Reef fish community structure of the Fernando de Noronha Archipelago (Equatorial Western Atlantic): the influence of exposure and benthic composition

João Paulo Krajewski · Sergio R. Floeter

Abstract We studied the reef fish assemblage of eight reefs within the oceanic archipelago of Fernando de Noronha, off northeastern Brazil. In a total of 91 belt transects (20×2 m) we recorded 60 species from 28 families. The 25 most abundant species accounted for about 98% of all fish recorded in this study and most of these species are widely distributed in the Western Atlantic. The majority of fish counted were planktivores (37.0%), followed by mobile invertebrate feeders (28.5%), territorial herbivores (11.3%), roving herbivores (10.5%), omnivores (7.1%), macro-carnivores (6.5%) and sessile invertebrate feeders (0.03%). In terms of biomass, roving herbivores were the most representative (41.8%), followed by mobile invertebrate feeders (19.9%), macrocarnivores (14.3%), omnivores (14.0%), piscivores (8.3%), planktivores (1.4%), territorial herbivores (0.3%), and sessile invertebrate feeders (0.03%). Overall, density and biomass of fishes were positively correlated with coral cover and depth, and negatively correlated with wave exposure. These relationships are probably a response to the habitat complexity provided by the higher coral cover in deeper reefs (>10 m) of the archipelago or to the lower water turbulence below 10 m deep. Carnivores and mobile invertebrate feeders were mainly influenced by depth and non-consolidated substratum, planktivores and omnivores by wave exposure and herbivores by algal cover. Although our results suggest that habitat characteristics may play a role in determining the distribution of some fish species, we also found several habitat generalists, suggesting that the community is dominated by versatile species.

J. P. Krajewski
Departamento de Biologia Animal,
Universidade Estadual de Campinas,
Campinas, SP 13083-970, Brazil

J. P. Krajewski · S. R. Floeter (✉)
Departamento de Ecologia e Zoologia, CCB,
Universidade Federal de Santa Catarina,
Florianópolis, SC 88010-970, Brazil
e-mail: floeter@ccb.ufsc.br

Introduction

One of the most important questions in coral reef ecology is the understanding of how fish communities are structured along a range of environmental variables (Jones and Syms 1998; Bellwood and Wainwright 2002). In this context, several studies have investigated correlations between fish density and biomass with a range of abiotic variables (e.g. Jones and Syms 1998; Jones and McCormick 2002). To date, wave exposure has been considered one of the key factors in shaping coral reef fish assemblages, as the abundance of fast-swimming fish species has been found positively correlate to water flow and wave exposure by a

number of studies in reefs around the world (e.g. Fulton and Bellwood 2002a; Fulton et al. 2005; Floeter et al. 2007; Johansen et al. 2007). Similarly, depth has been also found to play an important role in determining reef fish community structure, as particular species and trophic groups often favour specific depth zones on reefs (Clarke 1977; Green 1996; Fox and Bellwood 2007). Positive correlations have also been observed between fish abundance and other abiotic variables, such as reef topographic complexity (Roberts and Ormond 1987; Jones and Syms 1998). In general, the abiotic variables of reef systems seem to have critical roles on the distribution of associated fish species.

In addition to abiotic factors, the structure of fish communities may also be influenced by biotic variables, such as abundance of potential competitors (Jones 1987, 1988; Robertson 1996), abundance of prey (Hobson and Chess 1978, 1986; Bouchon-Navarro and Bouchon 1989; Jennings et al. 1996; Floeter et al. 2007), and relative abundance of some substratum types, such as corals and sponges, that may be used as food or shelter (i.e. living or temporary hiding grounds) (e.g. Munday et al. 1997; Rocha et al. 2000; Gardiner and Jones 2005). In general, stronger correlation between substratum composition and fish density has been found in coral reef fish species with more specialised diets (e.g. some butterflyfishes and angelfishes) and habitat requirements (e.g. coral dwelling gobies and some cardinal fishes) (e.g. Bouchon-Navarro and Bouchon 1989; Jennings et al. 1996; Munday et al. 1997; Gardiner and Jones 2005; Floeter et al. 2007).

Despite the recognized importance of relationships between fish assemblage structure and biotic and abiotic variables, most studies on this subject have been conducted in high diversity coral reef systems, focusing fishes with specialized habitat or diet requirements. As a result, very little information is available for low diversity systems, such as isolated tropical rocky reefs. However, while the diversity and complexity of coral reefs seem to promote the evolution of specialised relationships between fishes and reef microhabitats (e.g. Munday et al. 2004; Gardiner and Jones 2005), the relatively simpler reef topography, greater isolation and smaller reef area of some oceanic islands or tropical rocky reefs (Floeter et al. 2007, 2008) seem to offer less chance for these relationships to occur. The Brazilian

oceanic islands are an example of such structurally and biologically simple reef habitats, since they usually harbour only a fraction of the reef fish community of most of the Brazilian coastal reefs and have a relatively smaller reef area. As a consequence, the study of reef fish communities in these islands may provide important information regarding the identity of fish species managing to live in so isolated and simple habitats and whether these species are associated to specific environmental variables in their geographical range. To date the only community structure study on Brazilian oceanic islands was conducted on Atol das Rocas (Rosa and Moura 1997), one of the four Oceanic Islands/Archipelagos of Brazil (Gasparini and Floeter 2001; Feitoza et al. 2003; Floeter et al. 2008). Further studies of oceanic islands with low diversity reef fish assemblages are thus important to understand the processes driving reef fish assemblages in these unusual systems.

Fernando de Noronha is the largest Brazilian oceanic archipelago and lies 345 km off the northeastern Brazilian coast, about 150 km east of Atol das Rocas, on the same submarine volcanic chain: the Fernando de Noronha Ridge. Despite their proximity, these islands are structurally very different. Most of Atol das Rocas reefs are biogenic (composed by coralline algae matrix), shallow, and sheltered from wave impact (Rosa and Moura 1997; Gherardi and Bosence 2001), while Fernando de Noronha reefs are predominantly composed by volcanic rocks and exposed to wave action. Thus, the comparison of the reef fish community structure of these two oceanic islands provides a unique opportunity to understand how habitat structure may shape the community of tropical isolated reefs.

Here we conduct the first assessment of the fish assemblage in different reef habitats of Fernando de Noronha. The main goals of this study are to describe the reef fish community structure of the archipelago and to investigate the relationships between fish density and biomass with wave exposure, depth and benthic composition. We further investigate the degrees of association of the dominant species on the community with the studied environmental variables and also compare the structure of the reef fish community of Fernando de Noronha with Atol das Rocas and the Abrolhos reefs (NE Brazilian coast).

Materials and methods

Study sites

The study was conducted at the Fernando de Noronha Archipelago (FN) (03°50′ S; 32°25′ W), 345 km off north-eastern Brazil, from 22 June to 17 July 2007. FN has an area of approximately 27 km². Since 1998, 75% of the FN has been designated a Marine National Park (MNP), where fishing is prohibited up to 50 m depth (Fig. 1) (Linsker 2003).

We studied eight rocky reefs with different wave exposure and substratum composition in the archipelago (Fig. 1). Each reef was divided in the following depth zones, when possible: shallow (0–6 m), medium (6.1–12 m) and deep (12–20 m) (see Fig. 1 for the depth zones in each reef). Water transparency ranged from 5 to 30 m and water temperature from 28 to 29°C at all sites.

The reefs are mainly composed of volcanic rocks and coral cover was usually low (0–5%), with exception of the southern shore of Sancho Beach and Laje dos Dois Irmaos, which have coral cover of about 12 and 20%, respectively. Coral species richness is also low at FN reefs, as coral cover is dominated by a single species, the great-star-coral (*Montastraea cavernosa*). In general, substratum at FN reefs is predominantly composed by algal turfs (the epilithic algal matrix—EAM—sensu Wilson et al. 2003) and brown macroalgae. Most studied reefs have a steep and narrow (about 3–20 m wide) rocky wall that reaches up to 5 to 25 m deep, and an adjacent rocky bottom composed by large irregular volcanic rocks. The north-western shore of the archipelago is protected from the prevailing southeast winds from April to November, resulting in low wave exposure during this season. From November to March, higher swells are common even in the sheltered bays, like Cagarras and Sancho beach, on the north-western coast. The south-eastern coast faces strong winds and waves year-round, especially from April to November. Buraco da Raquel (RQ) (a reef lagoon) and Baia do Sueste (SU) (a sheltered bay) are sites protected from exposure to winds and waves year round and thus are less exposed compared to other reefs in the south-eastern coast (Linsker 2003).

Sampling surveys

We assessed the composition of reef fish communities at FN from a total of 91 belt transects (20×2 m). This transect size was chosen as it is feasible even in sites with lower visibility, fits in reef areas with similar habitat structure and because it has been previously applied in other Brazilian coastal reefs (Floeter et al. 2007). Each transect was sampled twice for fish counts. In the first count, the diver swan along the transect and recorded all larger mobile fishes. In the second count, only cryptic and bottom dwelling species were searched by carefully scanning the substratum and looking beneath rocks and crevices.
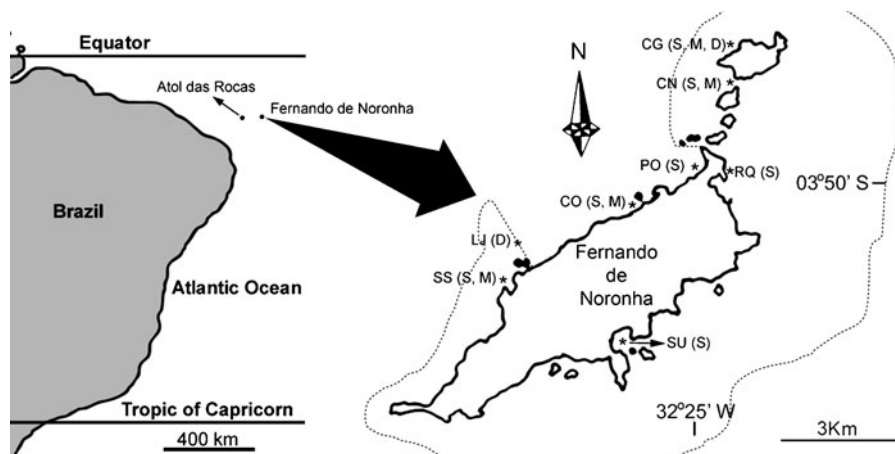

Fig. 1 The eight studied reefs at the Fernando de Noronha Archipelago: (CG) Cagarras, (CN) Canal, (PO) Porto, (RQ) Buraco da Raquel, (CO) Praia da Conceição, (LJ) Laje Dois Irmãos, (SS) Praia do Sancho and (SU) Baía do Sueste. Depth zones of each reef are shown in the *parenthesis*: *S* shallow, *M* medium and *D* deep. The *dashed line* embraces the Marine Park area

Each individual recorded in the transects was grouped into species and size class, 10 cm intervals of total length (TL). This size class classification was adopted as it is easily estimated in the field and because it has been used in other studies on Brazilian reef fish community. Each of the eight studied reefs was sampled 4 to 18 times. The number of samples in each reef was proportional to its total area. For each study site, the position of the transects was randomly placed within each depth zone.

All the surveys were conducted from 09:00 to 16:00 and care was taken to equally distribute samples along the day and among the different tide regimes for each study site. However, the sites SU and RQ were sampled only during high and low tide respectively, as these sites are accessible to divers only in these conditions. To standardise our observations, fish surveys were all conducted by the first author.

All species recorded in the surveys were grouped in trophic groups (see trophic groups in Table 1) following previous studies on Brazilian reef fish community structure (e.g. Ferreira et al. 2001, 2004; Floeter et al. 2007; Luiz et al. 2008). Fish biomass was estimated by length-weight transformations and allometric conversions: $W = a \cdot L^b$ where parameters a and b are constants for the allometric growth equation from Fishbase (www.fishbase.org). Fish length was calculated as the mid-point for each size class. When coefficient values were not found for the species, we used coefficients for the closest related species (see Floeter et al. 2008) or genera.

The relative abundance of each substratum type in each transect was estimated with photoquadrats (Preskitt et al. 2004). While the first diver performed the fish surveys, a second diver simultaneously swan behind him, keeping a distance of at least 5 m and taking five photographs of the substratum at random points along the transect. Photos were taken from a distance of ~80 cm from the substratum, and each photoquadrat corresponds to an area of 40×60 cm. The substratum was classified into one of seven categories (see Krajewski et al. 2011): 1) Non-consolidate (NC); 2) Epilithic algal matrix (EAM); 3) Green algae (GA); 4) Brown algae (BA); 5) Sponge (S); 6) Colonial cnidarians (CN) and 7) Bare rock (BR). The percent cover of each substratum was estimated using 20 random points on each photograph according to the seven categories above. The

photoquadrats were analysed with the Coral Point Count with Excel Extension software (CPCe v3.4) (Kohler and Gill 2006).

We also recorded each transect's depth and ranked each sampled site (specific depth zone in each studied reef) according to an arbitrary scale of wave exposure raging from 0 (lowest) to 9 (highest) (c.f. Krajewski et al. 2011).

Data analysis

The influence of wave exposure, substratum composition and depth on fish community structure was analysed with a redundancy analysis (RDA; Leps and Smilauer 2007). For this analysis, we used the total fish community (i.e. total of fish individuals recorded) in each site. Fish species were grouped in trophic categories and two analyses were performed: one for fish density and other for biomass. We also investigated the relationship between the three abiotic variables and the distribution of the 20 most abundant diurnal reef fish species. Each trophic group was analysed separately in a canonical correspondence analysis (CCA), in which fish density in each site was correlated to wave exposure, substratum percent cover and depth. In the CCA, some trophic groups with only one or two abundant species were pooled with similar groups to allow the use of this multivariate analysis (see Fig. 4a–c for pooled groups). Substrata with average frequency lower than 5% were excluded from the analysis. We obtained the ordination diagram and the marginal (or independent effect, i.e. the total amount of variability in the data that would be explained by that environmental variable alone) and conditional (the effect that the environmental variable brings in addition to other variables already in the model) effects of each environmental variable studied for the fish assemblage considered (Leps and Smilauer 2007). These effects were expressed by the λ value of each studied variable, which provides an estimate of relative variation (%) of the abundance and biomass of trophic groups (on RDA) or species abundance (CCA) that could be explained by each factor (Leps and Smilauer 2007).

To achieve statistical tests requirements, substratum cover (%) was arcsine transformed and species abundance and biomass data were LogX+1 transformed (Zar 1999; Leps and Smilauer 2007).

Table 1 Top 25 dominant species recorded in 13 sites (91 transects) at the Fernando de Noronha Archipelago. Species are ranked in decreasing numeric abundance. D density

Family	Species	Troph. Group	<10 cm	10–20 cm	21–30 cm	31–40 cm	Total	D 40 m² (±SE)	Biomass (g) 40 m² (±SE)	Biom. Rank	Freq. transects
Labridae	*Thalassoma noronhanum*	Plank./M. Invert.	1,600	0	0	0	1,600	17.58±2.14	20.34±2.48	22	81.31
Pomacentridae	*Chromis multilineata*	Planktiv.	1,119	76	0	0	1,195	13.13±4.32	43.54±14.34	23	28.57
Pomacentridae	*Stegastes rocasensis*	Terr. Herbiv.	826	0	0	0	826	9.07±0.97	25.32±2.72	29	90.10
Haemulidae	*Haemulon chrysargyreum*	M. Invert.	174	552	5	0	731	8.03±2.78	290.57±100.74	9	57.14
Labrisomidae	*Malacoctenus* aff. *triangulatus*	M. Invert.	611	0	0	0	611	6.71±1.12	9.28±1.56	37	52.74
Epinephelidae	*Cephalopholis fulva*	Carniv.	36	225	123	71	455	5±0.61	1120.74±137.41	2	73.62
Acanthuridae	*Abudefduf saxatilis*	Omniv.	168	232	0	0	400	4.39±0.82	206.01±38.69	13	62.63
Pomacentridae	*Acanthurus chirurgus*	Rov. Herbiv.	37	120	134	96	387	4.25±0.83	1413.80±278.39	1	61.53
Mullidae	*Mulloidichthys martinicus*	M. Invert.	1	250	28	17	296	3.25±2.32	260.14±186.02	11	14.28
Labridae	*Halichoeres radiatus*	M. Invert.	88	73	20	8	189	2.07±0.37	148.35±26.53	16	54.94
Balistidae	*Melichthys niger*	Omniv.	2	59	87	19	167	1.83±0.52	944.56±268.96	3	25.27
Labridae	*Sparisoma radians*	Rov. Herbiv.	137	5	0	0	142	1.56±0.32	6.73±1.40	40	37.36
Holocentridae	*Holocentrus ascensionis*	Carnivorous	3	8	59	59	129	1.41±0.49	437.90±153.34	7	42.85
Haemulidae	*Haemulon parra*	M. Invert.	1	64	34	18	117	1.28±0.43	267.02±90.13	10	37.36
Labridae	*Sparisoma axillare*	Rov. Herbiv.	7	6	25	76	114	1.25±0.17	854.45±122.26	5	50.54
Labridae	*Sparisoma frondosum*	Rov. Herbiv.	4	6	31	69	110	1.20±0.17	862.91±124.98	4	53.84
Gobiidae	*Coryphopterus* aff. *glaucofraenum*	M. Invert./Omn.	96	0	0	0	96	1.05±0.42	2.71±1.09	48	15.38
Blenniidae	*Ophioblennius trinitatis*	Ter. Herbiv.	91	0	0	0	91	1.00±0.21	1.49±0.31	53	26.37
Holocentridae	*Myripristis jacobus*	Planktiv.	2	77	2	0	81	0.89±0.21	9.34±2.28	36	25.27
Mullidae	*Pseudupeneus maculatus*	Mob. Invert.	1	21	29	12	63	0.69±0.28	156.86±64.38	15	26.37
Acanthuridae	*Acanthurus coeruleus*	Rov. Herbiv.	4	3	17	27	51	0.56±0.10	347.90±63.02	8	32.96
Pempheridae	*Pempheris schomburgki*	Planktiv.	50	0	0	0	50	0.54±0.54	3.55±3.55	45	1.01
Labridae	*Sparisoma amplum*	Rov. Herbiv.	8	2	7	30	47	0.51±0.12	259.03±61.39	12	24.17
Gobiidae	*Elacatinus phthirophagus*	Invert.	38	0	0	0	38	0.41±0.13	0.01±0.003	60	15.38
Haemulidae	*Anisotremus surinamensis*	M. Invert.	1	5	9	16	31	0.34±0.07	132.80±30.59	17	24.17

Results

Community general characteristics

A total of 8,195 fish individuals of 60 species, from 28 families, were recorded in the transects. The 25 most abundant species accounted for about 98% of all fish recorded in this study (Table 1). From these 25 species, 17 were also among the 25 species with the highest biomass (Table 1). Mean species richness and number of individuals per census was 11.71 ± 0.34 and 90.05 ± 6.64, respectively, fish biomass was 9.20 ± 0.76 kg per transect (mean $\pm$ SE for all variables).

Planktivores accounted for 37% of all fish individuals recorded in all censuses, followed by 28.5% of mobile invertebrate feeders, 11.3% of territorial herbivores, 10.5% of roving herbivores, and 7.1% of omnivores (Fig. 2). Macrocarnivores represented 6.5% of all fish individuals from which carnivores were 6.0% and piscivores 0.5%, and sessile invertebrate feeders accounted for mere 0.03%. In terms of biomass, roving herbivorous fishes summed 41.8%, mobile invertebrate feeders 19.9%, carnivores 14.3%, omnivores 14.0%, piscivores 8.3%, planktivores 1.4%, territorial herbivores

with 0.3% and sessile invertebrate feeders with 0.03% (Fig. 2).

Relationship between environmental variables and density and biomass of fishes

Depth, coral cover and exposure explained most of the variation in fish density and biomass in the study sites (Table 2, Fig. 3). All of these variables were cross-correlated, as indicated by the decrease in the conditional effects of coral cover and exposure after depth has been selected (Table 2). Fish density usually increased with depth and coral cover and decreased with exposure for most trophic groups, but mobile invertebrate feeders and roving herbivorous fishes, had slightly higher density and biomass in sites with higher exposure and non-consolidate substratum (Fig. 3). The biomass of all trophic groups, except for omnivores, mobile invertebrate feeders and roving herbivores, appeared to be influenced by the environmental variables the same way as fish density. However, the biomass of omnivores increased with exposure, while the biomass of mobile invertebrate feeders and roving herbivores were not highly correlated with any of the environmental variables (Fig. 3, Table 3).

Fig. 2 The trophic groups recorded at the Fernando de Noronha Archipelago, their mean (+SE) abundance (Ab.) and biomass (Biom.), number of species and composition. Abbreviations: *Macr. Carn.* macrocarnivores, *Mob. Invert.* mobile invertebrate feeders, *Rov. Herbiv.* roving herbivores, *Terr. Herbiv.* territorial herbivores
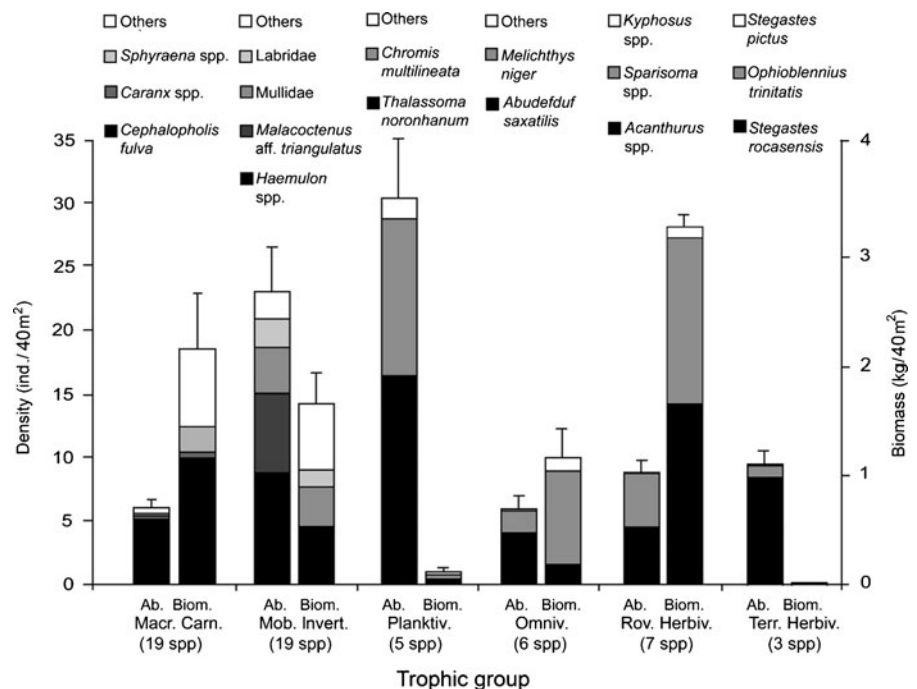
Table 2 Marginal and conditional effects of depth, exposure and benthic composition on the biomass and density of reef fishes of Fernando de Noronha recorded in the study sites. Legends for substratum types are as follows: *BA* brown algae, *EAM* epilithic algal matrix, *GA* green algae, *NC* non-consolidated

	Marginal effects		Conditional effects			
	Variable	λ	Variable	λ A	P	F
Biomass	Depth	0.27	Depth	0.27	0.064	3.99
	Coral	0.23	GA	0.12	0.152	2.07
	Exposure	0.16	Exposure	0.12	0.216	2.08
	GA	0.09	NC	0.14	0.048	3.38
	NC	0.09	EAM	0.04	0.644	0.88
	EAM	0.03	BA	0.04	0.780	0.76
	BA	0.02	Coral	0.03	0.644	0.78
Density	NC	0.23	NC	0.23	0.026	3.33
	Coral	0.14	GA	0.14	0.096	2.23
	GA	0.14	Exposure	0.16	0.070	3.08
	Depth	0.12	Coral	0.09	0.138	1.93
	Exposure	0.09	Depth	0.05	0.380	1.07
	EAM	0.03	BA	0.06	0.424	1.30
	BA	0.02	EAM	0.06	0.220	1.43

Fish-habitat relationships within trophic groups

The density of fishes in different trophic groups was influenced by different environmental variables (Table 3). The most important variables explaining the variation in the density of carnivores and mobile invertebrate feeders were depth and non-consolidated substratum (Table 3). Within this group, *Halichoeres radiatus* had higher density in shallow, more exposed sites and with higher cover of non-consolidated substratum. *Malacoctenus* aff. *triangulatus* was not strongly associated to any environmental variable; while the densities of *Pseudupeneus maculatus* and *Haemulon chrysargyreum* were positively correlated to brown algae. *Cephalopholis fulva* did not present any strong correlations with substratum type, while *Mulloidychthys martinicus* was positively correlated with EAM and green algae, but distribution of both species was strongly correlated with depth (Fig. 4a).

The most important variable explaining density variation of planktivores and omnivores (grouped for this analysis as all omnivorous fishes also eat plankton) was wave exposure (Table 3). *Melichthys niger* abundance was highly correlated with exposure, while *Chromis multilineata* and *Thalassoma noronhanum* were generalists for all the analysed variables (exposure, depth and substratum cover). *Abudefduf saxatilis* had higher density in sites with lower exposure and higher non-consolidated substratum cover (Fig. 4b).

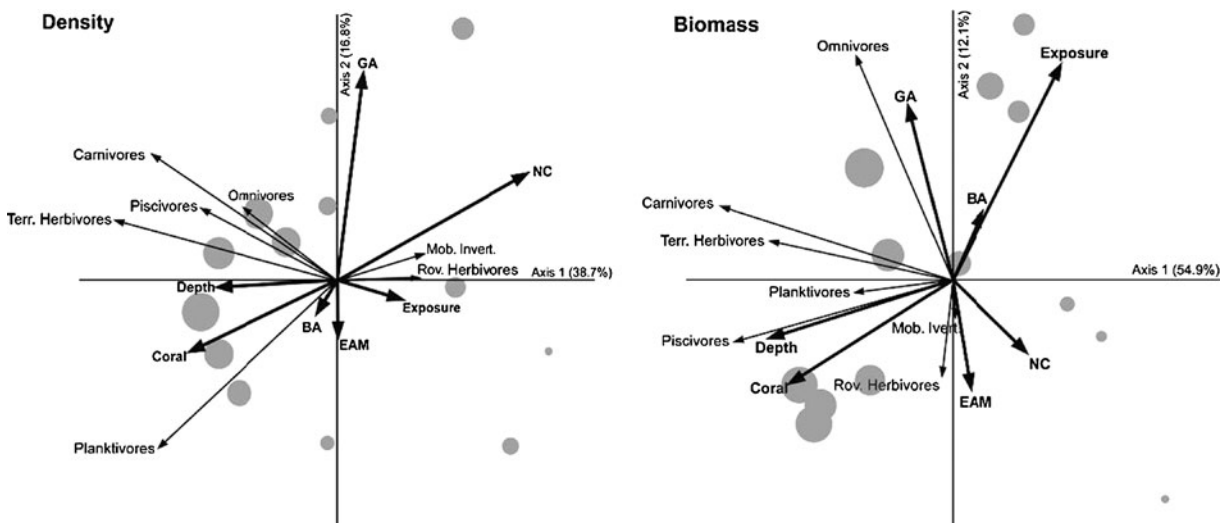Most herbivorous fishes were versatile and not strongly associated to any measured environmental

Fig. 3 Redundancy analysis (RDA) diagram for the relationship between three habitat variables (depth, exposure and benthic composition) with density and biomass of seven reef fish trophic groups at the Fernando de Noronha Archipelago. *Circles* correspond to each study site and their sizes are proportional to the mean density (**a**) or biomass (**b**) of all trophic groups combined. Substratum types: *BA* brown algae, *EAM* epilithic algal matrix, *GA* green algae, *NC* non-consolidated

Table 3 Marginal and conditional effects of depth, exposure and benthic composition on the density of different reef fish trophic groups at the Fernando de Noronha Archipelago. Legends for substratum types are as follows: *BA* brown algae, *EAM* epilithic algal matrix, *GA* green algae, *NC* non-consolidated

Troph. Gr.	Marginal effects		Conditional effects			
	Variable	λ	Variable	λ A	P	*F*
Carnivorous + Mob. Invert	Depth	0.12	Depth	0.12	0.096	2.11
	NC	0.09	NC	0.08	0.296	1.57
	BA	0.08	GA	0.08	0.236	1.65
	Co	0.07	EAM	0.07	0.488	1.38
	EAM	0.07	Expos	0.07	0.274	1.47
	GA	0.06	Co	0.01	1	0.28
	Expos	0.03	BA	0.02	0.728	0.42
Plantivorous + omnivorous	Expos	0.09	Expos	0.09	0.026	3.95
	GA	0.08	NC	0.08	0.056	4.15
	NC	0.07	GA	0.03	0.138	1.82
	EAM	0.04	Co	0.03	0.13	1.93
	Co	0.02	EAM	0.01	0.696	0.71
	Depth	0.02	BA	0.02	0.238	0.91
	BA	0.02	Depth	0.001	0.966	0.05
Herbivorous	GA	0.08	GA	0.08	0.128	2.63
	Expos	0.07	NC	0.09	0.086	3.38
	Depth	0.07	Depth	0.07	0.052	3.37
	Co	0.07	Co	0.04	0.254	1.82
	NC	0.03	BA	0.02	0.898	1.14
	BA	0.02	Expos	0.01	0.48	0.84
	EAM	0.01	EAM	0.01	0.586	0.32

variable (Fig. 4c, Table 3). However, density of *Ophioblennius trinitatis* was higher in sites with greater exposure and cover of green algae. Also, the densities of *Acanthurus chirurgus* and *Sparisoma radians* were slightly associated to brown algae, non-consolidated substratum and shallower sites (Fig. 4c).

Discussion

General patterns of community structure

Reef fish community of FN is dominated by few very abundant species, as typical of low diversity systems as oceanic islands in the Atlantic (Floeter et al. 2001, 2008; Ferreira et al. 2004). The fish community at FN also seems to be dominated by species with wide geographic range and versatile in their relationship with habitat features. This pattern is clearly noticed as 18 out of the 20 most abundant species at FN are widely distributed in the Brazilian coast and/or the Caribbean

(Floeter et al. 2008). The exceptions among the top most abundant species at FN are *Stegastes rocasensis* and *Malacoctenus* aff. *triangulatus*, endemics to Atol da Rocas (AR) and FN, where they occurs in a wide range of depths and hydrodynamic regimes (Rosa and Moura 1997; Floeter et al. 2001, Souza et al. 2011).

The dominance of more versatile species in terms of habitat use at FN may be explained by several physical and geographic characteristics of the archipelago. FN has a relatively small area when compared to Brazilian coastal reefs and is isolated from the Brazilian coast and other oceanic Islands. The bottom composition in several reefs around the archipelago is similar and the reefs do not have large expansion of shallow (<10 m) area and may be subject to fast and unpredictable variation in wave exposure, as it is typical of oceanic habitats (Linsker 2003). These environmental characteristics seem to diminish the chance of colonisation and establishment of more specialised reef fishes, which require more specific and stable habitat conditions (e.g. Munday 2000; Garpe and Öhman 2003, 2007).

Fig. 4 Canonical correspondence analysis (CCA) diagram for the relationship between environmental variables and the abundance of the main species of **a** herbivores, **b** planktivores and omnivores and **c** carnivores and mobile invertebrate feeders recorded in each study site
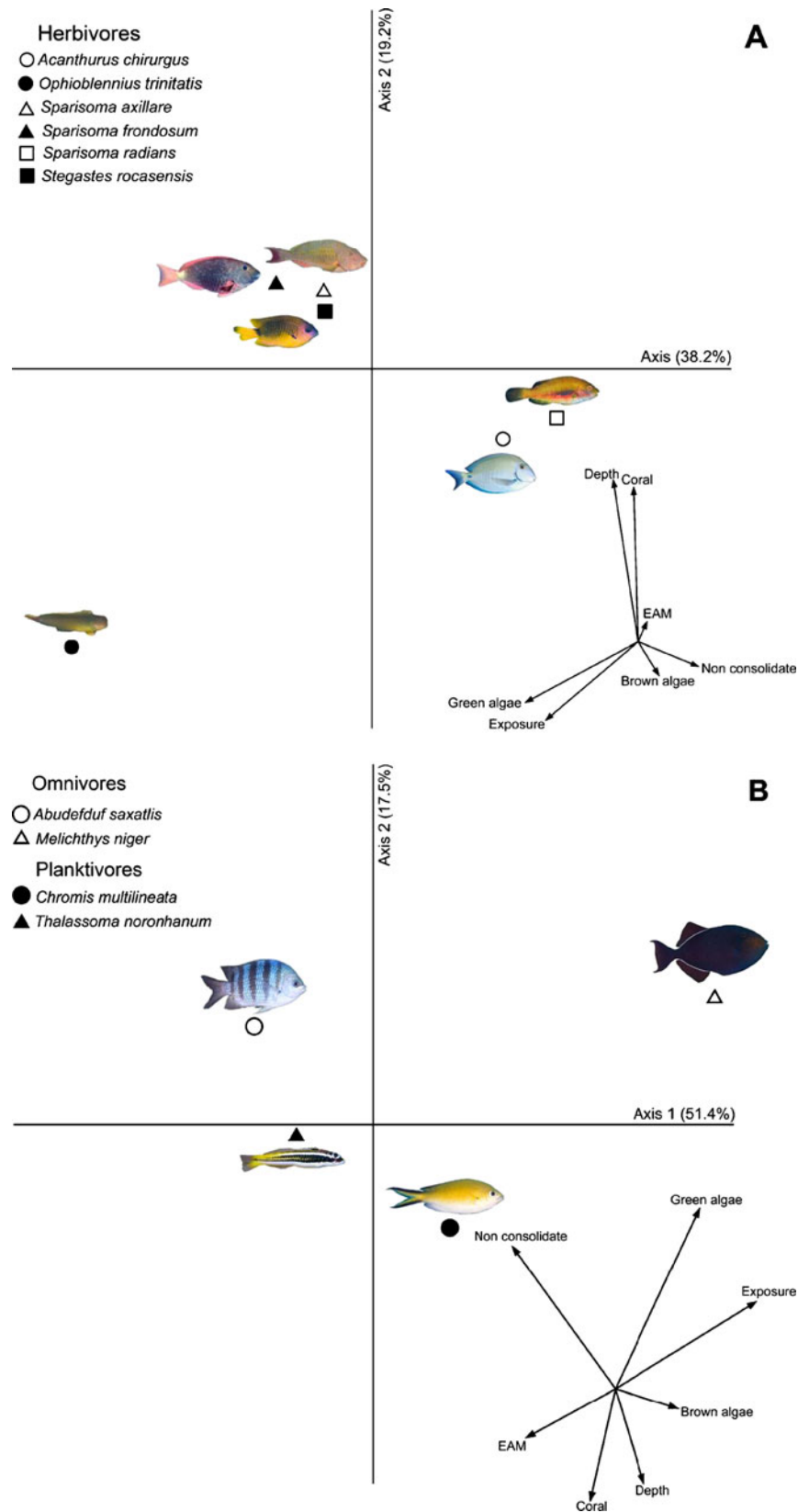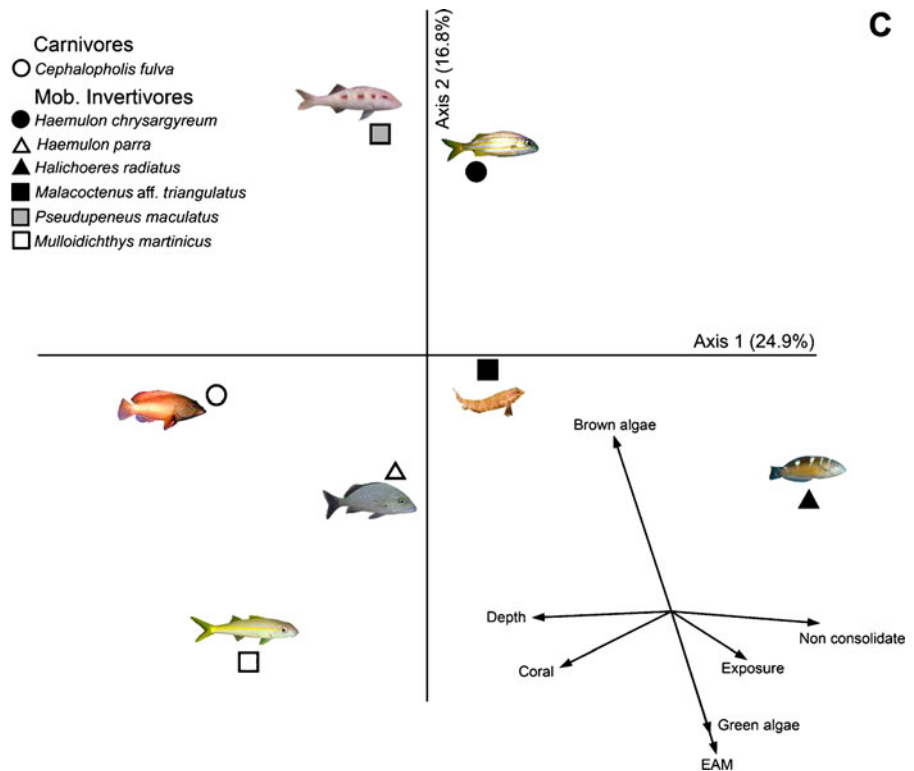
Fig. 4 (continued)

In terms of reef fish community structure, FN is more similar to AR than any other Brazilian reef studied so far (Ferreira et al. 2004), both in terms of species composition (Floeter et al. 2008) and trophic structure (this paper). This similarity between these two oceanic islands is expected, as both of them are located on the same volcanic ridge. However, some differences seem to exist, as FN has a higher relative abundance of mobile invertebrate feeders (27% vs. ~5% in AR) and a lower relative abundance of roving herbivores (11% vs. 22% in AR) and omnivores (7% vs. 15% in AR) (Fig. 5). The abundance of roving herbivores at AR is high even when compared to other relatively undisturbed Brazilian reefs (Rocha and Rosa 2001).

The differences in community structure between AR and FN could be explained by the fact that Rosa and Moura (1997) did not include "small sized and nocturnal/cryptobiont species" in their samples. However, even if we exclude these species from our data, the differences between the community structure of these two oceanic islands practically do not change. It is more plausible, however, that the differences in the fish community between these two oceanic archipelagos

reflect their different reef structure. FN is a high volcanic island with rocky reefs exposed to variable wave exposure and dominated by macroalgae (Linsker 2003; Bonaldo et al. 2006), while AR is an atoll mainly composed by coralline algae with a large enclosed lagoon (Maida and Ferreira 1997; Rosa and Moura 1997; Gherardi and Bosence 2001). More specifically, the reefs sampled by Rosa and Moura (1997) at AR are mainly located in the lagoon of the atoll, which is relatively protected from wave action. For example, haemulids prefer higher water movement and are very abundant at FN, while roving herbivores (mainly *Acanthurus* and *Sparisoma*) and the omnivore *Abudefduf saxatilis* prefer sites with lower water motion and abound in the lagoon of AR (Rosa and Moura 1997). Thus, differences in wave exposure between the sampled sites in the present study and in Rosa and Moura (1997) may account for the differences in community structure between AR and FN. It is possible that the community of FN is more similar to habitats found at the reefs outside the lagoon of AR (i.e. deeper or more exposed to waves), where no studies on fish community structure have been conducted to date.

Fig. 5 The relative abundance of different reef fish trophic groups Atol das Rocas (data from Rosa and Moura 1997 and Ferreira et al. 2004) and Fernando de Noronha (this paper). Abbreviations: *Pisciv.* piscivores, *Carn.* carnivores, *Mob. Inv.* mobile invertebrate feeders, *Sess. Inv.* sessile invertebrate feeders, *Omniv.* omnivores, *Rov. Herbiv.* roving herbivores, *Terr. Herbiv.* territorial herbivores
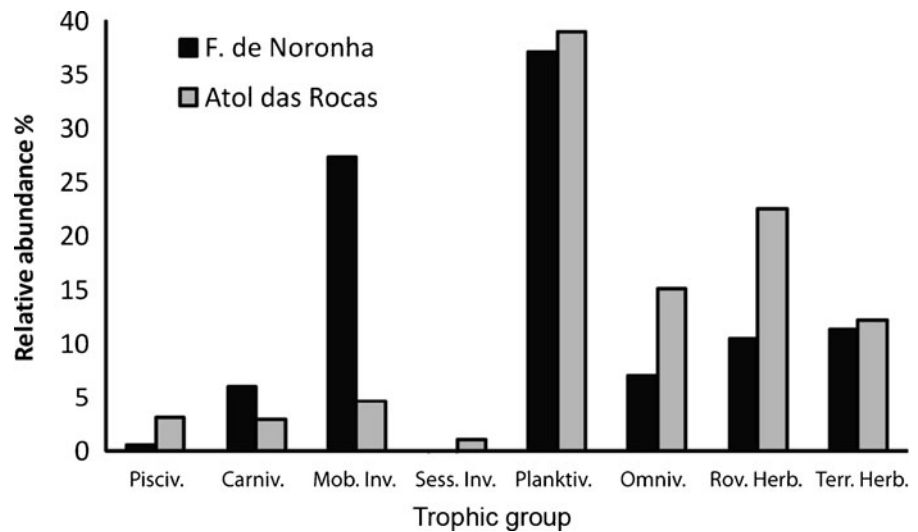
Another important factor that may influence the differences between fish community of AR and FN is the differential human impact in each island. AR is uninhabited and is effectively protected from fisheries (no-take area) since 1991 (Rosa and Moura 1997), while FN is a Marine Park with 2,500 inhabitants where fishing by locals is allowed in some areas of the archipelago (Linsker 2003). The main target species of local fisherman on FN are macrocarnivorous fishes (Krajewski, pers. obs.), thus, it would be expected that large top predators are less abundant at FN than in AR. However, the present results indicate that FN has proportionally more carnivorous fishes than AR as well as most of other Brazilian coastal reefs (e.g. Rosa and Moura 1997; Ferreira et al. 2001, 2004; Floeter et al. 2001, 2007). Nonetheless, carnivores at FN were dominated by *Cephalopholis fulva*, a medium size epinephelid species. In AR, in contrast other larger and important carnivorous and piscivorous fish species from Lutjanidae, Carangidae and Carcharhinidae were abundant in many reef zones (Rosa and Moura 1997). Similarly, in Parcel de Manoel Luiz, an undisturbed reef area about 85 km off north-eastern coast of Maranhão state, large predator species from Epinephelidae and Lutjanidae have been reported to be more abundant than in FN (see Rocha and Rosa 2001). Moreover, anecdotal accounts from older spearfisherman (Arduino Colassanti and Alfredo Carvalho-Filho, pers. comm.) state that sharks and big groupers (other than *C. Fulva*) were once abundant in FN 40 years ago. Thus, there is significant evidence that fishing has changed the abundance of top predators, especially large species, at FN.

Fish biomass is probably the most important factor in accessing the status of reefs (Sabater and Tofaeono 2007; Francini-Filho and Moura 2008; Sandin et al. 2008) and, thus, this variable has direct implications for coral reef management. However, the only previous study, to our knowledge, that sampled the biomass of reef fishes in a Brazilian reef has been conducted at the Marine National Park of Abrolhos (see Francini-Filho and Moura 2008 for further details), a reef system with higher fish, coral diversity and coral cover than FN (Leão et al. 1988; Floeter et al. 2001; Francini-Filho and Moura 2008). However, when the same trophic groups considered by Francini-Filho and Moura (2008) are compared between FN and Abrolhos, there is a general similarity between these two reef areas (Fig. 6). However, Abrolhos has a larger biomass of roving herbivorous fishes, which may be explained by the abundance of *Scarus trispinosus*, a large parrotfish species absent from FN (Ferreira and Gonçalves 1999, 2006; Francini-Filho and Moura 2008).

Relationships of fish density and biomass and environmental variables

In a number of tropical systems, positive relationships between coral cover and fish density and biomass have been considered as indicative of high habitat complexity (e.g. Jones and Syms 1998; Bergman et al.

Fig. 6 Biomass of different trophic groups in old no-take areas of the Abrolhos reefs (data and categories according to Francini-Filho and Moura 2008) and Fernando de Noronha Archipelago
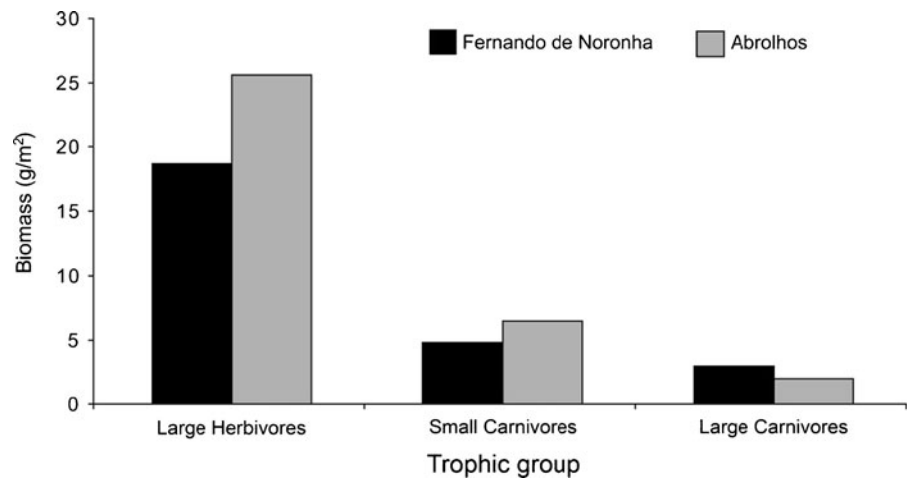
2000; Munday 2000; Garpe and Öhman 2003). At FN, the highest coral cover (about 20%) is found in Sancho beach and Laje Dois Irmãos, which also had higher habitat complexity and seem to offer more refuges to medium sized (about 20–40 cm TL) fishes compared to sites with lower coral cover (Fig. 7). Thus, the increase of fish biomass with coral cover in the present study indicates a positive response of fish biomass to reef structural complexity.

Higher coral cover at FN was also positively associated to depth, as highest coral cover was recorded about 12–18 m deep. This pattern is probably explained by the fact that depth reduces wave impact (i.e. the physical impact on the reef), thus facilitating the growth of some coral species (Dollar 1982; Storlazzi et al. 2002). Similar relationships between wave exposure and coral growth have

been found in other oceanic islands with high and unpredictable wave exposure in general (Dollar 1982; Storlazzi et al. 2002). The higher fish biomass in deeper reefs at FN, thus, is probably caused by an indirect effect of depth, which allowing higher coral growth. This later correlation would explain the positive relationship of fish density and biomass to depth and negative to exposure.

Macrocarnivores The distribution of macrocarnivores (piscivores + carnivores) in the present study was strongly related to depth and coral cover, a similar pattern recorded for other predatory fish species elsewhere (e.g. Connell and Kingsford 1998; Benfield et al. 2008). However, as carnivores at FN were dominated by *Cephalopholis fulva*, the positive association of this group with depth and coral may

Fig. 7 A view of "Laje dos Dois Irmãos" reef, at the Fernando de Noronha Archipelago. The higher coral cover (mostly represented by *Montastraea cavernosa* colonies), typical of reefs of Sancho beach (SS) and Laje (LJ), adds structural complexity to deeper (10–22 m) reefs of the archipelago
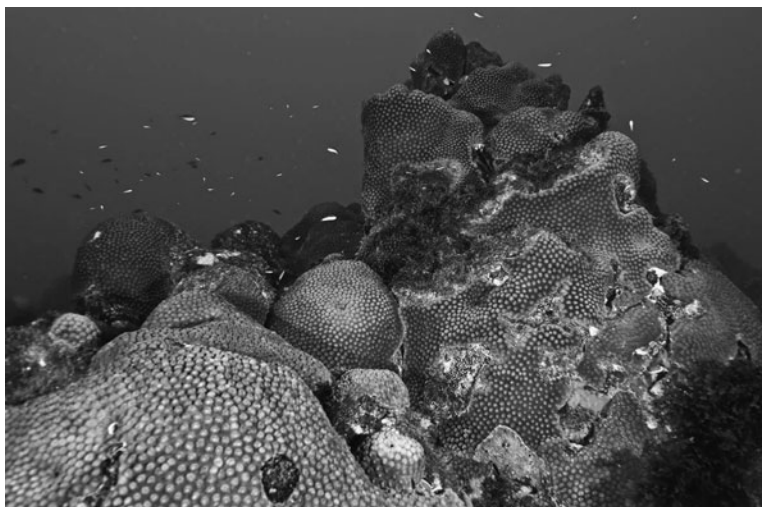
mostly reflect the distribution of *C. fulva* itself (Fig. 3). Thus, although the present results agree with other studies on carnivorous fishes, general conclusions on the distribution of carnivorous fishes at FN would require further detailed studies on a wider range of species within this trophic group.

Mobile invertebrate feeders Interestingly, the density and biomass of mobile invertebrate feeders were not strongly related to any environmental factor. This pattern is likely the result of the versatility (in terms of association with measured environmental variables) of the species within this group (Bellwood et al. 2006). This idea is further strengthened due to the high abundance of many of these species in all studied sites in FN, despite their environmental variations.

As invertebrate feeders usually select foraging substratum (e.g. Fulton and Bellwood 2002b; Berumen et al. 2005; Bonaldo et al. 2005; Krajewski et al. 2006), these species would be expected to be more abundant in sites with higher cover of their preferred foraging substrata. However, our overall results are not clear enough to evaluate whether fish abundance is correlated to foraging substratum availability at FN. For example, the mobile invertebrate feeder *Haemulon chrysargyreum* was more abundant in sites with higher brown algae cover, the preferred foraging substratum for this species (Krajewksi et al. in prep.). *Haemulon parra*, on the other hand, forages mostly on non-consolidated substratum and the EAM during the day at FN (Krajewski et al. in prep.), and its abundance was not associated to any of these substrata. However, *H. parra* is active during both day and night time and, as the current study has only assessed reef fish feeding and distribution during the day, further information on feeding of this species at night would be necessary to corroborate the current findings. It seems that the positive correlation between reef fish and their preferred foraging substratum varies among species and is more evident for specialised spongivores and coralivores (e.g. Bouchon-Navarro and Bouchon 1989; Jennings et al. 1996; Floeter et al. 2006) that actually ingest the reef substratum itself, and not only fauna associated to it. Thus, studies that found this correlation between fish and their preferred foraging substratum (e.g. Bouchon-Navarro and Bouchon 1989; Jennings et al. 1996; Floeter et al. 2007) have actually measured a direct relationship between fish and its prey. Also, as

most benthic carnivorous fish species at FN seem not to be specialist in habitat nor in prey use (Randall 1967; Krajewski et al. 2011), it is more likely that densities of most of these species are not affected by shortage of suitable foraging substratum and/or prey.

Planktivores Several studies have found positive correlations between the abundance of planktivores and water flow, a pattern explained by the higher influx of plankton in sites with higher water turbulence (e.g. Hobson and Chess 1978; Hammer et al. 1988; Floeter et al. 2007). In the present study, however, planktivorous fishes seem not to be positively associated with exposure. There are two plausible explanations for this result. The first is that the distribution of planktivores would be biased by the response of a single dominant species, *Thalassoma noronhanum* (Fig. 2), which is abundant everywhere at FN and known for its versatile feeding behaviour and diet (Sazima et al. 2005). Indeed, although the current study has followed previous suggestions to classify *T. noronhanum* as a planktivore (e.g. Floeter et al. 2001, 2007; Ferreira et al. 2004), further studies on the diet of this species are needed to confirm its major trophic category. The distribution of planktivores in the present study may also be explained by the overall high abundance of this group in all of the study sites, a pattern that could difficult the detection of inter-site differences. The high abundance of planktivores at FN is probably explained by the fact that most studied reefs are suitable habitats for planktivores, as they are directly exposed high wave exposure and currents, and present excellent visibility for picking zooplankton (cf. Floeter et al. 2007).

Omnivores The higher abundance of omnivores in FN reefs with higher exposure and green algal cover is clearly a response of the two main species in this group, *Abudefduf saxatilis* and *Melichthys niger* (Fig. 2). Both species are versatile foragers that feed on a variety of food items (including algae) collected both on the reef bottom and water column (Randall 1967). *M. niger* is a typical species found in high abundance at oceanic islands and associated to high wave exposure (Gasparini and Floeter 2001; Feitoza et al. 2003; Kavanagh and Olney 2006), what may explain its correlations with wave exposure (Fig. 4b).

Territorial herbivores We expected to find a higher density of territorial herbivores in shallower places with greater abundance of light, since these fishes depend on algal growth in their territories to feed on (Barneche et al. 2008). However, density of *Stegastes rocasensis* (the dominant territorial herbivore at FN) increased with depth and was low in very shallow waters (<1.5 m), especially in sites with higher wave exposure (e.g. shallow reefs of the Baía do Sueste and Canal). In a more detailed study of the distribution of *S. rocasensis* at FN, Souza et al. (2011) sampled four sites (Porto, Boldró, Conceição and Sancho) and found that adult individuals preferably inhabit shallow areas, while sub-adults and juveniles occupy deeper areas with lower wave exposure. The greater abundance of adults in shallower areas was hypothesised to be related to their stronger territorial behaviour, which resulted in their permanence within their territory even during "adverse situations", such as low tides and high wave impact (Souza et al. 2011). Even with the probable resistance of some adult individuals of *S. rocasensis* to these adverse situations, we noticed that this species may avoid some very shallow places. This pattern is probably explained by the wider variation in wave exposure of the sampled sites by the present study compared to the study by Souza et al. (2011). As a consequence, it is possible that even adult individuals of *S. rocasensis* are not able to sustain their territories in the shallows of some of our sampled sites. An alternative explanation for the scarcity of *S. rocasensis* in some shallow sites is that the population in these sites would be dominated by juvenile individuals that prefer deeper sites (Souza et al. 2011). However, as *S. rocasensis* individuals were not classified into ontogenetic phases in the present study, further studies would be necessary to test this hypothesis.

Roving herbivores Roving herbivores at FN seemed to be a versatile group, occurring in a range of habitats, but slightly more associated to shallow places with higher EAM cover. This relationship is probably explained by the feeding preferences of herbivorous fish species at FN. For example, the three large *Sparisoma* species, which accounted for about half of the abundance of roving herbivores at FN, are very active foragers and feed mostly over the EAM (Bonaldo et al. 2006), a substratum associated with shallow places in the study sites. Similarly, acanthurids

feed mostly on filamentous algae, organic debris and fine sedimentary particles found in the EAM (Randall 1967; Dias et al. 2001; Ferreira and Gonçalves 2006) and, thus, are also likely to be associated with this substratum.

Despite of some relationships between species and the environment, we found that, overall, reef fish species were not strongly associated to environmental variables at FN. In several studies conducted in coral reefs, some fish species (specially site-attached and specialised foragers) were found to be strongly limited or affected by some key environmental variables (e.g. Bouchon-Navarro and Bouchon 1989; Jennings et al. 1996; Munday et al. 1997; Jones and Syms 1998; Berumen et al. 2005). In contrast, fish community at FN seems dominated by versatile species that tolerate the range of environmental variables found in most of the reefs of the archipelago. The different patterns of reef fish distribution between the present study and previous studies on coral reefs emphasise the importance of investigating community structure of reefs with different reef structure and biodiversity. Extrapolations of general patterns found in high diversity coral reefs to low diversity rocky reefs could lead to misinterpretations and wrong estimates of the importance of factors structuring fish communities in rocky reefs.

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