

Post-doc Research Proposal

Diversity, biogeography and macroecological patterns of Atlantic reef fishes

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Short Title – Atlantic Reef fishes

Summary

This proposal aims to develop the great potential of reef-fishes as model taxa for biogeographical and macroecological analysis of reef areas in the Atlantic. Detailed large-scale studies of Atlantic reef fishes were always hampered by the lack of reliable geographical distribution of species. Now a multi-institutional international team of researchers is building the most accurate species distribution database possible for the entire tropical and subtropical Atlantic. This extensive new database covering 2404 species from 74 families will be used to **1)** synthesize current knowledge of reef fish diversity and endemism in the Atlantic, **2)** search for large-scale patterns and affinities among zoogeographical provinces, and **3)** advance our understanding of biogeographical and macroecological marine patterns through the test of a series of hypothesis including the operation of biogeographical barriers, dispersal potential, biotic invasions, and the stepping stones concept.

Problem Statement

Reef fish as model taxa

Any shallow (< 100m) tropical/subtropical benthic fish, which occurs associated, either permanently or temporarily, with hard substrates (i.e. coral, algae or rocky 'reefs') will be considered as 'reef-fish'. Reef-fish could be viewed as model taxa for biogeography and macroecology analysis of reef areas because: **1)** they are a highly speciose group; **2)** they are not limited to tropical reef areas (like reef-building corals) and thus are ideal for comparison between centers of high diversity and peripheral areas; **3)** reef-fishes are relatively easy to identify comparatively to other groups (e.g. sponges, ascidians); and **4)** distributions of soft-bottom species are usually less known.

The Atlantic reef fish database

Until now the biogeographical provincial divisions proposed by Ekman (1) and Briggs (2, 3) were based on fewer (and less reliable) checklists, and they did not use statistics for data organization. Taking advantage of the dynamic exchange of information through the internet, a team of researchers from both sides of the Atlantic is building an up-to-date, comprehensive geographical distribution database for the entire tropical and subtropical Atlantic (23 defined areas, see Figure 1). As the project leader, I am responsible for the creation and updating the database, which is now nearly completed in taxonomical terms with 74 families and 2404 species. Recent field and taxonomic research focusing on previously poorly-explored areas like the tropical West Africa (4, 5, P. Wirtz, unpubl.), the Brazilian coast (6), and oceanic islands (7), revealed new species (8–10), and added considerable new information about the geographical distribution of tropical reef fishes. Concurrently, new data are available on the tectonic, eustatic, climatic, and oceanographic characteristics of the tropical Atlantic (11, 12), and on the phylogeography of Atlantic species (13–15).

In order to explore if biological/ecological traits are linked with biogeographic or macroecological patterns found, each species in the database will be attributed a series of biological/ecological and functional characteristics (e.g. habitat – hard substrata only and soft substrata adjacent with reefs, maximum size, spawning mode, diet category). These data relative to each species will be inserted in the geographical distribution database from direct observations from all the collaborators, unpublished stomach content analysis, as well as data from the available literature (16, 17). The analyses will be done at the species, genus and family levels. Relative importance of genus and families will also be conducted.

Analytical tools

- Advanced analytical tools will be used to calculate similarity matrixes using various indexes, such as PAUP (Phylogenetic Analysis Using Parsimony – 18), cluster analyses;
- For statistical robustness a series of univariate and multivariate statistics, as well as randomization algorithms to estimate p-values will be conducted when applicable;
- Number of species in common among regions, and their biological/ecological characteristics will be analyzed;
- Map plots with possible migration or biogeographical links will be generated;
- Mantel tests will be applied to compare clustering of sites vs. geographic distance and vs. genetic differences matrix (i.e. comparisons with phylogeography works).

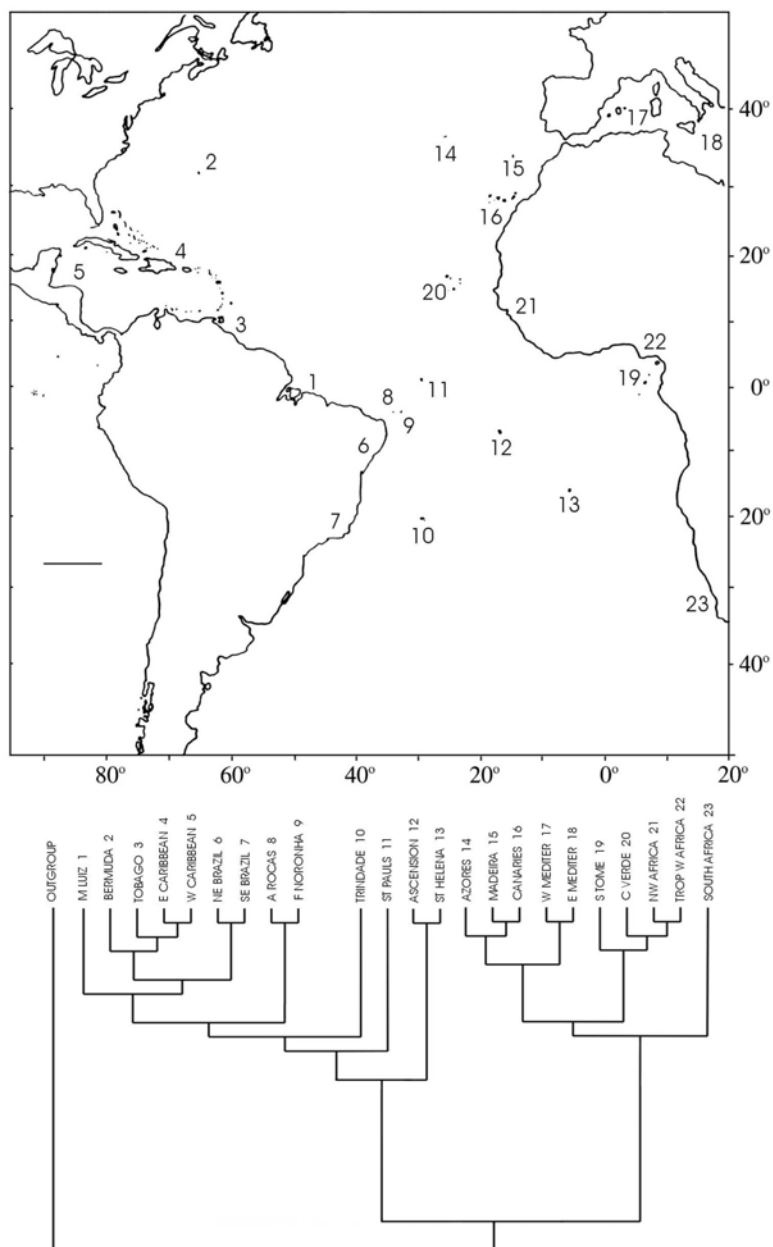


Figure 1. Preliminary clustering of the areas using PAUP (matrix has 23 sites, 2404 taxa). Number of bootstrap replicates = 100. Trees are unrooted.

Searching for large-scale patterns and testing causes of those patterns

Operation of zoogeographical barriers

Four major zoogeographical barriers are known to operate in the Atlantic, namely **1)** the Amazon ‘freshwater’ Barrier, separating the Caribbean reef fauna from Brazil. A recent faunal reevaluation revealed significant endemism on both sides (*19, 20*); **2)** the Mid-Atlantic Barrier, a broad, deep-water region that separates the western Atlantic tropics from those of the west African coast. However, approximately 92 reef fish species are amphi-atlantic; **3)** the Old-World Land Barrier, which was established by the collision between Africa and Asia. Currently, the only possible connection between the Indo-Pacific and the Eastern Atlantic is around the southern tip of Africa, but it is not easily transposed by tropical species due to the upwelling conditions of the Benguela current; and **4)** the Isthmus of Panama, which blocked the movement of tropical marine species between the eastern Pacific and the western Atlantic. How these barriers operate or operated in the past, and how porous they are (or were) is unclear from a general perspective (*14, 15, 21*). For example, what types of species are able to cross the Amazon? and what are the relative abundances of these types in both the Caribbean and Brazil? The proposed study will shed light in these questions.

Synthesis and exploration: Now we have an extensive database on the distributions of reef-fish species of the Atlantic and substantial recent information is available on two previously poorly-known key faunas – Brazil and west Africa. Thus, it is now possible to synthesize data in species composition, taxonomic diversity, total and relative richness (at the species, genus, and family level), and endemism found throughout the tropical and subtropical Atlantic reefs. The provincial divisions proposed by Briggs (*2, 3*) will be statistically explored and updated. For example, Gilbert (*22*) and Briggs (*2, 3*), divided the tropical western Atlantic fauna in three regions: the Caribbean (or continental), the West Indian (or insular) and the Brazilian. However, recent studies on the extent of genetic differentiation among reef fishes showed considerable gene flow throughout the northwestern Atlantic (*23*). This agrees with the low level of endemism found on the islands of the northwestern Atlantic (*24*).

Dispersal potential

Virtually all reef species have larvae that spend some time adrift in the plankton (*25*). Short planktonic durations (usually 15–25 days) and inshore development of demersal-spawners may result in relatively short average dispersal distances and more restricted distributions (*26*). The long planktonic duration (typically 20–50 days) and offshore development of many pelagic spawning species (e.g. Acanthurids, labrids, chaetodontids) suggest a more extensive dispersal (*27*). Furthermore, Hughes et al. (*28*) utilizing an extensive database for the entire Indo-Pacific region found that the five families that have significantly more pandemics than expected are all broadcast spawners, whereas the three families that have significantly fewer pandemics than expected are benthic spawners with extended period of parental care.

Hypothesis: Amphiatlantic species, i.e. species that migrated from one side to the other, are predominantly pelagic-spawning species (i.e. their larval duration in the planktonic phase enable these species to cross the Atlantic from time to time with the aid of oceanic currents).

Asymmetric invasions

Are invasions symmetric from one side to the other of a zoogeographical barrier (29, 30)? For example, the affinities of the Tropical Eastern Atlantic (TEA) fauna to other regions is a matter of much debate (31 – molluscs, 3 – shore fish), and the relative importance of its links with the Western Atlantic (Eastward migrations), the Mediterranean, and the SW Indian faunas need to be reassessed with up-to-date geographical distribution of reef-fishes. Briggs (3), stated that ~25% of the composition of TEA shore fish fauna derived from eastward trans-Atlantic invasions from the Caribbean or Brazil and that TEA was also invaded by at least 24 Indo-Pacific species that rounded the Cape of Good Hope with the occasional aid of the Agulhas Current (32). On the other hand, Briggs (3) asserted that high diversity areas, like the Caribbean, demonstrate high level of resistance to invasions by species from other regions. However, Vermeij & Rosenberg (31) argue that extinctions allowed successful invasions of the western Atlantic by mollusks.

Hypothesis A: Biotic exchange occurs primarily in a unidirectional way, from more to less diverse areas, i.e. towards areas where the biota is poorer and the competition is supposedly less. Thus in the tropical Atlantic migration occurs from the Caribbean to Brazil and from the Caribbean or Brazil to West Africa.

Hypothesis B: The Eastern Atlantic region has more faunal affinities with the Indo-Pacific than to the Western Atlantic, due to the higher probability of invasions from the species-rich Indo-Pacific region comparatively to the Western Atlantic (33).

The stepping stones concept

Since the seminal work of MacArthur & Wilson (34) on the theory of island biogeography, the concept and actual functioning of stepping stones for biotic exchange are a controversial issue (35–37). The islands of the mid-Atlantic ridge were always considered to have relevant importance as stepping-stones for Atlantic crossing (37, 38). However, the actual number of trans-Atlantic species that are also found in these islands is not known. Now the new database could be used to revisit the ‘presumed’ relative importance of oceanic islands as stepping stones for the reef fish fauna. Characteristics of island faunas will be compared to those on both continents.

Hypothesis: The majority of the trans-Atlantic species are also present in oceanic islands, which were presumably used as stepping-stones for long-distance crossings.

Name of Participants

Project leader

Sergio R. Floeter, UENF (proponent).

Biogeographical analysis

Sergio R. Floeter, UENF; D. Ross Robertson, STRI; Alasdair J. Edwards, University of Newcastle; Luiz A. Rocha, University of Florida; Peter Wirtz, University of Madeira; Jean-Christophe Joyeux, UFES.

Macroecological analysis

Sergio R. Floeter, UENF; Michel Kulbicki, IRD-New Caledonia; Carlos E.L. Ferreira, IEAPM; Jean-Christophe Joyeux, UFES.

Atlantic phylogeography

Brian W. Bowen, University of Florida; Luiz A. Rocha, University of Florida.

Taxonomic experts

Western Atlantic – William Smith-Vaniz, USGS; D. Ross Robertson, STRI; Joao L. Gasparini, UFES; Ivan Sazima, UNICAMP; Luiz A. Rocha, University of Florida; Sergio R. Floeter, UENF; Carlos E.L. Ferreira, IEAPM.

Eastern Atlantic – Peter Wirtz, University of Madeira; Joao P. Barreiros, University of Azores; Alasdair J. Edwards, University of Newcastle; Dennis Polack

Mid-Atlantic Ridge – Alasdair J. Edwards, University of Newcastle; D. Ross Robertson, STRI; Luiz A. Rocha, University of Florida.

Rationale for Support from NCEAS

The NCEAS is the ideal place for me to conduct the project described in this proposal, because it involves a number of aspects of its mission. First, the proposed research integrates well with and benefits much from interaction with a number of current working groups (e.g. the proposed project is a natural complement to Cliff Cunningham's CORONA – Coordinating Research On the North Atlantic). Second, this project applies advanced analytical tools (PAUP, univariate & multivariate statistics, randomization algorithms to estimate p-values) to address contemporary biogeographical and macroecological theories and hypotheses. Analyses will be computer-intensive and facilitated by the computational power available at the center. Finally, the close relationship between the center and the UCSB will provide collaborative opportunities with reef-fish scientists like Dr Robert Warner and Dr Sally Holbrook, and PISCO program scientists like Dr Steven Gaines.

Proposed Activities and Timetable

This one-and-a-half year project will begin on 1 September 2003.

1 September 2003 to 1 March 2004 – Compilation, refinement, and integration of ecological/biological data to the database.

1 March 2004 to 1 March 2005 – Synthesize reef fish diversity and endemism in the Atlantic. Conduct analyses to test the proposed hypotheses regarding biogeographical and macroecological issues. Manuscripts preparation.

Anticipated Results and Beneficiaries

Analyses of the new database will contribute to the advance of our knowledge on the diversity, biogeography and macroecology of the Atlantic reefs through (1) synthesis of extensive information not currently integrated, and (2) testing relevant hypotheses.

The entire database will be available on-line to future research and hypotheses refinement. It will also be useful in the detection of natural and human-induced invasions. Furthermore, it will allow the monitoring of recent changes in geographical ranges of tropical fish that are being recently detected in subtropical or temperate waters, probably due to the ‘global warming’ phenomena. At least three publications (in collaboration with the participants) will be derived from this project.

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