

Correspondence

Two letters on reef fish biogeography

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

INTRODUCTION

Even though biogeography deals with spatial and temporal scales that generally preclude experimental manipulation and formal hypothesis testing (Brown & Lomolino, 1998), there is limited room for speculations regarding the mechanisms responsible for the geographical and evolutionary patterns displayed by living organisms (Humphries & Parenti, 1984). Based on a selection of thirtyfive species (out of a pool of more than 1500 Atlantic reef fish species), Joyeux et al. (2001) stated that 'the South Atlantic reef fish biogeography proved to be an intricate tapestry', and tried to adjust a number of hypotheses in order to explain the 'puzzling' distributions they found. Here, I propose to demonstrate that Joyeux et al. (2001) overstepped the limits imposed by currently available evidence, introducing a number of incorrect or unsubstantiated distributional and phylogenetic patterns into the literature.

It has long been recognized that the Southwestern Atlantic harbours a considerable number of endemic species (Ekman, 1953; Briggs, 1974). In the late 1970s, as SCUBA diving began to be employed as a tool for collecting reef fishes along the Brazilian coast, it became evident that the number of endemic species was much greater than previously thought, as noted by Greenfield (1988). Several new species were discovered during these initial collecting efforts along the Brazilian coastal margin (Williams & Smart, 1983; Greenfield, 1988, 1989) and oceanic islands (Emery, 1972; Lubbock & Edwards, 1980, 1981; Edwards & Lubbock, 1981). The number of reef-associated species recognized as endemic to the South-western Atlantic has been steadily increasing in the last decade (e.g. Moura, 1995; Sazima et al., 1997, 1998; Rocha & Rosa, 1999), with no recent trend to stabilization (e.g. Burgess, 2001; Moura et al., 2001; Moura & Castro, 2002). Despite this considerable taxonomic progress, few works addressed the phylogenetic relationships within Pan-Atlantic groups that span multiple biogeographical provinces. The historical pathways underlying Briggs (1974) Atlantic faunal provinces have just started to be unveiled (e.g. Bernardi et al., 2000; Heiser et al., 2000; Muss et al., 2001; Rocha et al., 2002), and many questions still remain unanswered (Joyeux et al., 2001).

A review of the literature, together with the examination of museum specimens and data from recent and comprehensive collections, reveals that most distribution patterns and phylogenetic relationships used by Joyeux et al. (2001) to conjecture about the 'puzzling' biogeographical patterns in the South Atlantic represent either imperfections in their database or misinterpretation of recent literature. I argue that Joyeux et al. (2001) have introduced into the literature a considerable amount of erroneous data and added unnecessary explanations for each of the 'puzzling distribution patterns' they found within a selected set of species. At the same time, these authors add few (or no) relevant data to the recent efforts for a better understanding of biogeographical patterns among Atlantic reef fishes (e.g. Moura et al., 1999a; Bernardi et al., 2000; Floeter & Gasparini, 2000; Heiser et al., 2000; Moura et al., 2001; Muss et al., 2001; Moura & Castro, 2002; Rocha et al., 2002).

METHODS

The phylogenetic relationships used by Joyeux *et al.* (2001) were reassessed through a critical examination of the literature references cited by them (e.g. Goman & Lubbock, 1979; Bernardi *et al.*, 2000; Bowen *et al.*, 2001; Moura *et al.*, 2001; Muss *et al.*, 2001).

G. Bernardi and collaborators provided data from an unpublished molecular study on the specific status of an undescribed Brazilian species of *Sparisoma*, similar to the Caribbean species *S. atomarium* (Poey 1861). Depth and distribution ranges were also obtained from literature records (e.g. Günther, 1880; Randall & Böhlke, 1965; Heemstra & Randall, 1993), as well as from specimens deposited at the Museu de Zoologia da Universidade de São Paulo, which holds the largest and most extensive collection of Brazilian marine fishes (Menezes *et al.*, 1997; Moura *et al.*, 1999a; Menezes & Buckup, 2000).

RESULTS

Distribution patterns

Joyeux et al. (2001) used two examples to demonstrate 'accentuated antitropical distributions': Chromis flavicauda (Günther, 1880) and Halichoeres bathyphillus (Beebe & Tee-Van 1932). However, both 'antitropical' examples are species that are deep reef dwellers (Randall & Böhlke, 1965; Smith-Vaniz & Emery, 1980; Heemstra & Randall, 1993). An examination of the C. flavicauda type locality reveals that the species was originally described from Pernambuco State (Günther, 1880), well off the north-eastern tropical coast of Brazil. As the type specimen was collected by H.M.S. Challenger, it was most probably collected from a deep reef (Thompson, 1877). A great number of Atlantic deep-dwelling reef fishes, including H. bathyphillus, occur in shallower waters near their distribution ranges limits, and a close examination of depth records clarifies this pattern (e.g. Randall & Böhlke, 1965). Moreover, the lack of deep reef surveys in the Brazilian coast does not allow any speculation about the absence of *H. bathyphillus* - or any other deep reef species - in the tropical portion of the eastern coast of South America.

Two examples of widely distributed species with disjunct populations in the Caribbean and in southern Brazil presented by Joyeux et al. (2001) are either misidentifications or represent a lack of information about actual distribution ranges. The parrotfish Sparisoma atomarium (Poey) is restricted to the Caribbean, while its South-western Atlantic counterpart is an undescribed species (Moura et al., 2001; G. Bernardi, unpublished). The snowy grouper, Epinephelus niveatus (Valenciennes 1828), is recorded from the Carolinas throughout the northern coast of South America, and also along most of the north-eastern Brazilian coast (Heemstra & Randall, 1993). In addition, this species is another deep reef dweller, occurring in depths to 525 m, being most common between 100 and 200 m. Besides ignoring the wide depth range of the snowy grouper, Joyeux' distribution map (showing the species' range restricted to a narrow stretch along south-eastern Brazil) does not correspond to the most current taxonomic review (Heemstra & Randall, 1993). In fact, the snowy grouper is neither rare nor absent along the tropical Brazilian coast. It is an important commercial species that figures in fisheries statistics for the Abrolhos Bank, the largest coral reefs of Brazil (Paiva & Fonteles-Filho, 1997).

The secretive marbled grouper, Dermatolepis inermis (Valenciennes 1833), was considered by Joyeux et al. (2001) as a vagrant species along most of its South-western Atlantic range, despite being present on most Brazilian oceanic islands, including Trindade, as well as being positively recorded several times along the south-eastern Brazilian coast (e.g. Figueiredo & Menezes, 1980; Heemstra & Randall, 1993). It is unclear what criteria the authors used for classifying this (and several other) species as vagrants or if this classification is an outgrowth of the high dispersion/low establishment rates model they postulate. In another instance, Joyeux and colleagues state that the Holacanthus tricolor (Bloch 1795) population of Trindade is indeed resident, explaining that it 'replaces' P. paru (Bloch 1787) around that island. It is unclear what Joyeux et al. (2001) meant by replacement and why the Holacanthus individuals are classified as a resident population where as the marbled grouper individuals are considered vagrants. The postulated absence of Chaetodon striatus (Linnaeus 1758) and B. pulchellus from the Atol das Rocas, 'while present in the neighbouring Fernando de Noronha', reflect an incomplete distributional database, since both species occur at both islands (pers. observ.).

Finally, in order to support the idea of a prevailing south to north colonization across the Amazon delta, Joyeux *et al.* (2001) state that several 'Brazilian species' are found in the

southern Caribbean and only a few Caribbean species, namely '*Chromis scotti* (Emery 1968)' (*sic*) and *Halichoeres radiatus* (Linnaeus 1758), are found 'in a few sites south of the Amazon, generally on isolated locations'. In fact, *C. scotti* Emery 1968 is a common reef fish along the northern Brazilian coast, occurring on the States of Maranhão, Ceará and Rio Grande do Norte (Moura *et al.*, 1999b; Rocha & Rosa, 2001, Pers. Observ.), and *H. radiatus* does not occur south of the Equator (Rocha & Rosa, 2001).

Recent transatlantic migrations

Immigration from the African coast was advocated by Jouyeux et al. (2001) as the prime factor explaining the presence of Aulostomus strigosus Valenciennes 1842, Acanthurus monroviae Steindachner 1876 and Epinephelus marginatus (Linnaeus 1758) along the Brazilian coast. Although there is strong evidence for a recent east-to-west transatlantic migration in the first species (Bowen et al., 2001), the idea that A. monroviae and E. marginatus (one of the most common groupers along the southern and southeastern Brazilian coast) have also recently colonized the Brazilian coast is completely devoid of phylogeographical evidence. The fact that A. strigosus was able to perform an east-to-west migration does not imply that the same track was followed by other species. Although a plausible hypothesis, there are no genetic or long-term ecological studies showing that either A. monroviae or E. marginatus have recently arrived from West Africa. Distribution data alone cannot be construed as evidence to support the hypothesis of a recent arrival of these two species in the eastern coast of South America.

South-western Atlantic endemism and phylogenetic relationships

In order to provide evidence for vicariance through the parapatric speciation model, Joyeux *et al.* (2001) stated that the differences between the Caribbean and the Brazilian provinces are at the species or subspecies level, with no genus restricted to the southwestern Atlantic. However, no such endemic 'subspecies' are presented by them and the clinid genus *Ribeiroclinus* Pinto 1965, endemic to the eastern subtropical and temperate coasts of South America (Springer, 1970), was not taken into account. Besides the unsubstantiated data and wrong information, it is important to consider that there are many pitfalls inherent to the usage of subspecific ranks in reef fish biogeography, a topic that was thoroughly covered by Gill (1999).

The phylogenetic relationships presented by Joyeux et al. (2001) represent either wrongly compiled data or imaginary phylogenies. According to the source used by Joyeux and colleagues (Bowen et al., 2001), Aulostomus strigosus Valenciennes 1842 is not the sister species of the clade A. maculatus (Valenciennes 1837) + A. chinensis (Linnaeus 1766). In fact, Bowen et al. (2001) demonstrate that A maculatus is the sister species of the clade A strigosus + A. chinensis. Also, there are no studies supporting the sister species relationships presented by Joyeux et al. (2001) between Centropyge aurantonotus (Burgess 1974) and C. argi (Woods & Kanazawa 1951), Pomacanthus paru and P. arcuatus (Linnaeus 1758), and 'Bodianus insularis (Goman & Lubbock, 1979)' [sic] and the clade B. rufus (Linnaeus 1758) + B. pulchellus (Poey 1860). In the later case the source quoted by Joyeux and colleagues (Goman & Lubbock, 1979) explicitly mention that 'B. insularis resembles four of the six species of Bodianus occurring in the Atlantic and eastern Pacific', without specifying any candidate to be its closest relative. Akin to the aforementioned example, a number of ambiguous literature quotations permeate Joyeux et al. (2001) database on phylogenetic relationships of Atlantic reef fishes. Most of the references used to justify the phylogenetic relationships simply do not present such information. Neither Bernardi et al. (2000) nor Moura et al. (2001), both referred to as sources by Joyeux and colleagues, state that Sparisoma axillare (Steindachner 1878) is the sister species of S. rubripinne (Valenciennes 1839) + an East Atlantic undescribed Sparisoma species. Also, neither Allen (1991) nor Gasparini et al. (1999), both referred to as sources by Joyeux and colleagues, state that Stegastes fuscus (Cuvier & Valenciennes 1830) is the sister species of the clade S. imbricatus (Jenyns 1840) +S. variabilis (Castelnau 1855). Rocha et al. (2001), cited as a source by Joyeux and colleagues, do not state that T. noronhanum (Boulenger 1890) is the sister species of T. bifasciatum (Bloch 1791). Though the aforementioned relationships might be corroborated by future studies, literature sources do not support the phylogenetic relationships that Joyeux et al. (2001) have introduced.

Ongoing differentiation of reef fishes on South Atlantic remote oceanic islands

Are island populations of reef fish vulnerable to large population structure fluctuations within a few years? With the evidence presented by Joyeux et al. (2001), a positive answer is just as valid as a negative one. The authors did not state the approximate time span encompassing their 'recent expeditions to St Paul Rocks' in which they observed a 'rarefaction of the semialbinotics' colour morphs of H. ciliaris (Linnaeus 1758) and an increase in the abundance of its 'blue morph' (Lubbock & Edwards, 1981). The lack of such basic information casts serious doubt on the precision and accuracy of their proportional estimates. How many are a 'few years'? How did they assess the declining proportions of H. ciliaris colour morphs in St Paul's Rocks? Visual censuses? How many, at what depths, etc.? It would be useful for reef fish biogeographers, as well as for the Brazilian agencies responsible for the management of St Paul's Rocks (a Marine Protected Area), if Joyeux and collaborators could provide the methods they used to reach such conclusions. If a population restructuring is indeed happening, the rarefaction of certain endemic morphs of H. ciliaris may require emergency measures from the Brazilian environmental agencies, especially if the increased pressure of the aquarium trade reported by Joyeux and colleagues is indeed taking place in that area.

Joyeux et al. (2001) presented no genetic or morphologic evidence that a founder effect and subsequent inbreeding has induced some kind of differentiation on Chromis multilineata (Guichenot 1853) populations in St Paul's Rocks. It is unclear whether any 'ongoing differentiation' is really taking place in that area, and/or what particular characters (colour pattern, morphology, DNA?) were examined by Joyeux and colleagues in order to corroborate this idea. As recently demonstrated by Rocha et al. (2002), West Atlantic reef fish lineages with strong genetic differentiation can retain an almost complete morphological integrity. It would be useful if Joyeux and collaborators add to this emerging idea, presenting their hard data on the St Paul's Rocks' C. multilineata population.

CONCLUSIONS

Even though the database used by Joyeux *et al.* (2001) contains errors and several unsubstantiated speculations, the interaction of long distance dispersal abilities, allopatric

speciation and local extinctions as important mechanisms shaping the present composition of the Atlantic faunal provinces is clear. These are well-corroborated biogeographical mechanisms (see Kodric-Brown & Brown, 1993). Before the new phylogeographical models proposed by Bowen and collaborators (e.g. Bowen *et al.*, 2001; Muss *et al.*, 2001; Rocha *et al.*, 2002) can be reliably integrated, in order to give birth to a meaningful and falsifiable general hypothesis, they must be confirmed with additional cladograms from various unrelated reef fish lineages (Humphries & Parenti, 1984).

The cautionary message is that the evidence provided by Joyeux et al. (2001) should not be used uncritically in further biogeographical analyses. In order to avoid additional complications and misinterpretations, it would be preferable to examine the original literature sources. Also, when distribution ranges of selected reef fish species present major unexpected gaps, it is important to consider if such species present secretive or deep dwelling habits. Depth range is a crucial, but generally neglected, information for reef fish biogeographers. It is not surprising that deep dwellers are most frequently collected in shallow waters near the subtropical limits of their distribution ranges, as these areas present water temperature and oceanographic conditions compatible with that of deep tropical reefs.

Most of the examples of 'intriguing' disjunct distribution patterns of widely distributed species in Joyeux et al. (2001) are flawed. If such distribution patterns indeed exist among Atlantic reef fishes, they still remain poorly documented. In several instances, such disjunctions can be related to ecological rather than to evolutionary constraints, providing little support for the socalled 'tropical extinction theory' (Briggs, 1999). The fact that both historical and ecological factors can produce similar distribution patterns adds to the complexity of the issue (Endler, 1982), which should be dealt with through phylogeographical data together with robust data on distribution and ecology. The clarification of several methodological concerns expressed herein would be extremely useful for biogeographers and conservation biologists aiming to explore some of the interesting ideas presented by Joyeux et al. (2001).

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BIOSKETCH

Research interests of the author include systematics, biogeography and macroecological patterns of Atlantic reef fishes. Current projects include extensive marine fish collections along the Southwestern Atlantic, together with the development of a specimen-based data resource at the Museu de Zoologia da Universidade de São Paulo, Brazil (http://www.mnrj.ufrj.br/ pronex/).

Critical reply

Solving the South Atlantic puzzle requires more data, not more speculation

In his critique of our study on biogeographic patterns of South Atlantic reef fishes (Joyeux *et al.*, 2001), Moura (2003) argues that we wrongly compiled data, superficially read and ambiguously quoted the literature, imagined phylogenetic relationships, and described flawed biogeographic patterns. Here, we propose to demonstrate that Moura (2003) greatly misrepresented our data and hypotheses and used much ambiguous or wrongly quoted literature.

DISTRIBUTIONAL PATTERNS

In his critical comment, Moura (2003) seems to be worried about the introduction of erroneous data in the current literature. However, divergent interpretations of the literature may generate the so-called 'unsubstantiated patterns'. A clear example can be found in his own comment: Moura (2003) cites Williams & Smart (1983) in his second paragraph to illustrate new species discoveries in Brazil during the 1980s. However, Williams & Smart (1983) did not discover a new species; they provided new information about *Starksia brasiliensis*, a species that had been previously described by Gilbert (1900).

Moura (2003) also states that the Brazilian Sparisoma atomarium (Poev 1861) is an undescribed species but, contrarily to his claimed principles against 'unsubstantiated distributional and phylogenetic patterns', partly bases his statement on his 2001 paper (Moura et al., 2001), which does not explicitly say so. In his words, S. atomarium is 'considered widespread in the west Atlantic' and 'appear[s] to be absent from north-eastern Brazil and [is] restricted to the continental area between Espírito Santo and São Paulo'. Phylogenetic relationships of Sparisoma, proposed by G. Bernardi and colleagues (unpublished), were simply not available at the time of our writing. Further, when Moura (2003) indicates the presence of 'Chaetodon striatus (Linnaeus 1758) and B. pulchellus in Atol das Rocas' [sic], he corroborates his statement about our 'incomplete distributional database' by citing his own unpublished and inaccessible information. Indeed, Chaetodon striatus was independently detected in Atol das Rocas, but seems to be very rare (C. Buitrón, pers. comm.).

The maps in our study (Fig. 1 in Joyeux et al., 2001) were never intended to exactly represent the distribution of all indicated species, but to best synthesize distributional information available at the time across a series of unrelated taxa. Such multi-specific patterns are always described in detriment to a high precision that is generally not useful for the detection and comprehension of general patterns. It is possible, for example, that the deep water species Halichoeres bathyphilus (Beebe & Tee-Van 1932) does not present an antitropical distribution since one individual was recorded in Bahia 12°S (A. Carvalho-Filho, pers. comm.). Thus, we agree with Moura (2003) that the term used in the legend of the figure may have been too vague to adequately cover or describe all presented distributions. A better expression for both Chromis flavicauda (Günther 1880) and H. bathyphilus (Fig. 1c in Joyeux et al., 2001) would be 'anti-Caribbean' (but see Cervigón, 1993). However, ongoing meristic and genetic studies by L. Rocha and colleagues with C. flavicauda and J. L. Gasparini and colleagues with the Brazilian H. bathyphilus may reveal that the northern and southern com-

ponents of these disjunct distributions are indeed different species. Regarding the presence of Epinephelus niveatus (Valenciennes 1828) along the north-eastern coast, new records were published by Ferreira & Cava (2001) for Pernambuco (08°S) and various specimens were caught or sighted in Paraíba (L.A. Rocha, pers. comm.) and in Amapá (A. Carvalho-Filho, pers. comm.) (07°S and 00°N, respectively). At the time of our writing (Joyeux et al., 2001), the unpublished information (P.S.A. Costa, pers. comm.) indicated that the northern limit of distribution of this species was southern Bahia, 16°S. This led us to state that it was restricted to the southern coast, a limit that may be politically and geographically incorrect but that seemed justified at the time.

Holacanthus tricolor (Bloch 1795) was considered resident at Trindade due to its abundance (Gasparini & Floeter, 2001). Sightings of 10-20 individuals per dive were common. Dermatolepis inermis (Valenciennes 1833) is very rare on the coast and this prompts us to consider the species vagrant (i.e. 'exceedingly rare'; Joyeux et al., 2001). The terms 'ecological replacement' or 'competitive exclusion' were probably too strong, but it is interesting to note that Pomacanthus paru (Bloch 1787) is common at St Paul's Rocks (Feitoza et al., in press), Atol das Rocas (L. Candisani, pers. comm.) and Fernando de Noronha (S.R. Floeter, pers. obs.), whereas H. tricolor is rare or absent at these locations (Floeter et al., 2001). However, H. tricolor is common at Trindade Island and on the Vitória-Trindade Chain, locations where P. paru and Holacanthus ciliaris (Linnaeus 1758) were never recorded to date (Gasparini & Floeter, 2001). The reason why some of these spongivores are common in some islands and absent in others needs further investigation.

DISPERSAL ROUTES AND SOUTH-WESTERN ENDEMISM

Since the publication of our paper ('Jouyeux *et al.*, 2001' [sic] in Moura, 2003), the idea of prevailing south-to-north colonization across the Amazon delta has been further reinforced by new records of species previously considered Brazilian endemics at the southern tip of the Caribbean (Rocha, in press). Although *Chromis scotti* Emery 1968 has been collected from a few sites in north-eastern Brazil (information already presented in our paper; e.g. Fig. 1g in Joyeux *et al.*, 2001), it is still

not known southwards from the hump of Brazil. Moura (2003) also made a mistake stating that *Halichoeres radiatus* (Linnaeus 1758) does not occur south of the Equator, as the species is present in Atol das Rocas and Fernando de Noronha (3°50'S) (Rocha & Rosa, 2001b) and strays (i.e. vagrants) were found in the NE Brazilian coast (L.A. Rocha, pers. comm.).

East-to-west migration was hypothesized (e.g. the expressions 'most probably crossed the other way' and 'putative colonisers' in Joyeux et al., 2001, p. 837; see also p. 832) for Acanthurus monroviae (Steindachner 1876), Epinephelus marginatus (Linnaeus 1758) and Aulostomus strigosus Valenciennes 1842. We assume their eastern origin based on the large geographic area that these species occupy in the eastern Atlantic vs. their narrow distributional range in the western Atlantic (for an extreme example, only a few vagrant A. monroviae were recorded so far; O.J. Luiz-Júnior et al., submitted to Journal of Fish Biology). This same criterion was used by Briggs (1974, 1995) when asserting a western origin of other amphi-Atlantic fish species, and Rocha (in press) when discussing the Brazilian origin of a few species that are, in the northern part of their range, restricted to the southernmost areas of the Caribbean. Actually, most amphi-Atlantic fishes are believed to originate from the western Atlantic (Briggs, 1974). Of ninety-two reef-associated amphi-Atlantic teleost species, only four (3.68%) seem to have migrated from east to west (S.R. Floeter, pers. obs.): the three discussed above and Parablennius pilicornis (Cuvier 1829; Blenniidae) (O.J. Luiz-Júnior et al., submitted). We anxiously await the 'genetic or long-term ecological studies' that may support or falsify our hypothesis.

Concerning the absence of south-western Atlantic endemic genera, both Joyeux et al. (2001) and Moura (2003) are wrong. There are (at least) two endemic monotypic genera in the south-western Atlantic: Ribeiroclinus Pinto 1965 (R. eigenmanni [Jordan 1888]; from Rio de Janeiro to Argentina) and Storrsia Dawson 1982 (S. olsoni Dawson, 1982; apparently endemic to Fernando de Noronha). These two unique and atypical species (from a pool of more than 400 Brazilian reef fish) do not invalidate the fact that all other reef-associated species are from genera also found in the Caribbean. They can be nicely incorporated in Fig. 1i of Joyeux et al. (2001), although neither is large or conspicuous. Finally, concerning the use of subspecies, we followed Nelson (1999) who considered the subspecies concept 'useful in studies of biodiversity or conservation where we wish to draw attention in formal taxonomy to cases where there has been some recognisable divergence [...] within a species'.

PUTATIVE SISTER SPECIES

Many of the phylogenetic relationships we hypothesized (e.g. 'PUTATIVE sister species' in Table 1 in Joyeux et al., 2001) proved to be right. New molecular studies (G. Bernardi and collaborators, unpublished) confirmed Thalassoma noronharum (Boulenger 1890) and Thalassoma bifasciatum (Bloch 1791) as sister species and raised the chances for a specific status for the Brazilian population of S. atomarium (species currently being studied by Gasparini and collaborators). Similarly, a phylogenetic study of Pomacanthidae using allozymes (Chung & Woo, 1998) established that Pomacanthus paru and P. arcuatus (Linnaeus 1758) are closely related, as are H. tricolor and H. ciliaris (a relationship we were not aware of). In all cases, we based our suppositions on general likeliness, extreme similarity in colour pattern and/or total overlap in meristic data for all counts [e.g. Stegastes fuscus (Cuvier & Valenciennes 1830) and S. imbricatus Jenyns 1840 - for photographs, see Allen, 1991, p. 175, and Rocha, 2002, p. 464; Gasparini et al., 1999; G. Allen, pers. comm.]. Rocha (in press) used similar criteria to analyse speciation in the western Atlantic by considering similar species as closely related pairs: '...those pairs are very similar in general morphology, colour and ecological requirements (being herein tentatively considered sister species)...'. The case of Aulostomus is complex and unresolved, mainly because the population genetics study of the ring species (Bowen et al., 2001) was not intended as a phylogenetic study and lacks an outgroup.

Moura (2003) stated that we presented no evidence of differentiation of *Chromis* cf. *multilineata* (Guichenot 1853) at St Paul's Rocks. It, therefore, seems appropriate to comment that an aberrant coloured *C. multilineata* was recently photographed, just like some fishes described by Lubbock & Edwards (1981) 22 years ago (B. Feitoza, pers. comm.). Also, the blue colour morph of *H. ciliaris* from St Paul's Rocks was recently photographed by Yataka Niino at a Japanese aquarium, leaving no doubt that the aquarium collectors are now operating even at this remote islet (R. Kuiter, pers. comm.).

In conclusion, it has been 2 years since we presented our opinions as hypotheses to be

further tested (Joyeux et al., 2001). Instead of attempting to demolish our work, Moura should have dedicated his time and energy to use his own work and analyses to falsify (or confirm) our hypotheses. Moreover, his unpublished information on distributional records would greatly improve future analyses if it were made available to the ichthyological community. However, the only comprehensive Brazilian reef fish lists published are those by Lubbock & Edwards (1981), Rocha et al. (1998), Ferreira & Cava (2001), Gasparini & Floeter (2001) and Rocha & Rosa (2001a). Neither minor mistakes in distributional data nor new data published since our paper invalidate the hypotheses presented by us.

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