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**RESEARCH LETTER**

# Geographic variation in reef-fish assemblages along the Brazilian coast

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## ABSTRACT

The species composition of reef-fish assemblages from nine Brazilian major coastal sites and four oceanic islands are compared. Canonical correspondence analysis (CCA) was utilized to identify groups of sites based on similarity of composition, and to correlate environmental trends with such groups. Five distinct groups of sites were recognized: (1) the South and South-eastern coastal reefs (from Guarapari Islands to Santa Catarina, the southernmost Brazilian reefs); (2) the North-eastern coast (extending from the Manuel Luis Reefs to Abrolhos Archipelago); (3) Trindade Island; (4) Fernando de Noronha and Atol das Rocas; and (5) St Paul's Rocks. Water temperature, coral richness, distance from mainland, primary production and shelf width strongly correlated with the diversity and composition of the reef sites.

**Key words** Brazil, distribution patterns, diversity, environmental factors, macroecology, oceanic islands, reef fishes, South Atlantic, zoogeography.

## INTRODUCTION

The tropical fish fauna of the western Atlantic ranges from about 35°N–28°S (Robins, 1971; Nunan, 1992; present study), and a considerable part of this region (4°N–28°S) is included in Brazilian waters. Although the reef ichthyofauna of the western North Atlantic has been subject to substantial study, the reef fishes of the Brazilian coast and its oceanic islands have remained poorly known. This lack of information on species distributions and assemblage composition has left a significant gap in the understanding of the biogeography of the tropical Atlantic, especially that of the western South Atlantic (Sale, 1991; Briggs, 1995).

A significant increase in sampling effort in Brazilian waters occurred only after the mid-1990s, when the growing use of scuba by Brazilian ichthyologists led to the extension of the known geographical range of many species (e.g. Nunan, 1992; Guimarães, 1996a,b; Moura *et al.*, 1999), the description of new species (e.g. Sazima *et al.*, 1997, 1998; Gasparini *et al.*, 1999; Rocha, 1999), and the first representative collections from major reef areas (e.g. Nunan, 1992; Rocha *et al.*, 1998; Rocha, 1999b; Gasparini & Floeter, in press).

Large-scale patterns in the composition of reef fish assemblages have distinct causes: (1) evolutionary histories of different regions, (2) dispersal

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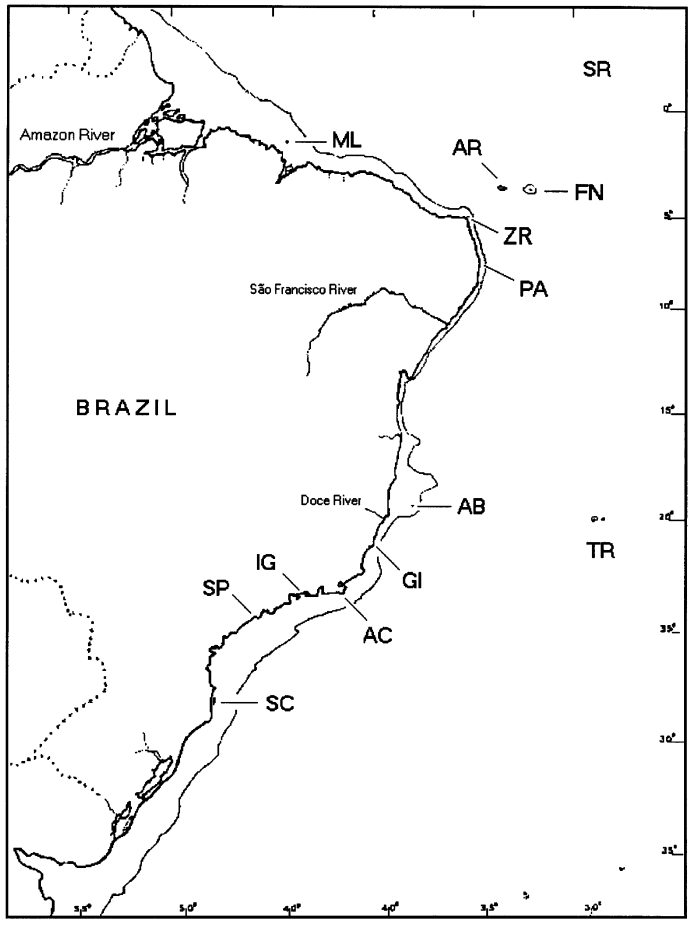


**Fig. 1** Location of the 13 Brazilian reef sites. Legend: ML = Manuel Luis Reefs, AR = Atol das Rocas, FN = Fernando de Noronha, SR = St Paul's Rocks, ZR = Zumbi Reefs, PA = Paraíba, AB = Abrolhos Archipelago, TR = Trindade Islands, GI = Guarapari Islands, AC = Arraial do Cabo, IG = Ilha Grande Bay, SP = São Paulo, SC = Santa Catarina. The 100 m isobath is included.

processes and (3) underlying environmental gradients. The latter is the central element addressed in this study. The Brazilian coast extends through *c.* 9500 km and is under the influence of a diverse set of oceanographic and ecological conditions. Locally, areas may be under the continuous influence of the oligotrophic tropical waters of the Brazilian Current, or seasonally affected by upwelling of cold, nutrient-rich waters (cf. Castro & Miranda, 1998; Ekau & Knoppers, 1999). The nature of the substrate varies from rocky (cf. Maida & Ferreira, 1997) to considerable coral cover (cf. Leão *et al.*, 1988). A further factor to consider is the enormous sediment and freshwater input from the Amazon and other Rivers (e.g. São Francisco and Doce River). Hypothetically, the fish faunas of the major Brazilian reefs vary according to these factors.

For the first time the opportunity has arisen to examine some aspects of the distributional patterns of the Brazilian reef fishes. In this paper, we will focus on the variation of fish assemblages among nine Brazilian coastal reef sites and four oceanic islands (Fig. 1), investigating distinctive environmental factors that possibly shaped the observed patterns.

**Table 1** Characteristic features of the major Brazilian reef sites

| Reef sites (coordinates) | Distance from the coast (km) | Coral species[1,2] (Scleractinian + Hydrocorals) | SWT[1,3] (°C) winter–summer | Water regime[4] | Primary production[3] (gC $m^{-2}$ $d^{-1}$) | Shelf width[3] (km) |
|---|---|---|---|---|---|---|
| North-eastern Brazil | | | | | | |
| Manuel Luis Reefs (0°52′S; 44°15′W) | 86 | 16 | 26–28 | NBC | 0.3–0.8 | ~130 |
| Zumbi Reefs (5°S; 35°W) | 10 | 8 | 26–28 | NBC and SEC | 0.02–0.2 | ~35 |
| Paraíba Coast (7°S; 34°50W) | — | 12 | 25–28 | SEC | 0.02–0.2 | ~35 |
| Abrolhos Archipelago (17°20′S; 39°W) | 50 | 18 | 22–27 | BC | 0.3–1.1 | ~180 |
| South-eastern Brazil | | | | | | |
| Guarapari Islands (20°40′S; 40°22′W) | 5 | 14 | 19–24 | BC and SACW | 0.3–1.1 | ~50 |
| Arraial do Cabo (23°S; 42°W) | — | 5 | 18–23 | BC and SACW | 0.3–1.3 | ~120 |
| Ilha Grande Bay (23°05′S; 44°20′W) | — | 2 | 18–23 | BC and SACW | 0.3–1.3 | ~150 |
| São Paulo Coast (24°30′S; 46°W) | — | 2 | 18–22 | BC and SACW | 0.1–0.5 | ~170 |
| Santa Catarina Coast (27°30′S; 48°W) | — | 1 | 17–21 | BC and SACW | 0.1–0.5 | ~150 |
| Oceanic islands | | | | | | |
| Atol das Rocas (3°50′S; 33°49′W) | 267 | 8 | 25–28 | SEC | 0.02–0.2 | ~10 |
| Fernando de Noronha (3°51′S; 32°26′W) | 345 | 11 | 24–25 | SEC | 0.02–0.2 | ~15 |
| St Paul's Rocks (0°55′N; 29°21′W) | 1000 | 2 | 26 | SEC | 0.02–0.2 | ~1.5 |
| Trindade Island (20°30′S; 29°20′W) | 1160 | 4 | 25 | BC | 0.02–0.5? | ~3 |

SWT = surface water temperature; NBC = North Brazil Current; SEC = South Equatorial Current; BC = Brazil Current; SACW = South Atlantic Central Water. Sources: [1] Maida & Ferreira, 1997; [2] Belém *et al.* (1986); and C.B. Castro, personal communication; [3] Ekau & Knoppers, 1999; [4] Castro & Miranda, 1998.

## STUDY SITES

Thirteen reef complexes were studied, encompassing the whole area of occurrence of reef-associated fishes in the western Atlantic south of the Amazon River mouth (Fig. 1 and Table 1). Nine sites are located in the continental shelf. Four are located on the North-eastern coast: Manuel Luis Reefs (ML), the northernmost Brazilian reef formation, consisting of coralline algal crusts over a rocky substrate, sparsely covered with hermatypic and fire corals; Zumbi Reefs (ZR), a rocky formation dominated by sponges and calcareous algae; Paraíba Coast (PA), where several calcareous algae reefs grow parallel to the shoreline, mainly over a sandstone base; and Abrolhos Archipelago (AB), the largest and more diverse coral reef complex in the South Atlantic, with large isolated 'mushroom shaped' pinnacles and wide platform-bank reefs. Five are located on the South-eastern and Southern coast: Guarapari Islands (GI), a rocky insular complex scattered with corals,

milleporines, octocorals and calcareous algae beds; Arraial do Cabo (AC), which consists of rocky shores with a veneer of corals, and depicts the southern limit of the distribution of fire corals; Ilha Grande Bay (IG) and São Paulo Coast (SP), with rocky habitats overgrown with macrobenthos (e.g. zoanthids, sponges); and Santa Catarina Coast (SC), the southernmost limit of reef-fish occurrence in the Brazilian Province, with rocky shore habitats covered with algae and sponges. The other four sites included are the Brazilian oceanic islands: Atol das Rocas (AR), an atoll constructed mainly by coralline algae and vermetids, with a veneer of hermatypic corals; Fernando de Noronha (FN), a volcanic formation covered with calcareous algae, vermetids, and corals; St Paul's Rocks (SR), a small isolated rocky archipelago overgrown with algae and zoanthids; and Trindade Island (TR), with volcanic rocky reefs covered with coralline algae.

## METHODS

This study was based on the tropical teleost species associated primarily with hard substrates in the continental shelf and oceanic islands, referred to here as 'reef fishes'. To minimize potential bias due to taxonomic problems and misidentification, we included 10 of the most characteristic reef-associated families (Muraenidae, Holocentridae, Serranidae, Haemulidae, Chaetodontidae, Pomacanthidae, Pomacentridae, Labridae, Scaridae, Acanthuridae). These families were chosen for the following reasons: (1) they are taxonomically well documented; (2) they are conspicuous and relatively easy to identify underwater; and (3) most of these families are consistently among the 10 most speciose in the Western and Central Atlantic (Floeter & Gasparini, 2000).

The composition and species distribution of the reef ichthyofauna have been determined primarily through original field studies in the 13 reef sites (Fig. 1) by the authors and colleagues, as well as by compilation of data from the literature (e.g. Figueiredo & Menezes, 1978; 1980; Menezes & Figueiredo, 1980, 1985; Lubbock & Edwards, 1981; Nunan, 1992; Böhlke & Chaplin, 1993; Randall, 1996; Rosa & Moura, 1997; Carvalho-Filho, 1999) and museum collections [Museu Nacional Rio de Janeiro (MNRJ), Laboratório de Biodiversidade de Recursos Pesqueiros da Universidade Federal do Rio de Janeiro (LBRP), Museu de Zoologia da Universidade de São Paulo (MZUSP), Universidade Federal da Paraíba (UFPB), Museu de Biologia Professor Mello Leitão (MBML), British Museum of Natural History (BMNH), Universidade Federal do Espírito Santo (UFES), Laboratório de Ictiologia da Universidade Estadual de Feira de Santana (LIUEFS), Museu de Zoologia da Universidade Estadual de Campinas (ZUEC)].

Canonical correspondence analysis (CCA) was utilized to identify the main groups of sites and to describe the relationships between reef-fish species and environmental factors (ter Braak & Verdonschot, 1995). With this intent, we ran together the binary data matrix of reef fish and a matrix of environmental and oceanographic data including distance from mainland, number of coral species, mean surface water temperature, primary production [i.e. phytoplankton production ($gC\ m^{-2}\ d^{-1}$)] and shelf width (distance from the coast to the 100 m isobath). The main characteristics of the studied sites, including all environmental data used in the CCA analysis, are presented in Table 1. The explanatory variables in the output are represented by vectors pointing towards the maximum change in the value of the associated variable. The length of an environmental line indicates a variable's relative importance. In order to improve the robustness of the conclusions, classical cluster analysis was also performed (the sites were clustered according to Sorensen's similarity coefficient using complete linkage, although varying the clustering routine had no effect on the grouping of sites).

## RESULTS

### Distribution patterns and related environmental factors

In the CCA ordination, the 13 sites are represented by points and the environmental variables by arrows (Fig. 2). Together, they account for 71.4% of the variance in the weighted averages. Five major groups are identified in the analysis: (1) SE coastal reefs (GI, AC, IG, SP and SC); (2) the NE coast (ML; PA, ZR, and AB); (3) Trindade Island (TR); (4) Fernando de Noronha and Atol das Rocas (FN and AR); and

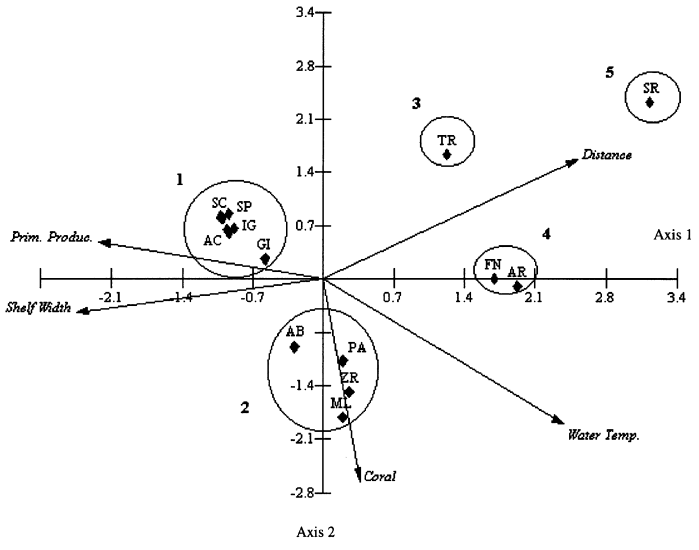


**Fig. 2** CCA ordination diagram with reef sites (points) and environmental variables (arrows). The length of the environmental arrows indicate their relative importance. Sites: (1) SC = Santa Catarina, SP = São Paulo, IG = Ilha Grande Bay, AC = Arraial do Cabo, GI = Guarapari Islands; (2) AB = Abrolhos Archipelago, PA = Paraíba, ZR = Zumbi Reefs, ML = Manuel Luis Reefs; (3) TR = Trindade Is.; (4) FN = Fernando de Noronha, AR = Atol das Rocas; (5) SR = St Paul's Rocks.

(5) St Paul's Rocks (SR). The same five groups were also obtained from the cluster analysis.

In the CCA biplot, the first axis approximates a gradient of fish species richness, which is highly influenced by distance from mainland (intraset correlation = 0.813), shelf width (–0.787), water temperature (0.765) and primary production (–0.707). Group 1, which includes all rocky-shore sites of the South and SE coast, is placed at one extreme of the temperature vector due to their lower mean annual water temperature. These sites also show relatively higher primary production and large shelf width. On the other hand, the oceanic islands (TR, FN, AR and SR) are characterized by relatively oligotrophic warmer water, narrower shelf width and greater isolation. Along the second ordination axis, the sites are distributed as a function of the gradient of coral richness (–0.762). Group 2, which includes the sites of the NE, is characterized by its relatively warm waters and high diversity of coral species. Both TR and SR sustain low coral species richness and are placed at the opposite extreme of the axis.

## Composition and geographical ranges

The most speciose families among those included in this study are: Serranidae (25 spp.), Labridae (16), Pomacentridae (13) and Haemulidae (11). Although there is considerable homogeneity in the composition of the reef-fish fauna along the Brazilian coastal reefs (Table 2), slight differences were found in some families. The haemulids and labrids are richer in the NE sites, scarids and serranids in the SE, and muraenids in the oceanic islands, particularly FN and AR. The coastal areas sustain richer fish assemblages when compared to the oceanic islands, as expected. However, the rocky shores and rocky reefs of the SE exhibit the most diverse assemblages.

Approximately 20% of the reef ichthyofauna occurring in all the study sites are restricted to the SW Atlantic (Table 3). Species that possess wider distributions (pan-Atlantic + western Atlantic and mid-Atlantic) represent a greater fraction of offshore assemblages. As expected, the coastal reefs presented a higher proportion of western Atlantic continental margin species. Only St Paul's Rocks

**Table 2** Number of species in each of the 10 most characteristic Brazilian reef-fish families in the five reef complexes determined by CCA (see Methods)

| Families (total number of spp.) | SE Brazil | | | | | NE Brazil | | | | F. de Noronha Ridge | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Santa Catarina | São Paulo | I. Grande Bay | Arraial do Cabo | Guarapari Islands | Abrolhos Reefs | Paraíba | Zumbi Reefs | Manuel Luis Reefs | Trindade Island | Atol das Rocas | F. de Noronha | St Paul's Rocks |
| Acanthuridae (3) | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 0 |
| Chaetodontidae (6) | 2 | 4 | 4 | 4 | 3 | 2 | 3 | 2 | 3 | 2 | 1 | 2 | 2 |
| Haemulidae (11) | 6 | 6 | 6 | 6 | 8 | 8 | 9 | 8 | 6 | 1 | 3 | 4 | 0 |
| Holocentridae (4) | 2 | 3 | 3 | 4 | 4 | 1 | 3 | 3 | 2 | 2 | 2 | 3 | 2 |
| Labridae (16) | 6 | 9 | 9 | 10 | 10 | 9 | 12 | 9 | 11 | 7 | 5 | 7 | 4 |
| Muraenidae (8) | 3 | 3 | 3 | 4 | 5 | 3 | 7 | 3 | 3 | 4 | 7 | 8 | 5 |
| Pomacanthidae (5) | 4 | 4 | 5 | 5 | 5 | 3 | 5 | 4 | 3 | 2 | 2 | 3 | 2 |
| Pomacentridae (13) | 6 | 7 | 7 | 7 | 7 | 6 | 8 | 6 | 6 | 4 | 4 | 4 | 3 |
| Scaridae (9) | 4 | 9 | 9 | 9 | 9 | 7 | 7 | 6 | 8 | 3 | 3 | 3 | 3 |
| Serranidae (25) | 15 | 18 | 18 | 20 | 22 | 13 | 12 | 8 | 9 | 8 | 5 | 6 | 2 |
| Total (100) | 50 | 66 | 67 | 72 | 76 | 55 | 69 | 52 | 54 | 35 | 35 | 43 | 23 |

**Table 3** Geographic range of the species within the 10 most characteristic reef-fish families in the five reef complexes determined by CCA (see Methods). Numbers refer to percentage of fish species

| Geographic range | SE Brazil | | | | | NE Brazil | | | | F. de Noronha Ridge | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Santa Catarina | São Paulo | I. Grande Bay | Arraial do Cabo | Guarapari Islands | Abrolhos Reefs | Paraíba | Zumbi Reefs | Manuel Luis Reefs | Trindade Island | Atol das Rocas | F. de Noronha | St Paul's Rocks |
| Pan Atlantic + circumtropical | 23.5 | 20.9 | 22 | 21.9 | 21.8 | 23.2 | 21.4 | 20.8 | 21.4 | 28.6 | 34.3 | 27.9 | 36.2 |
| Western + mid-Atlantic | 7.8 | 7.5 | 7.4 | 6.8 | 6.5 | 8.9 | 8.6 | 9.4 | 8.9 | 11.4 | 17.1 | 16.3 | 15.8 |
| Mid-Atlantic[1] | — | — | — | — | — | — | — | — | — | — | — | — | 4.2 |
| Western Atlantic margin | 51 | 50.7 | 50 | 52.1 | 53.8 | 46.5 | 48.6 | 47.2 | 51.8 | 42.9 | 25.7 | 37.2 | 11.8 |
| South-western Atlantic[2] | 17.7 | 20.9 | 20.6 | 19.2 | 17.9 | 21.4 | 21.4 | 22.6 | 17.9 | 17.1 | 22.9 | 18.6 | 32 |

[1] St Paul's Rocks + Ascension + St Helena; [2] continental margin + oceanic islands.

 

holds species restricted to the mid-Atlantic Ridge islands (St Paul's Rocks + Ascension + St Helena).

## DISCUSSION

### NE coastal reefs

The NE reef-fish assemblages are influenced by the warm and oligotrophic South Equatorial Current (SEC) and the relatively high coral diversity. The SEC impinges on the Brazilian coast between 7° and 17°S, further dividing into two branches, the north-westward flowing North Brazil Current, and the south-eastward-flowing Brazil Current (Evans *et al.*, 1985). Maximum shelf widths are attained off the Abrolhos bank (245 km). In contrast, the majority of the NE shelf is only 20–50 km wide.

The NE Brazilian assemblages are characterized by the dominance of tropical species. Many of these occur in the Caribbean and have not expanded their distributions southwards [e.g. the serranid *Serranus annularis* (Günther); the haemulid *Haemulon melanurum* (Linnaeus); the chaetodontid *Chaetodon ocellatus* (Bloch); and the labrids *Xyrichtys splendens* (Castelnau) and *X.* cf. *martinicensis* (Cuvier)]. Haemulids and labrids are richer and more abundant in the NE (Ferreira *et al.*, 1995) than in the SE sites, indicating that water temperature is a constraint in these two typical tropical families.

The largest coral reefs of the South Atlantic are located in the Abrolhos Archipelago (Leão *et al.*, 1988; Leão, 1996) and, as a consequence, the greatest reef-fish species richness was expected to occur in this area (Moura *et al.*, 1999). However, its fish assemblage is poorer in species than those of the SE sites (Table 2).

Some conspicuous reef fishes [e.g. *Holacanthus tricolor* (Bloch), *Myripristis jacobus* (Cuvier), and many zooplanktivores] are notably missing in the Abrolhos Archipelago. The reasons for these gaps are yet to be determined, but certainly some 'filters' could be acting in the region (e.g. particulate suspension matter, the São Francisco and Doce River freshwater and sediment barriers).

### South and SE coastal reefs

No true coral reefs are found along the SE coast, where rocky shores represent the main habitat for reef fishes. Rocky reefs occur with minor interruptions from the State of Espírito Santo to about 28°S, in Santa Catarina Coast. Nevertheless, the reef-fish fauna living in this area appears to be the richest of Brazil (Table 2), due to the mix of tropical and subtropical elements. The Abrolhos reefs and the Vitória–Trindade Ridge form a topographical barrier to the Brazil Current, inducing fundamental changes and spatial variability in physical, chemical and biological features over the SE shelf, which is generally larger than in the NE (Schmid *et al.*, 1995; Castro & Miranda, 1998). The SE reefs are subjected to a relatively intense seasonal upwelling promoted by the South Atlantic Central Water (SACW), bringing low-temperature (< 18 °C) and nutrient-rich waters close to the coastline (Ekau & Knoppers, 1999).

Serranids and scarids reach their peak diversity in the SE sites. Interestingly, a considerable number of Caribbean reef fishes found in this region are absent from the NE sites [e.g. the serranids *Epinephelus niveatus* (Valenciennes), *Mycteroperca microlepis* (Goode & Bean), *M. tigris* (Valenciennes), *Serranus phoebe* (Poey), and the scarid *Sparisoma atomarium* (Poey)]. However, a gradual faunal impoverishment is observed southwards of São Paulo, with Santa Catarina (28°S) being the southern limit of rocky reef bottoms under the influence of the warm Brazil Current (Evans *et al.*, 1985; Stramma, 1989) and consequently of tropical reef fish species. In Santa Catarina, shallow sheltered bays are little affected by seasonal intrusions of subtropical waters from the south and provide habitat for about half of the reef-fish species known from the Brazilian continental shelf.

### Offshore islands

Oceanic sites experience extreme isolation and relatively small shallow water area, thus diminishing the chances of larval input from the continental margins as well as limiting the availability of suitable habitats for the adults. The numbers of species decline impressively (Table 3). Haemulidae and Scaridae, although consistently speciose in the Brazilian coastal reefs, are poorly or not represented in the oceanic sites. The larger scraper parrot-fishes of the genus *Scarus*, which occur at oceanic sites in the Indo-Pacific and North Atlantic (Smith-Vaniz *et al.*, 1999; L. Rocha, personal observation), are absent from the South Atlantic oceanic islands. On the other hand, members

of the genus *Sparisoma* are present on the offshore islands, possibly reflecting the broader feeding habits of this genus, which includes not only algae but sponges as well (Deloach, 1999).

The two insular groups within the Fernando de Noronha Ridge, Atol das Rocas and Fernando de Noronha, have very similar fish faunas, with five shared endemic species. In contrast, St Paul's Rocks and Trindade Island are extremely isolated (> 1000 km from mainland) and sustain poorer assemblages, aside from harbouring a considerable number of endemic species (Floeter & Gasparini, 2000).

Some intriguing distribution patterns were found in the offshore islands. Of special interest is the absence of the family Acanthuridae from St Paul's Rocks, probably the only tropical island in the world missing this conspicuous reef-associated family. In addition, the wide-ranging banded butterfly-fish *Chaetodon striatus* (Linnaeus) has never been recorded at Atol das Rocas. The pomacanthids, *Holacanthus ciliaris* (Linnaeus) and *Pomacanthus paru* (Bloch), are common in the Caribbean, the Brazilian coast, Atol das Rocas, Fernando de Noronha and St Paul's Rocks. Surprisingly, both species are missing in Trindade Island, where *H. tricolor* and *Centropyge aurantonota* (Burgess) are known to occur (Gasparini & Floeter, in press). *H. ciliaris* and *P. paru* are common at Fernando de Noronha, where only a few vagrant juveniles of *H. tricolor* and *C. aurantonota* were recorded.

Theoretically, all these pelagic-spawning species do not have larval dispersal restrictions since the Acanthurids, *C. striatus* and *P. paru*, have successfully colonized extremely isolated sites such as Ascension and Bermuda. We assume, therefore, that ecological factors such as food availability, competition for space, temperature or requirements for proper larval development are influencing these disjunct patterns of distribution.

In summary, the geographical variation in fish assemblages among the Brazilian reefs is correlated strongly with some general environmental variables. The same analysis was run including about 250 fish species belonging to 55 families known to occur in the Brazilian reefs, and the same pattern of site association was found (not illustrated). Despite these results, other specific variables should be investigated (e.g. particulate suspension matter, freshwater input, habitat complexity) to avoid possible misinterpretation of locally specific patterns. Future studies focusing on quantitative aspects of the fish fauna on this coastal gradient, and revealing more detail of the distributional patterns, are to be encouraged.

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