.10	0.11 ± 0.07	0.12
Cephalopholis fulva	Carnivore	–	–	0.06 ± 0.03	0.08	0.56 ± 0.13	0.62

Table 1 continued

Family/Name	Trophic group	ITA		TRE		ESC	
		Density	%	Density	%	Density	%
Dermatolepis inermis	Carnivore	–	–	–	–	0.04 ± 0.03	0.04
Diplectrum radiale	Carnivore	–	–	0.07 ± 0.04	0.10	–	–
Mycteroperca acutirostris	Piscivore	–	–	0.01 ± 0.01	0.02	–	–
M. interstitialis	Piscivore	0.03 ± 0.03	0.04	0.03 ± 0.02	0.04	–	–
Paranthias furcifer	Planktivore	–	–	–	–	0.02 ± 0.02	0.02
Rypticus saponaceus	Carnivore	–	–	0.07 ± 0.04	0.10	0.22 ± 0.06	0.24
Serranus baldwini	Mob. Invert.	–	–	0.06 ± 0.03	0.08	0.05 ± 0.03	0.06
S. flaviventris	Mob. Invert.	0.05 ± 0.04	0.08	0.46 ± 0.12	0.63	–	–
Sparidae							
Diplodus argenteus	Omnivore	0.03 ± 0.03	0.04	0.14 ± 0.07	0.19	**14.93** ± 4.49	16.32
Synodontidae							
Synodus intermedius	Piscivore	–	–	0.08 ± 0.03	0.11	0.07 ± 0.04	0.08
S. synodus	Piscivore	–	–	0.03 ± 0.02	0.04	0.15 ± 0.05	0.16
Tetraodontidae							
Canthigaster figueiredoi	Sessile Invert.	0.05 ± 0.04	0.08	0.19 ± 0.05	0.27	0.73 ± 0.13	0.80
Sphoeroides spengleri	Mob. Invert.	0.23 ± 0.09	0.35	0.28 ± 0.07	0.38	0.25 ± 0.07	0.28

Bold numbers indicate the ten most abundant fishes in each study site. ITA = Itatiaia Archipelago; TRE = Três Ilhas Archipelago; ESC = Escalvada Is. Families displayed in alphabetic order

Considering trophic structure (Fig. 2) striking differences were observed regarding omnivores, planktivores, carnivores and piscivores, all significantly increasing in abundance towards more exposed areas related to water motion. On the other hand, territorial herbivores were more abundant toward sheltered sites. Sessile invertebrate feeders and roving herbivores showed no significant differences among sites and mobile invertebrate feeders are dominant in the inter-mediate exposed site (TRE). When within-family patterns are analyzed in detail, such as the abundance of damselfishes (Pomacentridae), a similar pattern reflecting the major trophic guilds emerges in relation to exposure gradient (Fig. 3). For example, the planktivore *Chromis multilineata* is significantly more abundant in the more exposed and clear water site (ESC) and the common territorial herbivore *Stegastes fuscus* have its abundance inversely proportional to the exposure

Table 2 Total number of transects and number per depth strata at each site

Exposure	ITA	TRE	ESC	Signif.
Total number of transects	39	72	55	
Transects per depth*				
2–5 m	30	30	8	
6–9 m	9	30	22	
10–16 m	–	12	25	
Total number of fish counted	2500	5244	5030	
Mean density (± SE)	69.42 ± 11.57	72.83 ± 8.58	91.47 ± 6.95	$p < 0.05$**
Richness	47	68	75	
Mean number of species per transect (± SE)	17.64 ± 0.72	13.85 ± 0.47	12.91 ± 0.60	NS
Horizontal water transparency	3–5 m	4–7 m	6–15 m	
Distance from the coast	0.5 km	3.5 km	10 km	

Total and mean number of fish species and mean density (± SE) per 40 m^2, plus the one way ANOVA results of comparisons among the gradient of exposure. SNK post-hoc results are indicated. Gradients of exposure: ITA = Sheltered; TRE = Moderately Exposed; ESC = Exposed

*The number of transects per depth reflects habitat availability at the sites. Mean fish density among depths was not significantly different at each site (ANOVA)

**F = 3.28; SNK: ITA = TRE < ESC
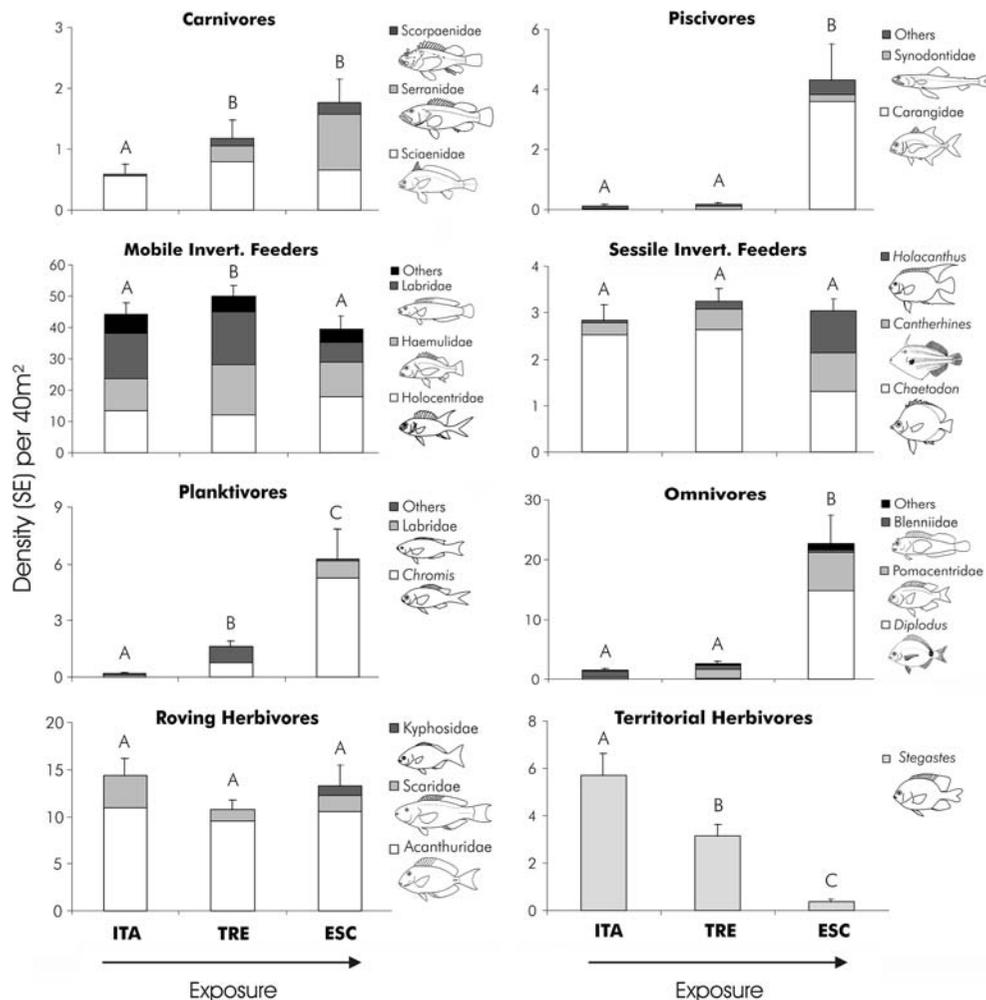
Fig. 2 Density of fish trophic groups (±SE) in the Guarapari Is. in relation to the exposure gradient of the sites. Note that different scales were used. ANOVA showed significant differences in fish abundance among sites ($p < 0.05$). Capital letters show statistical groupings (SNK post hoc) with bars having different letters being significantly different. Bars with the same letter are not significantly different. ITA – Itatiaia Archipelago, (**D**) TRE – Três Ilhas Archipelago, (**E**) ESC – Escalvada Is

gradient, being much more abundant towards the sheltered sites (Fig. 3). Within trophic categories some taxa behaved in a different way (Fig. 2), for example, no significant difference were shown by the sessile invertebrate feeders as a whole, whilst the sponge-eating angelfishes of the genus *Holacanthus* were significantly more abundant (ANOVA $p < 0.001$, $F = 21.623$) at the exposed site (ESC; Table 1). On the other hand, the butterflyfishes (mostly *Chaetodon striatus*) were significantly more abundant at sheltered and moderately exposed sites (ANOVA $p < 0.001$,

$F = 8.279$). Among the roving herbivores, kyphosids were only found at ESC, while parrotfishes (Scaridae) were found in higher densities at the sheltered site (ITA).

In terms of the size structure some evident differences were found among size classes in two of the four studied families (Fig. 4). Haemulids and serranids were found in larger sizes at ESC, while herbivorous acanthurids and scarids showed no differences in the larger sizes, although presenting higher densities of juveniles (<10 cm) in the sheltered site (ITA).
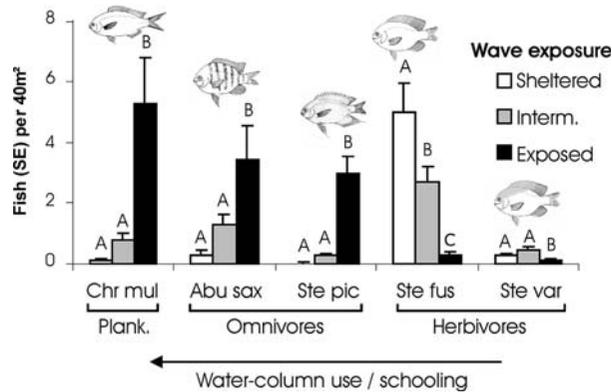
Fig. 3 Pomacentridae habitat use at the Guarapari Is. regarding wave exposure. ANOVA showed significant differences in fish abundance among exposures ($p < 0.05$). Capital letters show statistical groupings (SNK post hoc) with bars having different letters being significantly different. Species: Chr mul – *Chromis multilineata*, Abu sax – *Abudefduf saxatilis*, Ste pic – *Stegastes pictus*, Ste fus – *Stegastes fuscus*, Ste var – *Stegastes variabilis*. Wave exposure: sheltered – ITA, moderately exposed – TRE, exposed – ESC

Regarding the benthic composition, turf algae are significantly more abundant at the sheltered and moderately exposed sites (Table 3). Octocorals, macroalgae, sponges and encrusting calcareous red algae are all significantly associated with greater exposure. Zoanthids, fire corals, *Millepora*, and massive corals are more abundant at the moderately exposed site; however the latter two are not statistically significant (Table 3).

Some expected associations of the benthic composition (as food resource) and exposure were found. For example, the territorial herbivores are significantly more abundant towards the sheltered sites as well as their main source—the turf matrix (Fig. 5). The density of sponge-feeding angelfishes (Pomacanthidae) increases towards the exposed sites as well as sponge cover (their favored food items; Randall 1967; SRF personal observation) (Fig. 5). The sea chubs (Kyphosidae) are only present in the exposed site (ESC) where their main food source—macroalgae is also abundant (Table 3).

Within-family patterns of habitat use by damselfishes (Pomacentridae; Fig. 3 and description above) and wrasses (Labridae) reveals a distinct utilization of the rocky habitats regarding exposure by different species (Fig. 3) Among the wrasses, *Clepticus* and *Thalassoma* possess higher pectoral fin aspect ratios which is related to increasing swimming ability and water column use (Wainwright et al. 2002). They were found either exclusively or in higher abundances at exposed

areas in the reefs (i.e. shallow areas at Escalvada Is., see Table 1). On the other hand, the blackear wrasse *Halichoeres poeyi* (which possess low pectoral fin aspect ratio) was clearly more abundant at sheltered or moderately exposed sites.

In the CCA ordination diagram axis 1 represents the exposure gradient and explains 88% of the variance in the weighted averages (Fig. 6). Axis 2 accounts for other differences and responds for only 12% of the variability. Among the most abundant fish species, one planktivore (*Chromis multilineata*) and two omnivore pomacentrids and two schooling species *Diplodus argenteus* and *Caranx crysos* were associated with the higher hydrodynamic level at ESC (Fig. 6—the right end of the graph). Other species were associated with intermediate (TRE) or sheltered sites (ITA) like *Stegastes fuscus*, *Halichoeres poeyi*, *Haemulon steindachneri*, and *Sparisoma* spp. (the left hand of the graph). Some species show a plastic behavior regarding the exposure gradient with similar density in all sites (e.g. *Holocentrus adscensionis*, *Haemulon aurolineatum*, *Acanthurus bahianus*), thus positioned in the center of the plot.

Discussion

Interrelated gradients at southeastern Brazilian rocky reefs

In the studied sites, the water motion gradient is correlated with distance off the coast and the

Fig. 4 Mean density (individuals per 40 m² ± SE) of acanthurids, haemulids, serranids and scarids in four size classes at the three studied sites
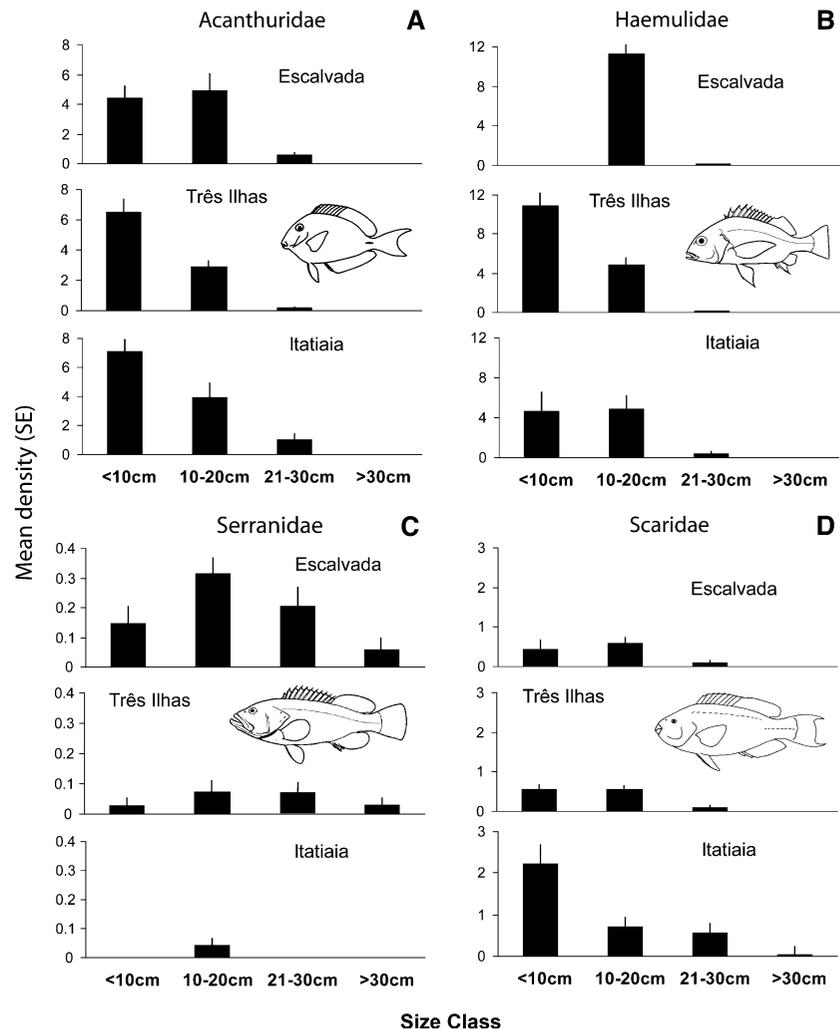
morphology of the islands (see island morphologies in Fig. 1). This exposure gradient seems to be the most important driving force structuring both reef fish and benthic communities. When exposure and benthic cover were analyzed in conjunction in the CCA, the exposure gradient alone explained most of variability. Gust (2002) found similar results studying how these same factors influence scarid biomass on the northern Great Barrier Reef.

Two main habitats are derived from the close interrelation between exposure and benthic coverage and could be described as follows: (1) exposed areas, i.e. areas subjected to major hydrodynamic forcing, and presenting less tri-dimensional complexity derived from sessile

organisms, although some sparse microhabitats with octocorals were present, and (2) sheltered or moderately exposed areas presenting higher structural complexity derived from fire-corals, zoanthids and massive corals.

The first combination is associated with mid-water schooling species like *Chromis* (planktivore), planktivore labrids and *Caranx* (piscivore) as well as the gregarious *Diplodus* (omnivore) that clearly prefer the exposed site and are primarily found in the edges of islands where there is a maximum water movement. Water visibility is very important for planktivores since they rely on visual cues to detect their food (Mussi et al. 2005), and also strong water motion is known to be related with plankton provision (Hobson and

Table 3 Mean benthic percent cover (±SE), plus the one way ANOVA results of comparisons among the gradient of exposure

Exposure	ITA	TRE	ESC	Signif.	F	SNK
Total number of quadrats	44	120	59			
Turf matrix	48.23 ± 2.40	42.06 ± 2.25	33.11 ± 2.76	*	6.16	ITA = TRE > ESC
Macroalgae	1.29 ± 0.59	8.97 ± 1.71	8.82 ± 2.32	**	19.72	ITA < TRE = ESC
Enc. calcar.	6.44 ± 1.34	3.83 ± 0.96	13.17 ± 2.83	**	8.67	ITA = TRE < ESC
Sponges	3.34 ± 0.75	3.03 ± 0.66	7.06 ± 1.19	**	9.45	ITA = TRE < ESC
Millepores	2.36 ± 0.67	4.89 ± 1.03	2.71 ± 0.65	NS	1.92	
Mass. corals	1.36 ± 0.44	2.06 ± 0.50	0.34 ± 0.15	NS	3.23	
Zoanthids	5.97 ± 1.71	12.94 ± 1.53	0.23 ± 0.23	**	18.66	ITA < TRE > ESC
Octocorals	3.64 ± 1.05	10.11 ± 0.97	10.23 ± 1.13	*	8.33	ITA < TRE = ESC

SNK post-hoc results are indicated. ITA = Sheltered; TRE = Moderately exposed; ESC = Exposed. Enc. calcar. = Encrusting calcareous algae; Mass. = Massive

$*p < 0.05$; $**p < 0.001$

Chess 1978; Hammer et al. 1988; Hobson 1991). Piscivores (e.g. carangids) take advantage of the typical plankton-feeding situation by frequently patrolling the reef searching for mid-water fishes (Hobson 1991; authors personal observations). Also, omnivore damselfishes (*Abudefduf saxatilis* and *Stegastes pictus*) which explore both algae and transient zooplankton and herbivorous kyphosids which feed on macroalgae (especially fucoids) are also conspicuous components of the community living in this environment. Kyphosids are typical inhabitants of exposed reefs along the coast and on isolated oceanic islands (Gasparini and Floeter 2001). Fishes in this habitat rely on schooling behavior for defense or attack (if predator). In terms of benthic composition, macroalgae and encrusting calcareous algae prevail in this high-energy habitat (cf. Steneck and Dethier 1994).

The second group is characterized by site-attached and reef associated species related to sheltered or moderate exposure regimes. Herbivores (mainly territorial pomacentrids), invertebrate feeders such as *Halichoeres poeyi* and *Chaetodon striatus*, and small cryptobenthic fishes (e.g. blenniids and labrisomids) flourish in these protected environments, where turf algae, zoanthids and massive corals dominate. Regarding the herbivorous species, juvenile scarids and territorial herbivores are more abundant at shallow depths in the sheltered site, where they can find appropriate hydrodynamic level and more turf algae matrix cover.

It is interesting to note however that environmental plasticity is also common in reef fish communities. Some genera showed high abundances in all sites, encompassing both kinds of habitats described above (e.g. *Holocentrus*, *Haemulon*, *Acanthurus*).

Some observed size structure differences could be attributable to ontogenetic factors related to life history (e.g. juveniles more abundant in the sheltered site—Scaridae, Haemulidae) or the abundance of food resources. For example, the macrocarnivores clearly take advantage of the higher density of mid-water schooling species as potential preys at the more exposed site (ESC). Nevertheless their increase in abundance and body size with exposure clearly has other cause as well. These species are the primary target by spear fisherman. Densities of these species especially larger size classes were higher at progressively greater distances from the coast. This trend is consistent with the expectation that harvesting pressure is lower in areas away from the coast, due to progressive access difficulties. These species are clearly experiencing heavy fishing pressure all along the Brazilian coast (Floeter et al. 2006). For example, not a single specimen of the goliath grouper, *Epinephelus itajara*, or the black grouper, *Mycteroperca bonaci*, were observed at any of the sites, despite that these sites fall within the historic range of the species (and older fishermen report that these species used to be common), indicating heavy threat to certain species. The studied islands are relatively close to Vitória city (with a population of one million people) and some form of actual management (fishing regulations or marine reserves)
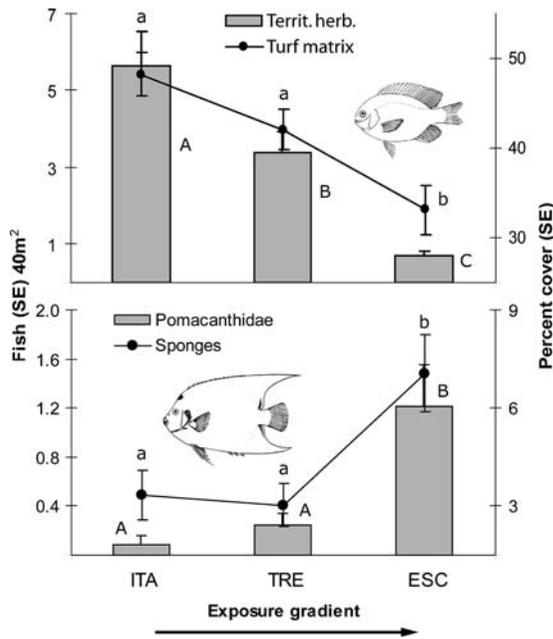
Fig. 5 Territorial herbivores (Pomacentridae) and spong-
ivores (Pomacanthidae) density (±SE) and substrate
percent cover (±SE) of their preferred food items at the
different sites. ANOVA showed significant differences
between sites for fishes and benthic cover ($p < 0.05$).
Capital letters show statistical groupings (SNK post hoc
test) with bars having different letters being significantly
different (capitals for fish and small letters for benthic
group)

is clearly needed in this region to help recover
fish populations (see Floeter et al. 2006 for de-
tailed discussion).

Typical coral reefs present marked structural
zonation and each characteristic habitats (e.g. flat,
crest, slope) usually spans over hundreds to
thousands of meters (review in Williams 1991).
Rocky shores, on the other hand, are typically
small in terms of horizontal extension (cf. Ferre-
ira et al. 2001) and consequently display mixed
habitats at various scales. As a result, the com-
munity structure is rather simple (basically the
two main combinations discussed above), and
dominated by species showing high plasticity
when compared with coral reef models (e.g. Russ
1984a, b, Williams 1991).

Food resources and hydrodynamics

The underlying causes of exposure gradients as a
major force structuring reef fish communities
seem to be related to shelter and food availability
(Hobson 1991; Williams 1991; Beukers and Jones
1997). In the present work a series of examples of
food availability (i.e. benthic cover of the pre-
ferred resource) associated with fish abundance
seem to corroborate this view as planktivores,
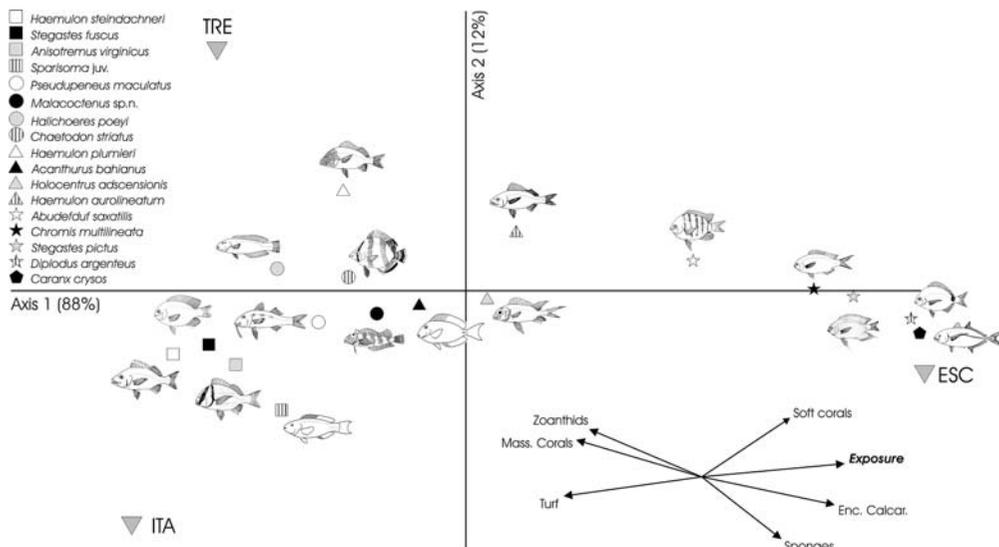
Fig. 6 Canonical correspondence analysis ordination dia-
gram with the 17 most abundant species of reef fishes
(symbols) at the studied sites. The sites are represented by

inverted triangles, and benthic organisms represented by
arrows. Sites: Itatiaia (ITA) – sheltered, Três Ilhas (TRE)
– moderately exposed, Escalvada (ESC) – exposed

territorial herbivores, macroalgae browsers and spongivores were positively related to the abundance of their preferred food items along the exposure gradient. Moreover, the utilization of these resources are mediated by swimming 'ability' and associated feeding performance that ultimately influence their abundance in particular habitats.

Detailed analyses of two speciose families (Pomacentridae and Labridae) showed that niche partitioning is likely occurring within both families. It seems that swimming 'ability' is influencing their abundances in relation to the exposure gradient, similarly to the patterns found in other tropical reefs (Bellwood et al. 2002; Dominici-Arosemena and Wolff 2006). For example, the planktivorous pomacentrid *Chromis* which has longer bifurcated caudal fins than other pomacentrids is found primarily in the exposed site. On the other extreme, the territorial herbivore *Stegastes fuscus* was found mainly in shallow and sheltered areas. The omnivorous *Stegastes pictus* is more abundant at the exposed site, but in deeper areas, less subjected to strong water motion (Fulton and Bellwood 2002). Similar pattern emerged from the most abundant labrids. The two planktivore species (*Clepticus brasiliensis* and *Thalassoma noronhanum*) possessing the higher pectoral fin aspect ratios among all the labrids are found exclusively in the exposed site preferentially at shallow or intermediate depths. This particular environment is related to the strongest water motion found in the studied sites. The species *Halichoeres poeyi* present the lower pectoral fin aspect ratio and is more abundant at sheltered and moderately exposed sites. The pectoral fin aspect ratio is known to be a very good predictor of swimming ability in labrids (see Wainwright et al. 2002). The pattern found here (i.e. directly related to exposure gradient) is very similar to the pattern of labrid distribution based on 'swimming abilities' found in the Great Barrier Reef and the Caribbean (Bellwood and Wainwright 2001; Fulton et al. 2001; Bellwood et al. 2002; Wainwright et al. 2002).

In summary: (1) two main kinds of habitats were found to be derived from the close interrelation between exposure and benthic coverage, namely exposed areas subjected to major hydrodynamic forcing, and sheltered or moderately exposed areas. (2) Some examples of the coupling of food availability and fish abundance were found, with planktivores, territorial herbivores, macroalgae browsers and spongivores being positively related with the abundance of their preferred food items along the exposure gradient. (3) Within-family analyses showed that niche partitioning is likely occurring and seems to be mediated by swimming 'ability' and associated feeding performance.

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