



Biogeography of tropical reef fishes: the South Atlantic puzzle

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Abstract

Aim To reveal underlying distributional mechanisms of tropical reef fishes in the South Atlantic.

Location The tropical South Atlantic, with emphasis on the Brazilian province.

Methods The disjunct distributions of thirty-five reef fish species occurring in the Brazilian Province were analysed to allow a better understanding of present biogeographical patterns. To avoid potential bias because of taxonomic problems or misidentification, we only included families taxonomically well documented, with conspicuous species, and relatively easy to identify.

Results The low-level differentiation between Caribbean and Brazilian species/populations, as well as the presence of restricted populations of a few northern or southern species on the opposite side of the Amazon River, clearly indicate that this barrier to dispersion can be occasionally bridged. Transoceanic dispersal appears to be frequent and to occur along three routes: from the Caribbean to North East Atlantic, from northern Brazil to the Gulf of Guinea, and from Africa to southern Brazil. Intermediate stepping-stones are apparently not required along transatlantic routes because of the rarity of consecutive colonizations. However, intermediate stopovers are persistently used along short routes. In all cases, the long-term success of colonists, i.e. the establishment of stable local populations, appears to depend upon ecological factors.

Main conclusions The puzzling patterns of distribution found in the South Atlantic seem primarily the outcome of allopatric speciation and of the interaction of long distance dispersal abilities and ecological processes. Successfulness of the colonization of remote sites appears to be less dependent from dispersal ability than upon persistence ability or settlement preferences.

Keywords

Dispersal, islands, disjunct, colonization, speciation, Amazon barrier, Brazilian province, distribution.

INTRODUCTION

The South Atlantic Ocean has some peculiar biogeographical and ecological characteristics. The most obvious is the

freshwater outflow from the Amazon River that apparently acts as a major biogeographical barrier separating the shore fish faunas of Brazil and the Caribbean (Briggs, 1995; Floeter & Gasparini, 2000). The oceanic islands of the tropical South Atlantic are widely scattered and support shelf faunas that exhibit reduced species diversity and other effects of isolation (Floeter & Gasparini, 2000). Considering that the islands vary in age, size and distance from other shores, comparative studies of their faunas can reveal

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considerable information about general patterns of evolution and distribution (cf. Robertson, 2001). St Helena is the one of the world's most isolated tropical islands (located from 1270 km Ascension and 1870 km from Africa). Others lying far out from shore are Ascension, Trindade and St Paul's Rocks (Fig. 1a). Closer to the continental shores, but still far enough to demonstrate the effects of isolation, are other island groups located on both sides of the tropical South Atlantic. In addition to the oceanic islands, there are submerged seamounts (the Fernando de Noronha and the Vitória-Trindade chains) that remain to be explored.

Until recently, the tropical western South Atlantic presented a conspicuous gap in our knowledge of the distribution of tropical reef fishes (cf. Sale, 1991). In the late 1990s, an increase in exploration and specimen collection resulted in the publication of considerable new information about the geographical distribution of many species (e.g. Moura *et al.*, 1999; Floeter *et al.*, 2001), the description of new species (e.g. Sazima *et al.*, 1998; Rocha & Rosa, 1999; Heiser *et al.*, 2000; Burgess, 2001; Moura *et al.*, 2001), the first comprehensive collections for certain sites (e.g. Rosa & Moura, 1997; Rocha *et al.*, 1998; Gasparini & Floeter, 2001), and the first works on phylogeography (Bernardi *et al.*, 2000; Bowen *et al.*, 2001; Muss *et al.*, 2001). Also, there is now available new work on the tectonic, eustatic, climatic and oceanographic characteristics of the tropical Atlantic (e.g. Zebiak, 1993; Arz *et al.*, 1999; Knoppers *et al.*, 1999; Stramma & Schott, 1999). These recent advances permit us to draw a first picture of some aspects of the biogeography of the region.

METHODS

This study is based on the recorded occurrences of thirty-five tropical teleost species primarily associated with hard substrata (rocky shores, coral and coralline algae reefs), here referred to as 'reef fishes', in the South Atlantic continental shelf and oceanic islands (Fig. 1a). To avoid potential bias caused by taxonomic problems or misidentification, we only included families taxonomically well documented (e.g. Pomacanthidae, Labridae, Scaridae), with conspicuous (e.g. generally common, large, non-cryptic, colourful, etc.) species, and relatively easy to identify (Table 1). Species not presenting disjunct distributions (i.e. present on the coast while absent in all islands, or endemic to one lone island) were excluded because such 'even' distributions are unlikely to bring much insight. The distribution patterns have been determined primarily through original studies by the authors and colleagues, as well as compilation of data from the literature (e.g. Lubbock, 1980; Lubbock & Edwards, 1981; Edwards, 1990; Afonso *et al.*, 1999; Smith-Vaniz *et al.*, 1999). The species were considered to be resident at a particular location if they were sufficiently abundant to have established self-recruiting populations or to be vagrants if exceedingly rare and probably recruited from other sites. Although the Manuel Luis Reefs are not considered to be an oceanic island, they were included as such in this study for

their ecological and biogeographical significance, as they are the first reef formation south of the Amazon plume (Rocha & Rosa, 2001a).

RESULTS AND DISCUSSION

Distribution patterns

The South Atlantic reef fish biogeography proved to be an intricate tapestry (Fig. 1). The thirty-five selected species displayed intriguing distribution patterns. The wrasse *Halichoeres bathyphilus* and the damselfish *Chromis flavicauda* present strongly accentuated antitropical distributions (Fig. 1c). Other species such as the groupers *Epinephelus niveatus* and *Mycteroperca microlepis* and the parrotfish *Sparisoma atomarium* show discontinuous distribution on American coastal reefs (Fig. 1c). The tropical extinction theory (the loss of the centre of distribution) is commonly evoked to explain this type of distribution pattern (Théel, 1886; Briggs, 1995). Three species found in the south-west are presumed immigrants from African waters the trumpetfish *Aulostomus strigosus*, the grouper *Epinephelus marginatus* and the surgeonfish *Acanthurus monroviae* (Fig. 1d). Twenty-one species are indistinguishable from their Caribbean counterparts (Fig. 1e–i). The remaining six species (Fig. 1c and i) are southern endemics the butterflyfish *Prognathodes brasiliensis*, the damselfish *Stegastes fuscus*, the wrasses *Bodianus insularis*, *Halichoeres brasiliensis* and *Thalassoma noronbanum*, and the parrotfish *Sparisoma axillare*, with close relatives in the northern or eastern Atlantic [respectively, *P. aculeatus*, *S. imbricatus*, *B. pulchellus/B. rufus*, *H. radiatus*, *T. bifasciatum*, and *S. rubripinne* (Table 1)].

The south-western Atlantic is overall characterized by high endemism, about 18–20% for reef fishes (Floeter & Gasparini, 2000). However, differences between the Caribbean and the Brazilian provinces are at the species or subspecies level, with no genus restricted to the south-western Atlantic. Brazilian corals, in contrast, show a level of endemism of 33%. Twenty-three percent of these scleractinian species are considered relict forms only remotely related to recent Caribbean species (Laborel, 1970; Leão, 1983; J. Laborel, pers. comm.). It has been argued that the observed differentiation with respect to reef fishes is too low to be accounted for the initial establishment of a connection of the Amazon River system to the Atlantic in the late Miocene (5–6 Ma) (cf. Hoorn *et al.*, 1995). We suspect that 'complete' vicariance or allopatric speciation with stabilizing selection could not have produced such general closeness between north and south-western Atlantic ichthyofaunas across the whole spectrum of fish species and life histories. Thus, vicariance through parapatric speciation (separation with occasional contact) seems the most parsimonious hypothesis to explain the low morphological differentiation in spite of the wide and old Amazon barrier (cf. Briggs, 1995; Bowen *et al.*, 2001). The Amazon River first created a filter, not a full barrier, to dispersal within a once widespread distribution. During the Pliocene

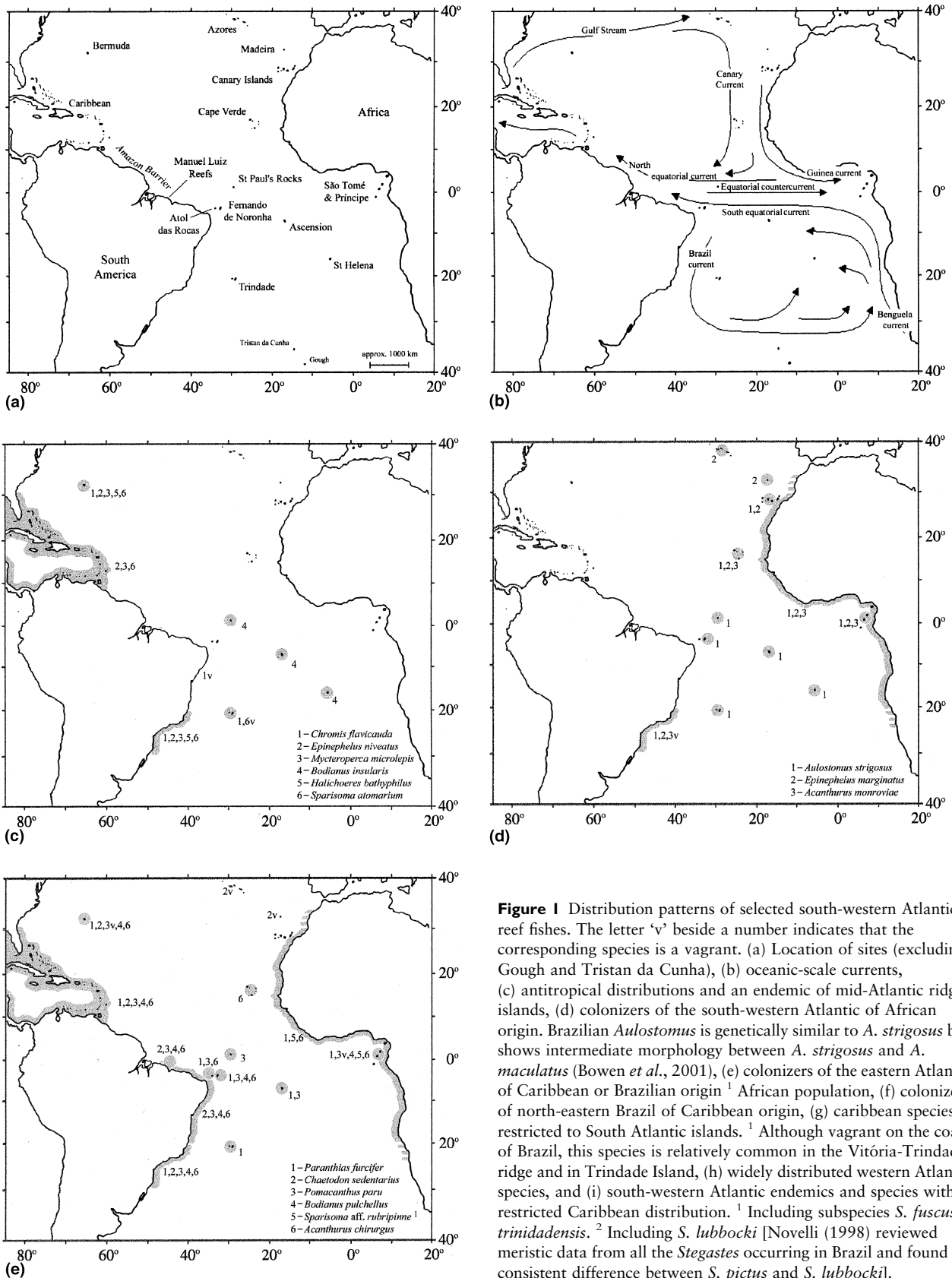


Figure 1 Distribution patterns of selected south-western Atlantic reef fishes. The letter 'v' beside a number indicates that the corresponding species is a vagrant. (a) Location of sites (excluding Gough and Tristan da Cunha), (b) oceanic-scale currents, (c) antitropical distributions and an endemic of mid-Atlantic ridge islands, (d) colonizers of the south-western Atlantic of African origin. Brazilian *Aulostomus* is genetically similar to *A. strigosus* but shows intermediate morphology between *A. strigosus* and *A. maculatus* (Bowen *et al.*, 2001), (e) colonizers of the eastern Atlantic of Caribbean or Brazilian origin¹ African population, (f) colonizers of north-eastern Brazil of Caribbean origin, (g) caribbean species restricted to South Atlantic islands. ¹ Although vagrant on the coast of Brazil, this species is relatively common in the Vitória-Trindade ridge and in Trindade Island, (h) widely distributed western Atlantic species, and (i) south-western Atlantic endemics and species with restricted Caribbean distribution. ¹ Including subspecies *S. fuscus trinidadensis*. ² Including *S. lubbocki* [Novelli (1998) reviewed meristic data from all the *Stegastes* occurring in Brazil and found no consistent difference between *S. pictus* and *S. lubbocki*].

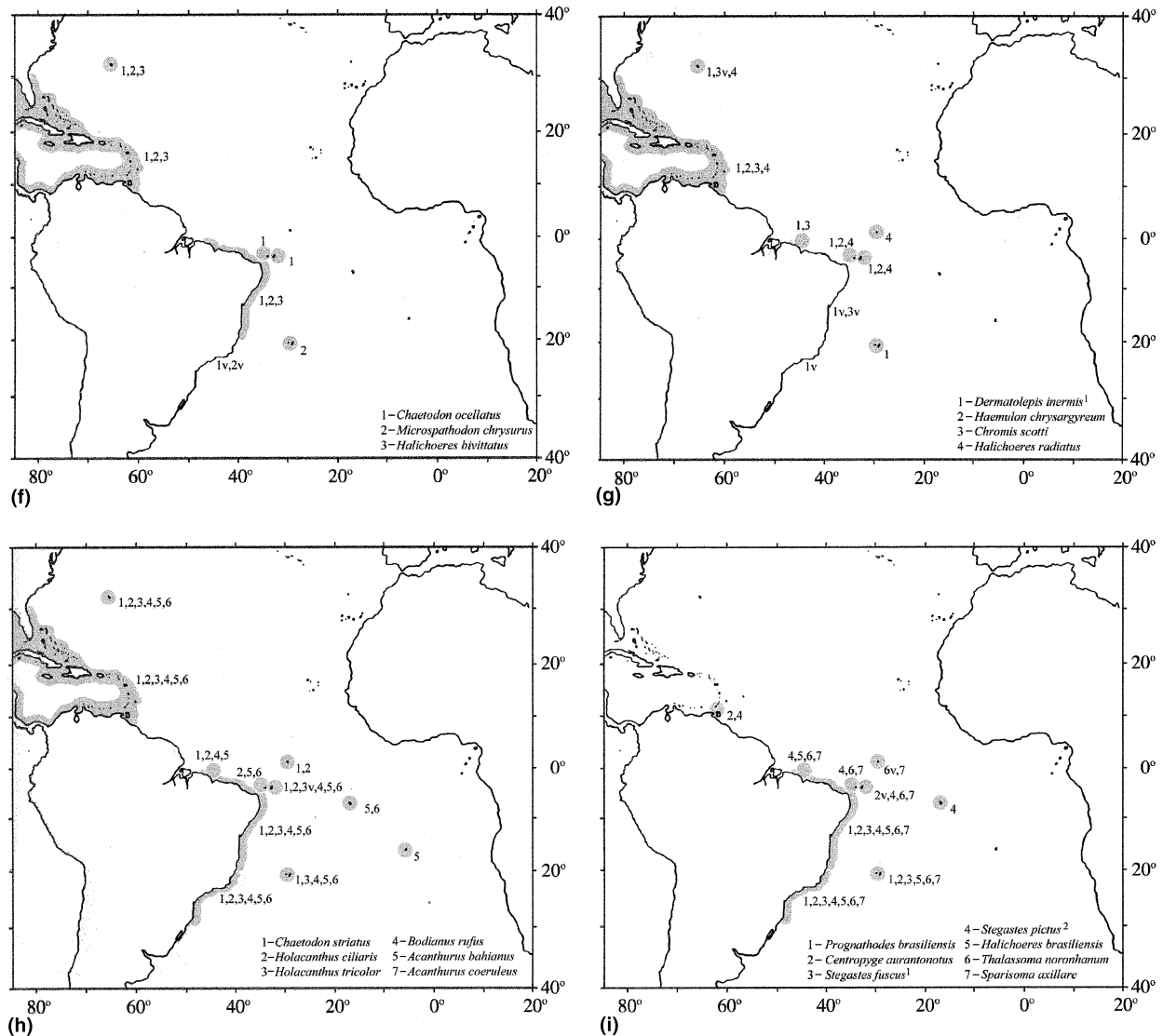


Figure I Continued.

(5.3–1.6 Ma) onwards, the delta experienced a rapid seaward growth caused by a major uplift and erosion of the Andes (Hoorn, 1994). Thus, it is possible that the filter interrupted faunal interchange for the most salinity or sediment sensitive species (Muss *et al.*, 2001), but that other species breached the barrier on occasion. We hypothesize a drastic but intermittent interruption of passage during high freshwater outflow periods (i.e. at the end of each glacial period). Another non-excluding possibility is that genetic flow would be completely severed during low sea-level periods (cf. Maslin & Mikkelsen, 1998; Arz *et al.*, 1999; Knoppers *et al.*, 1999). During one of the recent lowest stands (–50/70 m at 12.7–11.2 ka BP) (Arz *et al.*, 1999), the Amazon freshwater and material was directly exported to the upper shelf slope (present day shelf break is at 75–80 m). This event coincided with high sedimentation rates, possibly

cutting-off passage of shallow-water forms between the two biogeographical provinces.

It should be noted that the Brazilian province seems isolated from the Caribbean province because of the direction of prevailing currents, but that the reverse is possibly not true (Fig. 1b). It is conceivable that species unity between western Atlantic, the Brazilian and the Caribbean provinces may be maintained in some cases through genetic flow from south to north. For instance, some wide-ranging Brazilian species can only be found in the southern tip of the Caribbean (Fig. 1i). The grunt *Anisotremus moricandi* (Ranzani), the flameback angelfish *Centropyge aurantonotus*, the yellowtail damselfish *S. pictus* and the Brazilian puffer *Canthigaster* sp.n., among others, distribute according to this surprising pattern (Humann, 1996; L.A. Rocha, pers. comm.). On the other hand, some Caribbean species

Table 1 Geographic range and endemism level for the reef species selected for the present study. More details on the south-west Atlantic range are given in the figures. Exact range extension in the Caribbean Province and along the African coast is only provided in specific cases. Voucher references for Brazilian specimens can be obtained at the Biobase Project (<http://www.biobase.org/>)

Species	Geographic range	Level of endemism	References*	Putative sister species	Geographic range
Aulostomidae					
<i>Aulostomus strigosus</i> (Valenciennes, 1842)	W Indian + E Atlantic + Oceanic Isl. + Brazilian province		Bowen <i>et al.</i> (2001)	<i>A. maculatus</i> (Valenciennes, 1837) + <i>A. chinensis</i> (Linnaeus, 1766)	Caribbean province Indo-Pacific
Serranidae					
<i>Dermatolepis inermis</i> (Valenciennes, 1833)	Western Atlantic				
<i>Epinephelus marginatus</i> (Linnaeus, 1758)	Mediterranean + East Atlantic + Brazilian province				
<i>E. niveatus</i> (Valenciennes, 1828)	Western Atlantic + Eastern Pacific				
<i>Mycteroperca microllepis</i> (Goode & Bean, 1879)	Western Atlantic				
<i>Panathias furcifer</i> (Valenciennes, 1828)	East Atlantic + W Atlantic + Eastern Pacific		Afonso <i>et al.</i> (1999)		
Haemulidae					
<i>Haemulon chrysargyreum</i> (Günther, 1859)	Caribbean province + Brazilian islands				
Chaetodontidae					
<i>Chaetodon ocellatus</i> (Bloch, 1787)	Western Atlantic		Santos <i>et al.</i> (1997)		
<i>C. sedentarius</i> (Poey, 1860)	Western Atlantic				
<i>C. striatus</i> (Linnaeus, 1758)	Western Atlantic				
<i>Prognathodes brasiliensis</i> (Burgess, 2001)	Brazilian province	Species	Burgess (2001)	<i>P. aculeatus</i> (Poey, 1860)	Caribbean province
Pomacanthidae					
<i>Centropyge aurantonotus</i> (Burgess, 1974)	Brazilian province + S Caribbean province	Species	Lubbock & Edwards (1981); B. Feitoza, pers. comm.	<i>C. argi</i> (Woods & Kanazawa, 1951)	Caribbean province
<i>H. ciliaris</i> (Linnaeus, 1758)	Western Atlantic				
<i>H. tricolor</i> (Bloch, 1795)	St Paul's rocks SE Brazilian province NE Brazilian province + Caribbean province	Morphs Population Population	J.L. Gasparini, pers. obs.		
<i>Pomacanthus paru</i> (Bloch, 1787)	Western Atlantic + Oceanic islands			<i>P. arcuatus</i> (Linnaeus, 1758)	Western Atlantic
Pomacentridae					
<i>Chromis flavicauda</i> (Günther, 1880)	Brazilian province	Species ?	Smith-Vaniz <i>et al.</i> (1999)	<i>C. flavicauda</i>	Bermuda

Table 1 (Continued)

Species	Geographic range	Level of endemism	References*	Putative sister species	Geographic range
<i>Chromis scotti</i> (Emery, 1968)	Caribbean province + Brazilian province		Smith-Vaniz et al. (1999); Gasparini & Floeter (2001); Rocha & Rosa (2001a)		
<i>Microspathodon chrysurus</i> (Cuvier & Valenciennes, 1830)	Western Atlantic				
<i>Stegastes fuscus</i> (Cuvier & Valenciennes, 1830)	Brazilian coast Trindade island (<i>S. f. trindadensis</i>)	Species Subspecies	Allen (1991); Gasparini et al. (1999)	<i>S. imbricatus</i> (Jenyns, 1840) + <i>S. variabilis</i> (Castelnau, 1855) <i>Stegastes partitus</i> (Poey, 1868)	African coast + islands Brazilian province
<i>S. pictus</i> (Castelnau, 1855)	Brazilian province + Trindade & Tobago	Species	Novelli (1998); L.A. Rocha, pers. Comm.	+ <i>Stegastes lubbocki</i> Allen & Smith, 1992	Caribbean province Ascension
Labridae					
<i>Bodianus insularis</i> (Gomon & Lubbock, 1979)	Mid-Atlantic ridge islands	Species	Gomon & Lubbock (1980)	<i>B. rufus</i> (Linnaeus, 1758)	Western Atlantic
<i>Halichoeres bathyphilus</i> (Beebe & Tee-Van, 1932)	Brazilian province	Species ?	Smith-Vaniz et al. (1999)	+ <i>B. pulchellus</i> (Poey, 1860) <i>H. bathyphilus</i> (Beebe & Tee-Van, 1932)	Western Atlantic + São Tomé Bermuda
<i>H. bivittatus</i> (Bloch, 1791)	Western Atlantic	Species	Rocha & Rosa (2001b)	<i>H. radiatus</i> (Linnaeus, 1758)	Caribbean province + NE Brazilian islands
<i>H. brasiliensis</i> (Bloch, 1791)	Brazilian province	Species	Rocha et al. (2001)	<i>T. bifasciatum</i> (Bloch, 1791)	Caribbean province
<i>Thalassoma noronbanum</i> (Boulenger, 1890)	Brazilian province	Species	Rocha et al. (2001)		
Scaridae					
<i>Sparisoma atomarium</i> (Poey, 1861)	Western Atlantic				
<i>S. axillare</i> (Steindachner, 1878)	Brazilian province	Species	Bernardi et al. (2000); Moura et al. (2001)	<i>S. rubripinne</i> (Valenciennes, 1839) + <i>Sparisoma</i> aff. <i>Rubripinne</i> (Valenciennes, 1839)	Caribbean province Eastern Atlantic
Acanthuridae					
<i>Acanthurus bahianus</i> (Castelnau, 1855)	Brazilian province	Population	Briggs & Caldwell; (1957); Rocha et al., pers. comm.	<i>A. randalli</i> (Briggs & Caldwell, 1957)	Eastern Gulf of Mexico
<i>A. chirurgus</i> (Bloch, 1787)	Caribbean province	Population			
<i>A. coeruleus</i> (Bloch & Schneider, 1801)	West and East Atlantic	Population			
<i>A. monroviae</i> (Steindachner, 1876)	Western Atlantic	Population	Quéro et al. (1990); Golani & Somin (1996); Moura (2000); C.E.L. Ferreira, pers. obs.		

*General references used for the Western Atlantic are Böhlke & Chaplin (1968), Humann (1996) and Randall (1996), and for the Eastern Atlantic are: Quéro et al. (1990), Debelius (1997) and Edwards et al. (2001).

are restricted to a few sites south of the Amazon (e.g. the damselfish *Chromis scotti* and the wrasse *Halichoeres radiatus*), generally on isolated locations (Fig. 1g). Such distributions are a clear indication that the isolation between Brazil and the Caribbean is occasionally bridged – one way or the other. Periods of isolation can be interrupted by sporadic gene flow through larval transport by currents, active swimming abilities (Stobutski & Bellwood, 1997), rafting (Mora, 2001) or even through the colonization of deep-water sponge habitats under the Amazon River plume (Collette & Rutzler, 1977; Uyeno *et al.*, 1983; Rocha *et al.*, 2000).

Long-distance dispersal

Larvae of a number of species can successfully travel enormous distances before reaching suitable settling ground and colonizing new areas. Five species have thus apparently made the eastward transatlantic crossing. Two of them (*Chaetodon sedentarius* at Azores and Madeira, and the angelfish *Pomacanthus paru* in the Gulf of Guinea) were only found vagrants in the East Atlantic, presumably indicating recent arrival (Fig. 1e). The other three (Creolefish *Paranthias furcifer*, *B. pulchellus* and *Sparisoma* aff. *rubripinne*) established restricted populations (Afonso *et al.*, 1999; Bernardi *et al.*, 2000) (Fig. 1e). Two species with now resident western populations most probably crossed the other way (cf. Bowen *et al.*, 2001) (Fig. 1d). However, as shown by the relative commonness of vagrants from distant source populations, the establishment of founding populations appears much rarer than recruitment. In addition to the two recorded stray species in the East Atlantic, the African acanthurid *Acanthurus monroviae* was recently found as a vagrant in south-east Brazil (Moura, 2000; C.E.L.F. pers. obs.) and in the eastern Mediterranean (Golani & Sonin, 1996) (Fig. 1d). Other examples include the thirteen species that were recorded only as juveniles in Bermuda (including *Chromis scotti*; Fig. 1g) (Smith-Vaniz *et al.*, 1999). This pattern (comparative number of species crossings, limited distribution in colonized areas) fits with modern and fossil records for shell-bearing mollusks (Vermeij & Rosenberg, 1993). Invaders of the East Atlantic could have crossed the ocean from northern Brazil to the Gulf of Guinea via the Equatorial Under Current (Stramma & Schott, 1999; Muss *et al.*, 2001) (Fig. 1b and e), possibly favoured by ENSO-type or ENSO-induced events (Venegas *et al.*, 1996; Stramma & Schott, 1999). Alternatively, other species [e.g. *C. sedentarius* and *Adudefduf taurus* (Müller & Troschel)] (Debelius, 1997; Edwards *et al.*, 2001) appear to have crossed from the Caribbean to the Macaronesian islands off northern Africa via the Gulf Stream. In spite of the westward flowing South Equatorial Current, invasions from Africa to the west are rarer, as evidenced by the limited present distribution of the few putative colonizers of South America (Fig. 1d). Stepping stones do not appear necessary for transatlantic passage in either direction. The insular hogfish *B. insularis* is endemic and the lone member of its genus on the mid-Atlantic Ridge islands (Fig. 1c),

although its sister species *B. pulchellus* crossed the tropical Atlantic (Fig. 1e). It is unlikely that two or more consecutive and successful colonizations can occur. The presence of various species at oceanic islands is thus to be seen as reflecting the species' ability to disperse and colonize, not as a pre-requisite for further transport.

There has been an increasing attention given to the evolutionary significance of dispersal and retention of early life-history stage (e.g. Jones *et al.*, 1999; Swearer *et al.*, 1999). Overall, reef fish seem to have evolved and successfully dealt with the dispersion/retention duality. As evidenced by established populations at geologically recent volcanic islands such as Ascension (1.5 Myr) and by transoceanic vagrants, species may be dispersed far away, thus colonizing new areas and avoiding extinction. However, mass recruitment is essentially local (Jones *et al.*, 1999; Swearer *et al.*, 1999). Recruitment in isolated environments not only allows the persistence of endemic populations (Robertson, 2001), but also may permit allopatric speciation. A notable example is the possibly on-going differentiation of *Holacanthus ciliaris* (Fig. 2a–b) and *Chromis multilineata* (Guichenot) through possible founder effects and inbreeding at St Paul's (cf. Edwards & Lubbock, 1983). It would be of interest to know if *H. ciliaris* colour morphs perceive themselves as different 'species', as they apparently occupy different microhabitats (B. Feitoza and Osmar Luiz Jr, pers. comm.).

The type of spawning mode and the larval duration of the planktonic phase are often assumed to be major constraints on the dispersal abilities of marine species (see review in Sale, 1991, for a counter-example see Victor & Wellington, 2000). Among the Brazilian endemic reef fishes, 74% are small benthic demersal spawners, which evidently could not readily transgress the Amazon barrier (Floeter & Gasparini, 2000). A duality is readily apparent on oceanic islands where benthic spawners are more frequently endemic (through lack of genetic input), and pelagic spawners proportionately more speciose (through higher dispersal), than at continental shelves (Floeter & Gasparini, 2000). Recent expeditions to St Paul's Rocks (B. Feitoza *et al.*, unpubl. data) noted the rarefaction of the semi-albinotics *H. ciliaris*, and the comparatively higher abundance of the local blue morph (Fig. 2a) (cf. also Lubbock & Edwards, 1981). That such island populations can undergo large fluctuations within a few years appears to illustrate that reversal to ancestral population composition is unlikely without integrating new immigrants. Thus, concurrently with the high-observed frequency of vagrants, we infer that long-distance dispersal processes are more common than generally predicted. For both pelagic and benthic spawners, however, short route dispersal would be eased by the presence of stepping stones, and the south-western Atlantic is no exception to the rule. Trindade Island presents higher reef fish diversity than would be expected from its distance from the coast because of the seamounts of the Vitória-Trindade chain (Gasparini & Floeter, 2001). Further north, St Paul's Rocks' ichthyofauna could be considered as an impoverished caricature of Fernando de Noronha (Fig. 1h),

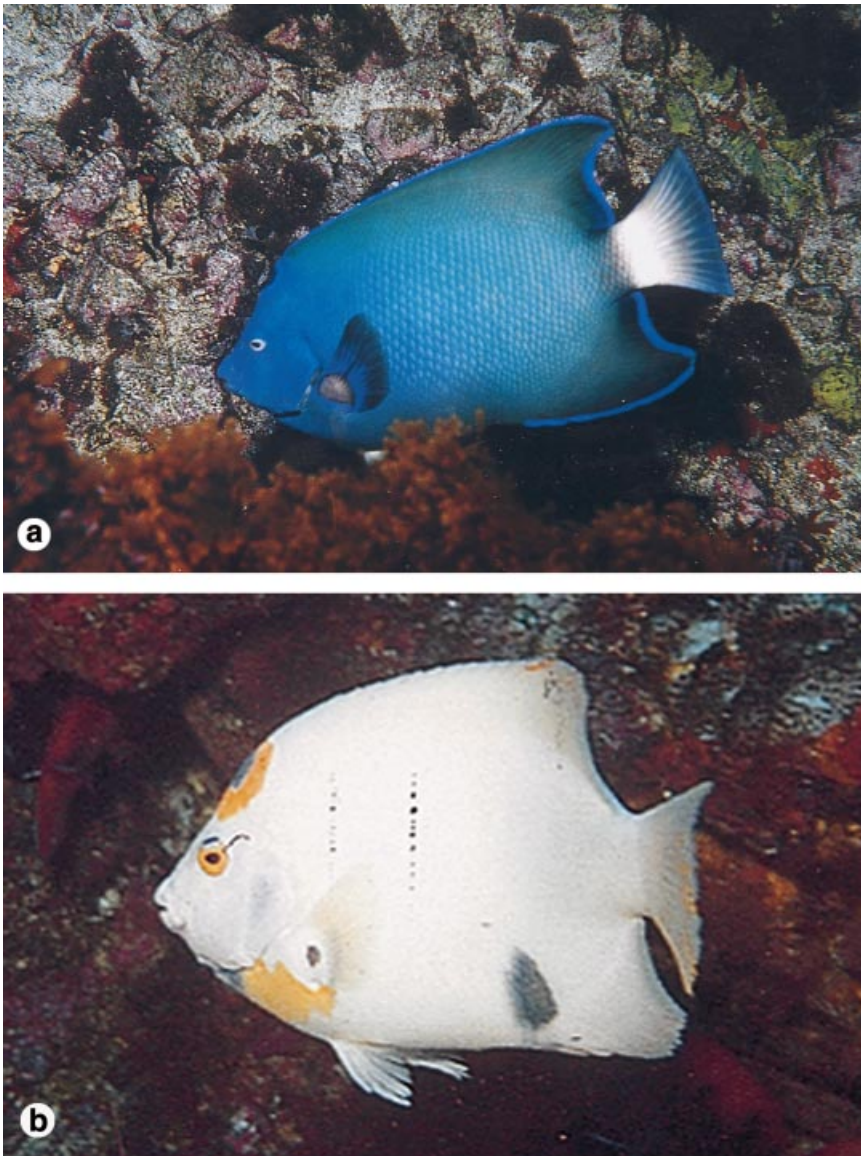


Figure 2 *Holacanthus ciliaris* colour morphs from St Paul's Rocks: (a) blue morph, and (b) semi-albinotic morph. *In situ* photographs by Osmar Luiz Jr.

thus showing the dependency of the former's fauna to the latter's colonization.

Long-term success of colonists

Some of the observed features cannot easily be linked to dispersal abilities or possible routes. Of special interest is the absence of the family Acanthuridae (surgeonfishes) from St Paul's Rocks, probably the only tropical island in the world missing this conspicuous reef associated family (Floeter *et al.*, 2001). Similarly, the wide-ranging butterflyfish *Chaetodon striatus* and the hogfish *B. pulchellus* were not recorded at Atol das Rocas while both are present in neighbouring Fernando de Noronha. These local absences could be related to the small size of the islands, and thus habitat availability together with possible post-settlement

difficulties. The genus *Scarus* (family Scaridae), which occurs at oceanic sites in the Indo-Pacific and North Atlantic (Smith-Vaniz *et al.*, 1999), is absent from the South Atlantic oceanic islands. On the other hand, all four scarid species that do occur on South Atlantic oceanic islands belong to the genus *Sparisoma*. This pattern could reflect the broader feeding habits of this genus (Bernardi *et al.*, 2000). The French angelfish *P. paru* is common in the Caribbean, on the Brazilian coast, Atol das Rocas, Fernando de Noronha and St Paul's Rocks. Surprisingly, on Trindade Island this species is apparently replaced by *H. tricolor*. The island is the only one in the South Atlantic that harbors a resident *H. tricolor* population (Gasparini & Floeter, 2001). These pelagic-spawning species certainly do not have larval dispersal restrictions, because the acanthurids, *C. striatus*, *B. pulchellus* and *P. paru* have successfully colonized very isolated sites

such as Ascension, Bermuda, and Africa. Thus, special ecological requirements for proper larval or post-settlement development, including habitat and predation rates, presumably determine the long-term success of colonists.

It has been argued that competition could hinder or prevent colonization of high diversity locations. Eastern Pacific fish and gastropod species have apparently been unable to colonize the Indo-western Pacific, while the opposite is frequent (Vermeij & Rosenberg, 1993; Briggs, 1995). As is known from shell-bearing mollusks (cf. Vermeij & Rosenberg, 1993), western Atlantic fishes that have colonized Africa generally have extremely limited distributions in the eastern Atlantic (Briggs, 1995) (Fig. 1d and e), most often occurring on the offshore islands of Cape Verde and São Tomé archipelago, where competition is probably lower.

Extinctions are usually believed to be rare events occurring only on a long time-span. Even in the smallest and most isolated islands, endemic fishes have survived through evolutionary time under very restricted areas in high-risk situations (Robertson, 2001). However, local extinction processes of apparently established populations are probably more frequent than generally expected. Historical disappearance or severe decline of population of reef fish species caused by natural (e.g. El Niño) or man-made disturbance (e.g. reef degradation, intensive aquarium collection, overfishing) is now documented (Smith-Vaniz *et al.*, 1999; Hawkins *et al.*, 2000), and has been related to the restricted geographical range of the species (Hawkins *et al.*, 2000). The survival of potentially valuable morphs or endemic species on south-western oceanic islands is under serious threat as the aquarium trade is moving in (J.L. Gasparini & S.R. Floeter, pers. obs.). Present-day distribution patterns may or may not provide indications of the local long-term history of species. An interesting feature found in the western Atlantic is that of species present in the entire Caribbean Basin but restricted to offshore localities in the south-western Atlantic (Fig. 1i). Assuming the latter are relict populations from a once widespread distribution, the pattern does not fit with the observation that generally the northern component of a disjunct antitropical or antiequatorial population is the first to disappear (Briggs, 1995). However, one can argue that inferences from observations in the Pacific are difficult to transpose into the Atlantic because the West Indies are considerably more extensive and diverse than the Brazilian province and thus more efficient at providing tropical habitats after range reduction, especially during glacial periods.

CONCLUSIONS

The puzzling patterns of distribution found in the South Atlantic seem primarily the outcome of allopatric speciation and of the interaction of long distance dispersal abilities and ecological processes. One emerging idea is that persistence ability or settlement preferences (see Öhman *et al.*, 1998) are more important than dispersal ability. Given enough time many species can reach extremely isolated reefs. The documented arrival of vagrants clearly indicates this capa-

bility, even within the short period of recent scientific investigations. However, not all vagrants can complete their life history there. No stepping stones are required along transoceanic routes because of the rarity of consecutive colonizations. However, intermediate stopovers are persistently used along short routes. Finally, some patterns cannot be given a satisfactory explanation. For example, why the spotfin hogfish *B. pulchellus* is present at the São Tomé archipelago when its closest relative (Sazima & Gasparini, 1999), and always sympatric, the Spanish hogfish *B. rufus* is not? Just chance?

The puzzle will certainly remain unclear for a long time. A great effort will be required to resolve central issues such as the importance of speciation, long distance transport, colonization success, etc. that shaped the biogeography of South Atlantic reef fishes.

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