

## Community structure of fishes and habitat complexity on a tropical rocky shore

Carlos E.L. Ferreira, José E.A. Gonçalves & Ricardo Coutinho  
*Instituto de Estudos do Mar Almirante Paulo Moreira (IEAPM), Departamento de Oceanografia,  
Rua Kioto 253, Arraial do Cabo, RJ, Cep:28930000, Brazil (e-mail: kadu@ax.apc.org)*

Received 24 May 2000      Accepted 30 November 2000

**Key words:** vertical distribution, benthic organisms, reef fish, Brazilian coast, fish diversity and richness, impacts, feeding niches

### Synopsis

The relationship between the variables of reef fish community structure (fish richness, fish diversity and total number of fishes) and those of habitat complexity (total surface area, substratum diversity, topographic complexity, number of holes, percent cover of turf algae, zoanthids, millepores, massive corals, bare rock, encrusting calcareous algae, urchins, other sessile organisms and *Sargassum*) were examined on three different rocky shores (FA, FB and FT) at Arraial do Cabo, a tropical region located on Brazilian southeastern coast (23° S, 42° W). Fish abundance and vertical distribution were assessed by a visual census technique using strip transects. Percentage cover of benthic organisms and other substratum types were calculated by replicated transects using a chain laid down on the substratum. Topographic complexity was determined by the chain link method and number of holes were estimated by direct counts on replicated transects. More than 91 fishes belonging to 37 families were seen in all study sites during one year of visual census effort. FA and FB sites had similar fish community structure and habitat complexity characteristics, while FT showed different habitat characteristics and higher fish diversity and richness, plus total number of fishes. Vertical distribution of fishes along the rocky shores studied seemed to be predictable and was determined by factors such as feeding habits and behavior, availability of refuges and social interactions. The habitat variables that best explained the higher diversity and number of fishes observed in FT site were total surface area of rocky shores and the abundance of benthic sessile invertebrates; these conditions were typical of rocky shores more exposed to wave surge.

### Introduction

Two decades of studies have passed, since the stochastic view was proposed as a main factor organizing the community structure of reef fishes in detriment to the deterministic view (Sale 1980, 1991). Today, it is widely recognized that communities of reef fishes are determined by several interacting factors including recruitment from the planktonic larva phase, interactions among the species and the history of disturbances (e.g. physical, biotic and even fishing, Hixon 1991, Russ & Alcala 1998).

One of the fundamental aims of community ecology is to determine what factors and respective roles influence the structure of natural communities. Also, community structure is related not only to the biological, but also to the physical structure of a community. Consequently, several studies have examined the effects of substratum variables on reef fish community structure (Luckhurst & Luckhurst 1978, Bell & Galzin 1984, Sale & Douglas 1984, Roberts & Ormond 1987, Chabanet et al. 1997, Öhman & Rajasuriya 1998).

In temperate reefs, kelps provide the additional dimension of plant canopy, increasing the availability

of food and refuges for fishes (Holbrook et al. 1990, Ebeling & Hixon 1991). On coral reefs, living corals form a complex framework, supporting a variety of microhabitats, thus increasing fish diversity (Luckhurst & Luckhurst 1978, Carpenter et al. 1981) and in some habitats, fish abundance (Chabanet et al. 1997). In other tropical regions, seaweed beds and seagrass meadows contribute significantly to the enhancement of fish diversity and abundance (Carr 1989, Jenkins & Wheatley 1998, Ornellas & Coutinho 1998). Likewise, artificial reefs have been widely deployed to attract fish to low productivity areas, simply by adding complexity (Bonhsack et al. 1997, Grossman et al. 1997). Whereas there is an extensive literature in this area of study of different reef ecosystems, the great majority have been carried out on coral reefs, few have tried the same thing on rocky shores (Falcón et al. 1996), but never on tropical rocky shores. Despite their lower complexity when compared to coral reefs, tropical rocky shores and adjacent environments can support a rich reef fauna and flora (Ferreira et al. 1998a,b, Guimaraens & Coutinho 1996, Ornellas & Coutinho 1998) and sustain a high primary productivity (Ferreira 1998).

The main objectives in this study were to examine the abundance and vertical distribution of fishes along different rocky shores, detect which habitat variables could be used to predict the presence and vertical distribution of the most abundant fishes, and which habitat variables can be used to predict whether a rocky shore could sustain more or less diversity and/or number of fishes.

## Methods

### *Study site*

This study was carried out in 1992 at Arraial do Cabo – Rio de Janeiro State (23° 44'S - 42° W), a tropical region on the Brazilian southeastern coast. Three study sites were chosen for sampling at Forno Inlet (Figure 1) in order to obtain data on communities of fishes and benthic organisms influenced by different conditions of wave movement: Fortaleza (FT), Forno-A (FA) and Forno-B (FB). From the first to the last, there is a decrease in intensity of wave surge measured by gypsum models (Lavrado 1992). The main physiographic structure of the study sites is characterized by rocky shores covered by granite boulders, ending in a sand bottom, with the presence of rock rubble in some

places. At FT the boulders are larger, and the slope more steeply. The protected conditions which Forno Inlet and most other sheltered sites in the region are included to provide conditions in which rich reef communities flourish (Castro et al. 1995, Guimaraens & Coutinho 1996, Viana<sup>1</sup>, Ornellas & Coutinho 1998, Ferreira et al. 1998a,b), with clear waters almost year-round and a mean average water temperature of about 22°C. The region is characterized by a coastal upwelling event in summer and spring periods, and is associated with local wind regime and bathymetry (Valentin 1984), although the cold nutrient rich water only bathe the study sites for short periods and generally in deeper parts (Ferreira et al. 1998b).

### *Fish community structure*

Abundance of fishes was assessed by a visual census technique adapted from Williams (1982), where a single SCUBA diver (CELF) swims, in a zigzag pattern up to the surface of the rocky shore and down to the sand bottom ( $\cong$  5 m long), recording fish species abundance and size 1 m each side in a strip transect 80 m long (total of 160 m<sup>2</sup>). All data were recorded on a prepared acrylic sheet while the diver followed an underwater tape measure. Replicated, random censuses (15–18) were performed monthly at each study site. The time limit, number of replicates and swimming velocity of each census were defined by plotting data against cumulative fish species number using presence-absence data of previous pilot studies. Vertical replicated visual censuses (12–15) were simultaneously performed for a better understanding of the vertical distribution of fishes on the rocky shores studied. Fishes were counted at each meter following an underwater tape measure, thus allowing a vertical profile of fish distribution and density to be build. All censuses were performed at high tide avoiding bias due to vertical migration of fishes. Nocturnal fishes were also sampled in nocturnal censuses but treated in another paper.

Fishes were grouped in major trophic categories, determined from direct behavioral observations, stomach content analysis (Ferreira & Gonçalves unpublished data) and available literature (Randall 1967, Moura 1998).

<sup>1</sup> Viana, M. 1997. Physiographic influence in the structure of the suprabenthic fish assemblage in the rocky shore of Arraial do Cabo, Rio de Janeiro, Brazil. *Boletim do Instituto de Pesca* 24: 25–35.

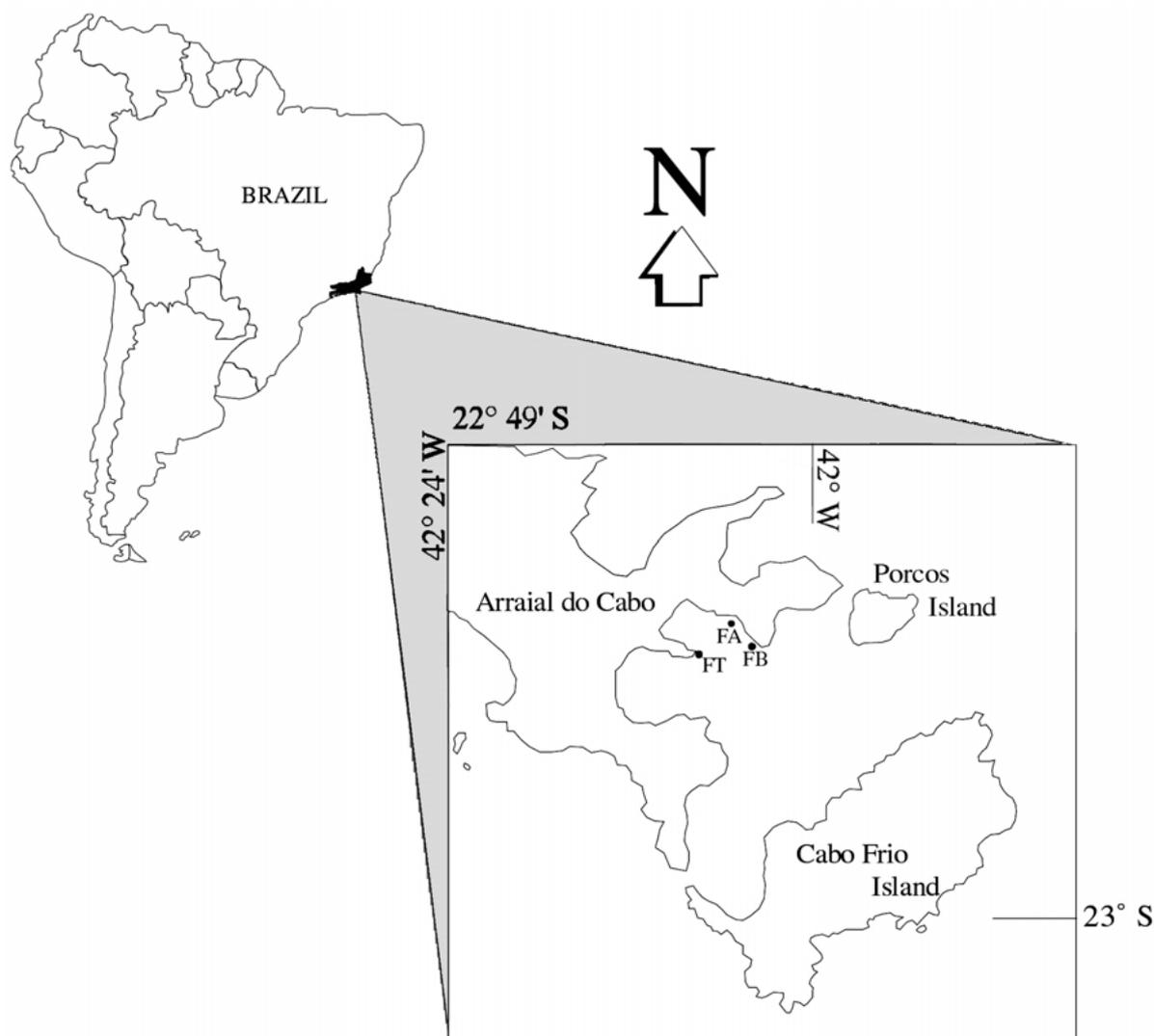


Figure 1. Map showing study sites: Fortaleza (FT), Forno-A (FA) and Forno-B (FB) in the Forno Inlet.

Some fish community variables, such as fish species richness, total number of fish and diversity of fishes per census (Shannon–Wiener index =  $\log_2$ ) were obtained in order to achieve good comparisons among study sites.

#### *Habitat complexity*

Percentage cover of benthic organisms (turf algae, zoanthids, millepores, massive corals, encrusting calcareous algae, urchins, *Sargassum*, other sessile

organisms) and bare rock were obtained, employing a chain 1 m long with links of 2 cm in length, laid parallel to depth contour of the rocky shore. The number of chain links covering each organism was then recorded and used to determine the proportion of rocky shore substratum composition (Porter 1972). Transects ( $n = 20$ ) were replicated in each study site at the beginning and at the end of the study.

Topographic complexity was estimated for all study sites by the ‘chain link method’ (Luckhurst & Luckhurst 1978), where a chain of 25 m was positioned to follow the contours and crevices as closely

as possible. A measure of the linear distance from surface to sand bottom was also recorded. The mean ratios of contour length/stretched length were used as a comparative index.

The number of existing holes were also assessed as a measure of environment complexity. A diver counted all holes found in 1 m of each side of a tape measure stretched along the substratum in replicated transects ( $n = 15$ ), from the surface of the rocky shore to the sand bottom. Hole size was also recorded. Although different size holes were detected, we only considered small holes for analysis, from about 1 m diameter to a few centimeters, those which could be promptly used as refuges by fishes. Other habitat variables, including total surface area of the rocky shore and substratum diversity (Simpson's index) were also estimated.

#### Data analysis

The fish and habitat related variables were compared among study sites using one way analysis of variance (ANOVA), and when necessary data were transformed to stabilize variances (Underwood 1997). Additional Student–Newman–Keuls (SNK) multiple comparisons of means test were performed as a *post-hoc* test (Zar 1996). Fish and benthic organisms vertical distribution plus relationships among them were analyzed through a Canonical Correspondence Analysis (CCA) utilizing MVSP 3.1 software. This ordination is considered to be a powerful multivariate technique which is useful to extract synthetic environmental gradients from ecological data (Ter Braak & Verdonschat 1995).

Additionally, in order to indicate which habitat complexity variables better explain the highest values of the fish community variables, a Multi Dimensional Scaling (MDS) ordination was used. Although this ordination method makes few assumptions about the data, distances between the points within the MDS configuration have the same rank order as the corresponding dissimilarity between samples (Clarke 1993), besides being more rapidly accessible to visual analysis. The one-way ANOSIN permutation test was used a posteriori to test for significant differences among formed groups. Both procedures were carried out utilizing Primer 4.0 software (Clarke & Warwick<sup>2</sup>).

<sup>2</sup> Clarke, K.R. & R.M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth. 64 pp.

## Results

### Fish composition

One year's visual census effort at Forno Inlet resulted in more than 91 species belonging to 37 families (Table 1). Communities in all the study sites were composed of: resident fishes (those which are specific site attached and were sighted in all censuses); wanderer fishes (those holding a larger home range, e.g. some scarids and acanthurids); and visitors (fishes that occasionally feed or rest on the rocky shore, e.g. pelagic fishes like some carangids). All communities of fishes sampled were lognormally distributed, with the dominance of few species and high number of rare species. Indeed, the ten most abundant fishes in the three sites corresponded to approximately 80% of all fishes censused during this study.

Fishes which occurred in huge schools (more than 500 individuals), like *Harengula clupeola* and *Selar crumenophthalmus*, were not included in Table 1 and in the results, since they were sighted sporadically and in high densities, consequently distorting the final statistical analysis. The ten most abundant fishes in Forno Inlet, considering all study sites collectively were in decreasing order *Haemulon aurolineatum*, *Stegastes fuscus*, *Diplodus argenteus*, *Abudefduf saxatilis*, *Halichoeres poeyi*, *Pseudupeneus maculatus*, *Chaetodon striatus*, *Acanthurus chirurgus*, *Haemulon steindachneri* and *Acanthurus bahianus* (Table 1).

### Comparison of fishes among study sites

The three sites sustained basically the same community of fish species, with the ten most abundant fishes in each site being detected in the others, despite differences in abundance (Table 1). Fish species richness, fish diversity ( $H'$ ) and total number of fishes per census were significantly higher at FT than in FA and FB sites (Figure 2). Such differences were due to approximately 15 fishes that were only sighted in FT site, even though all of them were found in low abundance (Table 1). In terms of trophic groups, composition seemed to be similar between FA and FB sites, with the majority of fishes ( $\cong 40$ –50%) being invertebrate predators, but including mainly mobile invertebrate feeders (Figure 2). In contrast, at the FT site, omnivores were the most important group, followed by invertivores and herbivores. Herbivores were the second most abundant group in FA and FB sites, including territorialist

Table 1. Total composition of visual census in one year effort: Density per 160 m<sup>2</sup> (mean ± SE), total number of specimens counted (n) and percent of total observed. Bold numbers indicate the ten most abundant fishes in each study site.

Family/Name	Trophic group	Fortaleza			Forno-A			Forno-B				
		Density	n	%	Density	n	%	Density	n	%		
Acanthuridae												
<i>Acanthurus bahianus</i>	Herbivore	<b>14.65 ± 1.43</b>	425	3.08	3.57 ± 0.52	118	1.15	2.97 ± 0.68	110	1.34		
<i>Acanthurus chirurgus</i>	Herbivore	<b>25.55 ± 1.63</b>	741	5.37	1.21 ± 0.32	40	0.39	1.27 ± 0.28	47	0.57		
<i>Acanthurus coeruleus</i>	Herbivore	1.03 ± 0.2	30	0.21	—	—	—	—	—	—		
Antennariidae												
<i>Antennarius multiocellatus</i>	Carnivore	—	—	—	0.09 ± 0.05	3	0.02	—	—	—		
Balistidae												
<i>Balistes vetula</i>	Invertivore	0.24 ± 0.08	7	0.05	0.24 ± 0.10	8	0.07	—	—	—		
Bleniidae												
<i>Parablennius</i> spp.	Omnivore	4 ± 0.68	116	0.84	2.36 ± 0.36	78	0.76	2.62 ± 0.32	97	1.18		
<i>Scartella cristata</i>	Herbivore	1.27 ± 0.26	37	0.26	0.78 ± 0.16	26	0.25	0.62 ± 0.12	23	0.28		
Bothidae												
<i>Bothus ocellatus</i>	Carnivore	0.48 ± 0.12	14	0.10	1.72 ± 0.22	57	0.55	2 ± 0.18	74	0.90		
Callionymidae												
<i>Callionymus bairdi</i>	Invertivore	—	—	—	0.09 ± 0.05	3	0.02	—	—	—		
Carangidae												
<i>Carangoides bartholomaei</i>	Carnivore	3.17 ± 1.31	92	0.66	—	—	—	0.75 ± 0.36	28	0.34		
<i>Carangoides crysos</i>	Carnivore	1.03 ± 0.57	30	0.21	—	—	—	0.16 ± 0.09	6	0.07		
<i>Caranx latus</i>	Carnivore	0.82 ± 0.46	24	0.17	—	—	—	—	—	—		
<i>Chloroscombrus chrysurus</i>	Planktivore	—	—	—	—	—	—	0.05 ± 0.03	2	0.02		
<i>Pseudocaranx dentex</i>	Planktivore	1.55 ± 0.61	45	0.32	2.06 ± 0.99	68	0.66	0.16 ± 0.09	6	0.07		
Chaenopsidae												
<i>Emblemaropsis signifera</i>	Invertivore	0.10 ± 0.08	3	0.02	0.09 ± 0.05	3	0.02	0.16 ± 0.06	6	0.07		
Chaetodontidae												
<i>Chaetodon sedentarius</i>	Invertivore	3.89 ± 0.38	113	0.81	—	—	—	0.21 ± 0.06	8	0.09		
<i>Chaetodon striatus</i>	Invertivore	<b>13.93 ± 0.78</b>	404	2.92	<b>7.21 ± 0.49</b>	238	2.33	<b>9.24 ± 0.53</b>	342	4.18		
Cirrhitidae												
<i>Amblycirrhitus pinos</i>	Carnivore	—	—	—	—	—	—	0.16 ± 0.06	6	0.07		
Daelyopteridae												
<i>Daelyopterus volitans</i>	Invertivore	1.79 ± 0.81	52	0.37	—	—	—	0.16 ± 0.06	6	0.07		
Diodontidae												
<i>Chilomycterus spinosus</i>	Invertivore	0.10 ± 0.02	3	0.02	—	—	—	0.16 ± 0.06	6	0.07		
<i>Diodon hystrix</i>	Invertivore	0.31 ± 0.08	9	0.06	0.24 ± 0.07	8	0.07	—	—	—		
Fistulariidae												
<i>Fistularia tabacaria</i>	Piscivore	—	—	—	—	—	—	0.16 ± 0.06	6	0.07		
Gerreidae												
<i>Eucinostomus</i> spp.	Invertivore	0.06 ± 0.04	2	0.01	—	—	—	0.05 ± 0.03	2	0.02		
Gobiidae												
<i>Coryphopterus</i> spp.	Omnivore	2.68 ± 0.18	78	0.56	<b>5.42 ± 0.36</b>	179	1.75	<b>3.81 ± 0.44</b>	141	1.72		
<i>Elacatinus figaro</i>	Invertivore	4 ± 0.34	116	0.84	<b>5 ± 0.22</b>	165	1.61	1.83 ± 0.40	68	0.83		





Table 2. Summary of habitat structure and fish community structure variables ( $\bar{x} \pm SD$ ), plus the one way ANOVA results of comparisons among study sites.

	Fortaleza (FT)	Forno-A (FA)	Forno-B (FB)			
Fish species richness (number of species per census)	73 $\pm$ 10.06	61 $\pm$ 6.30	55 $\pm$ 6.28	$p < 0.05^*$	F = 4.66	FT $\neq$ FA = FB
Total number of fishes per census	468 $\pm$ 74.23	318 $\pm$ 51.53	233 $\pm$ 46.34	$p < 0.001^*$	F = 8.05	FT $\neq$ FA = FB
Fish diversity (H') per census	4.06 $\pm$ 0.49	3.26 $\pm$ 0.32	3.50 $\pm$ 0.29	$p < 0.01^*$	F = 6.14	FT $\neq$ FA = FB
Number of holes	12.33 $\pm$ 7.24	21.70 $\pm$ 8.94	22.60 $\pm$ 5.24	$p < 0.01^*$	F = 5.54	FT $\neq$ FA = FB
Surface area (total length of the rocky shore)	23.25 $\pm$ 4.37	15.57 $\pm$ 3.05	14.3 $\pm$ 3.19	$p < 0.01^*$	F = 18.61	FT $\neq$ FA = FB
Substratum diversity (Simpson's index)	0.68 $\pm$ 0.08	0.65 $\pm$ 0.05	0.69 $\pm$ 0.08	$p = 0.48$	F = 0.73	FT = FA = FB
Topographic complexity (rugosity index)	1.35 $\pm$ 0.16	1.36 $\pm$ 0.14	1.32 $\pm$ 0.11	$p = 0.77$	F = 0.26	FT = FB = FA
% cover of turf algae	11.41 $\pm$ 5.53	11.07 $\pm$ 5.08	11.43 $\pm$ 5.77	$p = 0.49$	F = 0.72	FT = FA = FB
% cover of zoanths	1.85 $\pm$ 0.05	23.02 $\pm$ 6.93	23.99 $\pm$ 15.99	$p < 0.001^*$	F = 20.18	FT $\neq$ FA = FB
% cover of millepores	1.63 $\pm$ 0.08	4.77 $\pm$ 1.33	5.01 $\pm$ 1.02	$p = 0.07$	F = 2.91	FT = FA = FB
% cover of massive corals	—	1.24 $\pm$ 0.78	4.45 $\pm$ 2.96	$p < 0.001^*$	F = 14.99	FT $\neq$ FA $\neq$ FB
% cover of bare rock	31.94 $\pm$ 18.11	51.53 $\pm$ 6.35	39.66 $\pm$ 17.20	$p < 0.05^*$	F = 4.81	FA $\neq$ FT = FB
% cover of encrusting calcareous algae	21.78 $\pm$ 11.62	2.89 $\pm$ 1.03	11.44 $\pm$ 8.90	$p < 0.001^*$	F = 10.73	FT $\neq$ FA $\neq$ FB
% cover of urchins	9.21 $\pm$ 4.78	2.11 $\pm$ 1.40	3.39 $\pm$ 0.51	$p < 0.001^*$	F = 24.46	FT $\neq$ FA = FB
% cover of other organisms (sessile invertebrates)	9.09 $\pm$ 4.51	5.76 $\pm$ 2.43	2.35 $\pm$ 1.64	$p < 0.001^*$	F = 8.24	FT = FA $\neq$ FB
% cover of Sargassum	9.63 $\pm$ 2.23	—	—			FT $\neq$ FA = FB

\*Indicates significant difference.

herbivores from which *Stegastes fuscus* was by far the most abundant, and roving herbivores such as scarids and acanthurids. The territorial herbivore, *S. fuscus*, sustained high densities in FA and FB sites, while overall roving herbivores were most abundant at FT site, although more species of these non territorial herbivores were found in the later area. Carnivores, piscivores and planktivores showed similar percentages in composition among sites, with the first group being richer at the FT site (Table 1). A quick view of the data shows that large fishes, not only predators but also herbivores, sustained higher densities in FT, while small fishes such as *S. baldwini* and *Coryphopterus* spp. were more abundant in FA and FB.

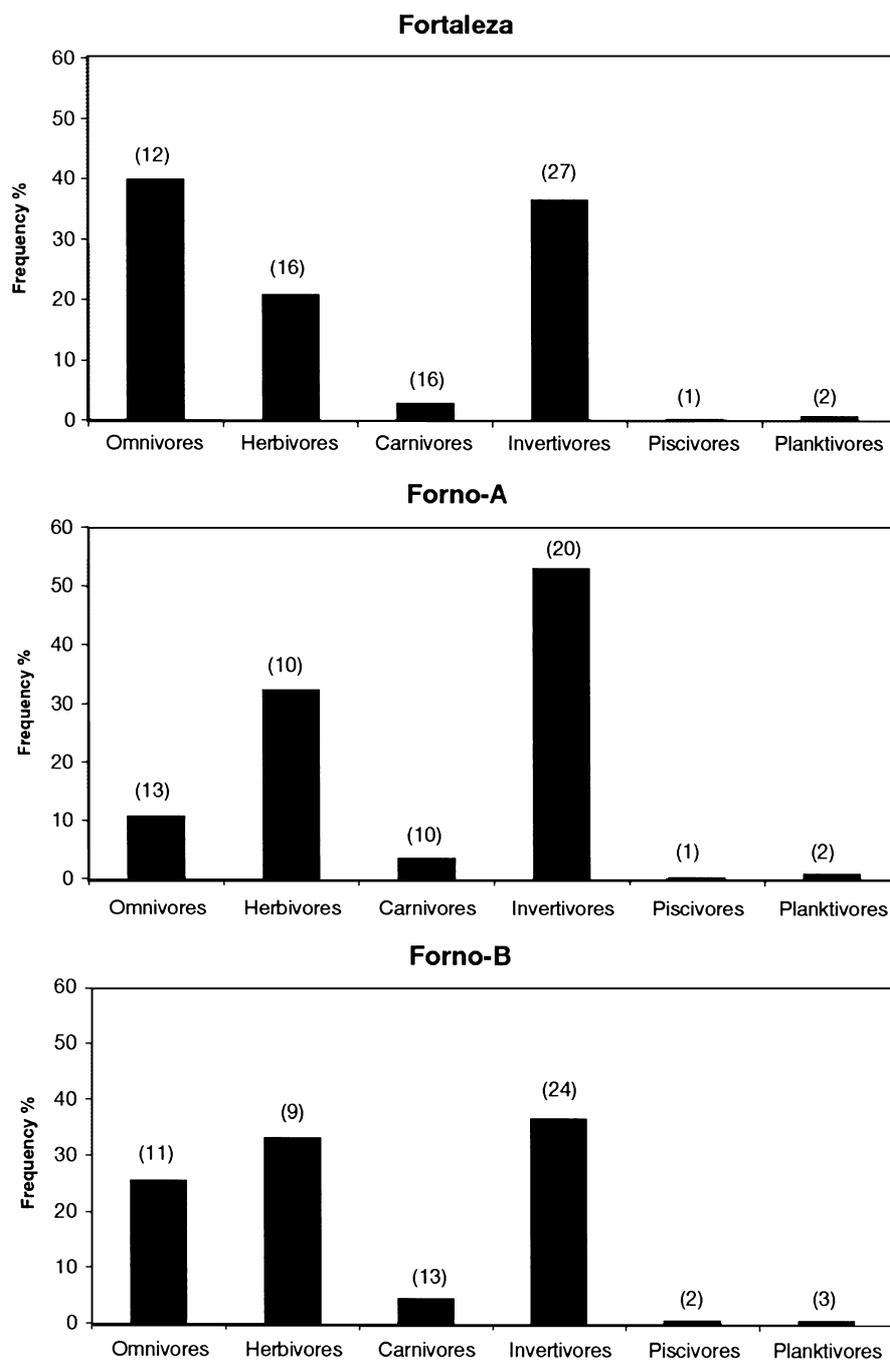
#### Habitat complexity

Within the habitat variables, substratum diversity, topographic complexity (rugosity), percentage cover of turf algae and of *Millepora alcicornis* were not significantly different among sites (Table 2). Although not revealed by statistical analysis, *M. alcicornis* was scarce at the

FT site. The same pattern was repeated with the other cnidarians, such as zoanths (e.g. *Palythoa caribaeorum*) and massive corals (e.g. *Siderastrea stellata* and *Mussismila hispida*). Similar number of holes were found at the FA and FB sites, almost the double found in FT site. The mean length of surface area was slightly higher in FT, and such a difference could influence the comparison to other sites for some organisms which possess an equal or a lesser percentage of cover. Abundance of sessile benthic invertebrates, the great majority being filterers, were also higher at FT, as this site is more exposed to predominant currents.

#### Fish and benthic organisms vertical distribution

The ten most abundant species of fishes are represented by points and the habitat variables represented by arrows in the CCA ordination diagrams for the three study sites (Figure 3). The fish species and habitat variables jointly reflected the species distribution along each of the habitat variables. Together, fish species and



*Figure 2.* Percentage of major trophic groups of fishes within study sites. Number in parentheses indicate the number of species in each group.

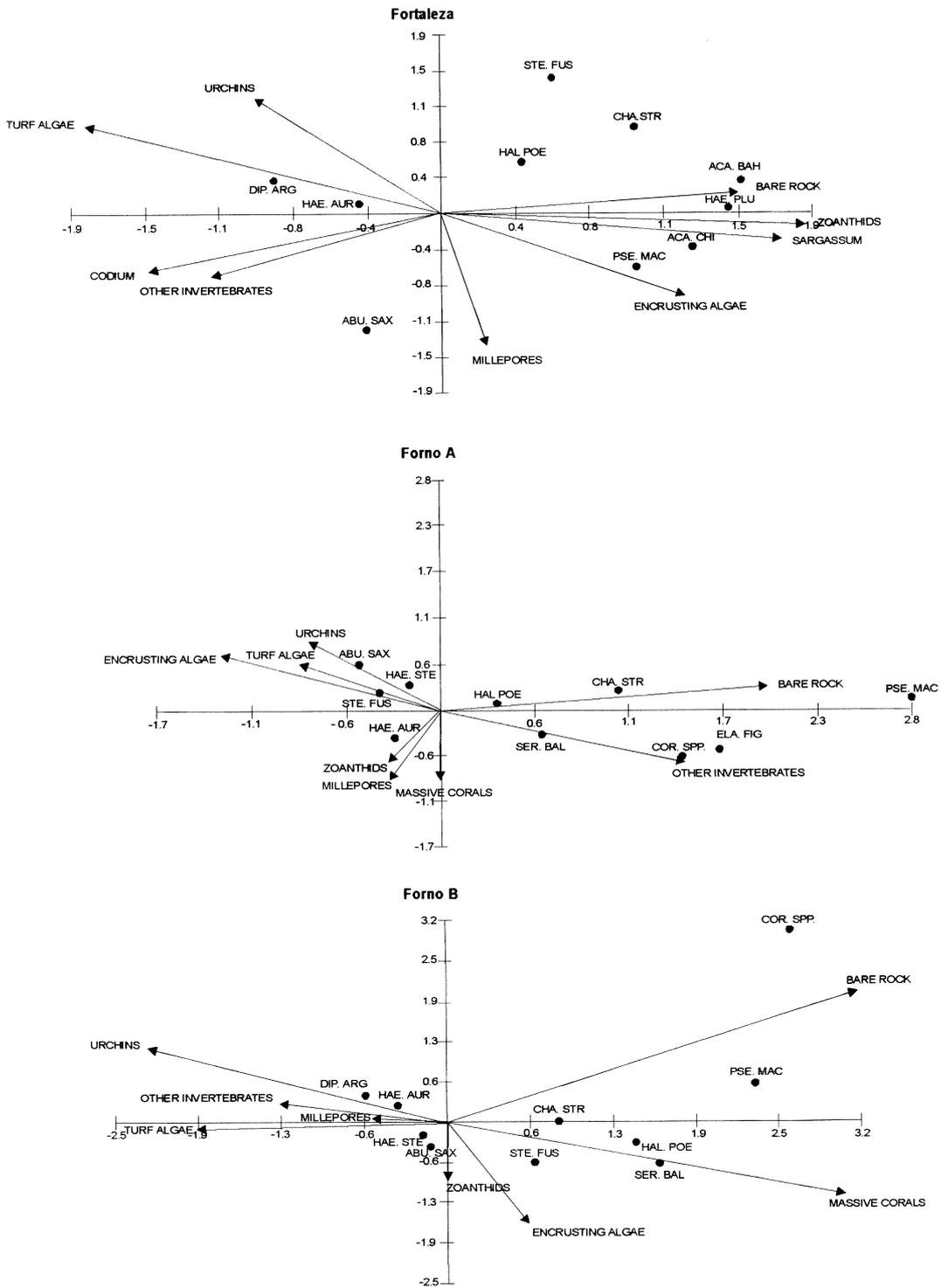


Figure 3. Canonical correspondence analysis of fish abundance vs. substratum type percent coverage obtained from vertical transects along the rocky shores of study sites.

habitat variables accounted for 65%, 89% and 93% of the variance in the weighted averages, respectively for FT, FA and FB sites; the corresponding sums of eigenvalues being 1.1, 0.6 and 0.81. In the three biplots, the axis 1 clearly represented the gradient of depth on the rocky shores studied, where the left side was characterized by shallow environments with increase in depth as one goes to the right (Figure 4).

In the FT site ordination, turf algae and *Codium intertextum* were the most important habitat variables describing the shallow habitat, followed by urchins, mainly *Echinometra lucunter*, and other sessile benthic invertebrates, including barnacles, mussels, anemones, sponges, ascidians, hydroids and bryozoans. Fishes abundant in this zone included *D. argenteus*, *H. aurolineatum* and *A. saxatilis*. The hydrocoral, *Millepora alcicornis*, showed an intermediate distribution at the FT site, being more associated with axis 2, which was responsible for the dispersing of points in the vertical position. *Stegastes fuscus*, which is a typical inhabitant of shallow areas, at the FT site did not present a well defined pattern, despite sustaining higher abundance in shallow areas (Figure 4a). *H. poeyi* and *C. striatus* were fishes which possessed an ample distribution along the rocky shore, while the herbivores *A. chirurgus* and *A. bahianus* and the benthic invertebrate feeders *H. plumieri* and *P. maculatus* were more commonly found in deeper zones. The later are more associated with the sand-rocky interface. The percent cover of zoanthids, together with that of *Sargassum furcatum*, which occurred only in summer periods, were the most important habitat variables influencing the distribution of fishes in deeper zones of the rocky shore. The amount of bare rock increases with depth and such a pattern predominated on all sites. The encrusting calcareous algae were more densely distributed on mid to deeper habitats at the FT site.

For FA site, the cover of encrusting calcareous algae was the best indication of a shallow environment, followed by the cover of urchins and turf algae. The most abundant fishes in this zone were *A. saxatilis*, *S. fuscus*, *H. aurolineatum* and *H. steindacneri*. The cover of millepores, zoanthids and massive corals, more densely represented in intermediate and deeper zones, were responsible for the vertical point dispersal of the biplot ordination. *H. poeyi*, *S. baldwini* and *C. striatus* are fishes with an ample distribution along the rocky shore in this site. The cover of bare rock and other sessile organisms characterized the deeper zones. Fishes occurring there were the gobiids, *Coryphopterus* spp., highly associated with soft bottom, the Brazilian

cleaner fish, *E. figaro*, and the goat fish, *P. maculatus* (Figure 4b).

In the ordination for the FB site, urchins and turf algae were the benthic organisms which most influenced the distribution of typically shallow habitat fishes, followed by the percentage cover of other sessile benthic organisms and millepores. The most abundant fishes in this zone were *D. argenteus*, *H. aurolineatum*, *H. steindacneri* and *A. saxatilis*. The percentage covers of zoanthids and encrusting calcareous algae were associated with axis 2 and at this site showed a high density in mid parts of the rocky shore. *S. fuscus* and *C. striatus*, despite being most abundant in shallow areas (Figure 4c), showed an ample distribution on the positive side of axis 1. *H. poeyi* and *S. baldwini*, as at FA, were fishes with an intermediate depth distribution, while *Coryphopterus* spp. and *P. maculatus* were common in deeper areas. At this site, the percent cover of bare rock, together with massive corals, also reflected the distribution of fishes on deeper areas.

#### *Relationship between fish community structure and habitat complexity*

The results of the MDS analysis demonstrate graphically what was explicit in Table 2. Ordination extracted 47% of the variance for the first two vectors. The one-way ANOSIN test confirmed a significant difference ( $R = 0.98$ ,  $p < 0.1\%$ ) between the two groups formed (Figure 5). Group 1 presented habitat variables more associated with the FT site, including percent cover of encrusting calcareous algae, urchins and other sessile invertebrates, as well as all fish variables (fish richness, fish diversity and total number of fishes). Group 2 showed habitat variables which were highly associated with the FA and FB sites, such as percent cover of millepores and zoanthids, and number of holes, together with the habitat variables not significantly different among study sites (percent cover of turf algae, rugosity and substratum diversity; see Table 2). The habitat variables that seemed to be highly associated with fish variables were percent cover of sessile invertebrates, total surface area, percent cover of urchins and encrusting calcareous algae.

## Discussion

### *Patterns of fish abundance*

Considering that Arraial do Cabo region is a high latitude tropical area and does not sustain true coral

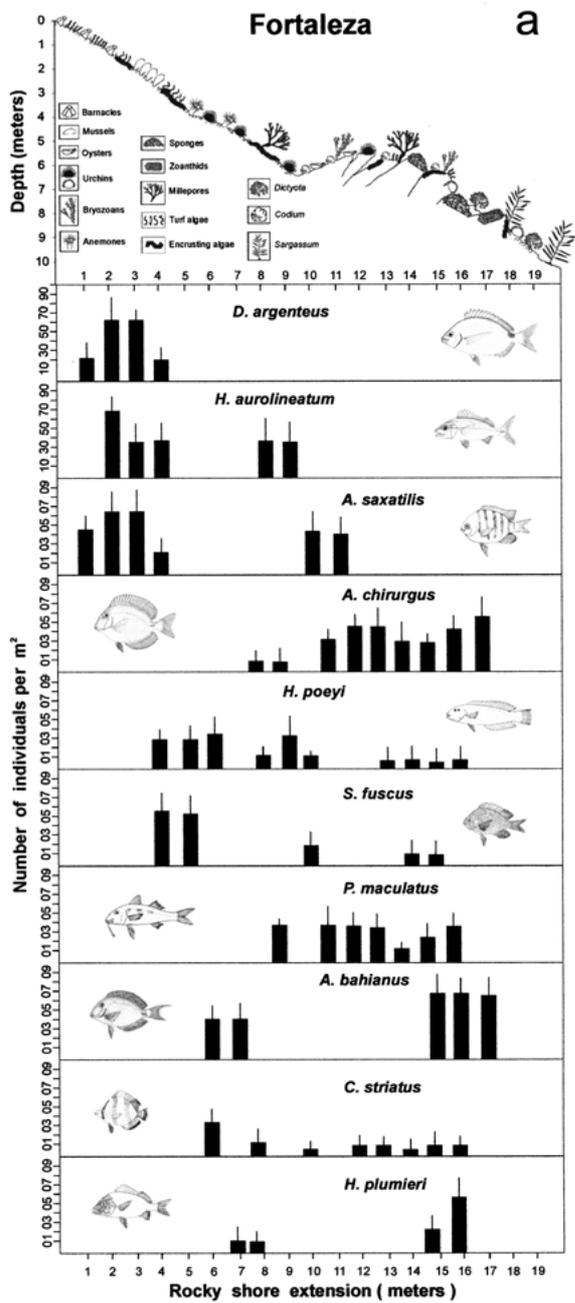


Figure 4a.

reefs, the patterns of fish abundance and diversity described here by means of visual census seem to be well comparable to some tropical coral reefs (Bell & Galzin 1984, Kaufman & Ebersole 1984, Sale & Douglas 1984, Núñez Lara & Arias Gonzáles

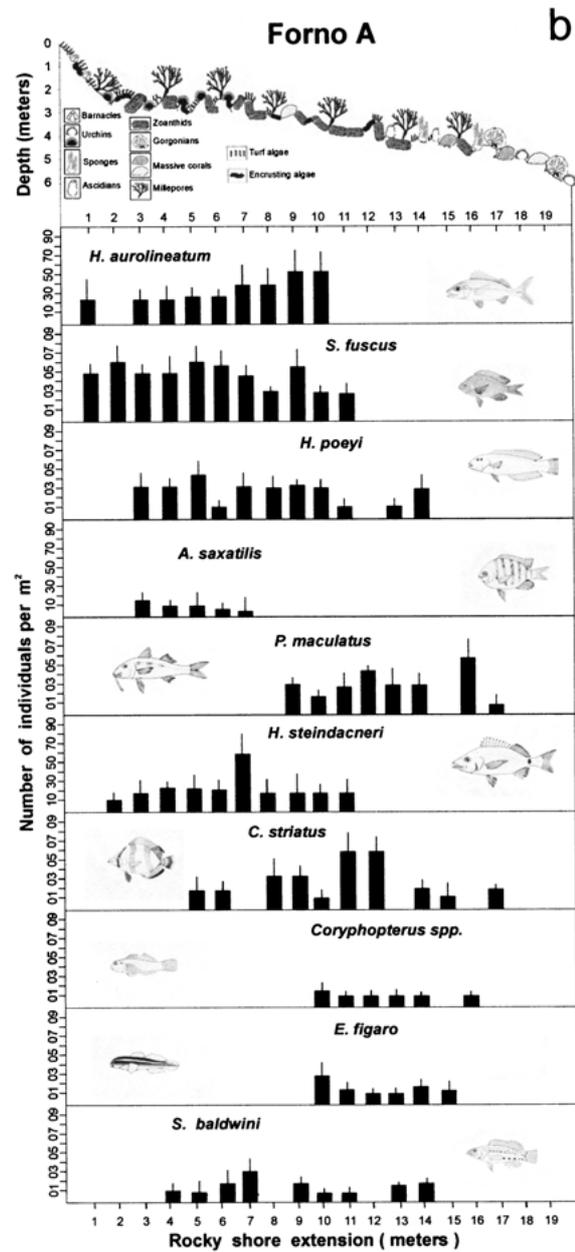


Figure 4b.

1998). Actually, the complete list of local reef fishes is at present greater than the list shown in Table 1 (Ferreira & Zaluar unpublished data). The whole region has been suffering from overfishing, including spearfishing and collecting of fishes for the aquarium trade. The first have major effects on the abundance and size of large fishes from families Serranidae,

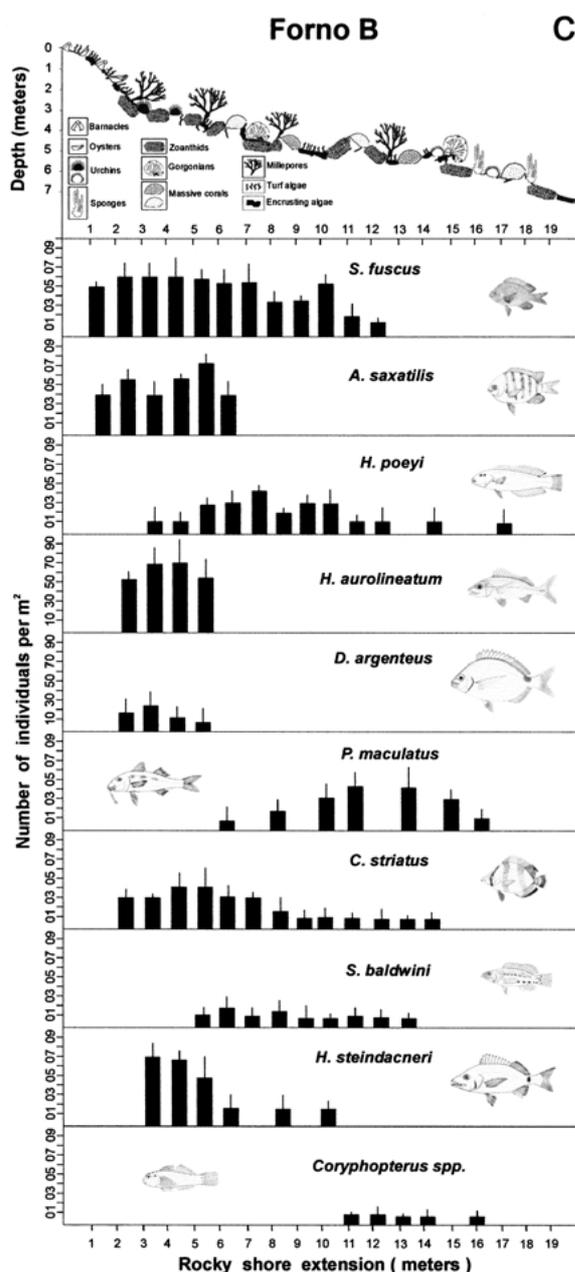


Figure 4c. Fish abundance and vertical distribution plus schematic view of vertical substratum composition of the three study sites: a – Fortaleza, b – Forno-A and c – Forno-B.

Carangidae, Balistidae and Scaridae; while the second affects most the abundance of fishes from families Labridae, Pomacanthidae, Pomacentridae and Syngnathidae. Fortunately, the whole region recently

became a harvest reserve, including a marine protected area. Therefore, the patterns of fish abundance detected here, mirror the community state at the time of present study, structured by known factors (Hixon 1991, Russ & Alcala 1998) and possible unknown synergistic factors driven by different local impacts.

The data showed that the basic difference in the community structure of fishes among study sites was that FT sustains a higher diversity and abundance of fishes than the other sites, which in turn are very similar, both in terms of fish community and environment. Omnivores, for example, were best represented in the FT site (Figure 2), where the cover of *P. caribaeorum* as well as other cnidarians is very meager, due mainly to high wave surge, thus giving space to the growth of a variety of sessile invertebrates, and consequently offering a greater diversity of food. Taking this into account, substratum diversity was not a good descriptor for the comparison of different study sites in this rocky shore system. Good examples of omnivores in this case are the filefish, *S. hispidus*, and the porgy, *D. argenteus* (Table 1), since despite them occurring in Forno-A and Forno-B sites, they reached higher densities at FT.

As FT sustains a great influx of water, more drift material is available (e.g. macroplankton) (Ferreira personal observation), which increases the density of restricted planktivores such as *C. multilineata*, along with occasional planktivores (e.g. pelagic pickers) such as *A. saxatilis* and *C. sedentarius*. As the abundance of virtual prey increased, an increase in abundance of large predators was detected (Table 1). Otherwise, abundances of more site attached, small fishes, like *Coryphopterus* spp. and *S. baldwini* were higher at the sheltered sites, where more size specific refuges were available and less predators were present. Roving herbivorous fishes were also most abundant at FT. A larger rocky shore as well as the lack of dominance of *P. caribaeorum* were the potential factors contributing to this pattern, since more space was available for algal growth. This contrasts with some authors, who found no relationship between the abundance of herbivorous fishes and algae cover (Wellington & Victor 1985, Chabanet et al. 1997). However, the most important factor in explaining the highest abundance of roving herbivorous fishes at FT site seems to be the low density of *S. fuscus* territories. In FA and FB sites, this species can occupy more than 70% of the substrate in shallow areas at some places, thus having a great influence on feeding behavior of scarids and acanthurids, which is a well reported interaction (Choat 1991).

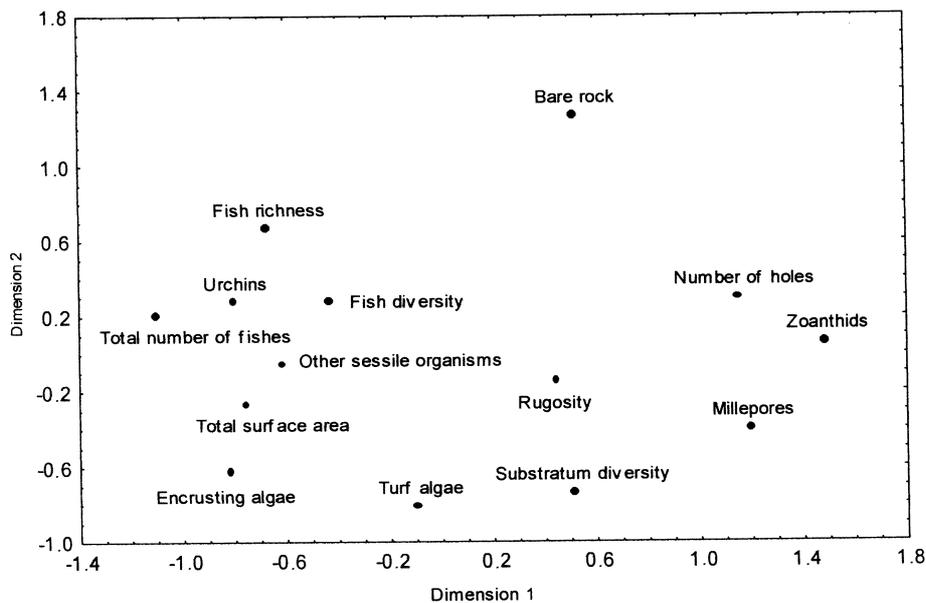


Figure 5. Multidimensional scaling analysis of the relationships between fish community variables and habitat complexity variables.

Since the three study sites described here were included in the same inlet, the community of fishes at all sites, as expected, was very similar, being influenced indirectly by local upwelling (Ferreira et al. 1998b). However, the rocky shores not included in the embayment conditions provided by the position of Cabo Frio island in relation to the continent (Figure 1) and directly influenced by upwelling cold waters and high wave surge, are remarkably different from the community of fishes discussed herein (Ferreira unpublished data). Moreover they provide good comparisons with the non-upwelling influenced sites. Such characteristics of a tropical system side by side to a subtropical system in such a small area as Arraial do Cabo, produce an edge effect (Krebs 1994), increasing total diversity, and also making the region a hot spot for the understanding of the limits of distribution of various marine organisms and the adaptations they make use in order to survive in such an unstable environment.

#### Vertical distribution of fishes

The data show that there is a fixed pattern of fish vertical distribution along the rocky shores, common to all study sites. This pattern is highly correlated with patterns of vertical distribution of benthic organisms (Figure 4) and it seems to be determined by factors

such as feeding habits and behavior, refuge from predation and social interactions. Some investigations have described distinct associations of fishes in different zonations with different substratum type and complexity, either in tropical or temperate environments (Ebeling & Hixon 1991, Holbrook et al. 1990, Ebeling & Hixon 1991). As an example, *S. fuscus* sustains its highest densities in shallow areas of the rocky shore, where its main food item, turf algae, reaches the highest diversity and biomass (Ferreira 1998, Ferreira et al. 1998a), since these algae are directly dependent of sunlight. However, despite the fact that FT also sustains a high biomass of turf algae, the availability of refuge (e.g. number of holes) was lower than in the other sites, and consequently a correlated decrease occurred with the abundance of *S. fuscus*. Abundant invertivores like *H. poeyi*, *S. baldwini* and *C. striatus*, feeding on mobile or sessile invertebrates, find their food in a large strip of the rocky shore, as these invertebrates are associated with different kinds of substratum. Other fishes like *D. argenteus* and *A. saxatilis* were frequently observed forming schools while foraging in the water column in shallow areas, although such feeding behavior could change regarding the size of a fish and wave exposure. In this way, larger individuals of *A. saxatilis* are more restricted to feed on benthos while small size fishes feed on the water column. This kind of intraspecific separation of feeding niches is conspicuous for

other species of fishes in this system. *P. maculatus* is a typical fossorial feeder, foraging mostly over sand, so being more abundant in the sand-rocky shore habitat. Notwithstanding, they detect and capture prey in quite different ways (McCormick 1995), thus they could extend their limits of distribution along the rocky shore.

As FT presented different habitat characteristics, some different fish species occurred there. Nevertheless, where the same species are present and comparisons are done, they tend to maintain the same vertical distribution as is shown in Figure 4. Thus, a good approach to understand the relationship between fishes and substratum type relies basically on continued field observations and gut analysis. Bearing this in mind, it is possible to infer a certain degree of predictability in terms of spatial distribution of fishes, especially for dominant species of fish on the investigated rocky shores and even, considering the differences reported between FT and FA and FB sites, to predict the presence or absence of a fish species (in terms of a stabilized community).

#### *Relationships between fish variables and habitat variables*

FT sustains the highest fish richness, fish diversity and total number of fishes sighted, and from the MDS results it was evident that the habitat variables more associated with those fish community structure variables are the cover of other sessile invertebrates, total surface of the rocky shore, density of urchins and the cover of encrusting calcareous algae. Rugosity (= topographic complexity) which has been widely used in coral reefs around the world as a good predictor of fish diversity and, in some locations, abundance (see Chabanet et al. 1997) was a poor descriptor of number of fishes in the rocky shores studied. Complexity on the rocky shore system seems to rely on the presence or absence of holes, which in turn are formed by accumulation and superposition of granite boulders. Indeed, if the rocky shore is characterized by large boulders, more large holes are formed (as was found at FT), while the reverse is characteristic of the FA and FB rocky shores. Although the number of holes was higher at FA and FB sites, they do not attract so many fishes as FT sustains. Indeed, the characteristic of a great number of holes is to offer refuges for fishes such as damselfishes and small site attached fishes, e.g. *Coryphopterus* spp. and *S. baldwini*, which reflect in the greater abundance

of these fishes at the sheltered sites (Table 1). Such a relationship has also been described to occur on coral reefs where architectural complexity of corals attracts more sedentary and small territorial fishes (Sale & Douglas 1984). Clearly, where there are large patches of *M. alcicornis* associated with rocky shores, similar to true coral reefs, the complexity is higher. Nevertheless, when comparisons were made the difference among study sites regarding rugosity was not significant, even though the *M. alcicornis* cover at FA and FB sites was greater than at FT. Actually, the contrast when comparing sites with huge cover of *M. alcicornis*, not analyzed herein, is the refuge that these hydrocorals provided by increasing the variety of microhabitats for recruits and juveniles, especially noted for *H. poeyi*, *S. pictus* and *C. striatus* (Ferreira personal observation). Since a positive correlation does not necessarily mean causation, careful detailed discussion, relying on fish-habitat interaction, become necessary (Öhman & Rajasuriya 1998).

Excluding recruits and juvenile urchins, adult urchins are food resources for quite a few fishes, including (in this study) *D. hystrix* and *B. vetula*, with the later occurring in very low densities, mainly due to fishing. Thus, urchins density does not seem to be a good indicator of high fish abundance, but as stressed in literature, the lack of their predators (Hay 1984, McClanahan et al. 1994). The percent cover of encrusting calcareous algae is often associated with the density of urchins, specially *E. lucunter*. In fact, due to its characteristic of high herbivore pressure, this urchin maintains huge barrens of such red encrusting calcareous algae in shallow areas of the rocky shores (Ferreira et al. unpublished data), the only algae which generally could keep itself growing under a such grazing pressure (Steneck 1988). Despite this, these algae were abundant on different parts of the rocky shores in each study site. Hence, the habitat variables which could better explain the association of all fish variables at FT were percent cover of other sessile invertebrates and total surface of the rocky shore. Firstly, with an increase in abundance and diversity of sessile invertebrates, a greater diversity of food is available, as suggested by the high abundance of omnivores recorded at FT site (Figure 2). Moreover, additional space on the substratum, provided not only by a wider rocky shore, but also by the lack of *P. caribaeorum*, means that more larvae could recruit in such space, consequently increasing the availability and diversity of food. Likewise, the exposure conditions to wave surge of this site, providing a great influx of drift material,

seems to be an additional determinant, contributing to increasing in the diversity of fishes. Therefore, it is suggested that a rocky shore with conditions of high wave surge, not affected directly by upwelling and larger than rocky shores like FA and FB sites, could sustain greater number and higher diversity of fishes than those rocky shores found in sheltered sites.

### Conclusion

The results presented in this study showed that Forno Inlet presented a rich reef fish fauna with fixed patterns of vertical distribution on local rocky shores. In protected areas, rocky shores in locations subject to more wave exposure sustain a higher diversity and number of fishes. This study demonstrated that some indicators of habitat complexity widely used for other reef systems, were not useful for describing and comparing rocky shores, wave exposure being the main structural factor. Although the factors which regulated community structure of reef fish have been intensely investigated and they are known to be determined by several interacting factors (Hixon 1991, Russ & Alcala 1998), fish diversity and distribution in the rocky shore system studied here seemed to be highly predictable. This kind of information is valuable in order to optimally manage local resources. In fact, since Arraial do Cabo is now in a process of evaluation for the regulation of the use of specific marine areas, these data will be useful for optimizing the management of the local marine resources. It is extremely important to produce basic knowledge, in terms of diversity and abundance of local resources, in order that the development of precise models can be accomplished and a better understanding of the local rocky shore system and its impacts can be gained. This will be important to help the local preservation efforts in the near future.

### Acknowledgements

Logistic and financial support was given by IEAPM. As usual, discussion with Helena Passeri contributed greatly to final work. Thanks to Terezinha Andrea and Joel Creed for improving the final English version. Thanks also to Seroma who helped with Figure 4 and to Eduardo Godoy, who helped to count holes in transects. Many thanks to two anonymous referees for comments and suggestions.

### References cited

- Bell, J.D. & R. Galzin. 1984. Influence of live coral cover on coral reef fish communities. *Mar. Biol. Prog. Ser.* 15: 265–274.
- Bonhsack, J.A., A.M. Ecklund & A.M. Szmant. 1997. Artificial reef research: is there more than the attraction-production issue? *Fisheries* 22: 14–16.
- Carpenter, K.E., R.I. Míclat, V.D. Albaladejo & V.T. Corpuz. 1981. The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *Proc. 4th Int. Coral Reef Symp.* 2: 497–502.
- Carr, M.H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *J. Exp. Mar. Biol. Ecol.* 126: 59–76.
- Castro, C.B., C.A. Echeverría, D.O. Pires, B.J. Mascarenhas & S.G. Freitas. 1995. Distribuição de cnidária e equinodermata no infralitoral de costões rochosos de Arraial do Cabo, Rio de Janeiro, Brasil. *Rev. Brasil. Biol.* 55: 471–480.
- Chabanet, P., H. Ralambondrainy, M. Amanieu, G., Faure & R. Galzin. 1997. Relationships between coral reef substrata and fish. *Coral Reefs* 16: 93–102.
- Choat, J.H. 1991. The biology of herbivorous fishes on coral reefs. pp. 120–155. *In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego.
- Clarke, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. *Aust. J. Ecol.* 18: 117–143.
- Ebeling, A.W. & M.A. Hixon. 1991. Tropical and temperate reef fishes: comparison of community structures. pp. 509–563. *In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego.
- Falcón, J.M., S.A. Bortone, A. Brito & C.M. Bundrick. 1996. Structure of and relationships within and between the littoral, rock-substrate fish communities off four islands in the Canarian Archipelago. *Mar. Biol.* 125: 215–231.
- Ferreira, C.E.L. 1998. Partitioning resources by herbivores in a tropical rocky shore. Doctorate Thesis, São Carlos Federal University, São Paulo. 100 pp.
- Ferreira, C.E.L., A.C. Peret & R. Coutinho. 1998. Seasonal grazing rates and food processing by tropical herbivorous fishes. *J. Fish Biol.* 53 (Suppl. A): 222–235.
- Ferreira, C.E.L., J.E.A. Gonçalves, R. Coutinho & A.C. Peret. 1998. Herbivory by the dusky damselfish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. *J. Exp. Mar. Biol. Ecol.* 229: 241–264.
- Grossman, G.D., G.P. Jones & W.J. Seaman, Jr. 1997. Do artificial reefs increase regional fish production? A review of existing data. *Fisheries* 22: 17–23.
- Guimaraens, M.A. & R. Coutinho. 1996. Spatial and temporal variation of benthic marine algae at Cabo Frio upwelling region, Rio de Janeiro, Brazil. *Aquatic. Bot.* 52: 283–299.
- Hixon, M.A. 1991. Predation as a process structuring coral reef fish communities. pp. 475–508. *In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego.
- Holbrook, S.J., M.H. Carr, R.J. Schmitt & J.A. Coyer. 1990. Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. *Bull. Mar. Sci.* 47: 104–114.

- Jenkins, G.P. & M.J. Wheatley. 1998. The influence of habitat complexity on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. *J. Exp. Mar. Biol. Ecol.* 221: 147–172.
- Kaufman, L.S. & J.P. Ebersole. 1984. Microtopography and the organization of two assemblages of coral reef fishes in the West Indies. *J. Exp. Mar. Biol. Ecol.* 78: 253–268.
- Krebs, C. J. 1994. *Ecology*. Harper & Row, New York. 550 pp.
- Lavrado, H.P. 1992. Prey selection by the gastropod *Thais haemastoma* (Linneus) in Arraial do Cabo region, RJ. Master Thesis, Campinas State University, São Paulo. 104 pp.
- Legendre, L. & P. Legendre. 1983. *Numerical ecology*. Elsevier, New York. 318 pp.
- Luckhurst, B.E. & K. Luckhurst. 1978. Analysis of the influence of the substrate variables on coral reef fish communities. *Mar. Biol.* 49: 317–323.
- McCormick, M.I. 1995. Fish feeding on mobile benthic invertebrates: influence of spatial variability in habitat associations. *Mar. Biol.* 121: 627–637.
- Moura, R.L. 1998. Activity, distribution and feeding tactics of a fish community from Atol das Rocas. Master Thesis, São Paulo University, São Paulo. 70 pp.
- Núñez Lara, E. & E. Arias González. 1998. The relationship between reef fish community structure and environmental variables in the southern Mexican Caribbean. *J. Fish Biol.* 53 (Suppl. A): 209–221.
- Öhman, M.C. & A. Rajasuriya. 1998. Relationships between habitat complexity and fish communities on coral and sandstone reefs. *Env. Biol. Fish.* 55: 19–31.
- Ornellas, A. & R. Coutinho. 1998. Spatial and temporal patterns of distribution and abundance of a tropical fish assemblage in a seasonal Sargassum bed, Cabo Frio Island, Brazil. *J. Fish Biol.* 53 (Suppl. A): 198–208.
- Porter, J.W. 1972. Patterns of species diversity in Caribbean reef corals. *Ecology* 53: 745–748.
- Randall, J.E. 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogra.* 5: 665–847.
- Roberts, C.M. & R.F.G. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar. Ecol. Prog. Ser.* 41: 1–8.
- Russ, G.R. & A.C. Alcala. 1998. Natural fishing experiments in marine reserves 1983–1993: community and trophic responses. *Coral Reefs* 17: 383–398.
- Sale, P.F. 1980. The ecology of fishes on coral reefs. *Oceanogr. Mar. Biol.* 18: 367–421.
- Sale, P.F. 1991. Reef fish communities: open nonequilibrium systems. pp. 564–598. *In*: P.F. Sale (ed.) *The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego.
- Sale, P.F. & W.A. Douglas. 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology* 65: 409–422.
- Steneck, R.S. 1988. Herbivory on coral reefs: a synthesis. *Proc. 6th Int. Coral Reef Symp.* 1: 37–49.
- Ter Braak, C.J.F. & P.F.M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57: 255–289.
- Underwood, A.J. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge. 504 pp.
- Valentin, J.L. 1984. Analyse des paramètres hydrobiologiques dans la remontée de Cabo Frio (Brésil). *Mar. Biol.* 82: 259–276.
- Wellington, G.M. & B.C. Victor. 1985. El Niño mass coral mortality: a test of resource limitation in a coral reef damselfish population. *Oecologia* 68: 15–19.
- Williams, D.McB. 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1: 35–43.
- Zar, J.H. 1996. *Biostatistical analysis*. Prentice Hall, Upper Saddle River. 662 pp.