Patterns of distribution and processes of speciation in Brazilian reef fishes

Luiz A. Rocha*† *Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, FL, USA*

Abstract

Aim To evaluate the state of knowledge about the biogeography of Brazilian reef fishes and propose processes that lead to the observed distribution patterns.

Location The tropical western Atlantic.

Methods The geological history of the Amazon barrier was obtained from the literature, and its potential influence on speciation of reef fishes was analysed. Species distributions were analysed based on literature records and material deposited at Brazilian and American collections.

Results Recent estimates indicate that about 12% of the Brazilian reef fish species are endemic, and most ichthyologists agree that this endemism is generated by the barrier formed by the freshwater and sediment discharge of large rivers in north-eastern South America, mainly the Amazon, Orinoco and their tributaries. However, little is known about the dynamics of this barrier, and recent studies have demonstrated that it can be crossed through deep sponge bottoms on the outer continental shelf off north-eastern South America. Moreover, the recent discovery of species regarded as Brazilian endemics in the extreme southern Caribbean is showing that the Amazon barrier is weaker than previously thought.

Main conclusions The Amazon freshwater and sediment outflow is a strong barrier to shallow water reef fish and other organisms, and it is probably responsible for most of the endemism found in Brazilian coastal habitats. However, sea-level fluctuations influence the effectiveness of such barrier and may play a large role in the generation of diversity in the western tropical Atlantic. Alternatively, larval exchange between Brazil and the Caribbean is small but constant, and contrasting selection pressures in divergent environments (continental Brazil vs. insular Caribbean) may be the central force driving speciation.

Keywords

Dispersal, vicariance, endemism, Amazon barrier, western Atlantic, Pleistocene sea level, paleo-oceanography.

INTRODUCTION

As pointed out by Randall (1998), the analysis of shore fish distributions can elucidate the placement of geographical barriers and their role in speciation. Processes leading to the high diversity of the Indo-Pacific tropical region have been studied in detail (Ormond & Roberts, 1997; Briggs, 1999),

*Correspondence: Luiz A. Rocha, Department of Fisheries and Aquatic Sciences, University of Florida, 7922 NW 71st Street, Gainesville, FL 32653-3071, USA. E-mail: rocha@mail.ifas.ufl.edu
†Present address: Smithsonian Tropical Research Institute, Unit 0948, APO, AA 34002-0948, USA

but less attention has been devoted to zoogeographical patterns in the tropical western Atlantic. The goal of this study is to evaluate the role of biogeographical barriers, especially the Amazon River, in influencing the speciation of reef-associated organisms in the shallow tropical western Atlantic, mainly by analysing species and population's distribution patterns, the barrier's geological history and its past and present oceanographical characteristics. Historical and ecological factors are taken into consideration and may explain much of the evolutionary dynamics in widely distributed western Atlantic reef fishes.

The north-eastern coast of South America, between the mouths of the Orinoco and Amazon rivers, is characterized

by soft bottoms, turbid waters and the world's largest freshwater runoff (Curtin, 1986). This area is recognized as a barrier to the dispersal of reef building corals (Cox & Moore, 2000), rocky shore gastropods (Vermeij, 1978) and shallow water reef fishes (Gilbert, 1972). The endemism found in corals, hydrozoans, molluscs and fishes in Brazil led Briggs (1974a) to consider the tropical Atlantic coast of Brazil and its oceanic islands a biogeographical province distinct from the Caribbean and the West Indian provinces. On the other hand, the limited data available on the Brazilian marine ichthyofauna and the discovery of reef fishes under the Amazon freshwater plume (Collette & Rützler, 1977), led Helfman et al. (1997) to conclude that there was no evidence for such a division.

However, in the past few years a large amount of data on Brazilian reef fishes became available, including species descriptions (Sazima et al., 1998; Rocha & Rosa, 1999; Heiser et al., 2000; Gasparini et al., 2001; Moura et al., 2001), redescriptions and revalidations of fishes endemic to Brazilian reefs (Rocha et al., 2001; Rocha & Rosa, 2001b), faunal surveys (Rocha et al., 1998; Gasparini & Floeter, 2001; Rocha & Rosa, 2001a) and consequently zoogeographical analyses (Floeter & Gasparini, 2000; Floeter et al., 2001; Joyeux et al., 2001). This increase in knowledge about western South Atlantic reef fishes was augmented by the discovery of several fish species previously considered to be Brazilian endemics in the southern Caribbean (Rocha, 2002). These findings warrant a re-examination of distribution patterns and speciation processes in tropical western Atlantic reef fishes.

METHODS

It is difficult to define what is a reef fish (Bellwood & Wainwright, 2002), and for this reason species lists and numbers (and consequently biogeographical analyses) show considerable variation depending on what the authors consider reef fish. The discussion herein is focused on tropical fishes and other organisms associated with reef or hard substrate, distributed to depths of up to 100 m. The distributions of tropical reef fishes in the western Atlantic ranges from Bermuda at 35° N (Robins, 1971) to Santa Catarina, in southern Brazil 28° S (Floeter et al., 2001), and locations of interest, major currents and the Amazon barrier are illustrated in Fig. 1.

Species distributions were obtained from the scientific literature (Rosa et al., 1997; Rocha et al., 1998, 2000; Feitoza, 1999; Gasparini & Floeter, 2001; Rocha & Rosa, 2001a) and analysis of preserved material in the following fish collections: Ichthyological Collection at the Universidade Federal da Paraiba, Brazil (UFPB), Museu de Zoologia da Universidade de Sao Paulo, Brazil (MZUSP), Florida Museum of Natural History at the University of Florida (UF), National Museum of Natural History at the Smithsonian Institution (USNM), and Museum of Comparative Zoology at Harvard University (MCZ). Recent phylogeographical analyses (e.g. Muss et al., 2001; Rocha et al., 2002) provided additional information about population structure within species distributed through coastal Brazil and the Caribbean.
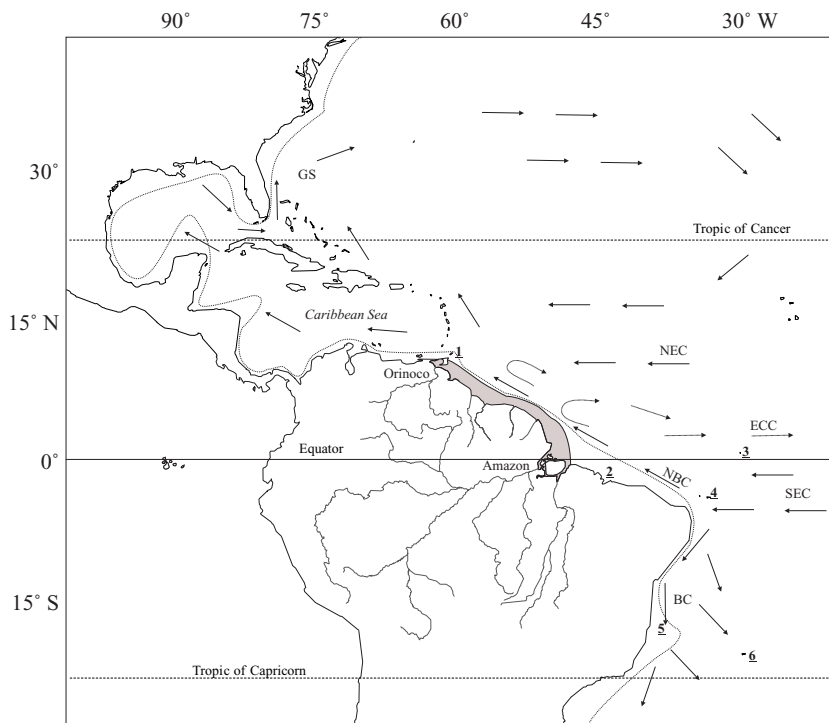
Figure 1 Tropical western Atlantic. Approximate area of influence of the Amazon barrier shaded in grey. Underlined numbers represent locations mentioned in the text, as follows: 1. Tobago; 2. Manuel Luiz reefs; 3. St Paul's Rocks; 4. Fernando de Noronha and Atol das Rocas; 5. Abrolhos reefs; 6. Trindade Island. Arrows indicate direction of mean surface oceanic currents; except for the ECC, which is a sub-surface current. Current abbreviations: GS, Gulf Stream; NEC, North Equatorial Current; ECC, Equatorial Countercurrent; NBC, North Brazil Current; SEC, South Equatorial Current; BC, Brazil Current. Dotted line represents approximate location of continental shelf break.

DISCUSSION

Endemism in Brazilian coastal reefs, the numbers

Recent inventories of Brazilian marine fishes give totals of 844 (Szpilman, 2000), or 962 (Carvalho-Filho, 1999) species. However, these lists include many vague records, based on popular Caribbean fish guides, which frequently state that some widely distributed species range 'south to Brazil'. A more realistic list, based on collections and literature records was recently compiled by Rosa *et al.* (in press), in which 518 marine shore fishes are recorded from the northeastern Brazilian continental shelf. In reviewing their list it was estimated that 323 of these species occur in or around coral or rocky reefs. When this number is combined with the reef fishes of south-eastern Brazil (S. R. Floeter and J. L. Gasparini, pers. comm.), a total of 353 reef fishes is obtained and seems to represent a realistic number. This is roughly half of the number of reef fishes found in the richer Caribbean region (Lieske & Myers, 1994; Smith, 1997).

Forty-five (12.7%) of the fish species found on reefs at the Brazilian shelf are not found in other biogeographical provinces, and are thus considered endemics. This level of endemism is less than previous estimates of 18% (Joyeux *et al.*, 2001), mainly because analyses of collections and underwater photographs from the southern Caribbean (Rocha, 2002) revealed that many species previously considered Brazilian endemics also occur in that region. Oceanic island endemics contribute to the endemism at their respective islands, and not the Province, so they are not among the forty-five species cited above.

The Amazon barrier

In present times (interglacial interval, high sea level), the Amazon discharges about one-fifth of the world's total freshwater runoff into the Atlantic (Curtin, 1986), or 6300 km^3 year^{-1} (Milliman & Meade, 1983), and the largest riverine sediment discharge (2.9×10^8 tonnes year^{-1}) into the world ocean (Degens *et al.*, 1991). The outflow is so large that seawater never enters the river mouth, and freshwater is transported offshore as a surface plume (Nittrouer & DeMaster, 1986), up to 500 km seaward (Lentz, 1995). This surface freshwater plume extends to a depth of *c.* 30 m over the Amazon area shelf, and subsurface ocean water is restricted to depths > 30–40 m over the outer shelf (Curtin & Legeckis, 1986; Masson & Delecluse, 2001). During the current interglacial period, most of the sediment carried by the Amazon is not deposited over the outer shelf, but is diverted towards the Guyana's shelf by the North Brazil Current (Fig. 2), where it forms extensive mud deposits up to 20 km wide, and 60 km long (Kuehl *et al.*, 1986; Allison *et al.*, 2000).

Sea-level fluctuations greatly influence the dynamics of the Amazon barrier. Sediment distribution is quite different during glacial maxima, when the sea level can be 130 m lower than at present. During low sea level the sediment from the Amazon is transported directly offshore through canyons in the continental shelf, and deposited in the Amazon deep-sea fan (Nittrouer & DeMaster, 1986). This fan-shaped area extends 700 km seawards and covers *c.* 375,000 km^2 at 1000–4300 m depths (Lopez, 2001). The lower ocean water layer of the continental shelf disappears and low salinity waters and sediment carried by the Amazon maintain contact with the shelf until its edge, which can be as shallow as 10 m with lower sea levels (Fig. 2). Stratigraphical data obtained in the Amazon fan revealed that sedimentation rates during the last glacial period were 5–25 m k^{-1}, compared with about 0.1 m k^{-1} in the present and previous interglacial periods (Lopez, 2001).
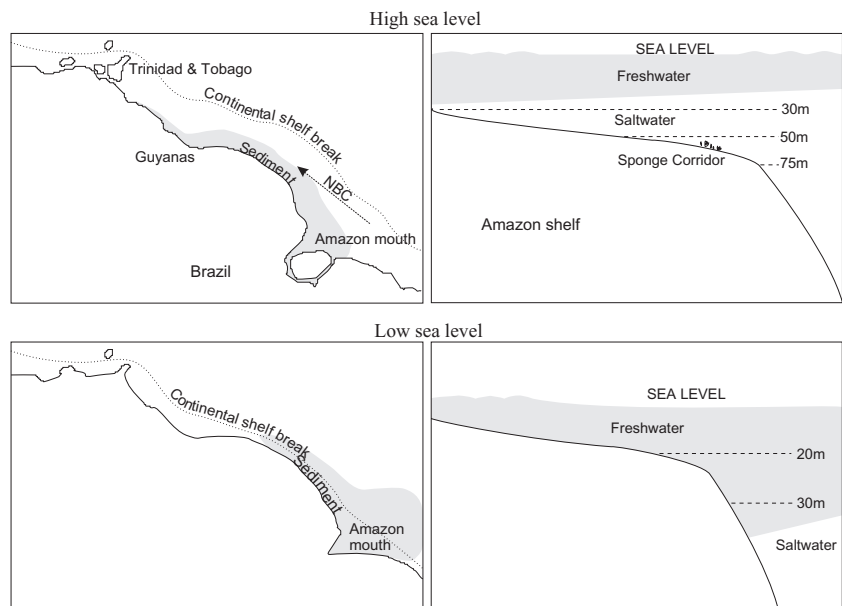
Figure 2 Schematic view of the Amazon freshwater discharge (above) and sediment deposition (below), during stands of high (left, present condition) and low sea level (right); NBC, North Brazil Current.

A key point for understanding the effects of the Amazon barrier on the tropical western Atlantic shore fauna lies on its age. There is some disparity about the Amazon geological history in the current Brazilian reef fish literature: Joyeux *et al.* (2001) state that the initial connection between the Amazon and the Atlantic was established at 5–6 million years ago (Ma), whereas Floeter & Gasparini (2001) consider that the Amazon influence started at the point of maximum sediment deposition 1.6 Ma. However, the geological literature is clear; Potter (1997) and Hoorn (1994) state that the origin of the sediment deposition by the Amazon in the Atlantic is confirmed by the presence of a large late Middle Miocene submarine fan (formed *c.* 11 Ma), coinciding with a major uplift of the Andes (Hoorn *et al.*, 1995), and Hoorn (1996) affirms that the connection between the palaeo-Amazon and the Atlantic has been well-established since the beginning of the Late Miocene (10.4 Ma).

Speciation and the Amazon barrier

The most important component of the classic model of allopatric speciation is the formation of a barrier that divides a species range into isolated portions, so that gene flow is eliminated, and (given enough time) genetic differences can accumulate (Brown & Lomolino, 1998). If the vicariant barrier collapses, previously isolated populations may be sufficiently divergent that intrinsic reproductive barriers (post-mating isolation) complete the process of speciation even in renewed sympatry. This model is the foundation for vicariance biogeography (Barton, 1988).

The soft bottoms, combined with the freshwater surface plume of the Amazon and high sedimentation, do not allow the development of coral reefs on the north-eastern coast of South America, separating the Brazilian from the Caribbean coral and reef-associated faunas (Veron, 1995; Cox & Moore, 2000). Several authors recognized the influence of this barrier in the formation of pairs of sister species of reef fishes in the western tropical Atlantic: *Apogon maculatus* and *A. americanus* (Gilbert, 1977); *Stegastes adustus* and *S. fuscus* (Greenfield & Woods, 1974); *S. partitus* and *S. pictus* (Emery, 1973); *Thalassoma bifasciatum* and *T. noronhanum* (Rocha *et al.*, 2001); *Lythrypnus mowbrayi* and *L. brasiliensis* (Greenfield, 1988); *Starksia ocellata* and *S. brasiliensis* (Williams & Smart, 1983).

Furthermore, the Amazon barrier is believed to be responsible for the formation of geminate species pairs in shallow water corals (Leao, 1986) and rocky shore gastropods (Vermeij, 1978). This barrier is also probably responsible for the deep DNA sequence divergences between Brazilian and Caribbean populations of the spiny lobster *Panulirus argus* (Sarver *et al.*, 1998), the redlip blenny *Ophioblennius atlanticus* (Muss *et al.*, 2001) and the ocean surgeonfish *Acanthurus bahianus* (Rocha *et al.*, 2002).

However, as noted by Gilbert (1977), a barrier to organisms that inhabit hard bottom in shallow, clear seawater is not necessarily a barrier to deep-water reef fishes. During periods of high sea level the deep outer shelf in the Amazon region (50–70 m) has low sedimentation and normal salinity, allowing colonization by sponges and some deep-water reef fishes (Collette & Rützler, 1977). At the same time the surface freshwater plume creates low light conditions, precluding coral development. This narrow area can be used as a corridor between the Brazilian and Caribbean biogeographical provinces by organisms that require clear, normal salinity seawater but not shallow reef habitats or corals.

A recent survey of sponge dwelling fishes off north-eastern Brazil (Rocha *et al.*, 2000) recorded several Brazilian endemic reef fishes, including many of the ones listed above, living in sponge bottoms off north-east Brazil in similar depths to those explored by Collette & Rützler (1977) off the Amazon mouth. Those Brazilian endemics that can live on deep sponge bottoms can potentially cross the Amazon barrier via the sponge corridor. If so, how can speciation occur in these groups? One explanation maybe related to oceanographical characteristics of the Amazon area shelf during Pleistocene glacio-eustatic cycles (Fig. 2). The physical configuration of the Amazon barrier changes dramatically during low sea-level stands: the low salinity waters and sediment are transported directly to the deep-sea fan in the Atlantic Ocean floor. This results in low salinity and high sedimentation conditions across the shelf, so that colonization by neither sponges nor reef fishes is possible, and the corridor between Brazil and Caribbean may be effectively closed during these intervals.

The geological record indicates that only rarely in the last 850 k was the global temperature as warm as it is in the present interglacial period (Gates, 1993). The last glacial period (Wisconsin) lasted for at least 100 k, the earth began warming around 18 k BP, and the oceans reached their present level 6 k BP and have been stable since then (Cox & Moore, 2000). If a glacial period is long enough, or if a species is not able to cross the barrier during the short periods of high sea level, vicariant isolation and speciation is possible.

In the Indo-Pacific, a dynamic barrier related to Pleistocene sea-level fluctuations was hypothesized by Randall (1998), and proposed as an explanation of distributions of sibling species of reef fish. It is possible that sea-level fluctuations also influence the speciation of western Atlantic reef fishes. As noted by Randall (1998) and Brown & Lomolino (1998), barriers are not always static, and variations in sea level can produce successive isolations and connections of areas through the creation of land bridges during low sea-level stands and subsequent inundation of those bridges by rising sea levels.

The intermittent (or semi-porous) nature of the Amazon barrier is indicated by the distribution of fish that occur primarily in Brazil, but also are found in sympatry with closely related taxa north of the Amazon. The following closely related species pairs co-occur in the southern Caribbean (Rocha, 2002): *Centropyge argi* and *C. aurantonotus* (Pomacanthidae), *Priolepis hipoliti* and *P. dawsoni* (Gobiidae), *Sparisoma chrysopterum* and *S. frondosum* (Scaridae) and *S. partitus* and *S. pictus* (Pomacentridae). As those pairs are very similar in general morphology, colour (see Humann

& Deloach, 2002) and ecological requirements (being herein tentatively considered sister species), sympatric speciation in the southern Caribbean followed by colonization of Brazil is unlikely. Also, most of the Brazilian components of those pairs are known to occur in deep sponge bottoms in northeast Brazil (Rocha *et al.*, 2000), indicating their potential to use the sponge corridor under the Amazon outflow to cross the barrier northwards, perhaps aided by the North Brazil Current which flows in a general south–north direction along the Amazon area continental shelf (Peterson & Stramma, 1991). The present-day distribution most probably indicates secondary contact after range expansion towards the southern Caribbean by the Brazilian component, probably through the sponge corridor during an interglacial period.

Moreover, the following species are widely distributed in the Brazilian province but recorded at only a few locations in the southernmost region of the Caribbean province, possibly indicating speciation in the South Atlantic followed by recent crossing of the Amazon towards the Caribbean: *Anisotremus moricandi* (Haemulidae), *Chromis jubauna* (Pomacentridae), *Heteroconger camelopardalis* (Congridae), *Opistognathus* sp. (Opistognathidae) and *Ptereleotris randalli* (Microdesmidae) (Rocha, 2002). In contrast, *Chromis scotti* (Pomacentridae), *Coryphopterus thryx* (Gobiidae), *Haemulon melanurum* (Haemulidae), *Halichoeres bivittatus* (Labridae) (Rocha & Rosa, 2001a) and *Lutjanus mahogoni* (Lutjanidae) (Feitoza, 1999) are widely distributed in the Caribbean, but are found only north of the 'hump' of Brazil (above 10° S). These maybe examples of recent crossing of the barrier southwards.

## The Caribbean region: a centre of origin or accumulation?

Evidence presented indicates that the Caribbean also accumulates fauna. According to Briggs (1974b), when a zoogeographical barrier separates two regions, 'the region that develops the greatest ecosystem stability will function as the more important evolutionary centre and will supply species to the lesser area but will accept few or no species in return', and this seems to be happening in the Caribbean region, as it supplies many species to Brazil and receives only a few in return.

There is no doubt that the Caribbean region has the most diverse reef fish fauna in the Atlantic, with more than 700 species, and is the centre of diversity in the Atlantic Ocean. Some of the most extreme examples are among New World genera that reach their greatest diversity in the Caribbean and are not present in the eastern Atlantic: *Elacatinus* (Gobiidae) with twelve species in the Caribbean (Collin, 1975) and two in Brazil; *Starksia* (Labrisomidae) with at least ten species in the Caribbean and two in the Brazilian coast (Rocha & Rosa, 2001a); and the entire family Chaenopsidae with nine genera in the Caribbean (Randall, 1996) and only two in Brazil (Ramos, 1994; Ramos *et al.*, 2003). Figure 3 shows contour lines of Labroidei diversity; most reef-associated groups in the western Atlantic show a similar pattern.

Recent faunal surveys in the southern Caribbean support the hypothesis that Brazil has exported a few species to the Caribbean. In this scenario the centre of diversity (the Caribbean) is enriched by the introduction of species from a
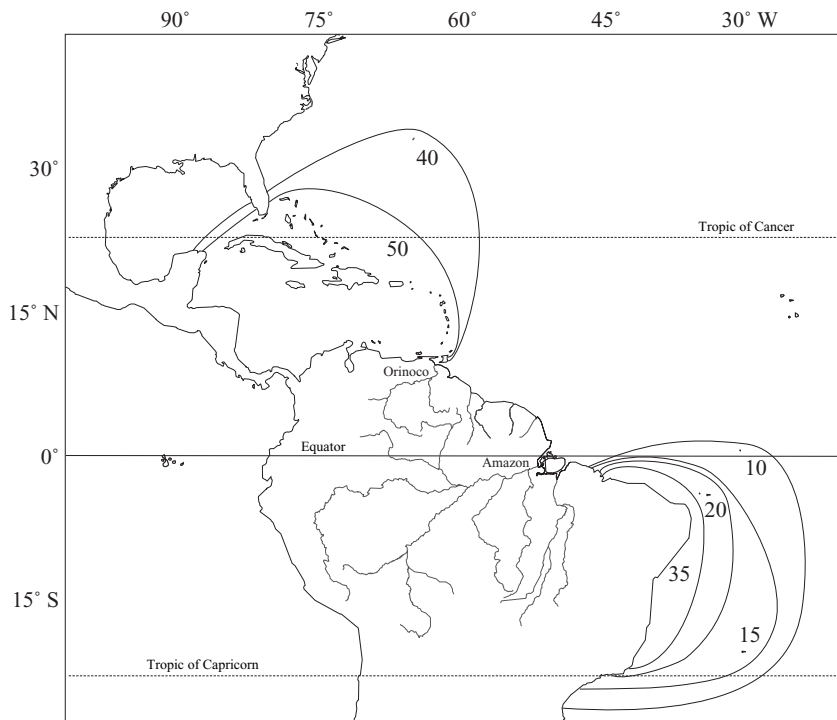
Figure 3 Contours of species diversity of the suborder Labroidei in the tropical western Atlantic.
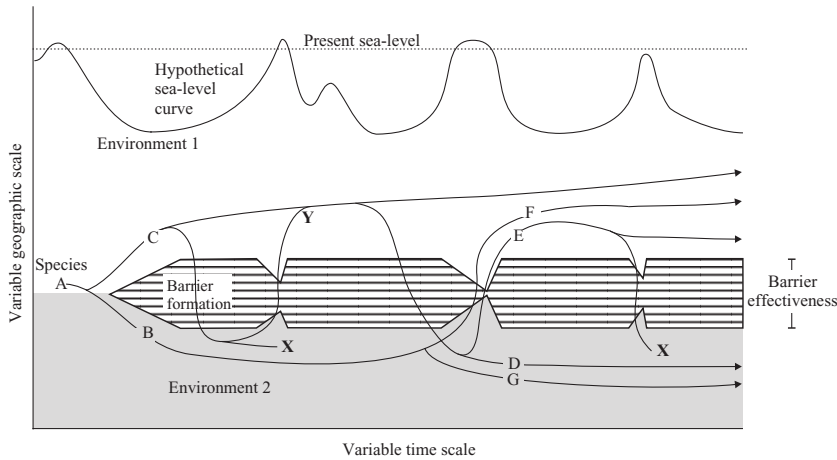
Figure 4 Schematic representation of the operation of the Amazon barrier on 'Species A'. Letters represent points where reproductive isolation occurs, splitting the A lineage into species B–C, D–E and F–G. X represents extinctions, Y coalescence. The sea-level curve is hypothetical and does not reflect the actual history.

peripheral area (Brazil). Thus the Caribbean may be a centre of origin and at the same time a centre of accumulation, by receiving a few species from peripheral areas (Fig. 4). Randall (1998) and Paulay (1997) reached a similar conclusion to explain the high diversity of the Indo-Malayan region.

Speciation in the western Atlantic: dispersal or vicariance?

In dispersal models speciation proceeds by rare colonization across pre-existing barriers, whereas in vicariance models speciation is achieved by the appearance of barriers fragmenting the ranges of widely distributed taxa (Humphries *et al.*, 1988).

Interestingly, geminate reef fish species pairs separated by the Amazon, which started discharging large amounts of sediment and freshwater in the Atlantic *c.* 10 Ma, look more similar to each other than pairs separated by the Isthmus of Panama, which closed *c.* 3 Ma (a clearly vicariant barrier). The dispersal model may explain this contradiction: many reef fish species have the potential to cross long distances of open ocean during their pelagic larval stage, and sporadic dispersal between isolated populations may retard the process of speciation (Avise, 2000).

Intermittent vicariance can also explain the similarity between geminate species pairs in the western Atlantic: considering the Amazon outer shelf as a corridor, and sea levels as switches, opening and closing this corridor, vicariance may operate during low sea levels when the barrier is more efficient. When the barrier weakens and the corridor re-opens in high sea-level stands, some species can disperse and isolated populations may potentially coalesce (Bowen *et al.*, 2001). However, if reproductive incompatibility is attained during one of the glacial periods, then the geminate species will subsequently follow distinct evolutionary paths.

A third, and more probable explanation is that both fluctuations in sea level (intermittent vicariance) and extended pelagic larval stage of some species (dispersal) decrease the effectiveness of the Amazon barrier (Fig. 4). If we treat barrier effectiveness as a percentage, 0% meaning free gene flow between populations, and 100% meaning complete isolation, a barrier that is 100% effective (the Isthmus of Panama) would promote speciation much faster than a less effective barrier such as the Amazon area shelf.

Environmental differences driving species distributions and speciation on Brazilian oceanic islands

All hypotheses above are based on the fact that an effective barrier has separated Brazilian and Caribbean populations for a relatively long period. Another explanation for speciation in western Atlantic reef fishes would be ecological speciation, which can occur without a physical barrier against dispersal. According to Schluter (2001) 'ecological speciation occurs when divergent selection on traits between populations or subpopulations in contrasting environments leads directly or indirectly to the evolution of reproductive isolation', either in allopatry, parapatry or sympatry. Mayr (1947) also recognized the importance of ecology in speciation, but regarded the process as much less frequent than geographical speciation.

The islands of the Caribbean Sea are characterized by clear waters all year round, relatively stable environmental conditions, and bottom sediments largely composed of calcium carbonate (Robins, 1971), whereas the north-eastern Brazilian coast is a typical continental environment, with terrigenous substrates, influenced by run off from rivers and high turbidity caused by wind driven suspension of bottom sediments (Leao & Dominguez, 2000). These differences may generate divergent selection pressures in the islands vs. mainland habitats, potentially promoting ecological speciation, even in the presence of some migration between populations.

Two groups of oceanic islands off Brazil appear to have similar environmental conditions, except for a much lower coral diversity, to those found in the Caribbean. The first and closer to the mainland are Fernando de Noronha Archipelago (340 km from the coast) and Atol das Rocas (270 km from the coast), the second is the very isolated

island of St Paul's Rocks (1000 km from the coast), just a few km north of the Equator (Fig. 1). Noronha and Rocas are probably formed by the Noronha hotspot, and the oldest volcanic rocks in Noronha were aged between 8 and 10 Myr (Rivalenti *et al.*, 2000), thus, if Rocas is formed downstream by the same hotspot it would be a few million years older. Saint Paul's Rocks is located close to the mid-Atlantic ridge and two putative ages are given for it: 9.5 Myr if it originated from a nearby ridge, or 35 Myr if it originated from a farther oceanic ridge (Melson *et al.*, 1972). They are all influenced by the warm South Equatorial Current, and are located upstream from the Brazilian coast, with the possible exception of St Paul's Rocks that is seasonally influenced by the Equatorial Countercurrent (Fig. 1, Edwards & Lubbock, 1983).

Several fish species show a biogeographical link between the Caribbean and Brazilian oceanic islands. The puddingwife (*Halichoeres radiatus*, Labridae) is widely distributed in the Caribbean region, and is also found in the Brazilian oceanic islands of St Paul's Rocks, Fernando de Noronha and Atol das Rocas (Rocha & Rosa, 2001b). The puddingwife's sister species, *Halichoeres brasiliensis*, is distributed throughout the Brazilian tropical coast. A similar distribution is found in *Elacatinus randalli*, which is found on the Caribbean and Fernando de Noronha off Brazil (Sazima & Moura, 2000) whereas *E. figaro* is endemic to the Brazilian coast. In addition, *Haemulon chrysargyreum* occurs in Fernando de Noronha, Atol das Rocas and the Caribbean, but is absent from the Brazilian coast. If there is sufficient migration to morphologically homogenize populations of *H. radiatus* and *E. randalli* separated by *c.* 4000 km (distance of open ocean between Atol das Rocas and the Caribbean), 'why can't this gene flow continue to the Brazilian coast?', or 'why can't *H. chrysargyreum* colonize the coast, only 270 km away from Atol das Rocas?'

Joyeux *et al.* (2001) suggested that this pattern might be a result of relictual distribution of a once wider geographical range. However, I believe that the simplest explanation is ecological speciation; the insular and coastal populations are subject to divergent selection pressures that are sufficient to overwhelm the homogenizing effect of sporadic gene flow. In extreme cases, environmental differences may prevent the colonization of continental locations by strictly oceanic species (or vice versa). Veron (1995) proposed a similar hypothesis for the coral fauna of the Indo-West Pacific to explain the greater similarity between widely separated locations with comparable physical environments, than that of adjacent locations with different environments. He concluded that environmental factors are more important than connectivity through currents and distance.

The distributions of some fishes in the north Atlantic may also be alternatively explained by the hypothesis of ecological speciation driven by environmental differences in continental vs. insular habitats. The following species show an insular vs. continental distribution: *Holacanthus ciliaris* (common throughout the Caribbean, Brazilian coast and islands), and *H. bermudensis* (mainly Gulf of Mexico and Florida, but hybrids between *H. ciliaris* and *H. bermudensis*

are found in Bermuda), *Ptereleotris helenae* (Caribbean islands) and *P. caliurus* (coastal Florida). The Gulf Stream has been tentatively considered a barrier between Florida and the Caribbean; however, some of these taxa are found on both sides of the barriers (like *H. bermudensis* at the Bahamas), weakening the hypothesis of vicariance. Moreover, the subspecies *Stathmonotus stahli stahli* (lesser Antilles) and *S. stahli tekla* (greater Antilles, coastal Central America and Florida) are allopatric, but each occupies a wide geographical area, and there is no apparent barrier between their ranges.

The southern oceanic islands

Oceanographical conditions at the Brazilian southern oceanic islands are very different from those at the north-east. Trindade and Martim Vaz are located 1160 km from the south-eastern Brazilian coast, and are downstream from the coast, under the influence of the Brazil Current. They are the youngest Brazilian oceanic islands (3–3.5 Myr), and were subject to a recent faunal survey (Gasparini & Floeter, 2001) and zoogeographical study (Floeter & Gasparini, 2000). There are six, relatively shallow (10–110 m) seamounts between these islands and the mainland. The seamounts are about 250 km apart, and potentially increase the population connections between the islands and the mainland.

Floeter & Gasparini (2000) found a biogeographical split between the South Atlantic oceanic islands and the ensemble of the Brazilian mainland, the Caribbean and Bermuda using a cluster analysis. Their study was based on presence and absence of all reef-associated fish species, and grouped Trindade Island with the north-eastern Brazilian oceanic islands. This was probably because of their similar total number of species, which is smaller than the remaining locations. In contrast, Rocha & Rosa (2001a) considered only distributions of labroid fishes and found the major division to lie between the North and South Atlantic. Trindade was grouped with the Brazilian coastal sites, outside the cluster formed by the north-eastern Brazilian islands (St Paul's Rocks and Atol das Rocas). Major current tracks (Fig. 1), the presence of seamounts between Trindade and the mainland and the close relationship between the island's endemics and coastal Brazil species (Gasparini & Floeter, 2001) clearly indicate that Trindade is more closely related to the Brazilian mainland than to the other Brazilian offshore islands.

Disjunct distributions

Anti-tropical and disjunct distributions are well-known phenomena in Indo-Pacific fishes, as reviewed by Briggs (1987) and Randall (1998). In the western Atlantic, Floeter *et al.* (2001) noted that four groupers (*Epinephelus niveatus*, *Mycteroperca microlepis*, *M. tigris* and *Serranus phoebe*) and one parrotfish (*Sparisoma atomarium*) were present in south-eastern Brazil and in the Caribbean, but absent or rare at the north-eastern Brazilian coast. Joyeux *et al.* (2001) stated that the wrasse *Halichoeres bathyphillus* and the damselfish *Chromis flavicauda* present 'strongly accentuated

antitropical distributions'. However, neither the wrasse, which is not *H. bathyphillus*, but a new species probably endemic to south-eastern Brazil (R. L. Moura, pers. comm.), nor the damselfish, which is abundant in and was described from low latitude waters (5° S) (Rocha *et al.*, 1998; Smith-Vaniz *et al.*, 1999), seem to represent anti-tropical distributions.

There are at least three species that may have disjunct distributions, being abundant in south-east Brazil and the Caribbean, but absent from most of the NE Brazilian coast: *Mycteroperca microlepis* (Serranidae), *Sparisoma atomarium* (Scaridae) and *Chaetodon sedentarius* (Chaetodontidae). The grouper *M. microlepis* may represent the only truly anti-tropical distribution in Atlantic reef fishes: it is found in cold waters of the Gulf of Mexico and north-east Florida, above the Tropic of Cancer (Humann & Deloach, 2002), and from Espirito Santo, slightly above the Tropic of Capricorn (21° S) to Santa Catarina (27° S), south-eastern Brazil (Figueiredo & Menezes, 1980), but has never been recorded at the Caribbean or north-eastern Brazil.

The parrotfish *S. atomarium* is common in the Caribbean (Randall, 1996; Humann & Deloach, 2002) and south-eastern Brazil (Joyeux *et al.*, 2001), but apparently absent from north-east Brazil (Rocha *et al.*, 1998; Rocha & Rosa, 2001a). The butterflyfish *C. sedentarius* occurs in the Caribbean (Randall, 1996), Parcel de Manuel Luiz reefs (Rocha & Rosa, 2001a), and south-eastern Brazil (Menezes & Figueiredo, 1985), but was not recorded in the eastern region of north-east Brazil, or the 'hump' of Brazil (Rocha *et al.*, 1998). Joyeux *et al.* (2001) suggested that this pattern is a consequence of the loss of the centre of distribution, or tropical extinction, however the centre of distribution of these species appears to be the Caribbean, not north-eastern Brazil. The geomorphology of the continental margin around the 'hump' of Brazil may offer clues to explain the absence of those species. The continental shelf in the area is very narrow (22–30 km), and relatively shallow (60–70 m maximum depth) (Chaves, 1979), thus the slope would be exposed during low sea levels, and habitat availability would be greatly reduced, probably causing extinction in many taxa.

CONCLUSIONS

The Amazon freshwater and sediment outflow is a strong barrier to shallow water reef fish and other organisms, and it is probably responsible for most of the endemism observed in Brazilian coastal habitats. However, during intervals of high sea level it can be crossed by fish that have broad habitat preferences, capable of living in deep sponge communities (50–70 m) off the Amazon outer shelf. The co-occurrence of closely related species pairs in the southern Caribbean indicates that speciation may occur during periods of low sea level, followed by dispersal across the barrier during high sea level. An alternative (but not mutually exclusive) hypothesis is that there is continuous, but relatively small dispersal between Brazil and the Caribbean, and ecology plays a larger role in shaping diversity in the western

Atlantic than previously thought, through divergent selection in environmentally different habitats.

There are two distinct groups of oceanic islands in Brazil, one in the north-east corner, with strong oceanic characteristics, little influence from coastal waters, and affinities with the Brazilian mainland, the Caribbean and central Atlantic islands; and another in the south-east, strongly influenced by the coast, and with affinities mostly with the Brazilian mainland. The geomorphology of the continental shelf in north-east Brazil indicates that the few cases of disjunct distributions are probably better explained by extinction as a result of habitat loss during low sea-level periods.

Despite recent advances in the knowledge of Brazilian reef fishes, there is still a need for reliable faunal surveys of the north-eastern Brazilian coast and oceanic islands. There is no recent checklist for fishes of Fernando de Noronha or Atol das Rocas, and recent visits to St Paul's Rocks by the author and colleagues indicate that several additions will be made to the checklist of Lubbock & Edwards (1981). Deep reefs off north-east Brazil are also understudied and may sustain a diverse reef fish community not seen on the adjacent near-shore, ecologically distinct reefs. The continental islands of the southern Caribbean (Trinidad and Tobago) form another area of interest that lacks reliable surveys. Once checklists from those areas are available, decisive evidence in favour of vicariance, dispersal and/or ecological speciation may become clear.

Comparative phylogeographical studies of closely related taxa may also contribute to the understanding of speciation processes in the tropical western Atlantic. Of special interest are the comparisons among taxa with varying levels of habitat preferences, but similar dispersal capabilities. If the pattern of genetic divergences strongly correlated to habitat preferences observed by Rocha *et al.* (2002), is confirmed in other taxa, then the hypothesis of ecology as a driving force in reef fish evolution will be favoured. Genus level phylogenies, either morphological or molecular, would also be welcome, especially in groups where endemism is greater such as blennies and gobies, but the relationships are less obvious, possibly because of greater phylogenetic depth. Population genetics surveys of species that have disjunct distributions may reveal if those species were recently extinct in the narrow NE Brazil shelf or if they are relicts of a wider, older distribution.

REFERENCES

Allison, M.A., Lee, M.T., Ogston, A.S. & Aller, R.C. (2000) Origin of Amazon mudbanks along the northeastern coast of South America. *Marine Geology*, **163**, 241–256.

Avise, J.C. (2000) *Phylogeography: the history and formation of species*, p. 447. Harvard University Press, Cambridge.

Barton, N.H. (1988) Speciation. *Analytical biogeography: an integrated approach to the study of animal and plant distributions* (ed. by A.A. Myers and P.S. Giller), pp. 185–218. Chapman and Hall, New York.

Bellwood, D.R. & Wainwright, P.C. (2002) The history and biogeography of fishes on coral reefs. *Coral reef fishes. Dynamics and diversity on a complex ecosystem* (ed. by P.F. Sale), pp. 5–32. Academic Press, New York.

Bowen, B.W., Bass, A.L., Rocha, L.A., Grant, W.S. & Robertson, D.R. (2001) Phylogeography of the trumpetfish (*Aulostomus* spp.): ring species complex on a global scale. *Evolution*, **55**, 1029–1039.

Briggs, J.C. (1974a) *Marine zoogeography*. McGraw-Hill, New York.

Briggs, J.C. (1974b) Operation of zoogeographic barriers. *Systematic Zoology*, **23**, 248–256.

Briggs, J.C. (1987) Antitropical distribution and evolution in the Indo-West Pacific Ocean. *Systematic Zoology*, **36**, 237–247.

Briggs, J.C. (1999) Modes of speciation: marine Indo-West Pacific. *Bulletin of Marine Science*, **65**, 645–656.

Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn, p. 692. Sinauer Associates, Inc., Sunderland, MA.

Carvalho-Filho, A. (1999) *Peixes costa brasileira*, 3rd edn, p. 320. Marca D'Agua, Sao Paulo.

Chaves, H.A.F. (1979) *Projeto REMAC: geomorfologia da margem continental brasileira e areas oceanicas adjacentes*. Serie Projeto REMAC, Rio de Janeiro.

Collette, B.B. & Rützler, K. (1977) Reef fishes over sponge bottoms off the mouth of the Amazon River. *Third International Coral Reef Symposium*, Miami, pp. 305–310.

Collin, P. (1975) *The neon gobies*, p. 304. TFH Publications, Inc., Neptune City, NJ.

Cox, C.B. & Moore, P.D. (2000) *Biogeography: an ecological and evolutionary approach*, 6th edn, p. 298. Blackwell Science, Oxford.

Curtin, T.B. (1986) Physical observations in the plume region of the Amazon River during peak discharge – II. Water masses. *Continental Shelf Research*, **6**, 53–71.

Curtin, T.B. & Legeckis, R.V. (1986) Physical observations in the plume region of the Amazon River during peak discharge – I. Surface variability. *Continental Shelf Research*, **6**, 31–51.

Degens, E.T., Kempe, S. & Richey, J.E. (1991) Summary: biogeochemistry of major world rivers. *Biogeochemistry of major world rivers* (ed. by E.T. Degens, S. Kempe and J.E. Richey), pp. 323–347. Wiley, New York.

Edwards, A. & Lubbock, R. (1983) Marine zoogeography of St Paul's Rocks. *Journal of Biogeography*, **10**, 65–72.

Emery, A.R. (1973) Atlantic bicolor damselfish (Pomacentridae): a taxonomic question. *Copeia*, **1973**, 590–594.

Feitoza, B.M. (1999) *Composicao da ictiofauna recifal do talude continental da Paraiba*, p. 79. Unpublished BSc Thesis. Departamento de Zoologia, Joao Pessoa.

Figueiredo, J.L. & Menezes, N.A. (1980) *Manual de peixes marinhos do sudeste do Brasil*, p. 90. University of Sao Paulo, Sao Paulo.

Floeter, S.R. & Gasparini, J.L. (2000) The southwestern Atlantic reef fish fauna: composition and zoogeographic patterns. *Journal of Fish Biology*, **56**, 1099–1114.

Floeter, S.R. & Gasparini, J.L. (2001) Brazilian endemic reef fishes. *Coral Reefs*, **19**, 292.

Floeter, S.R., Guimarães, R.Z.P., Rocha, L.A., Ferreira, C.E.L., Rangel, C.A. & Gasparini, J.L. (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecology and Biogeography*, **10**, 423–432.

Gasparini, J.L. & Floeter, S.R. (2001) The shore fishes of Trindade Island, western South Atlantic. *Journal of Natural History*, **35**, 1639–1656.

Gasparini, J.L., Rocha, L.A. & Floeter, S.R. (2001) A new *Ptereleotris* (Teleostei: Microdesmidae) from the Brazilian coast. *Aqua, Journal of Ichthyology and Aquatic Biology*, **4**, 109–114.

Gates, D.M. (1993) *Climate change and its biological consequences*, p. 280. Sinauer Associates, Inc., Sunderland, MA.

Gilbert, C.R. (1972) Characteristics of the Western Atlantic Reef-fish Fauna. *Quarterly Journal of the Florida Academy of Sciences*, **35**, 130–144.

Gilbert, C.R. (1977) Status of the western South Atlantic apogonid fish *Apogon americanus*, with remarks on other Brazilian species. *Copeia*, **1977**, 25–32.

Greenfield, D.W. (1988) A review of the *Lythrypnus mowbray* complex (Pisces: Gobiidae), with the description of a new species. *Copeia*, **1988**, 460–470.

Greenfield, D.W. & Woods, L.P. (1974) *Eupomacentrus diencaeus* Jordan and Rutter, a valid species of damselfish from the western tropical Atlantic. *Fieldiana Zoology*, **65**, 9–20.

Heiser, J.B., Moura, R.L. & Robertson, D.R. (2000) Two new species of Creole Wrasse (Labridae: *Clepticus*) from opposite sides of the Atlantic. *Aqua, Journal of Ichthyology and Aquatic Biology*, **4**, 67–76.

Helfman, G.S., Collette, B.B. & Facey, D.E. (1997) *The diversity of fishes*, p. 528. Blackwell Science, Inc., Malden, MA.

Hoorn, C. (1994) An environmental reconstruction of the palaeo-Amazon River system (Middle-Late Miocene, NW Amazonia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **112**, 187–238.

Hoorn, C. (1996) Miocene deposits in the Amazonian foreland basin. *Science* **273**, 122.

Hoorn, C., Guerrero, J., Sarmiento, G.A. & Lorente, M.A. (1995) Andean tectonics as a cause for changing patterns in Miocene northern South America. *Geology*, **23**, 237–240.

Humann, P. & Deloach, N. (2002) *Reef fish identification*, 3rd edn, p. 481. New World Publications, Jacksonville.

Humphries, C.J., Ladiges, P.Y., Roos, M. & Zandee, M. (1988) Cladistic biogeography. *Analytical biogeography: an integrated approach to the study of animal and plant distributions* (ed. by A.A. Myers and P.S. Giller), pp. 371–404. Chapman and Hall, New York.

Joyeux, J.C., Floeter, S.R., Ferreira, C.E.L. & Gasparini, J.L. (2001) Biogeography of tropical reef fishes: the South Atlantic puzzle. *Journal of Biogeography*, **28**, 831–841.

Kuehl, S.A., DeMaster, D.J. & Nittrouer, C.A. (1986) Nature of sediment accumulation on the Amazon continental shelf. *Continental Shelf Research*, **6**, 209–225.

Leao, Z.M.A.N. (1986) *Guia para identificacao dos corais do Brasil*, p. 57. Universidade Federal da Bahia, Salvador, Brasil.

Leao, Z.M.A.N. & Dominguez, J.M.L. (2000) Tropical coast of Brazil. *Marine Pollution Bulletin*, **41**, 112–122.

Lentz, S.J. (1995) The Amazon River plume during AMASS-EDS: subtidal current variability and the importance of wind forcing. *Journal of Geophysical Research*, **100**, 2377–2390.

Lieske, E. & Myers, R. (1994) *Coral reef fishes*, p. 400. Harper-Collins, London.

Lopez, M. (2001) Architecture and depositional pattern of the Quaternary deep-sea fan of the Amazon. *Marine and Petroleum Geology*, **18**, 479–486.

Lubbock, R. & Edwards, A. (1981) The fishes of Saint Paul's Rocks. *Journal of Fish Biology*, **18**, 135–157.

Masson, S. & Delecluse, P. (2001) Influence of the Amazon River runoff on the tropical Atlantic. *Physics and Chemistry of the Earth, Part B: Hydrology, Oceans and Atmosphere*, **26**, 137–142.

Mayr, E. (1947) Ecological factors in speciation. *Evolution*, **1**, 263–288.

Melson, W.G., Hart, S.R. & Thompson, G. (1972) St Paul's Rocks, equatorial Atlantic; petrogenesis, radiometric ages, and implications on sea-floor spreading. *Memoirs of the Geological Society of America*, **132**, 241–272.

Menezes, N.A. & Figueiredo, J.L. (1985) *Manual de peixes marinhos do sudeste do Brasil*, p. 105. University of Sao Paulo, Sao Paulo.

Milliman, J.D. & Meade, R.H. (1983) World-wide delivery of river sediment to the oceans. *Journal of Geology*, **91**, 1–21.

Moura, R.L., Figueiredo, J.L. & Sazima, I. (2001) A new parrotfish (Scaridae) from Brazil, and revalidation of *Sparisoma amplum* (Ranzani, 1842), *Sparisoma frondosum* (Agassiz, 1831), *Sparisoma axillare* (Steindachner, 1878) and *Scarus trispinosus* Valenciennes, 1840. *Bulletin of Marine Science*, **68**, 505–524.

Muss, A., Robertson, D.R., Stepien, C.A., Wirtz, P. & Bowen, B.W. (2001) Phylogeography of *Ophioblennius*: the role of ocean currents and geography in reef fish evolution. *Evolution*, **55**, 561–572.

Nittrouer, C.A. & DeMaster, D.J. (1986) Sedimentary processes on the Amazon continental shelf: past, present and future research. *Continental Shelf Research*, **6**, 5–30.

Ormond, R.F.G. & Roberts, C.M. (1997) The biodiversity of coral reef fishes. *Marine biodiversity: patterns and processes* (ed. by R.F.G. Ormond, J.D. Gage and M.V. Angel), pp. 216–257. Cambridge University Press, Cambridge.

Paulay, G. (1997) Diversity and distribution of reef organisms. *Life and death on coral reefs* (ed. by C.E. Birkeland), pp. 298–353. Chapman & Hall, New York.

Peterson, R.G. & Stramma, L. (1991) Upper-level circulation in the South Atlantic Ocean. *Progress in Oceanography*, **26**, 1–73.

Potter, P.E. (1997) The Mesozoic and Cenozoic paleodrainage of South America: a natural history. *Journal of South American Earth Sciences*, **10**, 331–344.

Ramos, R.T.C. (1994) Análise da composição e distribuição da fauna de peixes demersais da plataforma continental da Paraíba e Estados vizinhos. *Revista Nordestina de Biologia*, **9**, 1–30.

Ramos, R.T.C., Rocha, C.R. & Rocha, L.A. (2003). A new species of *Emblemaria* (Teleostei: Chaenopsidae) from Northern Brazil. *Copeia*, **2003**, 95–98.

Randall, J.E. (1996) *Caribbean reef fishes*, 3rd edn, p. 368. TFH Publications, Neptune City, NJ.

Randall, J.E. (1998) Zoogeography of shore fishes of the Indo-Pacific region. *Zoological Studies*, **37**, 227–268.

Rivalenti, G., Mazzucchelli, M., Girardi, V.A.V., Vannucci, R., Berbieri, M.A., Zanetti, A. & Goldstein, S.L. (2000) Composition and processes of the mantle lithosphere in northeastern Brazil and Fernando de Noronha: evidence form mantle xenoliths. *Contributions in Mineral Petrology*, **138**, 308–325.

Robins, C.R. (1971) Distributional patterns of fishes from coastal and shelf waters of the tropical western Atlantic. Symposium on investigations and resources of the Caribbean Sea and adjacent regions. FAO, *Fisheries Report* 71–2, Rome.

Rocha, L.A. (2002) Brazilian reef fishes. *Reef fish identification: Florida, Caribbean, Bahamas* (ed. by P. Humann and N. Deloach), pp. 462–479. New World Publications, Jacksonville.

Rocha, L.A. & Rosa, I.L. (1999) New species of *Haemulon* (Teleostei: Haemulidae) from the northeastern Brazilian coast. *Copeia*, **1999**, 447–452.

Rocha, L.A. & Rosa, I.L. (2001a) Baseline assessment of reef fish assemblages of Parcel Manuel Luiz Marine State Park, Maranhao, north-east Brazil. *Journal of Fish Biology*, **58**, 985–998.

Rocha, L.A. & Rosa, R.S. (2001b) *Halichoeres brasiliensis* (Bloch, 1791), a valid wrasse species (Teleostei Labridae) from Brazil, with notes on the Caribbean species *Halichoeres radiatus* (Linnaeus, 1758). *Aqua, Journal of Ichthyology and Aquatic Biology*, **4**, 161–166.

Rocha, L.A., Rosa, I.L. & Rosa, R.S. (1998) Peixes recifais da costa da Paraíba, Brasil. *Revista Brasileira de Zoologia*, **15**, 553–566.

Rocha, L.A., Rosa, I.L. & Feitoza, B.M. (2000) Sponge-dwelling fishes of northeastern Brazil. *Environmental Biology of Fishes*, **59**, 453–458.

Rocha, L.A., Guimarães, R.Z.P. & Gasparini, J.L. (2001) Redescription of the Brazilian wrasse *Thalassoma noronhanum* (Boulenger, 1890) (Teleostei: Labridae). *Aqua, Journal of Ichthyology and Aquatic Biology*, **4**, 105–108.

Rocha, L.A., Bass, A.L., Robertson, D.R. & Bowen, B.W. (2002) Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). *Molecular Ecology*, **11**, 243–252.

Rosa, R.S., Rosa, I.L. & Rocha, L.A. (1997) Diversidade da ictiofauna de poças de maré da praia do Cabo Branco, João Pessoa, Paraíba, Brasil. *Revista Brasileira de Zoologia*, **14**, 201–212.

Rosa, R.S., Nunes, C.R. & Rocha, L.A. (in press) Diversidade da ictiofauna do nordeste brasileiro: uma compilacao das especies de teleosteos marinhos costeiros. *Revista Nordestina de Biologia*.

Sarver, S.K., Silberman, J.D. & Walsh, P.J. (1998) Mitochondrial DNA sequence evidence supporting the recognition of

two subspecies of the Florida spiny lobster *Panulirus argus*. *Journal of Crustacean Biology*, **18**, 177–186.

Sazima, I. & Moura, R.L. (2000) Shark (*Charcharhinus perezi*), cleaned by the goby (*Elacatinus randalli*), at Fernando de Noronha Archipelago, western South Atlantic. *Copeia*, **2000**, 297–299.

Sazima, I., Gasparini, J.L. & Moura, R.L. (1998) *Gramma brasiliensis*, a new basslet from the western South Atlantic (Perciformes: Grammatidae). *Aqua, Journal of Ichthyology and Aquatic Biology*, **3**, 39–43.

Schluter, D. (2001) Ecology and the origin of species. *Trends in Ecology and Evolution*, **16**, 372–380.

Smith, C.L. (1997) *National Audubon Society field guide to tropical marine fishes of the Caribbean, the Gulf of Mexico, Florida, the Bahamas and Bermuda*, p. 720. Alfred A. Knopf, New York.

Smith-Vaniz, W.F., Collette, B.B. & Luckhurst, B.E. (1999) *Fishes of Bermuda: History, zoogeography, annotated checklist, and identification keys*, p. 424. American Society of Ichthyologists and Herpetologists, Special Publication 4, Allen Press, Lawrence, Kansas.

Szpilman, M. (2000) *Peixes marinhos do Brasil. Guia pratico de identificacao*, 2nd edn, p. 288. Aqualung, Rio de Janeiro.

Vermeij, G.J. (1978) *Biogeography and adaptation: patterns of marine life*, p. 332. Harvard University Press, Cambridge, MA.

Veron, J.E. (1995) *Corals in space and time: biogeography and evolution of the Scleractinia*, p. 321. Cornell University Press, Ithaca, NY.

Williams, J.T. & Smart, A.M. (1983) Redescription of the Brazilian labrisomid fish Starksia brasiliensis. *Proceedings of the Biological Society of Washington*, **96**, 638–644.

BIOSKETCH

Luiz A. Rocha is a post-doctoral fellow at the Smithsonian Tropical Research Institute, Panama. His research focuses on population genetics, systematics, biogeography and evolution of reef fishes. He has worked on Atlantic reef fishes for the last 10 years, with extensive field work in Brazil and the Caribbean.