



The southwestern Atlantic reef fish fauna: composition and zoogeographic patterns

S. R. FLOETER*‡ AND J. L. GASPARINI†

*Universidade Federal do Espírito Santo—Departamento de Ecologia e Recursos Naturais, 29060-900 Vitória, Espírito Santo, Brazil

†Universidade Federal do Espírito Santo—Departamento de Biologia, 29040-090 Vitória, Espírito Santo, Brazil

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The Brazilian coast, the Caribbean and the tropical South Atlantic oceanic islands reef ichthyofauna separated into two major clusters: (1) the western Atlantic continental margin and Bermuda, further divided into (1a) the western North Atlantic, and (1b) the Brazilian coast; and (2) the South Atlantic oceanic islands, also divided in (2a) the Brazilian offshore islands, and (2b) Ascension and St Helena. Species geographic ranges suggest the recognition of only two western Atlantic zoogeographic provinces for tropical marine shore fishes. A Brazilian Province, including the offshore localities of Atol das Rocas, Fernando de Noronha, Trindade and St Paul's Rocks, and an expanded West Indian Province that includes Bermuda. Ascension and St Helena should be regarded as a separated Central Atlantic Province.

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Key words: reef fishes; zoogeography; spawning modes; oceanic islands; South Atlantic; Brazil.

INTRODUCTION

The southwestern Atlantic reef ichthyofauna was one of the least known and it has been ignored in all interoceanic comparisons. However, recent research efforts led to the compilation of the first comprehensive fish lists for Brazilian coastal and offshore reefs (Moura, unpublished; Rocha *et al.*, 1998; Gasparini & Floeter, 2000). Until the mid-1980s, this fauna was thought to consist largely of wide ranging Caribbean species (Moura *et al.*, 1999a). It is now apparent that many of those, although similar to their northwestern Atlantic congeners, are endemic to the southwestern Atlantic (Greenfield, 1988, 1989; Sazima *et al.*, 1997, 1998; Rocha & Rosa, 1999).

The Amazon River has the largest freshwater discharge in the world and supplies *c.* 1 billion tons of sediment per year to the continental shelf (Meade *et al.*, 1985). The low-salinity plume that extends offshore and northwestward (this region is under the influence of the North Brazilian Current) and the differentiated sedimentation along the north Brazilian shelf has been suggested to represent a major barrier between the Caribbean and the southwestern Atlantic faunas (Gilbert, 1972; Briggs, 1974, 1995; Greenfield, 1988, 1989).

Virtually all reef species have larvae that spend some time adrift in the plankton (Leis, 1991; Victor, 1991). The duration of the planktonic stage varies

‡Author to whom correspondence should be addressed. Sergio R. Floeter, Village Ed. Degas, 204 Ilha do Boi, Vitória, ES, 29052-730 Brazil. Email: floeter.vix@zaz.com.br

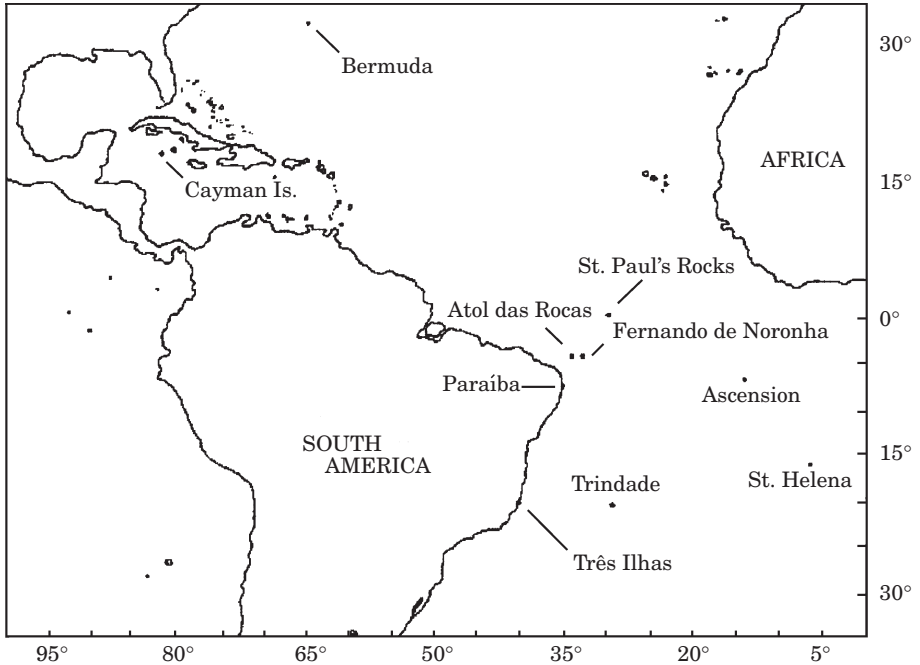


FIG. 1. Location of the 10 Atlantic reef sites.

according to the spawning mode. The pelagic and balistid-type spawners (mainly balistids, monacanthids, and tetraodontids) show typical larval duration of 20–50 days, while the normal demersal-spawners remain part of the plankton for 15–25 days (Thresher, 1991). Combined with extinction and speciation mechanisms, these varying dispersal abilities seem to be a key to understanding the complex characteristics of reef fish biogeography (MacArthur & Wilson, 1967; Victor 1986; Shulman & Bermingham, 1995).

This study addresses two major issues. The first is to compare the taxonomic composition and diversity of the reef fishes of the southwestern Atlantic. The second is to investigate the processes that may have influenced present patterns of species distribution, such as the Amazon outflow barrier, oceanic currents, geographic isolation and dispersal abilities.

METHODS

This study focused on the 40 primarily reef-associated teleost families (*sensu* Thresher, 1991). These included almost all species that live on coral, tropical rocky or coralline algal reefs found in the Atlantic. The taxonomic definition of the families followed Nelson (1994). Comparisons of the reef ichthyofauna between the western Atlantic continental margin and the oceanic islands were made after compilation of species checklists from 10 reef sites (Fig. 1 and Table I): two Brazilian coastal sites, the four Brazilian offshore islands, two central Atlantic sites, and an outside group represented by one site in the middle of the Caribbean Sea, the Cayman Islands (Burgess *et al.*, 1994), and Bermuda, the world's northernmost coral reef ecosystem (Smith-Vaniz *et al.*, 1999). The Brazilian coastal sites included Paraiba, northeastern Brazil (Rocha *et al.*, 1998), and a ten-year study at Três Ilhas Archipelago, southeastern Brazil (Gasparini & Floeter, 2000). Offshore islands were represented by St Paul's Rocks (Lubbock & Edwards, 1981;

TABLE I. Location, dominant reef type, area and distance from mainland for each Atlantic site

	Northwestern Atlantic		Brazilian province				Central Atlantic	
	Bermuda	Cayman Islands	Brazilian coast		Brazilian offshore islands		Ascension Island	St Helena Island
			Paraíba	Três Ilhas Archipelago	Atol das Rocas	Fernando de Noronha		
Latitude	32°18'N; 64°46'W;	19°30'N; 80°10'W;	07°00'S; 34°50'W;	20°36'S; 40°22'W;	03°51'S; 33°49'W;	20°30'S; 29°20'W;	07°55'S; 14°25'W;	15°58'S; 05°43'W;
Dominant reef type	Corals, calcareous algae and vermetid reefs	Corals	Calcareous algae, corals, and vermetid molluscs	Rocky with a veneer of corals, calcareous algae and vermetid reefs	Atoll built primarily by coralline algae and a veneer of corals	Rocky, algae and vermetid reefs	Poor in coral, calcareous algae reefs	Rocky, calcareous coralline algae cobbles
Shallow platform area >50 m deep (km ²)	~180	~300	~350	~10	~5.5	~50	~0.5	~150
Distance from mainland (km)	1049	—	—	—	267	345	1000	1870*
Surface water temperature (°C) (Winter-Summer)	18–28	25–28	24–27	20–26	25–28	24–27	25–27	21–26
References	Smith-Vaniz <i>et al.</i> , 1999	Burgess <i>et al.</i> , 1994	Maida & Ferreira, 1997	Gasparini & Floeter, 2000	Kikuchi & Leão, 1997	Maida & Ferreira, 1997	Edwards & Lubbock, 1983a	Price & John, 1980
								Edwards, 1990

*Distance from Africa (nearest land).

Ferreira *et al.*, 1999), a four-year study on Trindade Island (Gasparini & Floeter, unpublished) and Atol das Rocas and Fernando de Noronha Archipelago (Moura, unpublished; Rosa & Moura, 1997), the two insular groups within the Fernando de Noronha Ridge. The mid-Atlantic sites Ascension Island (Lubbock, 1980) and St Helena Island (Edwards & Glass, 1987; Edwards, 1990) completed the list.

Variation in the assemblage structure of the reef fishes was examined among the 10 Atlantic sites by analyses of species richness, species diversity within families (relative abundance, i.e. number of species per family divided by the number of species for all families), geographical ranges, and principal spawning modes (Table II). The spawning modes were divided according to Thresher (1991).

Changes in species composition within and among families were investigated using cluster analysis. Similarities between the sites were calculated from a binary data matrix based on the presence/absence of species or families. The similarity index adopted was Sorensen's coefficient, $S_s = 2a/(2a+b+c)$, where a is the number of species common to both localities, b and c the number of species occurring in only one of the two localities. The coefficient does not take absences into account, and stresses the value of common presence, broadening the range of values between the less and the more similar pairs of localities (Sneath & Sokal, 1973; Valentine, 1973; Pielou, 1979). Localities were clustered according to the similarity coefficient using complete linkage—where the distances between clusters are determined by the greatest distance between any two objects in the different clusters, i.e. by the furthest neighbours (Pielou, 1984).

RESULTS AND DISCUSSION

VARIATION IN THE TAXONOMIC COMPOSITION OF ATLANTIC REEFS

Two cluster analyses were performed. The first one was based on a matrix of presence/absence of all species (Fig. 2). The second one was based on the species richness of the 40 reef-associated families. Both analyses separated the 10 Atlantic sites into two major clusters: (1) The western Atlantic continental margin and Bermuda, further divided into: (1a) the North Atlantic–Caribbean and Bermuda and (1b) the Brazilian coast—Paraíba and Três Ilhas; and (2) the South Atlantic oceanic islands, also divided into: (2a) the Brazilian offshore islands—Atol das Rocas, Fernando de Noronha, St Paul's Rocks and Trindade, and (2b) Ascension and St Helena. Varying the clustering routine had no effect on the grouping of sites.

The differences between the geographic groups in the Atlantic is evidenced by the distributions of the relative abundance of species in the main reef associated taxa (Table III). Various families that are consistently speciose in the continental margin sites (and Bermuda) are poorly or not represented at all in the South Atlantic oceanic sites: Serranidae, Apogonidae, Gobiesocidae, Gobiidae, Labrisomidae, Lutjanidae, Haemulidae and Scaridae. Two taxa, Fistulariidae and Chaenopsidae are absent from the oceanic islands where the distributions are characterized primarily by the relatively higher abundance of Tetraodontiforms and Muraenidae. Although Muraenidae is one of the top ten richest families at every site in the Atlantic, the relative importance of this family increases on the oceanic islands, where they rank among the three most species-rich families (Table III). Only the Ascension–St Helena group include Antennariidae, Bothidae, Diodontidae and Scorpaenidae among their richest families.

Although the number of families remains constant along the east coast of the Americas, the Brazilian coast differs from the western North Atlantic in its lower

TABLE II. Total number of species, families, geographic range and reproductive mode of reef-associated fishes in the 10 Atlantic sites

	Bermuda	Cayman Islands	Paraíba	Três Ilhas Archipelago	Atol das Rocas	Fernando de Noronha	Trindade Island	St Paul's Rocks	Ascension Island	St Helena Island
Species	238	264	154	174	73	79	72	44	64	63
Families	37	39	39	39	28	31	29	20	30	29
Geographic Range (%)										
Pan Atlantic	18.9	12.9	20.4	20.9	26.4	30.4	30.0	38.6	35.9	35.7
Western Atlantic	44.5	32.7	53.9	58.1	37.5	34.2	35.6	16.0	4.6	3.3
Western and Central Atlantic	5.5	5.3	7.9	5.8	15.3	15.2	12.9	13.6	18.4	11.5
Western North Atlantic	29.8	48.7	—	—	—	—	—	—	—	—
Western South Atlantic	—	—	17.8	15.2	13.9	13.9	12.9	15.9	—	—
Central and Eastern Atlantic	—	—	—	—	—	—	—	—	4.6	8.2
Central Atlantic*	—	—	—	—	—	—	—	4.5	25.0	26.5
Endemic	1.3	0.4	—	—	6.9	6.3	8.6	11.4	11.5	14.8
Reproductive mode (%)										
Pelagic-spawning	68.7	50.2	60.4	65.0	63.9	65.7	65.0	66.5	76.2	71.4
Balistid-type	7.4	4.3	5.4	7.9	4.2	9.0	10.0	9.1	8.2	8.5
Demersal-spawning	23.9	45.5	34.2	27.1	31.9	25.3	25.0	24.4	15.6	20.1

*St Paul's Rocks, Ascension and St Helena.

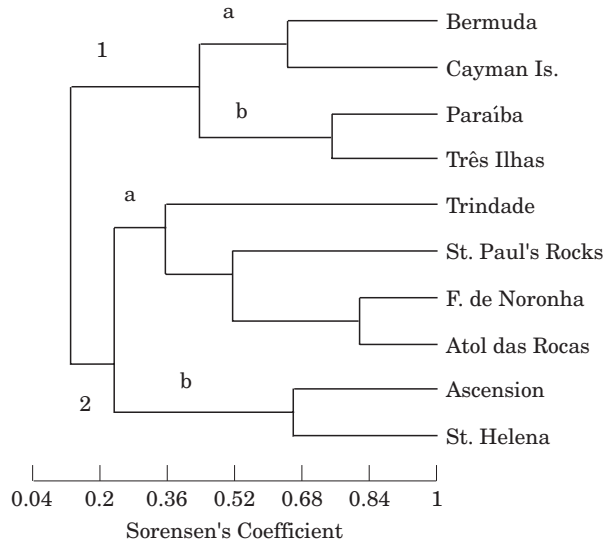


FIG. 2. Cluster analysis (complete linkage and Sorensen's coefficient) of the 10 Atlantic reef sites, based on the presence/absence of all species.

species richness ($\sim 35\%$ less) and a sizeable proportion of endemic components ($\sim 18\%$). In the South Atlantic oceanic islands the number of species and families decline impressively (see Table II) due to the extreme isolation, limited habitats and the relatively small area of shallow water surrounding them (Edwards & Glass, 1987). The level of endemism is high on oceanic islands, specially those on the mid-Atlantic Ridge (Table II and Fig. 3).

THE WESTERN NORTH ATLANTIC

The Cayman Islands are located in the Caribbean, the most speciose area in the Atlantic (Ekman, 1967; Briggs, 1974, 1995; Levinton, 1995). These islands were the richest site in this study (Table II) and presented a high similarity (Sorensen's coefficient=0.65) with Bermuda. The latter is a special case since, although located 1049 km SE of Cape Hatteras, U.S.A., ocean currents and continual influx of pelagic larvae from the Caribbean *via* the warm Gulf Stream have reduced the effectiveness of geographic isolation as a zoogeographic barrier and account for the relatively high diversity (at least three times higher than any South Atlantic oceanic island) (Smith-Vaniz *et al.*, 1999).

Robins (1971), Gilbert (1972) and Briggs (1974, 1995), divided the tropical western Atlantic fauna into three regions: the Caribbean (or continental), the West Indian (or insular) and the Brazilian. However, recent studies on the extent of genetic differentiation among reef fishes concluded that there was considerable gene flow throughout the northwestern Atlantic (Shulman & Bermingham, 1995; Bermingham *et al.*, 1997). This agrees with the low level of endemism found in the Bahamas (Smith-Vaniz & Böhlke, 1991), Cayman Islands (Burgess *et al.*, 1994) and Bermuda (Smith-Vaniz *et al.*, 1999). Therefore, the division of the tropical northwestern Atlantic into two faunal provinces was premature. The recognition of only two western Atlantic zoogeographic provinces for tropical

TABLE III. Number of species and families relative abundance (in parentheses) per reef-associated family in each site

Families	Bermuda	Cayman Islands	Paraíba	Três Ilhas Archipelago	Atol das Rocas	Fernando de Noronha	Trinidad Island	St Paul's Rocks	Ascension Island	St Helena Island
Acanthuridae	3 (1.3)	3 (1.1)	3 (2.0)	3 (1.7)	3 (4.2)*	3 (3.8)	2 (2.8)	—	2 (3.1)	1 (1.6)
Apogonidae	12 (5.0)*	13 (4.9)*	5 (3.3)	6 (3.4)	2 (2.8)	1 (1.3)	1 (1.4)	1 (2.2)	1 (1.6)	2 (3.1)
Balistidae	6 (2.6)	4 (1.5)	3 (1.0)	3 (1.7)	2 (2.8)	3 (3.8)	4 (5.6)*	2 (4.4)*	3 (4.7)*	2 (3.1)
Blenniidae	5 (2.1)	5 (1.9)	5 (3.3)	5 (2.9)	4 (5.6)*	3 (3.8)	3 (4.2)*	2 (4.4)*	3 (4.7)*	3 (4.7)*
Bothidae	4 (1.7)	3 (1.1)	1 (0.7)	1 (0.6)	2 (2.8)	1 (1.3)	1 (1.4)	—	3 (4.7)*	2 (3.1)
Chaenopsidae	1 (0.4)	13 (4.9)*	2 (1.3)	1 (0.6)	—	—	—	—	—	—
Chaetodontidae	5 (2.1)	5 (1.9)	2 (1.3)	3 (1.7)	1 (1.4)	2 (2.5)	2 (2.8)	2 (4.4)*	2 (3.1)	2 (3.1)
Diodontidae	3 (1.3)	2 (0.8)	3 (2.0)	3 (1.7)	1 (1.4)	2 (2.5)	2 (2.8)	1 (2.2)	3 (4.7)*	2 (3.1)
Gobiesocidae	1 (0.4)	6 (2.3)	3 (2.0)	3 (1.7)	1 (1.4)	—	1 (1.4)	—	—	—
Gobiidae	15 (6.4)*	37 (14.0)*	16 (10.5)*	9 (5.2)*	6 (8.3)*	6 (7.6)*	4 (5.6)*	1 (2.2)	2 (3.1)	2 (3.1)
Grammatidae	1 (0.4)	3 (1.1)	1 (0.7)	1 (0.6)	—	1 (1.3)	—	—	—	—
Haemulidae	7 (3.0)	10 (4.0)*	9 (5.9)*	8 (4.6)*	3 (4.2)*	4 (5.1)*	1 (1.4)	—	—	—
Holocentridae	8 (3.4)	9 (3.4)	3 (2.0)	3 (1.7)	2 (2.8)	2 (2.5)	2 (2.8)	2 (4.4)*	2 (3.1)	2 (3.1)
Labridae	16 (6.8)*	12 (4.5)*	11 (7.2)*	10 (5.7)*	5 (6.9)*	6 (7.6)*	7 (9.7)*	4 (8.9)*	4 (6.3)*	4 (6.3)*
Labrisomidae	3 (1.3)	20 (7.6)*	9 (5.9)*	9 (5.2)*	4 (5.6)*	3 (3.8)	2 (2.8)	2 (4.4)*	—	—
Lutjanidae	11 (4.7)*	13 (4.9)*	7 (4.6)*	5 (2.9)	1 (1.4)	2 (2.5)	1 (1.4)	1 (2.2)	1 (1.6)	—
Monacanthidae	8 (3.4)	5 (1.9)	4 (2.6)	7 (4.0)*	1 (1.4)	2 (2.5)	3 (4.2)*	2 (4.4)*	1 (1.6)	2 (3.1)
Mullidae	2 (0.9)	2 (0.8)	2 (1.3)	3 (1.7)	2 (2.8)	2 (2.5)	2 (2.8)	—	1 (1.6)	1 (1.6)
Muraenidae	14 (6.0)*	10 (4.0)*	8 (5.2)*	6 (3.4)	9 (12.5)*	8 (10.1)*	5 (6.9)*	8 (17.8)*	10 (15.6)*	6 (9.4)*
Opistognathidae	—	1 (0.4)	2 (1.3)	2 (1.1)	—	—	1 (1.4)	—	—	—
Ostraciidae	4 (1.7)	5 (1.9)	3 (2.0)	2 (1.1)	3 (4.2)*	2 (2.5)	1 (1.4)	—	1 (1.6)	1 (1.6)
Pomacanthidae	3 (1.3)	5 (1.9)	4 (2.6)	5 (2.9)	2 (2.8)	3 (3.8)	2 (2.8)	2 (4.4)*	2 (3.1)	—
Pomacentridae	10 (4.3)*	12 (4.5)*	7 (4.6)*	8 (4.6)*	4 (5.6)*	4 (5.1)*	5 (6.9)*	4 (8.9)*	3 (4.7)*	4 (6.3)*
Priacanthidae	4 (1.7)	2 (0.8)	1 (0.7)	2 (1.1)	1 (1.4)	1 (1.3)	1 (1.4)	—	1 (1.6)	3 (4.7)*
Scaridae	13 (5.5)*	11 (4.2)*	7 (4.6)*	9 (5.2)*	3 (4.2)*	3 (3.8)*	3 (4.2)*	4 (8.9)*	1 (1.6)	1 (1.6)
Scorpaenidae	5 (2.1)	6 (2.3)	2 (1.3)	4 (2.3)	—	—	1 (1.4)	1 (2.2)	3 (4.7)*	4 (6.3)*
Serranidae	33 (14.1)*	21 (8.0)*	12 (7.9)*	24 (13.8)*	5 (6.9)*	6 (7.6)*	10 (13.9)*	3 (6.7)*	5 (7.8)*	5 (7.8)*
Sparidae	4 (1.7)	2 (0.8)	3 (2.0)	8 (4.6)*	—	—	1 (1.4)	—	1 (1.6)	1 (1.6)
Syngnathidae	8 (3.4)	6 (2.3)	1 (0.7)	2 (1.1)	1 (1.4)	1 (1.3)	—	—	—	1 (1.6)
Tetraodontidae	3 (1.3)	2 (0.8)	1 (0.7)	3 (1.7)	—	2 (2.5)	—	—	1 (1.6)	2 (3.1)
Tripterygiidae	—	4 (1.5)	1 (0.7)	1 (0.6)	1 (1.4)	1 (1.3)	1 (1.4)	1 (2.2)	1 (1.6)	1 (1.6)
Other families†	25 (10.5)	18 (6.8)	13 (8.6)	19 (10.9)	4 (5.6)	8 (10.1)	4 (5.6)	3 (6.7)	9 (14.1)	13 (20.6)

*Families that constitute 4% or more of the total number of species.

†Antennariidae; Aulostomidae; Cirrihitidae; Congridae; Ehippididae; Fistulariidae; Kyphosidae; Pempheridae; and Synodontidae.

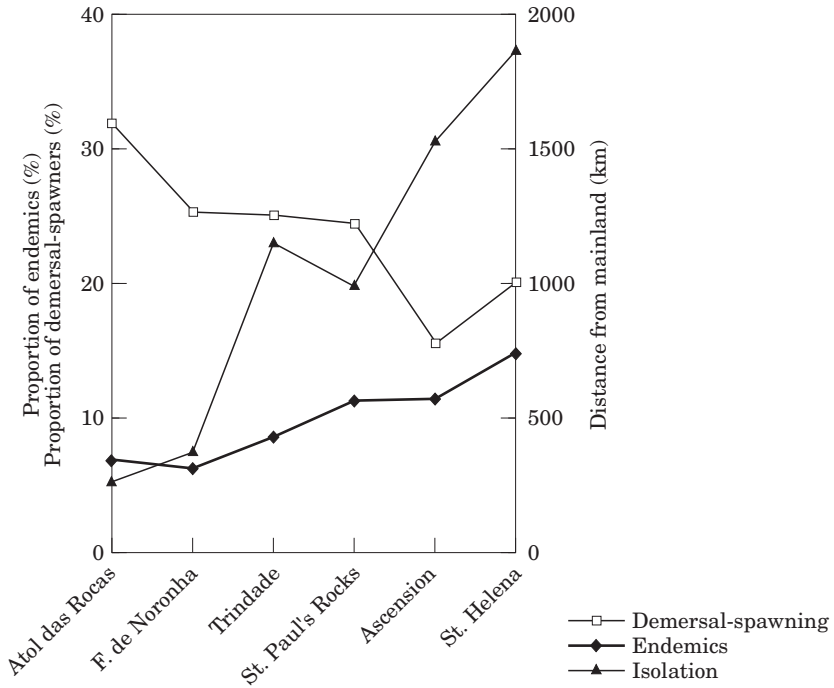


Fig. 3. Proportions of endemics and demersal-spawning species and distance from mainland (isolation) in tropical South Atlantic oceanic islands.

marine shore fishes (the Brazilian Province and an expanded West Indian or Caribbean Province), appears to be more appropriate (Burgess *et al.*, 1994; Smith-Vaniz *et al.*, 1999).

THE BRAZILIAN PROVINCE

The Brazilian Province occupies the area between the Orinoco and Amazon delta in the north (Briggs, 1974, 1995) and the State of Santa Catarina, the southernmost limit of rocky reef bottoms under influence of the warm Brazil Current (Evans *et al.*, 1985; Stramma, 1989). Although there is a considerable homogeneity in the composition of the reef fish fauna within the province (Paraíba and Três Ilhas showed a high similarity with Sorensen's coefficient = 0.76), some latitudinal trends exist possibly related to salinity, reef type, and water temperature (Moura *et al.*, 1999a; Floeter *et al.*, unpublished data).

The distinctiveness of the Province's biota is probably due to historic factors such as; sea level changes during glaciation periods (Leão *et al.*, 1988; Stanley, 1989; Briggs, 1995), and abrupt change in habitat when the Amazon river began to flow to the Atlantic in the Miocene—6.5 to 5.3 Mya (Nunan, 1992).

The northernmost Brazilian reefs, the Manuel Luis Reefs (Rocha, 1999; Moura *et al.*, 1999b), are isolated from the Caribbean by 2500 km of coastline subject to sedimentation and freshwater input from the Orinoco and Amazon Rivers drainage systems. This barrier is transgressed only by a small number of reef fish species that are found in association with sponge bottoms in offshore areas with oceanic salinity (Collette & Rutzler, 1977; Uyeno *et al.*, 1983). This

separation resulted in an impressive proportion of species being restricted to the western south Atlantic (Table II), especially shallow-water forms.

The Brazilian endemic reef fishes have been reported in the taxonomic literature as being closely similar to their western North Atlantic counterparts (allopatric replacements) (e.g. *Stegastes fuscus* (Cuvier, 1830) v. *S. dorsopunicans* (Poey, 1867); *Gramma brasiliensis* Sazima, Gasparini & Moura, 1998; v. *G. loreto* Poey, 1868; *Elacatinus figaro* Sazima, Moura & Rosa, 1997 v. *E. randalli* (Böhlke & Robins, 1968). This contrasts with the situation observed for the Brazilian fauna of scleractinians, which has a level of endemism of 44.4%, of which 23% of the species are considered relict forms only remotely related to recent western North Atlantic species (Leão, 1983). There is evidence suggesting an apparently Late Miocene separation of the coral faunas of Brazil and the western North Atlantic (Laborel, 1970; Leão, 1983). On the other hand, the endemic component of the Brazilian reef fish fauna seems to have a more recent origin, probably during the period of maximum terrigenous sediment deposition by the Amazon river initiated in the Late Pliocene (1.6 Ma) (Nunan, 1992).

BRAZILIAN OFFSHORE ISLANDS

There has been long standing interest in the relations among the offshore Brazilian islands from a biogeographical perspective. Atol das Rocas, Fernando de Noronha, Trindade and St Paul's Rocks harbour a considerable number of endemic species (Table II), which are locally very abundant (Lubbock & Edwards, 1981; Rosa & Moura, 1997; Gasparini & Floeter, unpublished). These islands share a sizeable portion of their reef fish fauna with the western Atlantic, including ~14% restricted to the western South Atlantic. They also lack species belonging to the eastern Atlantic fauna (Table II). Even St Paul's Rocks is more similar to the Brazilian offshore islands than to the other mid-Atlantic Ridge islands of Ascension and St Helena, as one should expect (Fig. 2). Therefore, as suggested by Edwards & Lubbock (1982b) and Briggs (1995), the Brazilian oceanic islands should be regarded as impoverished outposts of the Brazilian Province.

The two insular groups within the Fernando de Noronha Ridge, Atol das Rocas and Fernando de Noronha, have very similar shore fish faunas (Sorensen's coefficient=0.81), with five shared endemic species. They are the oceanic islands with the fish fauna most related to coastal areas [53% of their reef fish fauna shared with the western continental margin (Table II), possibly due to the relative proximity to the continent (Table I and Fig. 1)]. This island group is closer to St Paul's Rocks (Sorensen's coefficient=0.52), than Trindade (Sorensen's coefficient=0.37).

The endemism at Trindade Island (8.6%) and St Paul's Rocks (11.4%) is higher than at Rocas (6.9%) and Noronha (6.3%). Trindade lies 2300 km from Ascension Island; 2500 from St Paul's Rocks; 2500 from St Helena and 4200 from Africa (Fig. 1). In contrast to the mid-Atlantic Ridge islands, Trindade has a richer reef fish fauna and great affinity with the western Atlantic fauna (49%). This may be a consequence of the presence of the Vitória-Trindade Ridge. This chain includes six major, linearly arranged seamounts between the Brazilian coast and Trindade and it is under the influence of the warm southward flow of the Brazil Current. Distances of less than 250 km separate each seamount from

its closest neighbours. Summits of seamounts come close to the surface (15–150 m) and may function as ‘stepping stones’ for the fauna (Leal & Bouchet, 1991).

THE CENTRAL ATLANTIC

Lubbock (1980), Edwards & Glass (1987) and Edwards (1990) clarified the biogeographic affinities of Ascension and St Helena. These two mid-Atlantic Ridge islands are isolated from coastal ecosystems by more than 1500 km, therefore larvae and exogenous gene flow from such sources are very limited. They are similar to each other (Sorensen’s coefficient=0.67) with respect to the high numbers of endemic species (11.5%—AS and 14.8%—SH), the number of species that occur only in the mid-Atlantic (~25%) and the presence of eastern Atlantic species (4.9%—AS and 8.2%—SH). These data seem sufficient for the recognition of the Central Atlantic Province, following the suggestion of Edwards & Glass (1987) and Edwards (1990).

DISTRIBUTION PATTERNS WITHIN FAMILIES

The patterns of the distribution of species within families were analysed through six of the most characteristic reef-associated families (Thresher, 1991): pomacentrids, labrids, pomacanthids, serranids, scarids and gobiids. For each family, a cluster analysis based on the presence or absence of the species identified the same groups as previously described (see Fig. 2).

The pomacentrids are among the most speciose dwellers on tropical reefs (Allen, 1991) and together with the labrids rank among the ten richest families worldwide (Thresher, 1991). For the Pomacentridae the division among the Caribbean, the Brazilian coast and the oceanic islands probably reflects the high degree of endemism of this family at isolated localities. According to Wellington & Victor (1989), damselfish larvae appear to spend a relatively short period of time (two–five weeks) in the plankton. Population genetic studies suggested that damselfishes have more restricted dispersal (less gene flow) than other reef fishes, thus increasing the chance of endemism (Shulman, 1998). Five pomacentrids are endemic to the Brazilian coast and two species of *Stegastes* of the *fuscus-dorsopunicans-variabilis* complex (*sensu* Greenfield & Woods, 1974) are endemic to Brazilian offshore islands: *Stegastes rocasensis* (Emery, 1972), from Atol das Rocas and Fernando de Noronha and *S. sanctipauli* Lubbock & Edwards, 1981, from St Paul’s Rocks. The other species endemic to the South Atlantic oceanic islands, *Stegastes sanctahelenae* (Sauvage, 1879) from St Helena and *S. lubbocki* Allen & Smith, 1992 from Ascension, seem to belong to the *pictus-partitus* complex (D. R. Robertson, pers. com.). Interestingly, the purple reef fish *Chromis scotti* Emery, 1968 and the Caribbean cocoa damselfish *Stegastes* aff. *variabilis*, that do not occur along the eastern coast of South America, are common on the Manuel Luis Reefs (Rocha, 1999).

The family Serranidae is highly diverse in all the continental margin sites. Thirty-three species are present in the northwestern Atlantic sites, 24 occur in Três Ilhas Archipelago and three–nine species occurs at oceanic sites. *Cephalopholis fulva* (Linnaeus, 1758) is distributed along the Caribbean and the entire Brazilian Province, and is absent only in the St Helena–Ascension

Province. *Rypticus saponaceus* (Block & Schneider, 1801) is the only species present at all sites.

The pomacanthids are poorly represented in the Atlantic, with seven species on the continental margin and only four species at oceanic sites. This family has a curious zoogeographic pattern. *Holacanthus ciliaris* (Linnaeus, 1758) and *Pomacanthus paru* (Bloch, 1787) occur in the Caribbean, on the Brazilian coast, Atol das Rocas, Fernando de Noronha and St Paul's Rocks. Surprisingly, on Trindade Island both species are apparently replaced by *Holacanthus tricolor* (Bloch, 1795) and *Centropyge aurantonota* Burgess, 1974. Trindade is the only South Atlantic offshore island where the two latter species are present. Pomacanthids are absent from St Helena.

On the Brazilian coast almost all genera of Caribbean labrids were present, and the two regions were closely linked in the cluster analysis. *Bodianus insularis* Gomon & Lubbock, 1980 occurs only at the three mid-Atlantic Ridge islands. *Thalassoma noronhanum* (Boulenger, 1890), an abundant species endemic to the Brazilian Province, is present in all the Brazilian offshore and coastal sites.

Scaridae are well represented on the continental margin (14 species). All six species that occur on the oceanic islands belong to the genus *Sparisoma*. In the South Atlantic, the genus *Scarus* is restricted to the continental margin sites. This is interesting because this genus occurs at oceanic sites in the Indo-Pacific and all Caribbean species of *Scarus* are present at Bermuda (Smith-Vaniz *et al.*, 1999). The clustering for the scarids clearly separated the Brazilian offshore islands from Ascension and St Helena islands, where the relative abundances of this family were low (Table III).

The family Gobiidae is well represented in the tropical Atlantic (16 genera), and is present in the top three species-rich families in all three western Atlantic coastal sites and Bermuda. Only eight species (from six genera) are known from the Brazilian offshore islands, five of them endemic to the Brazilian Province: two *Lythrypnus* sp.n., *Priolepis dawsoni* Greenfield, 1989, *Elacatinus figaro* and *Elacatinus* sp.n. from Trindade (Gasparini & Floeter, unpublished).

Within all the 40 reef-associated families, only seven species—*Gymnothorax miliaris* (Kaup, 1856), *Holocentrus ascensionis* (Osbeck, 1765), *Myripristis jacobus* Cuvier, 1829, *Rypticus saponaceus*, *Kyphosus sectatrix* (Linnaeus, 1758), *Abudefduf saxatilis* (Linnaeus, 1758) and *Chromis multilineata* (Guichenot, 1855)—are present in all 10 Atlantic sites.

REPRODUCTIVE MODES AND ENDEMISM

The geographical affiliations among reef fish assemblages may reflect the distribution of the principal spawning modes (Thresher, 1991). Short planktonic durations and inshore development of normal demersal-spawners may result in relatively short average distances and more restricted distributions (Victor, 1991). Among the 32 species endemic to the tropical oceanic islands, half belong to demersal-spawning families (Pomacentridae; Tripterygiidae; Labrisomidae; Blenniidae and Gobiidae). Among the 46 species restricted to the Brazilian Province, 35 (74%) are benthic demersal-spawning species.

Oceanic islands have a consistently smaller proportion of demersal-spawning fishes than the continental margin (Table II). In the Caribbean the demersal-spawners Gobiidae, Chaenopsidae, Apogonidae and Labrisomidae are very rich

families. However these families are poorly represented or absent from the oceanic sites (Table III). The proportion of species in normal demersal-spawning families decreases from the Caribbean (45.5%) to the Brazilian coast (~30%), and with the distance from mainland—Atol das Rocas (30.1%), Fernando de Noronha, Trindade (24.3%) and St Paul's Rocks (22.7%). The lowest proportions were observed on Ascension (14.8%) and St Helena (19.6%) (Table II and Fig. 3). A notable exception is the goldspot goby *Gnatholepis thompsoni* Jordan, 1902 a demersal-spawner that has a mean larval life of 81.5 days (Bermingham *et al.*, 1997), and which is present throughout the Atlantic oceanic islands, including Ascension and St Helena.

Not all the species-rich families along continental margins are demersal-spawners. However most of those that produce pelagic eggs develop inshore (Leis, 1986). These families either have relatively short planktonic phase (lutjanids) or include large numbers of species with short development durations (serranids, chaetodontids) (Brothers & Thresher, 1985). The Lutjanidae, that are well represented in the western Atlantic coastal sites, have only one species at each oceanic site.

The long planktonic duration and offshore development of many pelagic and balistid-like species suggest a more extensive dispersal (Thresher & Brothers, 1985; Thresher *et al.*, 1989; Thresher, 1991). The number of pelagic plus balistid-type families in the ten most species-rich families is greater at oceanic sites (7–9 families), than on the Continental Margin (5–6 families) (Table III). For Labridae, only three genera *Bodianus*, *Thalassoma* and *Xyrichtys* occur consistently in the South Atlantic oceanic islands. All have long planktonic larval durations, between 40 to 80 days (Victor, 1986).

CONCLUSIONS

The geographic range of tropical reef fish species suggests the recognition of only two western Atlantic zoogeographic provinces: (1) the northwestern Atlantic or expanded Caribbean province (including the Atlantic coast from Florida to Cape Hatteras, North Carolina) and extending northward to Bermuda; and (2) the Brazilian province, which is separated from the Caribbean by the Amazon freshwater barrier and presents a high level of endemism (~18%). The Brazilian offshore islands share a sizeable portion of their reef fishes with the western Atlantic (including ~14% shared only with the Brazilian coast), and could be regarded as impoverished outposts of this fauna. Ascension and St Helena have *c.* 25% of their faunas not found outside the mid-Atlantic and should be considered as forming a Central Atlantic province.

The great majority (74%) of the Brazilian Province endemic species, as well as half of the species endemic to the tropical oceanic islands, are benthic demersal-spawning species that spend a relatively short period of time in the plankton and consequently have a restricted dispersal. The level of endemism and the proportion of demersal-spawning species of the South Atlantic oceanic islands varies according to geographic isolation.

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APPENDIX. List of the ten most species-rich families at each site

Site	Rank in species richness									
	1	2	3	4	5	6	7	8	9	10
<i>Western North Atlantic</i>										
Bermuda	Se	La	Go	Mu	Sc	Ap	Lu	Po	Ho	Mo; Sy
Cayman Islands	Go	Se	Lb	Ap	Cp	Lu	La	Po	Sc	Ha; Mu
<i>Brazilian coast</i>										
Paraíba	Go	Se	La	Ha	Lb	Mu	Lu	Po	Sc	Ap; Bl
Três Ilhas	Se	La	Go	Lb	Sc	Ha	Po	Mo	Ap	Mu; Bl
<i>Brazilian oceanic islands</i>										
Atol das Rocas	Mu	Go	La	Se	Bl	Lb	Po	Ac	Ha	Os; Sc
F. de Noronha	Mu	Go	La	Se	Ha	Po	Ac	Ba	Bl	Lb; Pa; Sc
St Paul's Rocks	Mu	La	Po	Sc	Se	Ba	Bl	Ch	Ho	La; Mo; Pa
Trindade Island	Se	La	Mu	Po	Ba	Go	Bl	Mo	Sc	Lb
<i>Central Atlantic</i>										
Ascension Island	Mu	Se	La	Ba	Bl	Bo	D	Po	Sp	Ac*
St Helena	Mu	Se	La	Po	Sp	An	Bl	Ba	Pr	Ap†

*Plus Ch; Go; Ho; Pa. †Plus Ba; Bo; Ch; D; Go; Ho; Mo.

Key for families: Ac=Acanthuridae; An=Antemmaridae; Ap=Apogonidae; Ba=Balistidae; Bl=Blenniidae; Bo=Bothidae; Cp=Chaenopsidae; Ch=Chaetodontidae; D=Diodontidae; Go=Gobiidae; Ha=Haemulidae; Ho=Holocentridae; La=Labridae; Lb=Labrisomidae; Lu=Lutjanidae; Mo=Monacanthidae; Mu=Muraenidae; Os=Ostraciidae; Pa=Pomacanthidae; Po=Pomacentridae; Pr=Priacanthidae; Sc=Scaridae; Se=Serranidae; Sp=Scorpaenidae; Sy=Syngnathidae.