

Physical, biological and human-induced effects on the reef fishes of Fernando de Noronha archipelago, Brazil

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Efeitos físicos, biológicos e antrópicos sobre os peixes recifais do arquipélago de Fernando de Noronha, Brasil

Resumo: Vários fatores têm o potencial de influenciar a distribuição e a composição das comunidades de peixes recifais. Entre os mais importantes estão a rugosidade, a exposição às ondas, a cobertura do substrato e as atividades humanas. O presente estudo avaliou a influência desses fatores nos peixes recifais de áreas com um gradiente de restrição a atividades humanas no arquipélago Fernando de Noronha, nordeste do Brasil e determinou suas importâncias relativas para a ecologia de peixes recifais. A rugosidade não influenciou a riqueza de peixes, mas influenciou o número de indivíduos, de jovens e de espécies residentes, enquanto a cobertura bêntica não pareceu ser um determinante importante para quaisquer das variáveis de peixes avaliadas. Esses resultados sugerem que a disponibilidade de abrigo (proteção física) é mais limitante que a disponibilidade de alimento (*i.e.* cobertura bêntica). Além disso, hidrodinamismo apresentou valores relativamente baixos, porém, influenciando negativamente os peixes. As atividades recreativas, apesar de aparentemente não-impactantes, tiveram um efeito negativo na abundância de peixes, com a área parcialmente protegida (Atalaia) mostrando uma estrutura semelhante à área não-protetida (Porto). Esses resultados sugerem que a presença humana, mesmo em áreas fiscalizadas, pode interferir na estrutura dos peixes recifais. É necessário uma proposta de gestão e de práticas de turismo de baixo impacto especialmente nas áreas parcialmente protegidas e não-protetidas.

Palavras chave: Oceano Atlântico, cobertura bêntica, peixes recifais, hidrodinamismo, turismo.

Abstract: Several factors have the potential to influence the distribution and composition of reef fish communities. Amongst the most important are rugosity, wave exposure, substrate cover and human activities. The present study evaluated the influence of these factors on reef fishes from sites following a gradient of human-induced effects on the Fernando de Noronha archipelago, northeast Brazil and determined their relative importance to reef fish ecology. Rugosity did not influence fish richness, but had a positive influence on number of individuals, juveniles and endemic species, whereas benthic cover did not seem to be an important determinant for any fish variable evaluated. These results suggest that availability of shelter (physical protection) is more limiting than availability of food (*i.e.* benthic cover). Furthermore, water flow showed somewhat low values, but even so, had negative effects on fish numbers. Recreational activities, albeit seemingly non-impacting, had a negative effect on fish abundance with the partially protected site (Atalaia) showing a similar community structure to the unrestricted site (Porto). These results suggest that human presence, even when supervised, may interfere on reef fish structure. Low-impact tourism practices are required especially in partially protected and unprotected areas.

Key words: Atlantic Ocean, benthic cover, reef fishes, hydrodynamics, tourism.

Introduction

Reefs are complex ecosystems in which interactions between biological and non-biological entities are highly conspicuous. The term habitat complexity is often used to illustrate a series of interacting factors of physical and biological nature which encompass the surface heterogeneity and the composition of the reef's substrate, respectively. Sites with high environmental heterogeneity and diverse benthic cover are often predictive of reef fish assemblages with high number of species and individuals (Luckhurst & Luckhurst 1978; Carpenter *et al.* 1981; Grigg 1994). Reef fishes of complex sites are benefited by an increase in the availability of temporary hiding places, spawning grounds, permanent shelter and/or feeding resources (Friedlander & Parrish 1998), which enhance recruitment (Beets 1989; Connell & Jones 1991). As a consequence, these sites support larger numbers of species and individuals by minimizing predator-prey encounter rates and relaxing competition via niche diversification (Hixon 1991).

In addition to habitat complexity, other factors may also play important roles on the distribution and structure of reef fish assemblages, and amongst the most important are wave action and human-induced effects (Milazzo *et al.* 2005; Floeter *et al.* 2006). Wave action may directly interfere with swimming performance and microhabitat utilization and, therefore, is often suggested as having a negative influence on most reef fishes (Dollar 1982; Grigg 1983). Further, reefs associated to human activities (e.g. boating, fishing, collections for the aquarium trade and recreational activities) usually sustain fish assemblages with lower diversity than human-free sites (Floeter *et al.* 2006). In fact, seemingly gentle activities such as guided snorkeling and reef visitation have also been proven to alter the structure of reef fish assemblages in areas where destructive activities such as fishing are strictly prohibited (Milazzo *et al.* 2005).

Although it is somewhat easy to determine how each of these factors may individually influence reef fish assemblage structure, the interdependency among these factors is also noteworthy. For example, wave action plays an important role in the zonation of benthic communities, particularly those of algae and corals (Björk *et al.* 1995; Connell *et al.* 1997), whereas habitat complexity may decrease in areas subject to high levels of human trampling (Rogers & Cox 2003; Milazzo *et al.* 2005). Therefore, it is important that these factors be investigated in combination in order to determine the breadth of influence of each particular factor to reef fish assemblage structure, as well as their association. However, few studies investigated a series of interdependent factors altogether covering the physical, biological and human-induced effects on reef fish assemblage (Friedlander *et al.* 2003), despite the fact that multi-factor studies are highly encouraged (e.g. Gratwicke & Speight 2005).

Furthermore, despite a substantial number of investigations on the effects of habitat complexity, wave action and human-activities on reef fish assemblages (Russel *et al.* 1974; Sale 1977; Luckhurst & Luckhurst 1978; Sale 1978; Talbot *et al.* 1978; Sale 1980; Wellington & Victor 1985; Hixon 1991; Denny 1994; Chabanet *et al.* 1997; Ferreira *et al.* 2001; Floeter *et al.* 2007), most studies focused on Caribbean and Indo-Pacific fish assemblages, whereas few investigations were conducted in the Southwest Atlantic region (i.e. Brazil). Reefs of this area are characterized by a high abundance of algae, and low diversity of coral species and coral growth forms, but with relatively high endemism (e.g. *Siderastrea stellata* and *Favia gravida*) (Maida & Ferreira 1997; Castro 2003). Similarly, fish assemblages are renowned for its low diversity and high levels of endemism (e.g. *Gramma brasiliensis* and *Apogon americanus*) (Floeter & Gasparini 2000). Given these inherent features, studies conducted in the Southwest Atlantic area may lead to results different than expected from Caribbean and Indo-Pacific counterparts. Two recent independent studies were the first to specifically address how multi-factor influence fish density in the Fernando de Noronha Archipelago, northeast Brazil (i.e. Medeiros *et al.* 2011; Krajewski & Floeter 2011). In these studies, important determinants included temporal variations (Medeiros *et al.* 2011), exposure (Krajewski & Floeter 2011), benthic cover (both studies) and structural complexity (both studies).

This study aimed to evaluate the influence of physical, biological and human-induced effects on reef fishes from an important oceanic archipelago in the Southwestern Atlantic in Brazil to determine the importance of these predictive variables to reef fish assemblage structure.

Material and Methods

Study area

Fernando de Noronha is a tropical oceanic archipelago consisting of 21 islands and islets in the Southwestern Atlantic region, 360 km off the Brazilian coast (**Figure 1**). The main island where the study was conducted makes up ~90% of the archipelago, with 18.4 km² of land area. It is under the influence of the westward South Equatorial Current (SEC), which is responsible for clear (up to 30 m of underwater visibility) and warm waters (25 to 30°C), with a low salinity fluctuation (3.4 to 3.6%) (Ferreira *et al.* 1990).

The archipelago is a Marine Protected Area (MPA, i.e. National Marine Park) under the Brazilian jurisdiction and controlled by the Chico Mendes Institute for Biodiversity Conservation (ICMbio), where fishing is strictly prohibited (permitted below the 50 m isobat line), but visitation and recreational activities (with distinguished levels of restriction) are permitted in some areas. The study was conducted between October and November of 2009 at four rocky reefs (depths between 0.6 and 2 m) following a gradient of human-induced effects: 1) Raquel: all recreational activities are prohibited, but certified scientific research is permitted; 2) Sueste bay: legally divided into two sectors with different levels of human restriction; in the southern sector, guided visitation is permitted and limited (restricted number of visitors per time section; use of fins prohibited; use of life vests required); in the northern sector only certified research activities are permitted; 3) Atalaia: visitation is guided and limited (restricted number of visitors per time section; use of fins prohibited); 4) Porto beach: open to visitation (no restriction whatsoever; located nearby the archipelago's port) (see **Figure 1**). Therefore, areas were characterized based on a decreasing gradient of protection from human activities, as follows: fully protected (Full; Raquel), fully and partially protected (Full/partial; Sueste bay), partially protected (Partial; Atalaia) and open to visitation (Open; Porto beach) (**Figure 1**).

Fish surveys and habitat evaluation

Fish assemblages and habitat characteristics (reef topography or rugosity, water flow and percent cover of benthic organisms and bare substrate) were assessed on randomly allocated belt transects of 20 x 2 m (between 3 and 5 replicates per site, depending on reef area, totaling 16 transects) during free dives on depths below 2 m.

Fish censuses began two minutes after the 20 m tape was laid in the substrate to allow fishes to settle back from possible diver disturbances. Following this, a diver spent one minute counting all fishes located within the limits of each transect segment (i.e. every 2 m² quadrat), totaling 20 minutes of observation per transect. Discriminating fishes among transect segments permitted a meticulous correlation with substrate characteristics (see below). Care was taken in order to avoid recounting fishes moving between transect segments. Further, juveniles were distinguished by coloration morphs and, with the exception of small, cryptic species, all individuals smaller than 5 cm were considered juveniles (Ornellas & Coutinho 1998). Identification of adults and juveniles followed the descriptions of Lieske & Myers (2001) and Humann & DeLoach (2002).

Rugosity was evaluated by draping and adjusting a 2 m long chain to the contour of the substrate, perpendicularly to the centerline of the transect (20 measures). A rugosity index was subsequently determined by calculating the ratio of the contoured chain to the linear horizontal distance (i.e. 2 m) at each point. Water flow was measured with a General Oceanic 2030 model flowmeter during one minute at each of three points of the transect (first, tenth and twentieth meters) and an average value of the transect was determined. The proportion of benthic cover

(turf algae, macroalgae, coralline algae and live coral) and bare substrate (unconsolidated and consolidated) was determined by laying a one meter tape perpendicular to the transect centerline and recording the substrate at three one-meter interval points. The relatively low coral diversity in the study area and low abundance of branching individuals, a characteristic of most Brazilian reefs (Maida & Ferreira 1997), precluded a distinction among coral growth forms.

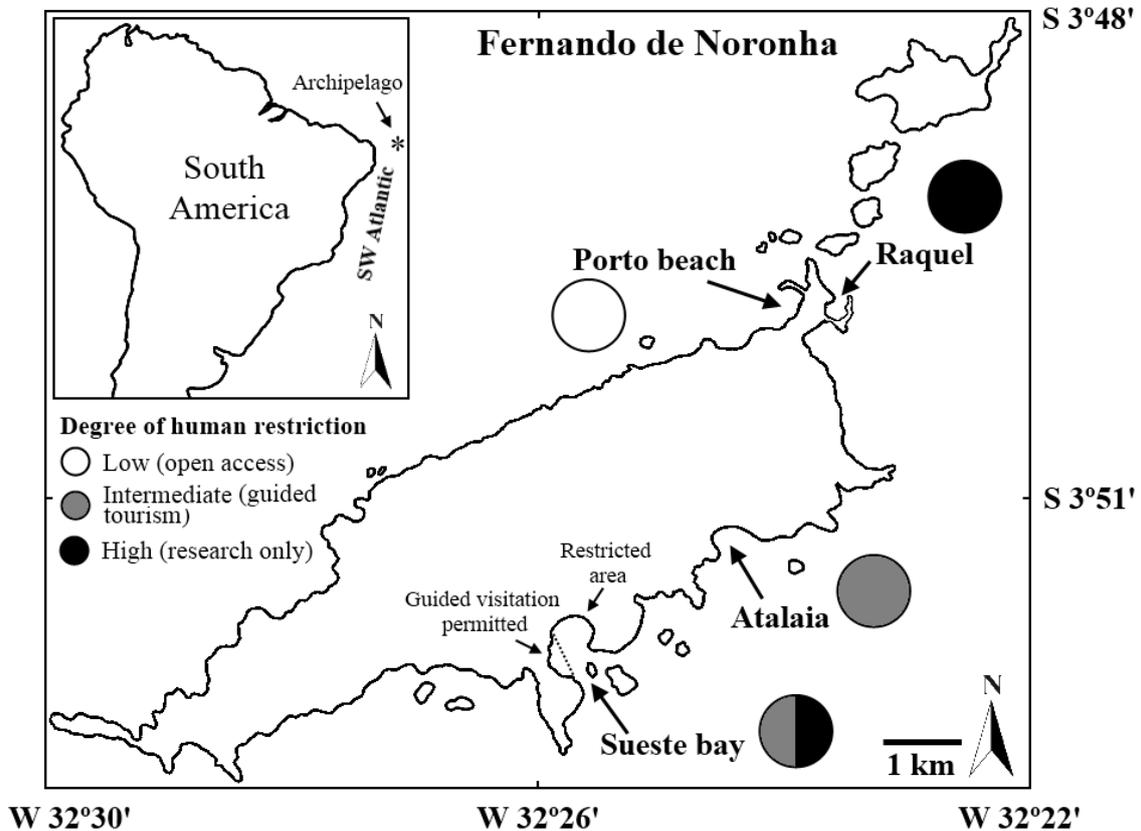


Figure 1. Location and map of study sites in Fernando de Noronha archipelago, Southwestern Atlantic ocean, northeast Brazil. Sites where samples were conducted followed a gradient of human restriction: fully protected (Full; Raquel), fully and partially protected (Full/partial; Sueste bay), partially protected (Partial; Atalaia) and open to visitation (Open; Porto beach).

Data analysis

Prior to the beginning of the analyses, normality and homogeneity of the data were tested via Kolmogorov-Smirnov and Levene's tests, respectively, and, when necessary, variables were transformed and their distribution re-tested (Sokal & Rohlf 1995). In all cases, a critical p-value < 0.05 was employed. All analyses were performed using Statistica software version 7.1 (Statsoft 2005).

Rugosity and water flow were compared among sites using one-way ANOVAs followed by Bonferroni multiple comparison tests. Percent cover of benthic organisms and bare substrate were arcsine square root-transformed and compared among sites using a one-way MANOVA (Pillai's trace test statistic) followed by Bonferroni multiple comparison tests.

Number of species and abundance of fishes per transect segment (i.e. per 2 m²) were square-root transformed. In order to minimize the effects of occasional fish schools in each transect segment (mostly haemulids), outliers were removed by excluding observations outside the range of two standard deviations (± 2 SD) from the mean value observed for the given sample. Less than 5% of the observations including all sites were excluded. The abundances of fish species was compared among sites using a one-way MANOVA (Pillai's trace test statistic) followed by Bonferroni multiple comparison tests. For this test, rare species (i.e. those which

accounted, individually, for less than 1% of the total abundance) were excluded and the analysis was carried out with eight species which comprised, together, 94% of the overall fish abundance. Rare species included: *Halichoeres cyanocephalus*, *Doratonotus megalepis*, *Sparisoma amplum*, *Sparisoma axillare*, *Sparisoma frondosum* (Labridae), *Mulloidichthys martinicus*, *Pseudupeneus maculatus* (Mullidae), *Muraena pavonina*, *Muraena retifera* (Muraenidae), *Acanthurus coeruleus* (Acanthuridae), *Bothus lunatus* (Bothidae), *Cephalopholis fulva* (Serranidae), *Chaetodon ocellatus* (Chaetodontidae), *Holocentrus adscensionis* (Holocentridae), *Malacanthus plumieri* (Malacanthidae), *Ophioblennius trinitatis* (Blennidae) and *Pempheris schomburgkii* (Pempheridae). Fish assemblage variables (number of species, individuals, juveniles and endemics) were compared among sites using one-way ANOVAs followed by Bonferroni multiple comparison tests. Endemic species are those which are endemic to the Brazilian province and not necessarily exclusive to the study area (Floeter & Gasparini 2001).

Linear discriminant function analysis (LDFA) using data from the most abundant species (same as mentioned above) was employed to classify the four study sites relative to fish abundance. This procedure is useful for classifying cases into different groups with a better than chance accuracy (Hill & Lewicki 2007).

To determine the contribution of physical, biological and human-induced effects on fish variables, general linear models (GLM) were employed. Number of species, individuals, juveniles and endemics were entered as dependent variables. Continuous independent variables included rugosity, water flow, and percent cover of benthic organisms and bare substrate. Status of reef protection was entered as a categorical independent variable following the level of protection from human activities for each site as described above (Full, Full/partial, Partial and Open).

Results

Rugosity differed significantly among sites, with higher values recorded at the Full and Full/partial sites, and lower values at the Partial and Open sites, albeit, in both cases, not significantly different from each other (ANOVA; $F = 6.48$; $p < 0.001$) (Figure 2a). Overall, water flow showed somewhat low values, with a clear opposing pattern to that of rugosity being observed (ANOVA; $F = 3.37$; $p < 0.05$) (Figure 2b). However, due to the high variance, particularly in the two less protected sites (Partial and Open), significant differences were only observed between the Full and Open sites (Figure 2b).

Percent cover of macroalgae accounted for the highest abundance of all categories at all sites, averaging between 27% (Full/partial site) and 68% (Open site) (Figure 3). Further, multivariate analysis of variance from percent cover of benthic composition and bare substrate identified significant differences among sites (Pillai's trace = 0.82; $F_{18,824} = 18.0$; $p < 0.001$). Pairwise comparisons between sites are shown in Table 1. Three general groups were distinguished according to benthic cover. The fully protected site (Full) was characterized by high percentages of macroalgae and coralline algae, which accounted together for over 78% of the benthic cover, with smaller contributions from bare unconsolidated substrate and live coral. The Full/partial and Partial sites showed similar benthic cover, the only difference being related to bare unconsolidated (higher values in the Partial site) and consolidated (higher values in the Full/partial site) substrates (see Figure 3 and Table 1). Finally, the Open site was largely dominated by macroalgae with a smaller contribution from turf algae. Percent cover of live coral did not differ significantly among sites and, pooled together across all sites, showed somewhat discrete values (less than 12%).

Highly significant differences among sites were observed for all fish variables investigated (Figure 4). Species richness differed due to lower values observed at the Open site (ANOVA; $F = 5.58$; $p < 0.001$) (Figure 4a). Also, a gradual decrease in the number of all individuals was observed among sites more and less protected from human-induced stress (ANOVA; $F = 4.30$; $p < 0.01$), although statistical significance was only detected between the Full

Determinants of fish numbers in Fernando de Noronha

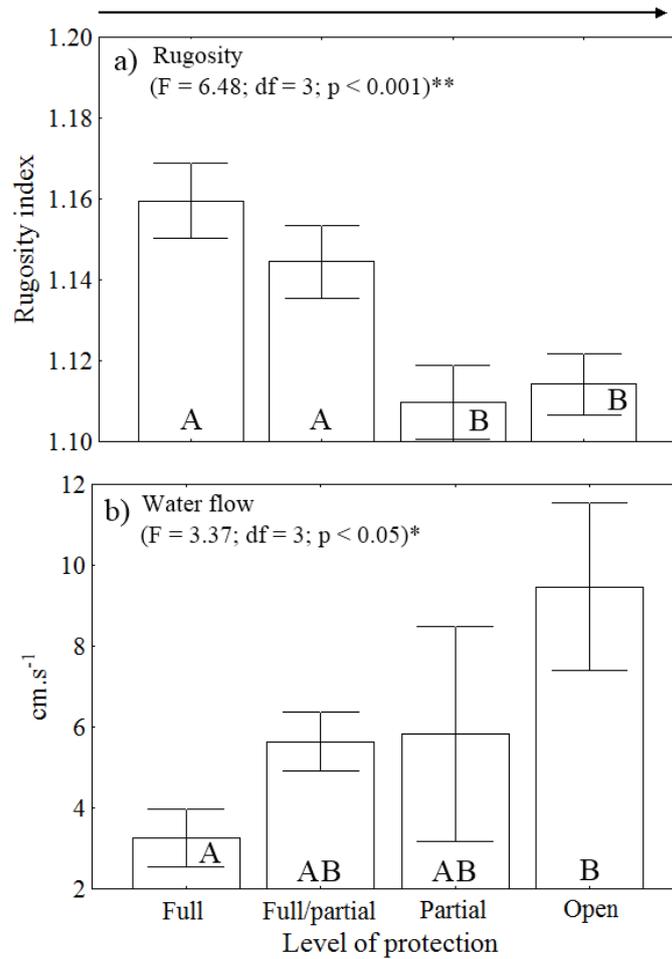


Figure 2. Mean values (\pm SE) of (a) rugosity and (b) water flow from four sites with ANOVA results indicated. Where different letters were assigned, significant differences were observed between pairwise sites. Arrows above panel indicate a decreasing gradient of protection from recreational activities (i.e. tourism).

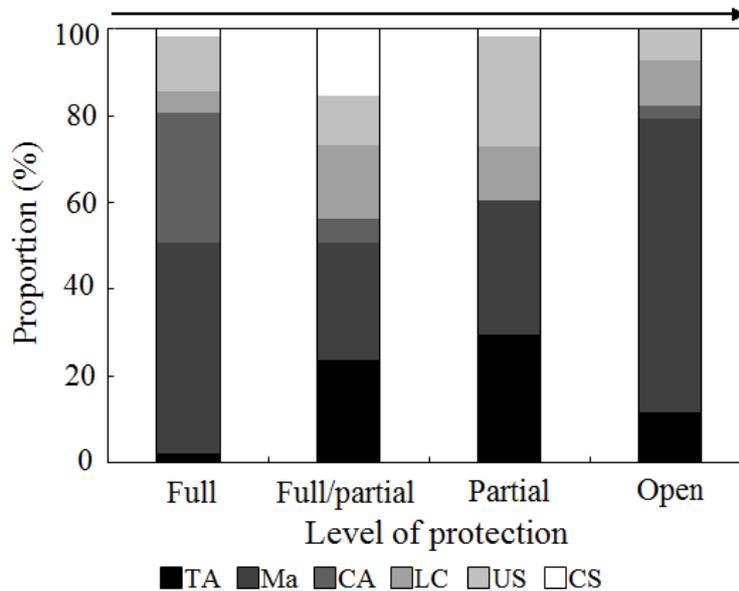


Figure 3. Relative proportion of benthic categories from four sites. TA: turf algae, ma: macroalgae, CA: coralline algae, LC: live coral, US: unconsolidated bare substrate, CS: consolidated bare substrate. Arrows above panel indicate a decreasing gradient of protection from recreational activities.

and Open sites and between the Full/partial and Open sites, with the Partial and Open sites showing statistical similarity (**Figure 4b**). For juveniles (ANOVA; $F = 5.93$; $p < 0.001$) (**Figure 4c**) and endemic species (ANOVA; $F = 14.17$; $p < 0.001$) (**Figure 4d**), number of individuals was over two orders of magnitude higher at the Full and Full/partial sites, which showed statistical similarity, compared to the Partial and Open sites, which also showed statistical similarity for both variables.

Multivariate analysis of variance carried out from the values of the most abundant species identified significant differences among sites (Pillai's trace = 0.41; $F_{24,873} = 5.67$; $p < 0.001$). However, an analysis of the abundance of each particular species (**Figure 5**) and *post-hoc* pairwise comparisons (**Table 2**) did not reveal clear patterns of segregation among sites.

Nevertheless, the discriminant function significantly distinguished among sites (Wilk's lambda: 0.65; $df = 24$; $p < 0.001$), and visual examination of discriminant function 1 plotted against discriminant function 2 clearly revealed this segregation among sites (**Figure 6**). Further, the data confirmed that all but one pairwise comparisons were significant (i.e. between Partial and Open sites) (**Figure 6**). These patterns are consistent with the observed differences detected among sites regarding number of individuals, juveniles and endemics, which showed higher values in the Full and Full/partial sites (**Figure 4**).

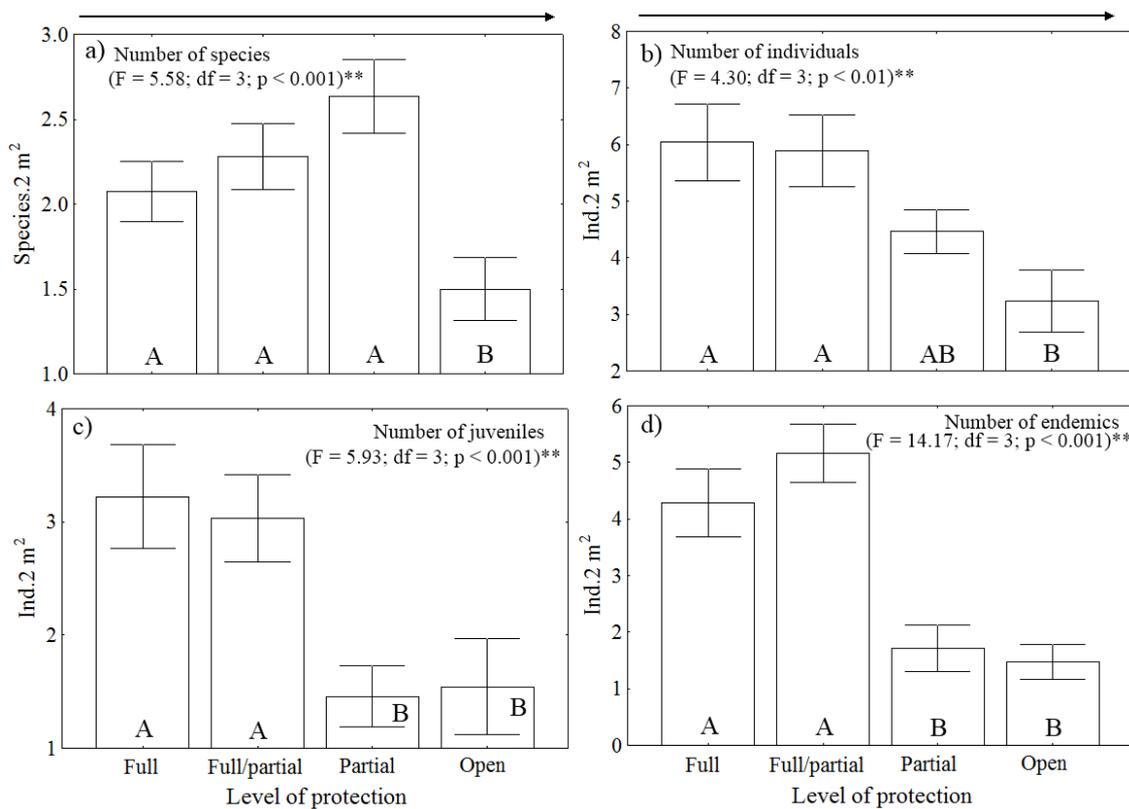


Figure 4. Mean values (\pm SE) of number of (a) species, (b) individuals, (c) juveniles and (d) endemics with ANOVA results indicated. Where different letters were assigned, significant differences were observed between pairwise sites. Arrows above panel indicate a decreasing gradient of protection from recreational activities.

General linear models, used to determine the importance of physical (rugosity and wave exposure), biological (benthic cover) and human-induced effects, identified significant responses of fish variables to some of these predictors (**Table 3**). Rugosity and protection from human-induced activities (positive effects) significantly explained the variability in species richness ($F_{10,289} = 4.50$; $p < 0.001$). Rugosity, protection from human-induced activities (positive effects) and wave exposure (negative effect) significantly explained the variability in fish abundance

(number of individuals) ($F_{10,289} = 3.99$; $p < 0.001$). Rugosity (positive effect) significantly explained the variability in the number of juveniles ($F_{10,289} = 5.70$; $p < 0.001$). Rugosity and protection from human-induced activities (positive effects) significantly explained the variability in the number of endemics ($F_{10,289} = 10.59$; $p < 0.001$). Despite differences in substrate composition among sites (Figure 3), percent cover of benthic organisms and bare substrate were poor predictors of fish numbers (Table 3).

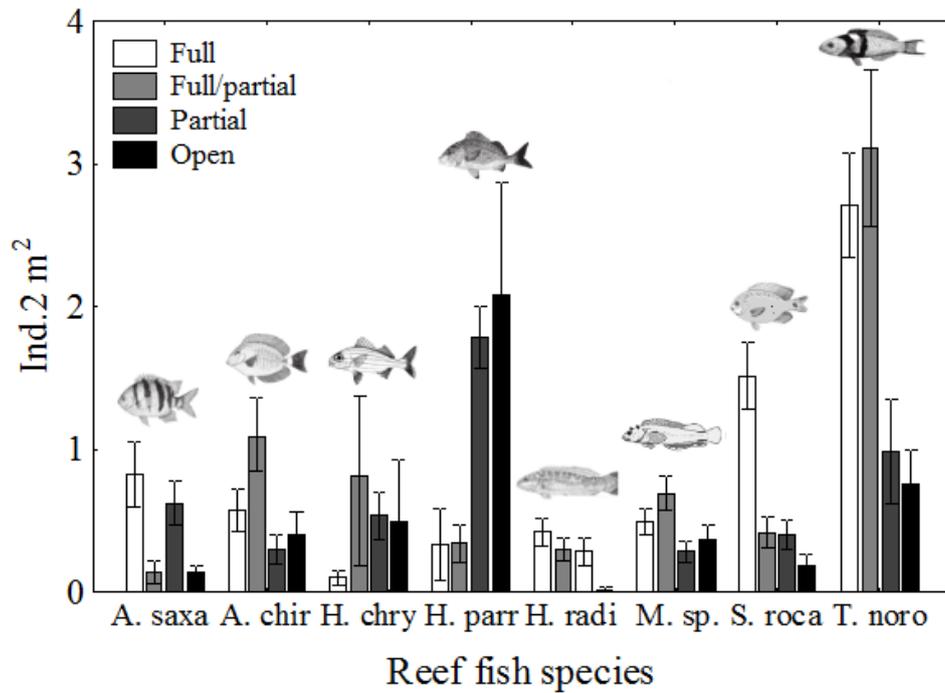


Figure 5. Mean values (\pm SE) of the abundance (ind.2 m²) of eight reef fish species at four sites with different degrees of restriction to recreational activities. Species names abbreviated (see Table 2).

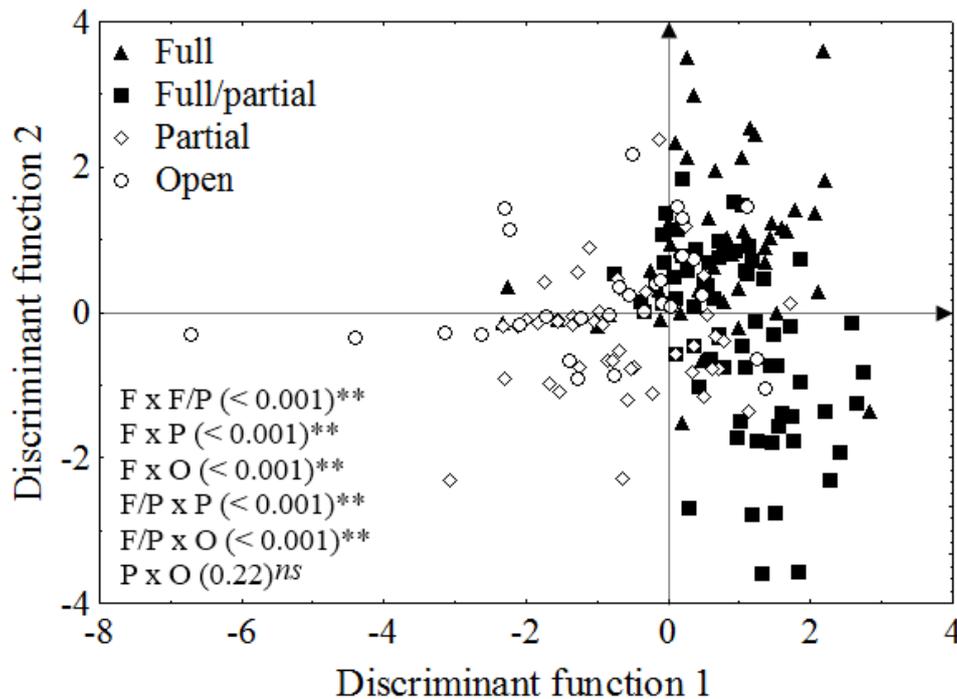


Figure 6. Discriminant function scatterplot on the abundance of eight reef fish species at four sites with different degrees of restriction to recreational activities. **: significant at 1%; ns: non-significant.

Determinants of fish numbers in Fernando de Noronha

Table 1. Bonferroni post hoc results of MANOVA (p values) for benthic cover estimates. Pairwise comparisons included four sites with different degrees of restriction to recreational activities. F: full; F/P: Full/Partial; P: Partial; O: Open.

Variables	Pairwise comparisons					
	F x F/P	F x P	F x O	F/P x P	F/P x O	P x O
Benthic cover						
Turf algae	< 0.001**	< 0.001**	0.04*	0.61	< 0.01**	< 0.001**
Macroalgae	< 0.001**	< 0.01**	< 0.01**	1.00	< 0.001**	< 0.001**
Coralline algae	< 0.001**	< 0.001**	< 0.001**	0.23	1.00	1.00
Live coral	< 0.001**	0.18	0.59	0.96	0.31	1.00
Bare substrate						
Unconsolidated	1.00	< 0.01**	0.97	< 0.001**	1.00	< 0.001**
Consolidated	< 0.001**	1.00	1.00	< 0.001**	< 0.001**	1.00

* significant at 5%; ** significant at 1%.

Table 2. Bonferroni post hoc results of MANOVA (p values) for the abundance of eight fish species. Pairwise comparisons included four sites with different degrees of restriction to recreational activities. F: full; F/P: Full/Partial; P: Partial; O: Open.

Variables	Pairwise comparisons					
	F x F/P	F x P	F x O	F/P x P	F/P x O	P x O
Family/fish species						
Acanthuridae						
<i>Acanthurus chirurgus</i>	0.17	1.00	1.00	0.03*	0.06	1.00
Haemulidae						
<i>Haemulon chrysargyreum</i>	1.00	1.00	0.48	1.00	0.62	0.93
<i>Haemulon parra</i>	1.00	< 0.001**	< 0.001**	< 0.001**	< 0.01**	1.00
Labridae						
<i>Halichoeres radiates</i>	1.00	1.00	< 0.01**	1.00	0.12	0.23
<i>Thalassoma noronhanum</i>	1.00	< 0.01**	< 0.001**	< 0.01**	< 0.01**	1.00
Labrisomidae						
<i>Malacoctenus</i> sp.	0.79	0.91	1.00	0.04*	0.17	1.00
Pomacentridae						
<i>Abudefduf saxatilis</i>	0.02*	1.00	0.06	0.06	1.00	0.13
<i>Stegastes rocasensis</i>	< 0.001**	< 0.001**	< 0.001**	1.00	1.00	1.00

* significant at 5%; ** significant at 1%.

Table 3. General linear model results (ANOVA) on the effects of physical (rugosity and wave exposure), biological (benthic cover) and protection from human recreational activities.

Predictors	Abundance		Richness		Juveniles		Endemics	
	F	p	F	p	F	p	F	p
Rugosity	15.49	< 0.001**	20.58	< 0.001**	29.95	< 0.001**	36.72	< 0.001**
Wave exposure	3.74	0.02*	2.74	0.07	1.96	0.14	3.73	0.03*
Benthic cover								
Turf algae	0.98	0.32	0.12	0.73	0.001	0.98	0.21	0.64
Macroalgae	1.57	0.21	0.49	0.49	0.002	0.96	0.54	0.46
Coralline algae	1.38	0.24	0.32	0.57	0.05	0.82	0.30	0.58
Live coral	1.41	0.24	0.28	0.60	0.02	0.89	0.64	0.42
Bare substrate								
Unconsolidated	1.69	0.19	0.66	0.42	0.001	0.98	0.99	0.32
Consolidated	0.93	0.33	0.08	0.77	0.01	0.94	0.40	0.53
Human-induced effects	2.66	0.04*	5.00	0.01**	2.54	0.06	6.76	< 0.001**

*Significant at 5%; significant at 1%.

Discussion

Rugosity

Rugosity positively influenced all fish parameters investigated (i.e. numbers of species, individuals, juveniles and endemics). Reef topography, a synonym for rugosity, has been considered one of the most important factors determining the abundances of many organisms, including several invertebrates (e.g. Crisp & Barnes 1954; Carleton & Sammarco 1987) and reef fishes (e.g. Roberts & Ormond 1987; Gratwicke & Speight 2005). For reef fishes particularly, physically complex areas (i.e. of high rugosity and high number of crevices) may improve effectiveness of recruitment (Connell & Jones 1991) and is often associated to higher availability of food and shelter (Hacker & Steneck 1990), increasing niche diversification and offering protection from predators and wave exposure.

Rugosity is a direct measure of the physical architecture of the reef's substrate and has been shown to positively influence fish richness, abundance and biomass at several reefs worldwide (e.g. McCormick 1994), albeit it is noteworthy that confusing results have also been acknowledged (reviews by Roberts & Ormond 1987; Gratwicke & Speight 2005). Nevertheless, artificial reefs have been used as fish-aggregating devices for centuries for fishery purposes (see Meier *et al.* 1989) and an increase in fish numbers is the obvious result of higher surface areas at complex substrates and its underlying increase in benthic coverage (i.e. increased food availability) and number of crevices (i.e. increased temporary refuge and hiding-sites). As a consequence, niche diversification increases and potential prey-predator encounter rates reduce (MacArthur & Levins 1964; Smith & Tyler 1972; Almany 2004). In fact, even biologically-poor sites have been benefited by simply increasing habitat complexity via artificial means (Bohnsack *et al.* 1997; Grossman *et al.* 1997).

As in the present study, Medeiros *et al.* (2011) and Krajewski & Floeter (2011) found that structural complexity (i.e. environmental heterogeneity) was a positive determinant of fish distribution and abundance. Although Sale & Douglas (1984) proposed that the influence of rugosity is only valid for sedentary, site-attached and/or territorial species, our results showed that not only site-attached, but also somewhat mobile species (e.g. acanthurids, haemulids and labrids) were, at least to a certain extent, positively influenced by rugosity. Although the influence of rugosity is markedly weak or coincidental for species which are not permanently associated to reefs (e.g. pelagic, migratory and schooling fishes), other mobile species (e.g. acanthurids, scarids and labrids) feed with higher frequency at sites with higher complexity in the study area (author's personal observation, Medeiros P.R.), supporting the positive effect of rugosity on these species. It is also likely that these species are attracted to complex sites for protection and hiding-places (see below).

Water flow

Despite the relatively low water flow at all sites, this variable had a negative influence on number of individuals and endemics, and was nearly significant for species richness (see **Table 3**). Similar results were previously observed in the study area (Krajewski & Floeter 2011) and on coastal reefs (Floeter *et al.* 2007). Also, water flow values showed an opposite pattern to those of rugosity, with sites of low level physical protection showing higher water flow values. Therefore, in addition to higher water flow, these sites also show lower quantities of protective shelter. Overall, although exposed sites may benefit some species (e.g. plankton feeders: Hobson & Chess 1978; Thresher 1983), it usually has a negative effect on the majority of species, thus limiting fish composition (Denny 1994), and this effect is particularly stronger at sites where shelter is not abundant. In fact, in a study carried out by Waldner & Robertson (1980) on the distribution of eight damselfishes, sites with similar substrates, but subject to different wave exposure regimes supported different fish species.

The high variance of values on two of the evaluated sites (i.e. Atalaia and Porto) suggests that these sites are subject to stronger water flow variations, whereas the other sites

showed a somewhat constant protection. Further, regardless of these values, the archipelago is located in an area subject to strong temporal fluctuations in wind conditions and sea currents (Eston *et al.* 1986; Ferreira *et al.* 1990).

Benthic composition

Benthic cover had a very small contribution to the observed variation in fish numbers. Studying fish assemblages on the same archipelago, Medeiros *et al.* (2011) found positive, albeit somewhat generalized relation between algal cover and fish density, whereas Krajewski & Floeter (2011) found that not only algae, but also coral, predicted fish abundance. Although benthic cover may play an important role in the distribution of several species, particularly for post-settled fishes, very confusing results arise on the influence of benthic cover when overall fish communities are evaluated. The available literature shows clear contrasting results, with some studies suggesting a positive influence of benthic cover on fish number (e.g. Carpenter *et al.* 1981; Bell & Galzin 1984; Lewis 1997) and others suggesting no influence whatsoever (e.g. Roberts & Ormond 1987). To elucidate these observed weak relationships in the present study, we propose one explanation which may be, at least to a certain extent, extrapolated to also clarify the divergences from the above mentioned studies. Species-specific responses to benthic cover are expected to be more pronounced at sites with higher diversity of fishes and benthic organisms, given that higher niche specialization is expected at diverse sites where competition is high (Eagle *et al.* 2001). Therefore, tighter relationships between some fish species and particular benthic components are expected at these high-diversity sites (e.g. some Caribbean and Indo-pacific reefs) compared to sites with lower diversity (e.g. Southwest Atlantic reefs).

An example of these relations comes about from chaetodontid fishes (e.g., butterflyfishes), which show strong feeding specialization of biological and morphological natures (i.e. high functional diversity). Obligate corallivorous chaetodontids are commonly observed in close association to sites with high coral cover in Caribbean reefs (Bouchon-Navaro *et al.* 1985). In Southwestern Atlantic reefs, chaetodontids are represented by four species which are not obligate corallivorous, but instead, feed on several benthic invertebrates (Randall 1967; Ferreira *et al.* 2004). Albeit of relatively high endemism, corals show lower species richness and morphotype diversity in Southwestern Atlantic reefs when compared to Caribbean reefs (Castro 2003), thus, minimizing species-specific responses from coral-feeders. This particular example supports our affirmation that, since the fish fauna of Southwestern Atlantic reefs encompass only a proportion of the fauna from Caribbean reefs, niche-specialization becomes less pronounced, with supposedly specialized fishes (e.g. chaetodontids) showing somewhat generalized habits. In fact, even in high-diversity Caribbean sites these relationships have been shown to result unexpectedly (see Bell *et al.* 1985; Eagle *et al.* 2001).

The important study of Risk (1972) conducted on the Virgin Islands, Caribbean Sea, showed similar patterns to the ones observed here. This author found no correlation between substrate diversity and fish numbers, but showed that structural complexity was a very important determinant. Similarly Roberts & Ormond (1987) found no relationships between substrate composition and fishes, but showed that number of holes from three different size classes was the most important predictor of fish abundance. As in the present study, these authors highlighted the importance of shelter to reef-associated fishes from all stages, prevailing over several other factors.

Human-induced effects

Human activities had a clear negative effect on most fish variable investigated. This is strong evidence that seemingly non-destructive human activities (i.e. tourism) may play a significant role in modifying reef fish structure, and that partial protection may not always yield expected results. Fishing has always been acknowledged as the most critical activity to reef fishes, but a substantial amount of studies have also been recently focusing on the effects of recreational activities (see review by Medeiros *et al.* 2007).

The most obvious effect of human activities was a decrease in fish abundance (individuals, juveniles and endemics) between the two most protected and the two less protected sites. This is likely to be a consequence of altered behaviors (i.e. evasion caused by human presence) such as observed elsewhere (Ferreira & Andrade 2012). One unexpected finding was the resemblance between the Open (Porto) and Partial (Atalaia) sites, where recreational activities are unrestricted and restricted, respectively. These sites shared similar rugosity values and similar number of individuals, juveniles and endemics, but differed extensively in benthic composition and fish richness. Furthermore, these two sites show contrasting area sizes, and although visitation is restricted in Atalaia (see Material and Methods) but not in Porto, it is possible that the former site is subject to a human-induced stress just as high as the latter, given the higher concentration of visitor per m².

Our findings support other studies which found that partial protection does not necessarily yield expected results (e.g. Francour *et al.* 2001; Denny & Babcock 2004; Floeter *et al.* 2006). Denny & Babcock (2004) found that partially protected sites showed no significant effect on the abundance of heavily targeted fishes compared to unprotected sites. Nevertheless, untargeted species were positively influenced by this protection. Floeter *et al.* (2006) suggested that fishes differ in their response to protection from human activities, particularly fishing, and that for most targeted fishes partial protection is not sufficient to guarantee reef fish community maintenance. Even for species that are not targeted or directly affected by human activities, cascades of trophic interactions are potentially threatening to the overall community. Within recreational activities, although several studies investigated the effects of fish feeding (Milazzo *et al.* 2005; Ilarri *et al.* 2008), trampling (Brown & Taylor 1999; Eckrich & Holmquist 2000), diving (Medio *et al.* 1997; Rouphael & Inglis 1997) and recreational fishing (Westera *et al.* 2003) on fishes, these community studies remain somewhat scarce, particularly in Southwest Atlantic sites.

The two sites with higher levels of protection from human activities also showed higher values of rugosity. The negative relationship between rugosity and recreational activities may be an indication that human trampling reduces the heterogeneity of reef topography and, consequently, played a significant role on fish abundance, as similarly observed elsewhere (Beauchamp & Gowing 1982; Liddle & Kay 1987; Liddle 1991; Brosnan & Crumrine 1994; Brown & Taylor 1999; Eckrich & Holmquist 2000). Nonetheless, these relationships need further investigation on the study site.

Our study highlights the importance of assessing several factors when investigating patterns of reef fish structure. Structural complexity, wave exposure (physical effects) and degree of protection from human activities were major correlates determining fish numbers, whereas substrate cover (biological) had minimal effects. Furthermore, the general awareness that algae-dominated substrates are indicative of historical changes to reefs (i.e. coral-algal phase shifts: McManus *et al.* 2000) seems not to be valid at the study area, given the abundance of algae on highly protected sites. Similarly, coral-rich reefs indicating high-quality environments seems not to be valid for southwest Atlantic sites, given the inherent coral characteristics of this area (Maida & Ferreira 1997; Castro 2003; but see Vroom *et al.* 2006). Furthermore, although the island is under governmental management to assure that human impacts are minimal, specific low-impact tourism practices are required in order to reduce the impact on benthic species and of fish evasion due to stress, especially in partially protected and unprotected areas.

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