ECOLOGY AND ZOOGEOGRAPHY OF DEEP-REEF FISHES IN NORTHEASTERN BRAZIL

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ABSTRACT

With the advent of SCUBA, the reef fish fauna has been substantially studied around the world, but the great majority of in situ studies have focused exclusively on a limited portion of this fauna, to depths of < 30 m. The present study represents the first SCUBA- based survey of the deep reef fishes off the Brazilian coast between 35 and 70 m. A species list was compiled based on visual observations, collections, video recording, and fishes obtained from commercial fishing boats. A total of 158 fish species belonging to 49 families was recorded. Thirty-two species were formally recorded for the first time from the study area, four of which [*Apogon robbyi* Gilbert, 1997; *Coryphopterus eidolon* Böhlke & Robins, 1960; *Psilotris batrachodes* Böhlke, 1963; and *Xanthichthys ringens* (Linnaeus, 1758)] represent new records for the western South Atlantic. Fifty-seven species had their depth range extended to depths > 40 m. The most species rich families were Carangidae (14 species), Gobiidae (12), Lutjanidae (11), Labridae (11), Serranidae (10), Haemulidae (8), and Scaridae (7). The presence of several species previously considered to have disjunct, or anti-equatorial distribution, indicates that the deep reefs may function as a faunal corridor between habitats in southeastern Brazil and the Caribbean.

With the advent of SCUBA, the coral reef ichthyofauna has been substantially studied around the world (see review by Sale, 1991). Even though ichthyologists have taken advantage of SCUBA technology for exploring and collecting specimens from coral reef habitats, the great majority of in situ studies have dealt exclusively with a limited portion of the reef fish fauna, to depths of < 30 m (Thresher and Colin, 1986; Itzikowitz et al., 1991; Pyle, 2000). Direct observations of deep reef fishes using conventional SCUBA are sparse (e.g., Lukens, 1981; Rocha et al., 1998) and limited both by the working depth (down to about 60 m) and the restricted bottom time (because of the limited quantities of breathing gas carried and decompression problems) (Pyle, 1996a, 1998, 2000).

The difficulties of working with direct observations on deep reefs have been overcome, in part, through the use of small research submersibles (e.g., Colin, 1974, 1976; Colin et al., 1986; Thresher and Colin, 1986; Pearcy et al., 1989; Itzikowitz et al., 1991; Stein et al., 1992). However, submersibles are extremely expensive to construct and operate, and require extensive logistical support. Moreover, submersibles cannot effectively approach organisms that inhabit cracks, crevices, caves, or overhanging ledges, being greatly limited in their ability to collect specimens of cryptic species, and thus are only adequate for broad observations of conspicuous organisms (Pyle, 2000). Only recently have the deep reef environments between 60 and 150 m (the "twilight zone") begun to be examined through diving, using an "open" and subsequently "closed" circuit mixed-gas breathing apparatus (see Pyle, 1998 for a review). The closed-circuit underwater apparatus, or "rebreather", is now considered the ideal tool for twilight zone exploration, providing as much as 10–12 hrs of underwater autonomy (Pyle, 1996a, 2000), however, rebreathers are extremely expensive, and their use requires extensive training.

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The Brazilian reef fish fauna has remained poorly known for a long time. Only after the mid-1990s, with the growing use of SCUBA by Brazilian ichthyologists, has a significant increase in sampling effort occurred (Moura, 1995; Rocha et al., 1998; Floeter and Gasparini, 2000; Floeter et al., 2001; Rocha and Rosa, 2001; Feitoza et al., 2003). Nevertheless, the Brazilian reef fish community beyond 30 m remains broadly unknown, with the exception of a few commercial species briefly treated by Rocha et al. (1998), who mentioned the necessity of detailed studies on the deep reef fish fauna. Consequently, there is a realm of unexplored reef habitat at depths between about 40 and 150 m. It is expected that this transition zone, from the highly complex and diverse coral reef environments that are fuelled by sunlight, to the relatively barren and perpetually dark abyssal depths where no photosynthesis can occur (Pyle, 1996b), hides a greater number of endemic species than the shallower or deeper regions (Pyle, 1998).

Deep reefs off the eastern coast of northeast Brazil (or the "hump" of Brazil) are important areas for local fisheries and are being increasingly fished. A 7-yr unpublished study on the Brazilian northeast coast carried out by the authors and other Brazilian ichthyologists has revealed that the deep reefs are one of the last refuges for large commercially exploited reef fishes, such as snappers (Lutjanidae) and groupers (Serranidae), where even globally threatened species such as *Lutjanus analis, Lutjanus cyanopterus*, and *Epinephelus itajara* are captured; see Hilton-Taylor, 2000. The present study is the first attempt to survey the deep reef ichthyofauna off the Brazilian coast between 35 and 70 m utilizing SCUBA. Despite the limitations of conventional SCUBA at depths beyond 30 m, it was possible to provide a baseline assessment of the deep reef ichthyofauna, including cryptic species, by describing and comparing its fish community with those of other western Atlantic reef sites.

Material and Methods

Study Area.—The study area is located off the eastern coast of northeast Brazil between the States of Rio Grande do Norte (4°59′S) and Pernambuco (7°51′S) (Fig. 1). This is a transition zone where the South Equatorial Current branches to become the northwestward flowing North Brazil Current and the southward flowing Brazil Current (Stramma et al., 1990; Silveira et al., 1994; Leão and Dominguez, 2000). The continental shelf in this area is very narrow (from 22 to 48 km wide according to the hydrographic charts) and shallow, reaching the escarpment between depths of 40 and 80 m (Chaves et al., 1979; França, 1979; Knoppers et al., 1999). Deep reef outcrops occur along most of the outer shelf-edge, almost always coinciding with the beginning of the shelf-break zone (see Kempf et al., 1967; Lana et al., 1996).

Fourteen deep reefs were investigated, six of which are over-shelf deep reefs and eight shelf-edge deep reefs. The water temperature ranged from 23 to 29.5 °C and visibility from 20 to 50 m. Because there are no systematic surveys of the corals, sponges, or algae for the study sites, superficial habitat descriptions are given here to provide only a general idea of the deep reef habitats of the area.

The two northernmost over-shelf deep reefs surveyed are located about 12 km from the outer shelf-edge ranging from 36 to 39 m in depth (Fig. 1B,C). These reefs consist of elongated sandstone outcrops reaching about 3 m from the sandy bottom, forming crevices and small caves. Living corals were present [*Montastrea cavernosa* (Linnaeus, 1767), *Siderastrea stellata* Verrill, 1868, *Meandrina braziliensis* Milne Edwards and Haime, 1848] along with tubular (*Aplysina* spp.), massive, and encrusting sponges. Algae (mainly brown and green) were abundant. The four southernmost over-shelf deep reefs are located at about 4 km from the outer shelf-edge ranging from 35 to 41 m depth (Fig. 1D,E,I,K). They consist largely of a flat

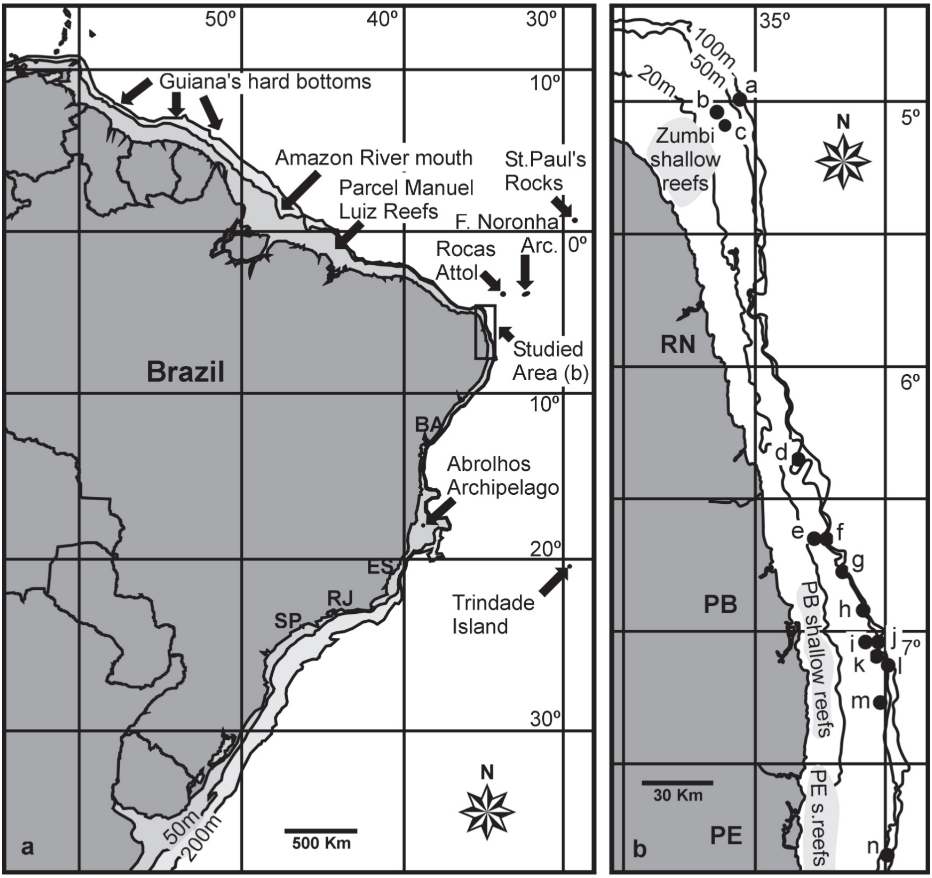

Figure 1. A) Map showing the location of the study area and other South Atlantic sites; B) Dive sites along the study area (letters a–n) and the general location of the main shallow reefs. State abbreviations: PE = Pernambuco; PB = Paraíba; RN = Rio Grande do Norte; BA = Bahia; ES = Espírito Santo; RJ = Rio de Janeiro; SP = São Paulo.

calcareous bottom with gentle inclination and small crevices, surrounded by patches of sand and deposits of algal nodules. Algae (mainly brown and green) and sponges (mainly tubular *Aplysina* spp.) covered most of bottom, with sparse coral growth (*Stephanocoenia michelini* Milne Edwards and Haime, 1848, *Porites branneri* Rathbun, 1887, *M. braziliensis, S. stellata*). Sharp thermoclines were not encountered at the six over-shelf sites.

The eight shelf-edge deep reefs surveyed are distributed along the outer-shelf (Fig. 1A,F–H,J and L–N), at depths of 45–70 m. Two distinct zones were observed at the shelf-edge deep reefs: (1) an upper flat zone, with gentle inclination; and (2) a deeper steep zone, composed of carbonatic rock outcrops (Fig. 2). The upper flat zone was similar to the four southernmost over-shelf reefs described above. The deeper steep zone was located at the beginning of the escarpment (shelf-break) and was marked by an abrupt change on the sea floor relief, from a gently sloping bottom of the upper flat zone to a steeply sloping nearly vertical face, with large rocks and caves. Algae and sponges (tubular, candle, and massive forms) covered most rocky surfaces. Living corals were common along rock ledges, with small colonies of *Agaricia fragilis* Dana, 1846, *P. branneri*, and *S. stellata*, sparse growth of *M. braziliensis* and *Scolymia wellsii* Laborel, 1967, and a few small heads of *M. cavernosa*. Long antipatharians (black corals) were also attached to the rocks. The reef at this depth is very similar to spur and grove formations of outer reefs in Caribbean islands, and probably consists of a drowned coral reef

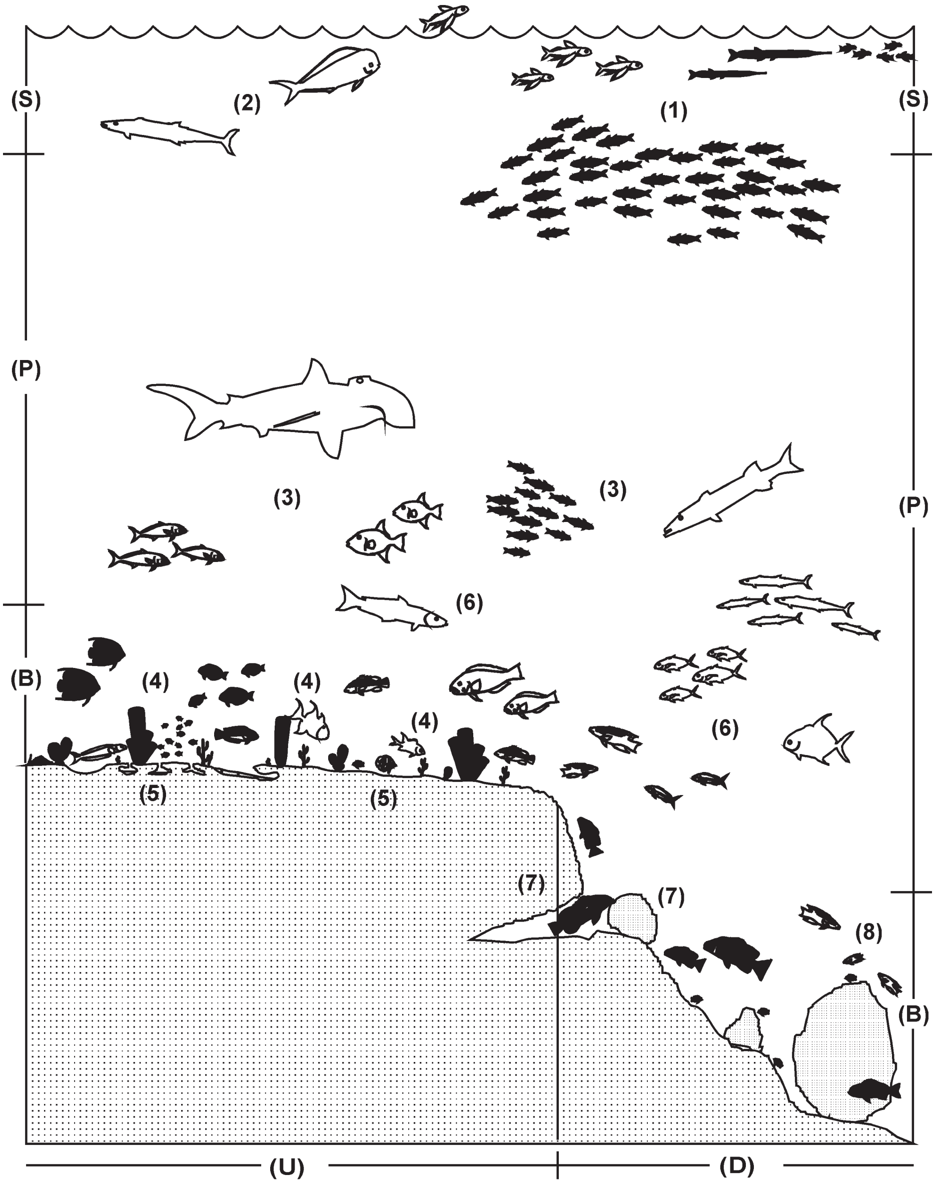

Figure 2. Spatial distribution of the shelf-edge deep reef fishes in water column: Note that figure is not drawn to scale. (U) upper flat zone; (D) deeper steep zone; (S) Surface dwellers; (P) Pelagic species; (B) Bottom dwellers. (1) Clupeidae, Exocoetidae, Belonidae; (2) Scombridae, Coryphaenidae; (3) Carangidae, Sphyrnidae, Balistidae (*Canthidermis*), Sphyraenidae, Scombridae; (4) Pomacanthidae, Scaridae, Holocentridae, Labridae, Lutjanidae, Serranidae, (*Cephalopholis*), Balistidae, Acanthuridae, Chaetodontidae, Haemulidae, Malacanthidae; (5) Gobiidae, Congridae, Pomacentridae, Apogonidae, Ophidiidae, Pomacanthidae (*Centropyge*), Opistognathidae, Microdesmidae, Muraenidae; (6) Scombridae, Carangidae, Rachycentridae, Serranidae (*Paranthias*), Labridae (*Bodianus*), Lutjanidae (*Ocyurus*); (7) Lutjanidae; Serranidae; Pomacentridae; Haemulidae; (8) Labridae, Lutjanidae, Pomacentridae, Malacanthidae, Acanthuridae.

that was built during lower sea levels. A sharp thermocline was usually encountered at about 50 m, where the water temperature changed abruptly from 28 to 29 °C to about 23–24 °C, decreasing gradually below that depth.

Data Collection and Species List.—This study was conducted between February 1998 and February 2003. Forty-eight SCUBA dives between 35 and 70 m were undertaken, and provided about 38 hrs of underwater activities, including collections, observations, and video recordings. Rebreathers are considered the ideal tool for deep reef exploration, providing as much as 10–12 hrs of underwater autonomy (Pyle, 1996a, 2000), however, due to our limited budget, only open-circuit SCUBA equipment was used in this study. Collecting gear included spear guns, dip nets, and fish anesthetics. Material obtained from commercial fishing boats was also examined. Specimens were deposited at the fish collections of the Universidade Federal da Paraíba, João Pessoa, PB, Brazil (UFPB) and University of Florida (UF) (see appendix for information on voucher specimens).

The species list was compiled based on visual observations, collections, and video recording. All species are listed in phylogenetic order of families following Nelson (1994), with species alphabetically organized within families. We have also included the following information for each species: (1) occurrence–presence along northeastern Brazilian reefs, where: 1 = shallow reefs, 2 = over-shelf deep reefs, 3 = shelf-edge deep reefs; (2) population status–a rough indication of relative abundance based on our observations; i.e., a diver's likelihood of observing a species on any given dive (adapted from Humann and DeLoach, 2002), where: AB = abundant (at least several sightings of many individuals —at least 50— can be expected on nearly every dive), VC = very common (at least several sightings can be expected on nearly every dive, but not necessarily many individuals), CM = common (sightings are frequent, but not necessarily expected on every dive), OC = occasional (sightings are not unusual, but are not expected on a regular basis), UN = uncommon (sightings are unusual), and RA = rare (sightings are exceptional), combinations can be used to better express the status of a given species among different sites. These abbreviations are used in Table 1 and through the text; (3) trophic category–determined from direct behavioral observations and available literature (Randall, 1967; 1996), where: TH = territorial herbivores, NH = non-territorial herbivores, C = carnivores, PL = planktivores, and O = omnivores; (4) habitat–where the species has usually been observed, with: B = bottom-dwellers (species seen in association with the substrate or moving up to 3–5 m above the bottom), P = pelagic (epipelagic forms that moved throughout water column), and S = surface-dwellers (species observed only near surface); (5) depth range–depth range where the species is commonly found over the deep reefs; (6) geographic range in the western Atlantic–where: WA = throughout western Atlantic, NWA = northwestern Atlantic; BP = Brazilian Province, NEB = northeastern Brazilian coast.

Zoogeographical Affinities.—Cluster analysis using presence or absence of species was used to investigate zoogeographic affinities between the deep reefs off the hump of Brazil and other western Atlantic sites. A dendrogram was constructed using the program MVSP (Multi-Variate Statistical Package) version 3.1. Sorensen's coefficient was used as a measure of similarity and farthest neighbor as clustering method (see Ludwig and Reynolds, 1988; Magurram, 1996). Data were based on species checklists available from the literature, and complemented by unpublished species checklists kindly provided by ichthyologists. Sources as follows: Florida, Caribbean, Bahamas, and Bermuda (Böhlke and Chaplin, 1993; Humann and DeLoach, 2002), the Guianas and northern Brazilian coasts (Lowe-McConnell, 1962; Collette and Rützler, 1977; Uyeno et al., 1983; Guéguen, 2000), Parcel de Manuel Luiz (Rocha and Rosa, 2001), northeastern Brazilian coast (Ferreira et al., 1995; Rosa et al., 1997; Rocha et al., 1998; Feitoza, 2001), Rocas Atoll (Rosa and Moura, 1997, complemented by an unpublished list compiled by L. A. Rocha and B. M. Feitoza, during two expeditions in May 1995 and March 2000), Fernando de Noronha Archipelago (an unpublished list compiled by B. M. Feitoza during 113 SCUBA dives in October 2002), Saint Paul's Rocks (Feitoza et al., 2003), Abrolhos reefs (an unpublished list compiled by C. L. S. Sampaio and B. M. Feitoza, during 37 SCUBA dives in March 2002), southeastern Brazilian coast (Figueiredo and Menezes, 1978, 1980, 2000; Menezes and Figueiredo, 1980, 1985; Moura et al., 1999) and Trindade Island (Gasparini and Floeter, 2001). In order to minimize sampling error, the analysis was restricted to 40 reef-associated low-mobility teleost fish families, including 129 genera and 484 species (see appendix for details). Epipelagic forms regularly found over reefs (such as clupeids, belonids, exocoetids, hemiramphids, coryphaenids, carangids, sphyraenids, scombrids, sharks, and pelagic rays) were not included.

Results and Discussion

In total, 158 fish species belonging to 49 families were recorded along the 14 deep reefs surveyed. Thirty-two species were formally recorded for the first time from the study area, four of which (*Apogon robbyi*, *Coryphopterus eidolon*, *Psilotris batrachodes*, and *Xantichthys ringens*) represent new records for the western South Atlantic. *Chromis jubauna*, a species previously known only from southeastern Brazil, was collected at the deep reefs at about 6°S, a distributional range extension of more than 1800 km to the north. Fifty-seven species had their depth range extended to depths > 40 m (Table 1).

Four species could not be identified to species: *Ophidion* sp., *Scorpaena* sp., *Psilotris* sp., and *Diodon* sp. The former two appear to be undescribed species and are being investigated by the authors; *Psilotris* sp. seems to be the same species collected by Ramos (1994) off Paraíba and Pernambuco coasts and still remains unidentified to the specific level; juveniles of *Diodon* sp. were seen but not collected and identification to the specific level was not possible. *Opistognathus* aff. *aurifrons* and *Malacoctenus* aff. *triangulatus* are undescribed species currently being studied by W. F. Smith-Vaniz (U.S. Geological Survey, Florida) and R. Z. P. Guimaraes (National Museum, Rio de Janeiro), respectively.

The most species rich family was Carangidae (14 species), followed by Gobiidae (12), Lutjanidae (11), Labridae (11), Serranidae (10), Haemulidae (8), and Scaridae (7). Fifty-six species (35.4%) were occasional, 34 (21.5%) common, 29 (18.4%) uncommon, 21 (13.3%) very common, 12 (7.6%) abundant, and six (3.8%) rare. A notable difference in fish abundance and community composition between the over-shelf and shelf-edge deep reefs was observed. Twelve species were visually more abundant at the two northernmost over-shelf deep reefs off Rio Grande do Norte coast: *Ginglymostoma cirratum* (VC), *Dasyatis americana* (AB), *Rachycentron canadum* (AB), *Carangoides bartholomaei* (AB), *Caranx latus* (AB), *Lutjanus apodus* (AB), *Anisotremus virginicus* (VC), *Kyphosus sectatrix* (AB), *Chromis multilineata* (VC), *Halichoeres bivittatus* (VC), *Xyrichtys martinicensis* (VC), *Scarus trispinosus* (CM), and *Chaetodipterus faber* (AB). Differences in fish composition and occurrence of fish along the shallow and deep reefs of the northeastern Brazilian coast are shown on Table 1.

Trophic Structure.—Despite the limited statistical power of our abundance estimates, it was possible to observe a great reduction in the number and density of herbivores at the deep reefs, when compared to shallow reefs at the same area. At the deep reefs, about two thirds (64.6%) of the species were carnivores, 16.5% planktivores, 11.4% omnivores, 6.3% non-territorial herbivores, and 1.3% territorial herbivores (Table 1). On the other hand, herbivores are the dominating trophic category in shallow reefs (Rocha et al., 1998; Rocha and Rosa, 2001). However, five herbivore species were still common or very common at the deep reefs, especially those shallower

Table 1. List of fish species on deep reefs off the hump of Brazil, showing the occurrence along northeastern Brazilian reefs, where: 1 = shallow reefs, 2 = over-shelf deep reefs, 3 = shelf-edge deep reefs; the population status, where: AB = abundant, VC = very common, CM = common, OC = occasional, UN = uncommon, and RA = rare; the trophic category, where: TH = territorial herbivores, NH = non-territorial herbivores, C = carnivores, PL = planktivores, and O = omnivores; the habitat where the species has usually been observed, with: B = bottom-dwellers, P = pelagic, and S = surface-dwellers; the depth range; and the geographic range in the western Atlantic, where: WA = throughout western Atlantic, NWA = northwestern Atlantic; BP = Brazilian Province, NEB = northeastern Brazilian coast.

Fish family/species	Occurrence	Pop. status	Trophic category	Habitat	Depth range (m)	Geographic range
GINGLYMOSTOMATIDAE						
Ginglymostoma cirratum (Bonnaterre, 1788)	1, 2, 3	OC	C	B	35–50	WA
CARCHARHINIDAE						
Rhizoprionodon porosus (Poey, 1861)	1, 2, 3	UN	C	P	40–50	WA
SPHYRNIDAE						
Sphyrna lewini (Griffith & Smith, 1834)	1, 2, 3	UN	C	P	10–70	WA
DASYATIDAE						
Dasyatis americana Hildebrand & Schroeder, 1928	1, 2, 3	OC	C	B	35–54	WA
Dasyatis marianae Gomes, Rosa & Gadig, 2000	1, 2, 3	OC	C	B	35–57	BP
MURAENIDAE						
Gymnothorax funebris Ranzani, 1840	1, 2, 3	OC	C	B	35–70	WA
Gymnothorax moringa (Cuvier, 1829)	1, 2, 3	OC	C	B	35–57	WA
Gymnothorax vicinus (Castelnau, 1855)	1, 2, 3	OC	C	B	35–47	WA
CONGRIDAE						
Heteroconger camelopardalis (Lubbock, 1980)	1, 2	AB	PL	B	35–40	NWA+NEB
Heteroconger cf. *longissimus* Günther, 1870	3	AB	PL	B	50–60	WA
CLUPEIDAE						
Opisthonema oglinum (LeSueur, 1817)	1, 2, 3	AB	PL	P	0–60	WA
OPHIDIIDAE						
Ophidion sp.	3	UN	C	B	54–57	NEB
BELONIDAE						
Ablennes hians (Valenciennes, 1846)	1, 2, 3	CM	C	S	0–3	WA
Strongylura timucu (Walbaum, 1792)	1, 2, 3	OC	C	S	0–3	WA
Tylosurus crocodilus (Peron & Lesueur, 1821)	1, 2, 3	UN	C	S	0–3	WA
SYNODONTIDAE						
Synodus synodus (Linnaeus, 1758)	1, 2, 3	OC	C	B	55–57	WA
EXOCOETIDAE						
Hirundichthys affinis (Günther, 1866)	1, 2, 3	OC	PL	S	0–3	WA
Cheilopogon cyanopterus (Valenciennes, 1847)	2, 3	CM	PL	S	0–5	WA
Cheilopogon melanurus (Valenciennes, 1847)	2, 3	CM	PL	S	0–5	WA
HEMIRAMPHIDAE						
Hemiramphus balao Lesueur, 1821	1, 2, 3	UN	PL	S	0–1	WA
HOLOCENTRIDAE						
Holocentrus ascensionis (Osbeck, 1765)	1, 2, 3	VC	C	B	35–70	WA
Myripristis jacobus Cuvier, 1829	1, 2, 3	CM	PL	B	35–54	WA
DACTYLOPTERIDAE						
Dactylopterus volitans (Linnaeus, 1758)	1, 2, 3	CM	PL	S	0–1	WA
SCORPAENIDAE						
Scorpaena sp.	2, 3	RA	C	B	47–54	NEB
Scorpaenodes caribbaeus Meek & Hildebrand, 1928	1, 2	UN	C	B	36–40	NWA+NEB
Scorpaenodes tredecimspinosus (Metzelaar, 1919)	3	OC	C	B	53–54	WA

Table 1. Continued.

Fish family/species	Occurrence	Pop. status	Trophic category	Habitat	Depth range (m)	Geographic range
SERRANIDAE						
Cephalopholis fulva (Linnaeus, 1758)	1, 2, 3	VC	C	B	35–70	WA
Epinephelus adscensionis (Osbeck, 1765)		CM	C	B	35–40	WA
Epinephelus itajara (Lichtenstein, 1822)	1, 2, 3	RA	C	B	35–60	WA
Liopropoma carmabi (Randall, 1963)	3	UN	C	B	53–54	WA
Mycteroperca bonaci (Poey, 1860)	1, 2, 3	VC	C	B	35–70	WA
Mycteroperca interstitialis (Poey, 1860)	1, 2, 3	UN	C	B	35–40	WA
Paranthias furcifer (Valenciennes, 1828)	1, 2, 3	AB	PL	B	35–70	WA
Rypticus saponaceus (Bloch & Schneider, 1801)	1, 2, 3	OC	C	B	35–40	WA
Serranus annularis (Evermann & Marsh, 1900)	2, 3	OC	C	B	51–57	NWA+NEB
Serranus baldwini (Evermann & Marsh, 1899)	1, 2, 3	CM	C	B	35–40	WA
OPISTOGNATHIDAE						
Opistognathus aff. *aurifrons* Jordan & Thompson, 1905	1, 2, 3	AB	PL	B	35–54	BP
APOGONIDAE						
Apogon americanus Castelnau, 1855	1, 2	CM	PL	B	35–40	BP
Apogon pseudomaculatus Longley, 1932	1, 2, 3	CM	PL	B	47–54	WA
Apogon quadrisquamatus Longley, 1934	2, 3	OC	PL	B	35–54	WA
Apogon robbyi Gilbert, 1997	2, 3	OC	PL	B	53–54	NWA+NEB
Astrapogon puncticulatus (Poey, 1867)	1, 2, 3	OC	PL	B	35–57	WA
MALACANTHIDAE						
Malacanthus plumieri (Bloch, 1786)	1, 2, 3	VC	C	B	35–70	WA
ECHENEIDAE						
Echeneis naucrates Linnaeus, 1758	1, 2, 3	OC	C	P	0–40	WA
RACHYCENTRIDAE						
Rachycentron canadum (Linnaeus, 1766)	1, 2, 3	CM	C	P	35–70	WA
CORYPHAENIDAE						
Coryphaena hippurus Linnaeus, 1758	1, 2, 3	OC	C	P	0–20	WA
CARANGIDAE						
Carangoides bartholomaei (Cuvier, 1833)	1, 2, 3	VC	C	P	5–70	WA
Carangoides ruber (Bloch, 1793)	1, 2, 3	UN	C	P	5–40	WA
Caranx crysos (Mitchill, 1815)	1, 2, 3	CM	C	P	5–57	WA
Caranx latus Agassiz, 1829	1, 2, 3	OC	C	P	5–57	WA
Caranx lugubris Poey, 1860	1, 2, 3	CM	C	P	5–70	WA
Decapterus macarellus (Cuvier, 1833)	1, 2, 3	UN	PL	P	0–40	WA
Decapterus tabl Berry, 1968	1, 2, 3	CM	PL	P	0–50	WA
Elagatis bipinnulata (Quoy & Gaimard,1824)	1, 2, 3	CM	C	P	3–50	WA
Selar crumenophthalmus (Bloch, 1793)	1, 2, 3	CM	PL	P	0–50	WA
Selene vomer (Linnaeus, 1758)	1, 2, 3	UN	C	P	35–40	WA
Seriola dumerili (Risso, 1810)	1, 2, 3	OC	C	P	51–54	WA
Seriola rivoliana Valenciennes, 1833	1, 2, 3	OC	C	P	51–54	WA
Trachinotus falcatus (Linnaeus, 1758)	1, 2, 3	OC	C	P	35–66	WA
Trachinotus goodei Jordan & Evermann, 1896	1, 2	AB	C	P	0–40	WA

Table 1. Continued.

Fish family/species	Occurrence	Pop. status	Trophic category	Habitat	Depth range (m)	Geographic range
LUTJANIDAE						
Lutjanus analis (Cuvier, 1828)	1, 2, 3	VC	C	B	35–70	WA
Lutjanus apodus (Walbaum, 1792)	1, 2, 3	OC	C	B	35–54	NWA+NEB
Lutjanus buccanella (Cuvier, 1828)	3	OC	C	B	47–54	NWA+NEB
Lutjanus cyanopterus (Cuvier, 1828)	1, 2, 3	UN	C	B	35–70	WA
Lutjanus jocu (Bloch & Schneider, 1801)	1, 2, 3	VC	C	B	35–70	WA
Lutjanus purpureus (Poey, 1875)	3	RA	C	B	66–70	WA
Lutjanus synagris (Linnaeus, 1758)	1, 2, 3	UN	C	B	35–54	WA
Lutjanus vivanus (Cuvier, 1828)	3	UN	C	B	60–70	WA
Ocyurus chrysurus (Bloch, 1791)	1, 2, 3	VC	C	B	35–70	WA
Rhomboplites aurorubens (Cuvier, 1929)	3	OC	C	B	47–54	WA
HAEMULIDAE						
Anisotremus surinamensis (Bloch, 1791)	1, 2, 3	VC	C	B	35–60	WA
Anisotremus virginicus (Linnaeus, 1758)	1, 2, 3	OC	C	B	35–40	WA
Haemulon aurolineatum Cuvier, 1829	1, 2, 3	VC	C	B	35–70	WA
Haemulon melanurum (Linnaeus, 1758)	1, 2, 3	CM	C	B	35–60	NWA+NEB
Haemulon parra (Desmarest, 1823)	1, 2, 3	VC	C	B	35–60	WA
Haemulon plumieri (Lacépède, 1802)	1, 2, 3	VC	C	B	35–70	WA
Haemulon squamipinna Rocha & Rosa, 1999	1, 2, 3	UN	C	B	35–40	NEB
Haemulon striatum (Linnaeus, 1758)	3	RA	C	B	66–70	WA
SPARIDAE						
Calamus pennatula Guichenot, 1868	1, 2, 3	CM	C	B	35–70	WA
SCIAENIDAE						
Equetus lanceolatus (Linnaeus, 1758)	1, 2, 3	OC	C	B	45–57	WA
Pareques acuminatus (Bloch & Schneider, 1801)	1, 2, 3	OC	C	B	35–54	WA
MULLIDAE						
Mulloidichthys martinicus (Cuvier, 1829)	1, 2, 3	OC	C	B	35–66	WA
Pseudupeneus maculatus (Bloch, 1793)	1, 2, 3	CM	C	B	35–70	WA
Upeneus parvus Poey, 1852	3	UN	C	B	53–54	WA
CHAETODONTIDAE						
Chaetodon ocellatus Bloch, 1787	1, 2, 3	VC	C	B	35–60	NWA+NEB
Chaetodon striatus Linnaeus, 1758	1, 2, 3	CM	C	B	35–60	WA
POMACANTHIDAE						
Centropyge aurantonotus Burgess, 1974	1, 2, 3	CM	TH	B	35–57	WA
Holacanthus ciliaris (Linnaeus, 1758)	1, 2, 3	CM	O	B	35–57	WA
Holacanthus tricolor (Bloch, 1795)	1, 2, 3	CM	O	B	35–57	WA
Pomacanthus arcuatus (Linnaeus, 1758)	1, 2, 3	OC	O	B	35–60	WA
Pomacanthus paru (Bloch, 1787)	1, 2, 3	VC	O	B	35–70	WA
KYPHOSIDAE						
Kyphosus sectatrix (Linnaeus, 1758)	1, 2, 3	OC	NH	B	35–40	WA
CIRRHITIDAE						
Amblycirrhitus pinos (Mowbray, 1927)	1, 2	OC	C	B	35–40	WA
POMACENTRIDAE						
Abudefduf saxatilis (Linnaeus, 1758)	1, 2, 3	UN	O	B	35–40	WA
Chromis flavicauda (Günther, 1880)	1, 2, 3	AB	PL	B	35–60	WA
Chromis jubauna Moura, 1995	3	CM	PL	B	54–57	BP
Chromis multilineata (Guichenot, 1855)	1, 2, 3	UN	PL	B	35–54	WA
Stegastes pictus (Castelnau, 1855)	1, 2, 3	VC	TH	B	35–70	BP

Table 1. Continued.

Fish family/species	Occurrence	Pop. status	Trophic category	Habitat	Depth range (m)	Geographic range
LABRIDAE						
Bodianus pulchellus (Poey, 1860)	1, 2, 3	CM	C	B	40–70	WA
Bodianus rufus (Linnaeus, 1758)	1, 2, 3	VC	C	B	35–70	WA
Clepticus brasiliensis Heiser, Moura & Robertson, 2000	1, 2, 3	OC	PL	B	35–54	BP
Halichoeres bivittatus (Bloch, 1791)	1, 2, 3	OC	C	B	35–54	NWA+NEB
Halichoeres dimidiatus (Agassiz *in* Spix & Agassiz, 1831)	1, 2, 3	VC	C	B	35–70	WA
Halichoeres penrosei Starks, 1913	1, 2	OC	C	B	35–40	WA
Halichoeres poeyi (Steindachner, 1867)	1, 2, 3	OC	C	B	35–54	WA
Halichoeres brasiliensis (Bloch, 1791)	1, 2, 3	OC	C	B	35–60	BP
Thalassoma noronhanum (Boulenger, 1890)	1, 2, 3	AB	PL	B	35–70	BP
Xyrichtys splendens Castelnau, 1855	1, 2, 3	OC	C	B	35–52	NWA+NEB
Xyrichtys martinicensis Valenciennes, 1840	1, 2, 3	OC	C	B	36–40	WA
SCARIDAE						
Cryptotomus roseus Cope, 1871	1, 2, 3	OC	NH	B	50–55	WA
Scarus trispinosus Valenciennes, 1840	1, 2, 3	OC	NH	B	35–60	BP
Scarus zelindae Moura, Figueiredo & Sazima, 2001	1, 2, 3	OC	NH	B	35–54	BP
Sparisoma frondosum (Agassiz, 1831)	1, 2, 3	CM	NH	B	35–54	BP
Sparisoma axillare (Steindachner, 1878)	1, 2, 3	OC	NH	B	35–54	BP
Sparisoma amplum (Ranzani, 1842)	1, 2, 3	OC	NH	B	35–54	BP
LABRISOMIDAE						
Malacoctenus aff. *triangulatus* Springer, 1958	1, 2	UN	C	B	35–40	BP
CHAENOPSIDAE						
Emblemariopsis signifera (Ginsburg, 1942)	1, 2, 3	UN	C	B	35–55	WA
CALLIONYMIDAE						
Paradiplogrammus bairdi Jordan, 1887	1, 2, 3	UN	C	B	53–54	WA
GOBIIDAE						
Coryphopterus dicrus Böhlke & Robins, 1960	1, 2, 3	OC	C	B	50–54	WA
Coryphopterus eidolon Böhlke & Robins, 1960	3	UN	C	B	51–54	NWA+NEB
Coryphopterus glaucofraenum Gill, 1863	1, 2	OC	C	B	35–40	WA
Coryphopterus thrix Böhlke & Robins, 1960	2, 3	CM	C	B	51–54	WA
Elacatinus figaro Sazima, Moura & Rosa, 1996	1, 2, 3	VC	C	B	35–70	BP
Gnatholepis thompsoni Jordan, 1902	1, 2, 3	CM	C	B	35–57	WA
Gobionellus saepepalens Gilbert & Randall, 1968	1, 2	UN	C	B	35–40	WA
Lythrypnus cf. *brasiliensis* Greenfield, 1988	1, 2, 3	UN	C	B	50–54	BP
Prioleps dawsoni Greenfield, 1989	1, 2, 3	CM	C	B	35–57	BP
Psilotris cf. *batrachodes* Böhlke, 1963	3	UN	C	B	54–55	NWA+NEB
Psilotris sp.	1, 2, 3	UN	C	B	54–55	NEB
Risor ruber (Rosén, 1911)	1, 2, 3	AB	C	B	35–58	NWA+NEB
MICRODESMIDAE						
Ptereleotris randalli Gasparini, Rocha & Floeter, 2001	1, 2, 3	AB	PL	B	35–60	BP
EPHIPIDAE						
Chaetodipterus faber (Broussonet, 1782)	1, 2, 3	OC	C	P	20–40	WA
ACANTHURIDAE						
Acanthurus bahianus Castelnau, 1855	1, 2, 3	OC	NH	B	35–40	WA
Acanthurus chirurgus (Bloch, 1787)	1, 2, 3	VC	NH	B	35–70	WA
Acanthurus coeruleus Bloch & Schneider, 1801	1, 2, 3	VC	NH	B	35–70	WA

Table 1. Continued.

Fish family/species	Occurrence	Pop. status	Trophic category	Habitat	Depth range (m)	Geographic range
SPHYRAENIDAE						
Sphyraena barracuda (Walbaum, 1792)	1, 2, 3	VC	C	P	3–70	WA
SCOMBRIDAE						
Acanthocybium solandri (Cuvier, 1831)	1, 2, 3	CM	C	P	3–51	WA
Euthynnus alletteratus (Rafinesque, 1810)	1, 2, 3	OC	C	P	0–50	WA
Scomberomorus cavalla (Cuvier, 1829)	1, 2, 3	OC	C	P	10–57	WA
Scomberomorus regalis (Bloch, 1793)	1, 2, 3	CM	C	P	3–51	WA
Thunnus obesus (Lowe, 1839)	2, 3	AB	C	P	0–54	WA
BALISTIDAE						
Balistes vetula Linnaeus, 1758	1, 2, 3	CM	C	B	35–70	WA
Canthidermis sufflamen (Mitchill, 1815)	1, 2, 3	CM	C	B	40–70	WA
Melichthys niger (Bloch, 1786)	2, 3	CM	O	B	40–70	WA
Xanthichthys ringens (Linnaeus, 1758)	3	RA	O	B	60–70	NWA+NEB
MONACANTHIDAE						
Aluterus monoceros (Linnaeus, 1758)	1, 2, 3	UN	C	B	35–40	WA
Aluterus scriptus (Osbeck, 1765)	1, 2, 3	OC	O	B	35–40	WA
Cantherhines macrocerus (Hollard, 1854)	1, 2, 3	OC	O	B	35–40	WA
Monacanthus ciliatus (Mitchill, 1818)	1, 2, 3	RA	O	B	35–50	WA
Monacanthus setifer Bennett, 1831	1, 2, 3	OC	O	B	35–40	NWA+NEB
Stephanolepis hispidus (Linnaeus, 1766)	1, 2, 3	OC	O	B	34–40	WA
OSTRACIIDAE						
Acanthostracion polygonius Poey, 1876	1, 2, 3	OC	O	B	35–40	WA
Acanthostracion quadricornis (Linnaeus, 1758)	1, 2, 3	OC	O	B	35–40	WA
Lactophrys trigonus (Linnaeus, 1758)	1, 2, 3	OC	O	B	35–40	WA
TETRAODONTIDAE						
Canthigaster figueiredoi Moura & Castro, 2002	1, 2, 3	CM	O	B	35–54	WA
DIODONTIDAE						
Diodon hystrix Linnaeus, 1758	1, 2, 3	UN	O	B	35–40	WA
Diodon holocanthus Linnaeus, 1758	1, 2, 3	UN	O	B	35–40	WA
Diodon sp.	1, 2, 3	AB	PL	P	3–40	WA

than 45 m, where algae were more abundant. The number of herbivores generally declines with depth because sunlight is filtered through the water column, limiting the development of algae (Itzkowitz et al., 1991). Thresher and Colin (1986) observed a gradual decline in abundance with increasing depth in all trophic categories except piscivores at the Marshall Islands, and at the same time, an increase in planktivores. The pattern observed in the previous two studies is very similar to the one reported herein, and seems to reflect the change in abundance of certain food groups: algae are less abundant and plankton more abundant.

Vertical Distribution of Fishes at the Deep Reefs.—More than three quarters of all fishes (77.2%; 122 species) were bottom-dwellers, 28 (17.7%) were pelagic fish that frequently visited the reefs, and eight species (5.1%) were mostly pelagic, inhabiting the upper area of the water column (Table 1). A notable difference was observed between the composition of bottom-dwellers at the upper flat zone and the deeper steep zone of the shelf edge reefs. The upper flat zone is inhabited mainly by small fishes, probably because of the low habitat complexity. Fishes in this zone inhabit small cracks and holes as well as the interior of sponges (see Rocha et al., 2000; Fig. 2). Bigger fishes inhabit the deeper steep zone, a much more complex habitat with large rocks and caves. Large, commercially important fishes such as black grouper (*Mycteroperca bonaci*), dog snapper (*Lutjanus jocu*), and also threatened species such as mutton snapper (*L. analis*), cubera snapper (*L. cyanopterus*), and queen triggerfish (*Balistes vetula*) are among the species observed in this habitat.

Pelagic species cruise the water column above the reefs. The presence of large oceanic fishes such as bigeye tuna (*Thunnus obesus*), dolphinfish (*Coryphaena hippurus*), wahoo (*Acanthocybium solandri*), and mackerel (*Scomberomorus regalis*) is certainly linked to the presence of blue, oceanic water, brought upon by the strong westward flowing south equatorial current.

Distribution and Zoogeography.—More than three quarters of all fishes (76.6%; 121 species) recorded at the deep reefs are widely distributed in the western Atlantic, 18 (11.4%) are endemic to the Brazilian Province, 15 (9.5%) are northwestern Atlantic species with a southern distribution limit at northeastern Brazil, and four (2.5%) are known only from the northeastern Brazilian coast. Twenty-three species (14.6%) are restricted to the deep reefs in northeastern Brazil, 14 of which (8.9%) were observed only over shelf-edge deep reefs (Table 1).

According to Floeter and Gasparini (2000), the geographic range of tropical reef fishes suggests the recognition of only two western Atlantic provinces: the northwestern Atlantic and the Brazilian Province, which are separated by a freshwater barrier of more than 1000 km between the Orinoco (Venezuela) and Amazon (Brazil) rivers (Rocha, 2003). The cluster analysis presented herein clearly shows the distinction between these two provinces (Fig. 3). Our results differ from those of Floeter and Gasparini (2000) who reported the presence of two clusters, one formed by the South Atlantic oceanic islands and the other by the ensemble of the Brazilian mainland, the Caribbean, and Bermuda. However, the analysis carried out by Rocha and Rosa (2001) agrees with ours, grouping Trindade Island with the Brazilian coastal sites, outside the cluster formed by the northeastern Brazilian islands, and separating Brazil from the Caribbean. Rocha (2003) attributed this discrepancy to the similar total number of species among the islands, (smaller than the remaining locations), and considered Trindade more closely related to the Brazilian mainland than to the other offshore islands due to the prevailing currents and the presence of a seamount chain between the island and the coast.

Despite the clear separation between the Brazilian and Greater Caribbean regions (Joyeux et al., 2001; Rocha, 2003; present study), recent analyses indicate that there is continuous, but relatively small dispersal between Brazil and the Caribbean (Rocha et al., 2002; Rocha, 2003). In addition, surveys carried out in the area between Guyana and the Amazon mouth have revealed the presence of hard bottoms at the continental shelf break, between depths of 36 and 80 m (Lowe-McConnell, 1962; Collette & Rützler, 1977; Uyeno et al., 1983). Typically, reef organisms such as sponges, gorgonians, and crustaceans inhabit these deep areas, where several species of Caribbean and Brazilian reef fishes were captured. Gilbert (1972) suggested that the Amazon barrier is not 100% effective as it only interrupts migration among populations of species that are restricted to depths shallower than 50 m and that cannot survive without reef coral. Collette and Rützler (1977) observed that salinity in deep water varied much less than at the surface (34.5–36.4 vs. 17–35.7). Consequently, no inhibitory effect caused by freshwater was observed at the bottom where sponges and reef fishes were found.

Bidirectional dispersal between Brazil and the Caribbean has been inferred from the distribution of some species that were previously considered to be endemic to one province, but are also found at locations in the other province. For example, the following species previously considered Brazilian endemics were recently observed at the southern Caribbean: *Stegastes pictus, Sparisoma frondosum, Ptereleotris randalli, Opistognathus* aff. *aurifrons*, *Canthigaster figueiredoi* and *Heteroconger camelopardalis* (Rocha, 2002). Exemplifying dispersal in the opposite direction, 14 species that are widely distributed in the Caribbean have their southern limit of distribution at northeastern Brazil, and four of these were recorded for the first time south of the Amazon. Despite being uncommon or rare, such records are a strong indication of reciprocal dispersal between the provinces.

The hard bottoms at the outer margin of the continental shelf seem to extend in a more or less continuous line from Guyana to northeastern Brazil. Organic carbonate sediments were detected at this line from the Para River mouth (0°) to the city of Recife (8°S), corresponding to a continuous formation extending for more than 2000 km (Kempf et al., 1967; Lana et al., 1996). In addition, the continental shelf of the hump of Brazil is somewhat similar to that of northern areas, such as Guyana. Characteristics of the bottom in these areas are strongly correlated with distance from shore: the bottom is soft and muddy close to shore, becoming progressively harder and more calcareous, and then building to organic reefs at its outer margin (Lowe-McConnell, 1962; present study).

The Parcel de Manuel Luiz (PML) is an important reef area sometimes considered a stepping-stone between Brazil and the Caribbean (Moura et al., 1999; Rocha and Rosa, 2001). It is located just south of the Amazon mouth, 86 km from shore and 51 km from the continental margin, with an area of approximately 40 km^2 (Rocha and Rosa, 2001), and is considered to be the northernmost Brazilian reef formation (Maida and Ferreira, 1997). Despite being located directly in front of several large river mouths, the distance from the coast and the strong northwestward flow of the North Brazil Current keep the waters around the PML clear throughout the year (Rocha and Rosa, 2001). However, the apparent absence of some very abundant Brazilian endemics (e.g., *Haemulon squamipinna* and *Stegastes fuscus*) suggests the presence of a barrier between the PML and other shallow reefs to the south (see Rocha and Rosa, 2001). On the other hand, our cluster analysis (Fig. 3) shows that, despite the distance of more than 1000 km that separates them, the PML is very closely related to deep reefs at the hump of Brazil. The coefficient of similarity between PML and the deep reefs (Sorensen's Coefficient = 0.69) is even larger than that between geographically closer shallow reefs (ZB, PB, and PE, Sorensen's Coefficient = 0.66). This suggests a connection between PML and the deep reefs, strengthening the hypothesis of continuity among these reefs along the northeast coast of South America. However, more detailed surveys of the area are necessary in order to understand connections between Brazilian and Caribbean faunas.

Floeter et al. (2001) points out that reef fish communities in northeastern Brazil are characterized by the dominance of tropical species, many of which are shared with the Caribbean but not with southeastern Brazil, possibly because of lower water temperatures.(e.g., *Haemulon melanurum*; *Chaetodon ocellatus*; *Halichoeres bivittatus*; *Xyrichthys splendens*). On the other hand, some widely distributed fishes are

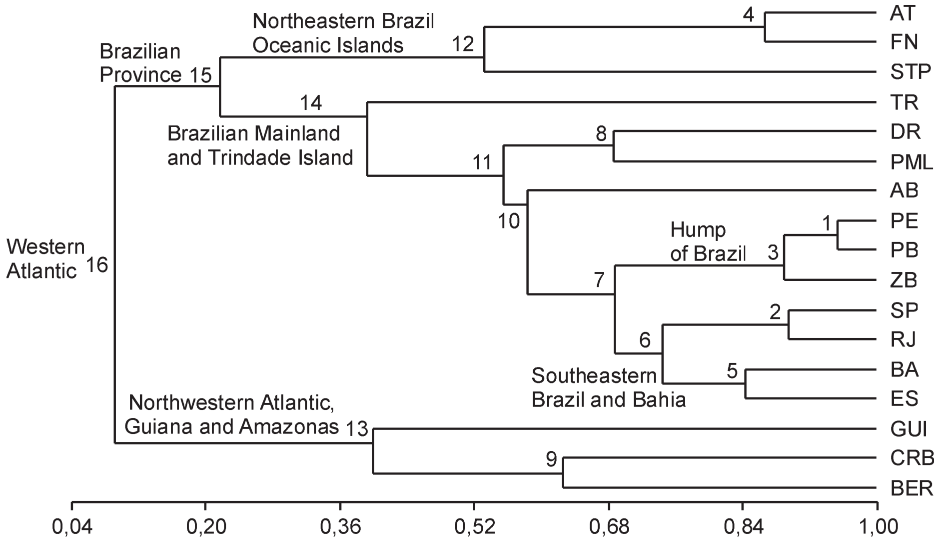

Figure 3. Cluster analysis (Sorensen's coefficient and farthest-neighbor) showing the zoogeographic affinities between the deep reefs off the hump of Brazil and other western Atlantic sites based on presence-absence of species. AT = Rocas Attol; FN = Fernando de Noronha Archipelago; STP = Saint Paul's Rocks; TR = Trindade Island; DR = Deep reefs off the hump of Brazil; PML = Parcel de Manuel Luiz Reefs; AB = Abrolhos Archipelago; PE = Pernambuco shallow reefs; PB = Paraíba shallow reefs; ZB = Zumbi shallow reefs; SP = São Paulo shallow reefs; RJ = Rio de Janeiro shallow reefs; BA = Bahia shallow reefs; ES = Espírito Santo shallow reefs; GUI = Guyana, Suriname, French Guiana and Amazon mouth hard bottoms; CRB = Caribbean reefs; BER = Bermuda.

shared between southeastern Brazil and the Caribbean, but were considered rare or absent in northeastern Brazil (e.g., *Centropyge aurantonotus, Liopropoma carmabi, Apogon quadrisquamatus, Heteroconger longissimus, Halieutichthys aculeatus, Equetus lanceolatus, Chromis flavicauda, Chaetodon sedentarius, Epinephelus niveatus,* and *Mycteroperca microlepis*).

At least seven of these ten species are recorded in deep reefs at the northeast by this study. The question then becomes: why are these species not present at the shallow reefs? A few years ago, these species were not known from northeastern Brazil, and historical explanations (such as ancient long distance colonization) were given to these apparently disjunct, anti-equatorial distributions (Joyeux et al., 2001). However, the presence of these species at deep reefs indicates that such barriers do not affect them. It is probable that ecological factors are linked to the observed pattern. Rocha (2003) points out that ecological factors play a larger role in shaping diversity in the western Atlantic than previously thought, through divergent selection in environmentally different habitats. Moura et al. (1999) also notes that there are trends in the composition of reef fish faunas within the Brazilian Province possibly related to salinity, bottom type, and temperature. In shallow reefs at our study area, very high temperatures (> 30 °C) combined with high rates of suspended sediment in the water, may prevent the colonization of the shallow reefs by species with strict habitat preferences.

Our survey indicated that the water in the deep reefs is up to 6 °C colder and much more transparent than the water around the shallow reefs. One clear example of the influence of temperature (or some biotic factor related to temperature) is the geographic distribution of *Chromis jubauna*. This species is common at depths between 10 and 21 m in southeastern Brazil (Moura, 1995; Moura et al., 1999) and at deep reefs in northeastern Brazil where the water is colder than 26 °C, but was never observed in the shallow, warmer reefs. Large aggregations of juvenile *C. jubauna* were observed on the deeper areas (60+ m), where the water is colder. *Chromis flavicauda* and *Centropyge aurantonotus* are two additional examples of species that occur in shallow water in southeastern Brazil, but only in deep water (45+ m) in the northeast. Surveys of reefs deeper than 70 m may reveal the presence of more species presently recorded only in southeastern Brazil and the Caribbean. Moreover, as emphasized by Pyle (2000), the greatest portion of the undiscovered reef fish biodiversity is found at those depths, and studies utilizing rebreather technology would greatly increase our knowledge of the Atlantic fish fauna.

Finally, the presented evidence indicates that the faunal corridor of South America (Collette and Rutzler, 1977) extends beyond the Amazon mouth area, includes the hump of Brazil and serves as a connection between cold habitats in south Brazil and the Caribbean. Additional studies on deep reefs to the north and south of the studied area may help us understand the dynamics of this corridor, and consequently, the patterns of distribution of reef fishes along the western Atlantic coast.

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Literature Cited

Böhlke, J. E. and C. C .G. Chaplin. 1993. Fishes of the Bahamas and adjacent tropical waters. 2nd. ed. University of Texas Press, Austin. 771 p.

Chaves, H. A. F., S. G. Zembruscki, and A. M. C. França. 1979. Introdução. Pages 11–23 *in* H. A. F. Chaves, ed. Geomorfologia da Margem Continental Brasileira e das Áreas Oceânicas Adjacentes. Projeto REMAC, vol. 7. PETROBRAS, Rio de Janeiro.

Colin, P. L., D. M. Devaney, L. Hillis-Colinvaux, T. H. Suchanek, and T. Harrison-III. 1986. Geology and biological zonation of the reef slope, 50-360 m depth at Enewetak Atoll, Marshall Islands. Bull. Mar. Sci. 38: 111–128.

________. 1974. Observation and collection of deep-reef fishes off the coasts of Jamaica and British Honduras (Belize). Mar. Biol. 24: 29–38.

________. 1976. Observations of deep-reef fishes in the Tongue-of-the-Ocean, Bahamas. Bull. Mar. Sci. 26: 603–605.

Collete, B. B. and K. Rutzler. 1977. Reef fishes over sponge bottoms off the mouth of the Amazon River. Proc. 3rd Int. Coral Reef Symp. 1: 305–310.

Feitoza, B. M. 2001. Composição e Estrutura da comunidade de peixes recifais da Risca do Zumbi, Rio Grande do Norte. MS Thesis, Universidade Federal da Paraíba, João Pessoa. 157 p.

___________, L. A. Rocha, O. J. Luiz Junior, S. R. Floeter, and J. L. Gasparini. 2003. Reef fishes of St. Paul´s Rocks: new records and notes on biology and zoogeography. Aqua. J. Ichthyol. Aquat. Biol. 7: 61–823.

Ferreira, B. P., M. Maida, and A. E. T. Souza. 1995. Levantamento inicial das comunidades de peixes recifais da região de Tamandaré – PE. Bol. Técn. Cient. CEPENE 3: 211–230.

Figueiredo, J. L. and N. A. Menezes. 1978. Manual de Peixes Marinhos do Sudeste do Brasil. Teleostei (1). Museu de Zoologia, Universidade de São Paulo, São Paulo. Vol. II, 110 p.

_____________ and _____________. 1980. Manual de Peixes Marinhos do Sudeste do Brasil. Teleostei (2). Museu de Zoologia, Universidade de São Paulo, São Paulo. Vol. III, 90 p.

_____________ and _____________. 2000. Manual de peixes marinhos do sudeste do Brasil. VI.Teleostei (5). Museu de Zoologia, Universidade de São Paulo, São Paulo. 116 p.

Floeter, S. R. and J. L. Gasparini. 2000. The southeastern Atlantic reef-fish fauna: composition and zoogeographic patterns. J. Fish Biol. 56: 1099–1114.

_____________, R. Z. P. Guimarães, L. A. Rocha, C. E. L. Ferreira, C. A. Rangel, and J. L. Gasparini. 2001. Geographic variation in reef-fish assemblages along the Brazilian coast. Global Ecol. Biogeogr. 10: 423–431.

França, A. M. C. 1979. Geomorfologia da Margem Continental Leste Brasileira e da Bacia Oceânica Adjacente. Pages 89–127 *in* H. A. F. Chaves, ed. Geomorfologia da Margem Continental Brasileira e das Áreas Oceânicas Adjacentes. Projeto REMAC, vol. 7. PETROBRAS, Rio de Janeiro.

Gasparini, J. L. and S. R. Floeter. 2001. The shore fishes of Trindade Island, western South Atlantic. J. Nat. Hist. 35: 1639–1656.

Gilbert, C. R. 1972. Characteristics of the western Atlantic reef-fish fauna. Quart. J. Florida Acad. Sci. 35: 130–144.

Guéguen, F. 2000. Distribution et abondance des poissons démersaux et de quelques autres organismes benthiques marins du plateau continental (0–60 m) de Guyane Française. Life Sci. 323: 775–791.

Hilton-Taylor, C. (Compiler). 2000. 2000 IUCN Red list of threatened animals. IUCN, Gland. xviii + 61 p.

Humann, P. and N. Deloach. 2002. Reef fish identification - Florida, Caribbean, Bahamas. 3rd Ed. New World Publications, Jacksonville. 481 p.

Itzikowitz, M., M. Haley, C. Otis, and D. Evers. 1991. A reconnaissance of the deeper Jamaican coral reef fish communities. NE Gulf Sci. 12: 25–34.

Joyeux, J. C., S. R. Floeter, C. E. L. Ferreira, and J. L. Gasparini. 2001. Biogeography of tropical reef fishes: the South Atlantic puzzle. J. Biogeogr. 28: 831–841.

Kempf, M., P. N. Coutinho, and J. O. Morais. 1967. Plataforma continental do Norte e Nordeste do Brasil I. Nota preliminar sobre a natureza do fundo. Trabs. Oceanogrs. Univ. Fed. PE 9/11: 9–26.

Knoppers, B., W. Ekau, and A. G. Figueiredo. 1999. The coast and shelf of east and northeast Brazil and material transport. Geo-Mar. Lett. 19: 171–178.

Lana, P. C., M. G. Camargo, R. A. Brogim, and V. J. Isaac. 1996. O bentos da costa brasileira: avaliação crítica e levantamento bibliográfico (1858-1996). FEMAR, Rio de Janeiro. 432 p.

Leão, Z. M. A. N. and J. M. L. Dominguez. 2000. Tropical coast of Brazil. Mar. Poll. Bull. 41: 112–122.

Lowe-McConnell, R. H. 1962. The fishes of the British Guiana Continental Shelf, Atlantic coast of South America, with notes on their natural history. J. Linn. Soc. London (Zool.) 44: 669–700.

Ludwig, J. A. and J. F. Reynolds. 1988. Statistical ecology: a primer on methods and computing. John Wiley and Sons, New York. 337 p.

Lukens, R. R. 1981. Observations of deep-reef ichthyofauna from the Bahama and Cayman Islands, with notes on relative abundance and depth distribution. Gulf Res. Rep. 7: 79–81.

Magurran, A. E. 1996. Ecological diversity and its measurements. Chapman and Hall, London. 179 p.

Maida, M. and B. P. Ferreira. 1997. Coral reefs of Brazil: an overview. Proc. 8th Int. Coral Reef Symp. 1: 263–274.
Menezes, N. A. and J. L. Figueiredo. 1980. Manual de Peixes Marinhos do Sudeste do Brasil. Teleostei (3). Museu de Zoologia, Universidade de São Paulo, São Paulo. Vol. IV, 96 p.
_____________ and ____________. 1985. Manual de Peixes Marinhos do Sudeste do Brasil. Teleostei (4). Museu de Zoologia, Universidade de São Paulo, São Paulo. V, 105 p.
Moura, R. L. 1995. A new species of *Chromis* (Perciformes: Pomacentridae) from the southeastern coast of Brazil, with comments on other species of the genus. Revue Fr. Aquariol. 21: 91–96.
___________, J. L. Gasparini, and I. Sazima. 1999. New records and range extensions of reef fishes in the western south Atlantic, with comments on reef fish distribution along the Brazilian coast. Revta. Bras. Zool. 16: 513–530.
Nelson, J. S. 1994. Fishes of the world. 3rd ed. John Wiley and Sons, New York. 600 p.
Pearcy, W. G., D. L. Stein, M. A. Hixon, E. K. Pikitch, W. H. Barss, and R. M. Starr. 1989. Submersible observations of deep-reef fishes of Heceta Bank, Oregon. Fisher. Bull. 87: 955–965.
Pyle, R. L. 1996a. How much coral reef biodiversity are we missing? Global Biodiv. 6: 3–7.
________. 1996b. The twilight zone. Nat. Hist. 105: 59–62.
________. 1998. Use of advanced mixed-gas diving technology to explore the coral reef "twilight zone". Pages 71–88 *in* J. T. Tanacredi and J. Loret, eds. Ocean pulse: A critical diagnosis. Plenum Press, New York.
________. 2000. Assessing undiscovered fish biodiversity on deep coral reefs using advanced self-contained diving technology. Mar. Tech. Soc. J. 34: 82–91.
Ramos, R. T. C. 1994. Análise da composição e distribuição da fauna de peixes demersais da plataforma continental da Paraíba e estados vizinhos. Rev. Nordest. Biol. 9: 1–30.
Randall, J. E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. 5: 665–847.
___________. 1996. Caribbean reef fishes. 3rd ed. T.F.H. Publications, Hong Kong. 368 p.
Rocha, L. A. 2002. Brazilian reef fishes. Pages 462–479 *in* P. Humann and N. Deloach, eds. Reef fish identification - Florida, Caribbean, Bahamas. 3rd ed. New World Publications, Jacksonville.
__________. 2003. Patterns of distribution and processes of speciation in Brazilian reef fishes. J. Biogeogr. 30: 1161–1171.
__________ and I. L. Rosa. 2001. Baseline assessment of reef fish assemblages of parcel Manuel Luiz Marine State Park, Maranhão, north-east Brazil. J. Fish Biol. 58: 985–998.
__________, ___________, and R. S. Rosa. 1998. Peixes Recifais da Costa da Paraíba, Brasil. Revta. Bras. Zool. 15: 553–566.
__________, ___________, and B. M. Feitoza. 2000. Sponge-dwelling fishes of northeastern Brazil. Env. Biol. Fishes 59: 453–458.
__________, A. L. Bass, D. R. Robertson, and B. W. Bowen. 2002. Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). Mol. Ecol. 11: 243–252
Rosa, R. S. and R. L. Moura, 1997. Visual assessment of reef fish community structure in the Atol das Rocas Biological Reserve, off northeastern Brazil. Proc. 8th Int. Coral Reef Symp. 1: 983–986.
_________, I. L. Rosa, and L. A. Rocha. 1997. Diversidade da ictiofauna de poças de maré da Praia do Cabo Branco, João Pessoa, Paraíba, Brasil. Revta. Bras. Zool. 14: 201–212.
Sale, P. F. 1991. The ecology of fishes on coral reefs. Academic Press, San Diego. 754 p.
Silveira, I. C. A., L. B. Miranda, D. L. Evans, M. R. Stevenson, and H. M. Inostroza. 1994. On the origin of the North Brazil Current. J. Geophys. Res. 99: 22501–22512.
Stein, D. L., B. N. Tissot, M. A. Hixon, and W. Barss. 1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. Fish. Bull. 90: 540–551.

Stramma L., Y. Ikeda, and R. G. Peterson. 1990. Geostrophic transport in the Brazil Current region north of 20°S. Deep-Sea Res. 37: 1875–1886.

Thresher, R. E. and P. L. Colin. 1986. Trophic structure, diversity and abundance of fishes of the deep reef (30–300 m) at Enewetak, Marshall Islands. Bull. Mar. Sci. 38: 253–272.

Uyeno, T., K. Matsuura, and E. Fujii, eds. 1983. Fishes trawled off Suriname and French Guiana. Japan Marine Fishery Resource Research Center, Tokyo. 519 p.

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