Peixes Recifais Brasileiros:
Diversidade e Endemismo

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Peixes Recifais Brasileiros: Diversidade e Endemismo

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II. Teses

Resumo

Os níveis de diversidade e endemismo da fauna de peixes que habita os ambientes recifais rasos de águas brasileiras são estabelecidos e os fatores ecológicos e históricos que os determinaram são apresentados e discutidos.

A diversidade é estimada com base na revisão crítica de recentes contribuições à taxonomia dos peixes recifais brasileiros, sendo tipificada por estudo de caso correspondente à uma revisão das espécies brasileiras do gênero *Paraclinus* (Teleostei, Blennioidei, Labrisomidae). Esta revisão indica que tanto a diversidade de espécies (três espécies de *Paraclinus*) quanto sua taxa de endemismo no Brasil (100 %) são maiores do que estava previamente descrito na literatura.

As informações contidas neste e em outros estudos similares revelaram níveis de diversidade e endemismo em peixes recifais brasileiros mais altos do que anteriormente descritos. A partir deste quadro, foram conduzidas duas avaliações sobre aspectos distintos da biogeografia desta fauna.

A primeira, restrita às dez famílias mais diversificadas em ambientes recifais brasileiros, é uma análise sobre a variação geográfica da composição de espécies encontrada nas principais formações recifais presentes em águas territoriais brasileiras. Esta análise indica a existência de dois agrupamentos de localidades na zona costeira do Brasil: o primeiro, que inclui as localidades presentes na região nordeste, apresenta correlação significativa com a riqueza coralínea da região. O segundo, constituído pelas localidades da região sudeste, está significativamente relacionado com a alta produtividade primária. Esta análise indica ainda que o principal fator que contribui para a diferenciação das ictiofaunas dos três complexos insulares da zona oceânica brasileira, *i.e.* Fernando de Noronha/Atol das Rocas, Ilha

da Trindade / Martin Vaz e Penedos de São Pedro e São Paulo é a distância geográfica que estas apresentam entre si e entre as demais localidades.

A segunda, restrita aos Acanthopterygii com desova não planctônica, é uma reavaliação das zonas de endemismo da ictiofauna dos ambientes recifais rasos de águas brasileiras, incluindo uma análise de suas relações hierárquicas e os fatores históricos relacionados ao surgimento das mesmas. Nesta análise são indicadas evidências de que foi a fauna da Ilha da Trindade a primeira a isolar-se das demais zonas de endemismo, e não a dos Penedos de São Pedro e São Paulo como previamente descrito na literatura. Entre os fenômenos históricos que moldaram estas zonas de endemismo, destacam-se, além das variações no nível do mar ocorridas durante as glaciações pleistocênicas, as mudanças nos padrões de circulação de termohalinas (THC) ocorridas no mesmo período.

Abstract

Levels of diversity and endemism of the ichthyofauna that inhabits Brazilian shallow reefs are established. Related ecological and historical factors are presented and discussed.

Diversity is estimated based on a critical review of recent contributions to the taxonomy of Brazilian reef fishes. These contributions are typified by a case study dealing with the revision of the Brazilian species of the genus *Paraclinus* (Teleostei, Blennioidei, Labrisomidae). This study indicated that actual levels of diversity (three species of *Paraclinus*) as well as endemism within Brazilian waters (100 %) are higher than previously sustained.

Information presented in this as well as in similar studies revealed levels of diversity and endemism in Brazilian reef fishes higher than previously described. From this standpoint, two analyses about distinct aspects of the biogeography of this fauna were conducted.

The first one, restricted to the ten most speciose fish families in Brazilian reefs, is an evaluation of the geographic variation of the species composition found in some of the main reef formations within Brazilian territorial waters. This analysis indicates the existence of two groups of localities along the Brazilian continental margin. The first one, which includes northeastern localities, is correlated with the richer coralline diversity observed in the area. The other group, composed of the southeastern localities, is correlated with the higher levels of primary production found in the area. This analysis further indicates that the main factor contributing for the differentiation of the oceanic islands' ichthyofaunas, *i.e.*, Fernando de Noronha / Atol das Rocas, Ilha da

Trindade / Martin-Vaz and St. Paul's / St. Peter's Rocks is their geographic distances from the remaining localities.

The second biogeographic study, restricted to the non-planktonic egg-laying Acanthopterygii, deals with a reevaluation of the ichthyofaunal zones of endemism from shallow reefs found within Brazilian territorial waters. This study also deals with the hierarchical relationships among these zones and the historical factors related to their origin. It indicates that Trindade Island's fauna was the first one to become isolated from the others, and not that of St. Paul's Rocks as previously sustained. Among historical phenomena that forged these zones of endemism, aside from sea-level changes that took place during Pleistocenic glacial cycles, are changes in thermo-haline circulation patterns (THC) that occurred during the same period.

Agradecimentos

Tudo começou quando meus pais me levaram pra pescar em Saquarema. Eu tinha quase três anos.

Depois me deram uma irmãzinha, que virou minha fiel companheira de aventuras marinhas.

Desde então, conheci várias pessoas tão apaixonadas pelo mar e suas criaturas quanto eu. O meu desenvolvimento como pesquisador e ser humano deve muito às interações que tive com elas. A lista não caberia aqui.

Entre elas, o meu orientador, Gustavo Nunan, me ajudou especialmente a diminuir minha ignorância sobre o vasto e maravilhoso mundo dos peixes recifais.

E meu companheiro de laboratório, Sérgio Anníbal, me ajudou a visualizar as conexões entre os peixes recifais e o "mundo real", sem as quais este trabalho não teria sentido.

Sobre apoio financeiro, que não é tudo, mas sem o qual ninguém vive ou faz tese, deixo registrado: Da graduação ao doutorado, vivi períodos onde a minha principal fonte de renda foi representada pelo auxílio que o governo do meu país (ou do meu estado) concede para estudantes sob a forma de bolsa. Enquanto doutorando, cheguei a figurar, por conta de bolsas concedidas pela CAPES e mais tarde pelo CNPq, entre os 30% da população ativa brasileira de melhor remuneração.

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DISCUSSÃO GERAL

1 - Introdução Geral

Antes mesmo que Linné publicasse a décima edição de seu *Sistema Naturae* (Linné, 1758), os peixes recifais brasileiros já eram objeto de estudo de viajantes europeus. O registro mais antigo que se conhece é o de Margraff (1648) que, pesquisando o nordeste do país, catalogou algumas dezenas de espécies, referindo-se a elas através de seus nomes indígenas. Expedições que partiam da Europa mercantilista em busca de novos conhecimentos sobre riquezas naturais brasileiras continuaram nos séculos seguintes, e informações dispersas sobre os peixes recifais brasileiros foram publicadas por diversos autores (ver revisão em Nunan, 1992).

Já no início do século XX, porém, surgiram as primeiras publicações sobre peixes recifais de autoria de um brasileiro. Trabalhando no Museu Nacional, Alípio de Miranda Ribeiro publicou diversos trabalhos, entre eles o catálogo *Fauna Brasiliense - Peixes* onde fez referência a mais de 370 espécies de peixes marinhos do Brasil, algumas delas exclusivas de ambientes recifais (Ribeiro, 1907 - 1918).

Nos anos seguintes surgiram vários outros estudos descritivos sobre esta fauna, até que Briggs (1974) apresentou a primeira indicação clara de que esta possui características únicas suficientes para ser reconhecida como uma unidade biogeográfica.

Posteriormente, com o desenvolvimento de técnicas de coleta associadas ao mergulho autônomo, o número de espécies de peixes recifais registradas na costa brasileira cresceu significativamente (Guimarães *et al.*, 2001). Neste contexto, Nunan (1992) apresentou uma extensa reavaliação sobre a composição e a biogeografia da fauna de peixes recifais brasileiros, indicando um grande número de adições em sua composição e o reconhecimento de sub-áreas de endemismo antes não reconhecidas, destacando-se, entre estas os complexos insulares oceânicos de Trindade e Martin Vaz e Fernando de Noronha e Atol das Rocas.

O presente estudo trata de uma reavaliação dos padrões de diversidade e endemismo da fauna de peixes recifais brasileiros, onde são apresentadas evidências de que esta é ainda mais diversificada do que previamente estabelecido tanto no que se refere ao número de espécies quanto ao número de zonas de endemismo que a compõe. São apresentadas ainda hipóteses sobre as relações hierárquicas entre estas zonas e discutidos os possíveis fatores bióticos e abióticos, históricos e instantâneos que as originaram e as mantém.

1.1 - A fauna estudada

Considera-se que a fauna de peixes associados a ambientes recifais figura como a mais complexa e diversificada comunidade de vertebrados do mundo (Helfman *et al.*, 1997). Estima-se, por exemplo, que somente nos recifes do Indo-Pacífico existam mais de 4.000 espécies de peixes, *i.e.*, 18% de todos os peixes conhecidos (Choat e Belwood, 1991). No Brasil, calcula-se que a ictiofauna recifal seja composta por aproximadamente 400 espécies (Guimarães *et al.*, 2001).

Historicamente, a designação "peixe recifal" surgiu como referência genérica a todos aqueles peixes observados por mergulhadores em ambientes de fundo consolidado, particularmente em recifes de coral (Sale, 1991).

No entanto, percebeu-se posteriormente que enquanto algumas espécies frequentam os recifes apenas ocasionalmente, outras são residentes obrigatórios. De fato, há tamanha diversidade nas relações que os peixes marinhos apresentam com os ambientes recifais que no espectro resultante são imprecisos os limites que separam os conceitos de "recifal" e "não-recifal" (*e.g.*, Bellwood, 1998; Robertson, 1998).

Dentre os grupos de peixes ditos recifais não obrigatórios, destacam-se os nadadores ativos como os actinopterígios das sub-ordens Carangoidei e Scombroidei e alguns Chondrichthyes, que visitam os recifes ocasionalmente, principalmente para alimentarem-se (Sale, 1991).

Entre os grupos encontrados com maior frequência em recifes, destacam-se alguns grupos de actinopterígios, entre os quais observam-se adaptações que refletem uma relação mais íntima com este ambiente. Essas adaptações vão desde o desenvolvimento de morfologias e coloridos complexos e exuberantes a especializações extremas no comportamento reprodutivo e alimentar (Deloach, 1999). De fato, a grande diversidade de formas e comportamentos é uma característica marcante dos recifes cujo surgimento está diretamente relacionado à complexidade tridimensional e temporal ali encontrada (Choat e Bellwood, 1991).

Tomando como exemplo as adaptações relacionadas ao ciclo reprodutivo das formas recifais, percebe-se que estas servem para refinar ainda mais o espectro conceitual que há entre os extremos "recifal" e "não recifal". Reconhece-se dois tipos básicos de postura entre os peixes encontrados em recifes: a planctônica, onde os ovos são lançados ao sabor das correntes e a demersal, onde os ovos são depositados em superfícies do recife e guardados pelos pais (Sale, 1991; Deloach, 1999). Há ainda aqueles onde os machos carregam os ovos, como é o caso dos Syngnathidae que carregam ovos em bolsas ou sobre a superfície do corpo, ou dos Apogonidae e Opistognathidae que carregam seus ovos na boca (Thresher, 1984).

Além disso, o tempo de duração da fase larvar planctônica pode variar de meses até menos de um dia (*e.g.*, Breder, 1941; Stobutzki e Belwood, 1997).

Destas observações decorre que, enquanto alguns grupos com postura demersal vivem em recifes apenas após o seu recrutamento, como é caso dos actinopterígios do gênero *Paraclinus*, têm fase larvar tão curta que passam todo o seu ciclo de vida nos recifes.

A constatação destas diferenças é importante para o entendimento sobre os diferentes padrões de diversidade e endemismo observados nos diferentes grupos, haja vista que os processos de especiação estão diretamente relacionados com a capacidade de dispersão dos organismos.

Neste sentido, cabe ressaltar que os artigos um e três referem-se apenas a espécies com desova não-planctônica, enquanto que o artigo dois somente a espécies com desova planctônica, exceto pelos Pomacentridae.

1.2 - O ambiente estudado

Recifes são ambientes de fundo consolidado, isto é, resistentes à ação de ondas e correntes marinhas (Hetzel *et al.*, 1994).

Os recifes biogênicos, ou chamados recifes de coral são formados por diversos organismos marinhos providos de esqueleto calcário, destacando-se, entre eles, os corais pétreos (Hetzel *et al.*, 1994). Ao longo dos anos, estes organismos crescem uns sobre os outros, criando um ambiente com alta complexidade onde se estabelece uma grande variedade de peixes (Chabanet *et al.*, 1997). No nordeste do Brasil, diferentes tipos de recifes orgânicos são encontrados, com destaque para os recifes cujo principal grupo de organismos presente é o dos corais escleractínicos (Castro, 1999).

Os recifes de origem inorgânica também podem ser de diversos tipos. Os costões rochosos, formados onde o mar se encontra com rochas do embasamento cristalino, representam, nas regiões sudeste e sul, o tipo predominante de recife

(Coutinho, 1999). Beirando grande parte da costa nordeste brasileira são encontrados ainda os recifes de arenito, formados pela compactação sedimentar de linhas de praia antigas (Hetzel *et al.*, 1994).

Existem também os recifes construídos pelo homem, os chamados recifes artificiais. São estruturas como pontes, quebra-mares, dutos ou plataformas marinhas que acabam servindo de base para o estabelecimento de algas e invertebrados. Estes, por sua vez, atraem os peixes que ali vêm buscar alimento e refúgio (*e.g.*, Love *et al.*, 2000; Bohnsack *et al.*, 1997).

O presente estudo concentrou seu foco nos ambientes recifais naturais.

1.3 Objetivos específicos de cada artigo

Artigo I: Neste artigo, o principal objetivo foi o de rever a taxonomia e a distribuição das espécies brasileiras dos peixes recifais do gênero *Paraclinus* (Teleostei: Blennioidei).

Artigo II: Este artigo teve por objetivo

1) rever as composições específicas das dez famílias de Acanthopterygii mais representativas nas principais formações recifais de águas brasileiras;
2) agrupar estas formações com base na similaridade entre suas composições ictiofaunísticas
3) analisar os possíveis fatores ambientais envolvidos na formação destes agrupamentos.

Artigo III: Neste artigo, objetivou-se

1) rever a composição e a distribuição da fauna de peixes acantopterígios de postura não-pelágica endêmicos de ambientes recifais brasileiros.
2) mapear e analisar a relação hierárquica entre as áreas de endemismo resultantes.
3) investigar possíveis associações entre os padrões hierárquicos observados e fenômenos da História da Terra previamente descritos.

Artigo I

Review of the Brazilian species of *Paraclinus* (Teleostei: Labrisomidae), with descriptions of two new species and revalidation of *P. rubicundus* (Starks)

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2.2 Abstract

The New World labrisomid genus *Paraclinus* comprises small, cryptic reef fishes and is represented by three endemic species on the coast of Brazil. *Paraclinus rubicundus* (Starks) occurs from Alagoas south to Santa Catarina and is removed from the synonymy of its Caribbean counterpart *P. nigripinnis* (Steindachner), from which it is separated by its lower numbers of dorsal-fin spines, lateral-line scales and rows of scales on the pectoral-fin base. The two remaining species were also historically misidentified as Caribbean forms. *Paraclinus arcanus* n. sp., known from Pernambuco south to Rio de Janeiro, is distinguished from the Caribbean *P. fasciatus* (Steindachner), by its higher numbers of dorsal-fin spines, nuchal cirrus morphology and the presence of a scaleless area along the anterior portion of the dorsal-fin base. *Paraclinus spectator* n. sp., known from Rio de Janeiro south to Santa Catarina, is distinguished from other large *Paraclinus* with an elongate first dorsal spine and three segmented pelvic-fin rays by the combined presence of a flattened, triangular opercular spine and a soft ray as the last dorsal-fin element.

2.3 Introduction

Paraclinus Mocquard comprises small reef-dwelling fishes distributed along the tropical and warm-temperate American coasts. Currently, twenty species are recognized, eight in the Western Atlantic (Springer, 1954; Böhlke, 1960) and twelve in the Eastern Pacific (Rosenblatt and Parr, 1969; Springer and Trist, 1969).

Literature records of Brazilian representatives of the group are scattered and frequently unsubstantiated. Starks (1913) described *Auchenopterus rubicundus* on the basis of a single specimen from a tide pool in Natal, northeastern Brazil. It was later placed in the synonymy of *P. nigripinnis* (Steindachner) by Springer (1954). All subsequent citations of *Paraclinus* from northeastern Brazil refer to *P. nigripinnis* (Eskinazi and Lima, 1968; Guedes and Azevedo, 1972; Koike and Guedes, 1981). Later, Menezes and Figueiredo (1985) recorded *P. nigripinnis* and *P. fasciatus* (Steindachner) from the southeastern coast of Brazil.

Examination of material from along the coast of Brazil indicated there are three species of *Paraclinus* in the area. Two of these species do not agree with any previous descriptions, as first indicated in a survey of the labrisomids occurring along the state of Rio de Janeiro, southeastern Brazil (Bacellar, unpubl.). We herein attempt to clarify some of these problems, and provide clear diagnostic features for identification of the three species occurring along the Brazilian coast.

2.4 Materials and Methods

Measurements were taken as described by Hubbs (1952) and are presented as hundredths of standard length. Following Springer (1954) and Rosenblatt and Parr (1969), counts of the dorsal and anal fins include all elements, and counts of the caudal fin include only the segmented elements. Counts of lateral-line scales were not made on damaged specimens. Counts of vertebrae were made on cleared and stained specimens, indicated by "cs" in the examined material sections. In the descriptions, the values in parentheses indicate the modes for counts. We have not examined systematic studies published prior to Springer's (1954) review, except for those that cited material from the coast of Brazil (i.e., Starks, 1913; Fowler, 1941). An aberrant specimen of *P. marmoratus* with 16 anal-fin rays (Table 1) was not used in calculation of averages or statistical tests. Institutional abbreviations are as listed in Leviton et al. (1985), with the addition of LBRP for Laboratório de Biodiversidade de Recursos Pesqueiros, Universidade Federal do Rio de Janeiro. The following comparative material was examined during this study: *Paraclinus fasciatus*: COLOMBIA: USNM 299984 (3), Cabruna. CUBA: USNM 171745 (2), Cardenas Bay; USNM 297482 (1), Varadero Beach. PANAMA: USNM 299986 (1), Colon. TOBAGO: USNM 320818 (2). USA, Florida: MZUSP 50197 (4), Crystal River; USNM 299989 (14), Monroe County. VENEZUELA: USNM 297481 (1), Mochima Bay. *Paraclinus nigripinnis*: ANTIGUA: MZUSP 50199 (6), Green Island. COLOMBIA: USNM 297452 (15), Cartagena Bay. MEXICO: USNM 192385 (1), Ascension Bay, Yucatan. PUERTO RICO: USNM 297464 (5). *Paraclinus marmoratus*: BAHAMAS: ANSP 147248 (3), Athol Island. BELIZE: USNM 327607 (3), Carrie Bow Cay. COLOMBIA: ANSP 143158 (6), Old Providence

Id.. USA, Florida: MZUSP 50198 (3), Key Largo; USNM 297510 (2), Monroe County; ANSP 75641 (3), Punta Gorda.

2.5 Key to the Brazilian species of *Paraclinus*

1A. Posteriormost dorsal-fin element a spinous ray; pelvic fins I, 2; orbital cirrus asymmetric, not palmate, with outermost branch longest (Fig. 1A); specimens to 32 mm SL -- *P. arcanus* n. sp.

1B. Posteriormost dorsal-fin element a segmented ray; pelvic fins I, 3; orbital cirrus symetrical, palmate, with branches equal in length (Figs. 2A and 2B) ; specimens to 46 mm SL or greater -- 2

2A. Opercular spine ending in a complex of 3 - 8 spines; first dorsal-fin spine not markedly longer than adjacent ones (9 to 10 % SL), without flap-like projections at its tip; distance between third and fourth dorsal-fin spines 3.9 to 4.7 % SL; segmented anal-fin rays usually 17 - 18; scaleless area at anterior portion of dorsal-fin base (Fig. 2A) -- *P. rubicundus*

2B. Opercular spine simple; first dorsal-fin spine markedly elongated (13 to 14 % SL), with flap-like projection at its tip; distance between third and fourth dorsal-fin spines 5.6 to 8.0 % SL; segmented anal-fin rays usually 19 - 20; without scaleless area at anterior portion of dorsal-fin base (Fig. 2B) ------------------------ *P. spectator* n. sp.

2.5.1. *Paraclinus rubicundus* (Starks) (Figs. 2A, 3A, 3B)

Auchenopterus rubicundus Starks, 1913: 74 (original description; Natal, Rio Grande do Norte; figure); Fowler, 1941: 179 (listed).

Paraclinus nigripinnis not of Steindachner, 1867. Springer, 1954: 434 (in part); Eskinazi and Lima, 1968: 169; Guedes and Azevedo, 1972: 310; Koike and Guedes, 1981: 70 (brief description); Menezes and Figueiredo, 1985: 52 (in part; brief description; figure = *P. spectator*).

Diagnosis.-Differs from all other species of *Paraclinus* in having the following combination of characters: pelvic-fin elements I, 3; dorsal fin typically with 29 spines followed by a segmented element; opercular spine ending in a complex of 3-8 spines (in specimens > 16.6 mm SL); anal fin typically with 17 soft rays.

Description.- Frequency distributions of fin-element counts are given in Table 1. Dorsal-fin elements XXVIII- XXX, 1 (XXIX, 1); anal-fin elements II, 16-18 (17); pectoral-fin rays 13–14 (13); segmented caudal-fin elements 13; pelvic-fin elements I, 3; lateral-line scales 31-34 (33). Branchiostegals 6; vertebrae 35. Pectoral-fin base usually without scales, rarely with one vertical row extending to half height of base; opercular spine ending in complex of 3-8 spines, this number tending to increase with growth. Distance between third and fourth dorsal-fin spines short (3.9-4.7 % SL in adults), only one interneural space vacant between 3rd and 4th dorsal proximal radials. Area around anterior portion of dorsal-fin naked, scales contacting dorsal-fin base at insertion of third dorsal-fin spine (Fig. 2A). Largest examined specimen 46 mm SL, largest reported 47 mm SL (Rosenblatt and Parr, 1969).

Sexual dimorphism.-The dimorphism observed in *P. rubicundus* is basically the same as discussed by Springer (1954) and Brooks (1991) for *P. nigripinnis*, i.e., males possess longer maxillaries, without marked enlargement on the posterior end and wider preopercular and interorbital areas.

Coloration.-Body of preserved specimens light brown with 6-9 (7) dark-brown bars on sides, varying in shape and intensity; dorsal fin with 7-8 (8) dark-brown bars; anal fin with 5-6 (6) bars; caudal base with dark bar followed sharply by narrow white bar; caudal fin otherwise cream to brown, sometimes stippled between rays; pectoral and pelvic fin membranes clear, rays spotted with brown, spots less visible in adult males. Some specimens with a uniformly tan body and darker vertical fins. Head with dark-brown markings radiating from orbit, lower markings longer and darker; head otherwise with numerous smaller dark-brown markings, these less visible in females. Dorsal fin with 1-3 (1) ocellated spots, spot over penultimate dark body bar always present and usually located around spines 23 to 24; no ocellated spot at anal fin. Live specimens darker overall, notably on body.

Remarks.-*Paraclinus rubicundus* is removed from the synonymy of *P. nigripinnis* based on the modal difference in number of dorsal-fin spines (Table 1), number of lateral-line scales (32-33 vs. 33-35 in *P. nigripinnis*) and number of rows of scales on base of pectoral (0 vs. 1 in *P. nigripinnis*). It also differs in number of ocelli on dorsal fin (1-3 vs. 0-1 in *P. nigripinnis*) and number of points at tip of opercular spine (3-8 vs. 2–5 in *P. nigripinnis*).

Distribution and habitat.-Restricted to the coast of Brazil, from Alagoas south to Santa Catarina (Fig. 4). In the Ilha Grande Bay, *P. rubicundus* inhabits clear water, on reefs heavily covered by algae. Most of the examined collections are from shallow-water environments, although it has previously been reported from depths of 14 m (Guedes and Azevedo, 1972) and 23 m (Eskinazi and Lima, 1968).

Material examined (22.6- 46 mm SL).- Alagoas State: MZUSP 50196 (3), Riacho Doce. Bahia State: MNRJ 14576 (1), MZUSP 50203 (4), Itaparica Island; MNRJ 14573 (4), MNRJ 14574 (7), MNRJ 14575 (5), Nova Viçosa; MNRJ 15881 (1), Coroa Vermelha Reef. Espírito Santo State: ZUEC uncat. (22), Santa Cruz. Rio de Janeiro State: MZUSP 50193 (2), LBRP 3475 (1), LBRP 5013 (2), Ilha Grande Bay. São Paulo State: MZUSP 50194 (1), São Sebastião; MZUSP 50195 (1), Ubatuba. Santa Catarina State: MNRJ 12018 (8, 2 cs), Bombinhas.

2.5.2 *Paraclinus arcanus* new species (Figs. 1A and 3C , 3D)

Paraclinus fasciatus, not of Steindachner, 1876. Menezes and Figueiredo, 1985: 52 (description).

Holotype: MNRJ 15900 (adult male, 29.5 mm SL), Itapinhoacanga Inlet, Ilha Grande Bay, Rio de Janeiro State, 23°02'S, 44°12'W, hand-net, 3m, 15th November 1995, R. Z. P. Guimarães and A. C. L. H. de Bacellar. Paratypes: Pernambuco State: MZUSP 50201 (1), Ponta de Pedras, 18th November 1972, Pierre Montouchet. Alagoas State: MZUSP 51604 (1), Riacho Doce, 13th December 1973, N. A. Menezes. Bahia State: MNRJ 14577 (112, 4 cs), USNM 345468 (3), MCZ 151298 (3), ANSP 175722 (3), Coroa Vermelha Reef, off Nova Viçosa, 23rd January 1995 to 1st February 1995, G. W. Nunan and D. Moraes Jr.; MZUSP 50202 (4), Barra do Gil, Ilha de Itaparica, 24th August 1972, N. A. Menezes and C. E. Dawson. Espírito Santo State: ZUEC 275-277 (3), Ilha do Frade, Vitória, 22nd July 1982, C. Zamprogno; ZUEC 3166 (3), tide-pool at

Santa Cruz, Aracruz, April-June 1993, J. L. Gasparini and D. V. Vervloet. Rio de Janeiro State: MZUSP 50200 (2), Ilha da Gipóia, Ilha Grande Bay, January 1982, A. Carvalho-Filho; LBRP 3399 (1), Itapinhoacanga Inlet, Ilha Grande Bay, 15th October 1995, R. Z. P. Guimarães and A. C. L. H. de Bacellar; LBRP 3431 (5), same data as holotype; LBRP 3464 (1), Itapinhoacanga Inlet, Ilha Grande Bay, 12th January 1996, R. Z. P. Guimarães; LBRP 3523 (1), Itapinhoacanga Inlet, Ilha Grande Bay, 31st January 1996, R. Z. P. Guimarães. Non-types: Bahia State: MNRJ 15878 (1), MNRJ 15879 (8), MNRJ 15880 (1), tide-pools at Viçosa Reef, Nova Viçosa.

Diagnosis.-*Paraclinus arcanus* is distinguished from other congeners with a spinous last dorsal-fin element and pelvic fins with one spine and two soft rays by the combined presence of a short nuchal cirrus with two to four small projections, cirrus never in the shape of a rounded lappet (vs. cirrus usually in the shape of a rounded lappet with short points on its margin in *P. fasciatus*, Fig. 1A, 1B); an asymmetric orbital cirrus with outermost branch longest (vs. cirrus symertical in *P. naeorhegmis*), presence of a wide scaleless area along the anterior portion of dorsal-fin base (vs. scaleless area along the anterior portion of dorsal-fin base narrow in *P. fasciatus*, Fig. 1A, 1B), and scales present on pectoral-fin base (vs. scales absent on pectoral-fin base in *P. cingulatus*) .

Description.- Frequency distributions of fin-element counts are given in Table 1. Dorsal-fin elements XXX - XXXII (XXXI); anal-fin elements II,18-20 (II, 19); pectoral-fin elements 12-14 (13); segmented caudal-fin elements 12-13 (13); pelvic-fin elements I,2; lateral-line scales 33-36 (35). Branchiostegal rays 6; vertebrae 36. One to three (two) vertical rows of scales on pectoral-fin base; opercular spine sharp, simple; first three dorsal-fin spines not markedly longer than remaining ones; distance between third and fourth dorsal-fin spines short (4.4-4.9 % SL), only one interneural space vacant between third and fourth dorsal proximal radials; nasal cirrus simple, cirri length usually equal to nasal tube length; orbital cirrus flattened, with 2-3 (rarely 4) tips, outermost tip longest and thickest (Fig. 1A); nuchal cirrus flattened, short, 2-4 (3) small tips (Fig. 1A); area around anterior portion of dorsal fin naked, scales contacting dorsal-fin base at insertion of second dorsal spine (Fig. 1A). Largest specimen examined 32 mm SL; smallest ripe female 22.5 mm SL (Table 2).

Sexual dimorphism.-Males with longer maxilla, females with greater preanal and pelvic-anal distances.

Coloration.-In alcohol, body of juveniles (< 20 mm SL) and adult females light brown, with 6-7 dark, diffuse irregularly shaped brown bars. Dorsal fin light brown with 6-8 dark-brown bars; rays between bars with small brown spots; anal fin light brown with 5-7 dark-brown bars; sharp dark-brown bar present at caudal-fin base; caudal fin otherwise clear except for few melanophores on rays; pelvic and pectoral fins clear with melanophores scattered on rays. Head light brown ventrally, with small, dark-brown spots. In life, brown markings may vary from reddish to orangish tones.

Body of adult males typically very dark brown in alcohol, sometimes dark brown with very weak bars. Diffuse dark bar at caudal-fin base; caudal fin otherwise dusky; pelvic and pectoral fins uniformly dusky brown. In life adult males entirely black. Dark stripe from ventro-posterior orbit margin to posterior tip of maxilla, stripe more evident in larger males. One or two (usually one) ocellated spots on dorsal fin; first spot always present and typically located at spines 23 to 25; second, when present, located around spines 27 to 30; spots difficult to distinguish in adult black-phased males. No spot on anal fin.

Remarks.-*Paraclinus arcanus* has been misidentified as *P. fasciatus* (Menezes and Figueiredo, 1985; Carvalho-Filho, 1992), which is known from many Caribbean localities (Springer, 1954; Greenfield and Johnson, 1981). The new species is distinguished from the latter by typically having 31 dorsal-fin spines (vs. 29 in *P. fasciatus*; Table 1), a forked nuchal cirrus (vs. cirrus in the shape of a rounded lappet in *P. fasciatus*; Figs. 1A, 1B), a scaleless area posterior to nape (vs. scaled in *P. fasciatus*; Figs. 1A, 1B), and by its smaller size (largest known specimen 32 mm SL vs. 49.8 mm SL in *P. fasciatus*).

Etymology.-From the Latin *arcanus*, meaning secretive, an allusion to its habit of hiding underneath rocks.

Distribution and habitat.-*Paraclinus arcanus* is a Brazilian endemic, known from Ponta de Pedras, Pernambuco State (ca. 5° S) south to the Ilha Grande Bay, Rio de Janeiro State (ca. 23° S) (Fig. 4). We have observed *P. arcanus* in shallow (1- 3 m deep) reef habitats at Ilha Grande Bay, where it is sympatric with *P. spectator* n. sp. and *P. rubicundus*. It has also been collected syntopically with *P. rubicundus* in the states of Bahia and Espírito Santo.

2.5.3 ***Paraclinus spectator*** new species (Fig. 2B, 3E, 3F)

Paraclinus nigripinnis, not of Steindachner, 1867. Menezes and Figueiredo, 1985: 52 (in part).

Holotype: MNRJ 15901 (adult male, 51 mm SL), Cataguás Island, Ilha Grande Bay, Rio de Janeiro State, 23°01'S, 44°17'W , hand-net, 5 m, 18th January 1996, R. Z.P. Guimarães and A. C. L. H. de Bacellar. Paratypes: Rio de Janeiro State, Ilha Grande Bay: ANSP 175723 (1), LBRP 3514 (2), USNM 345469 (1), Gambelo Point, 28th

January 1996, R. Z. P. Guimarães and A. C. L. H. de Bacellar; LBRP 3147 (4, 2 cs), no data, 1st April 1995, R. Z. P. Guimarães; LBRP 3430 (1), Itapinhoacanga Inlet, 14th October 1995, R. Z. P. Guimarães and A. C. L. H. de Bacellar; LBRP 3462 (1), Itapinhoacanga Inlet, 12th January 1996, R. Z. P. Guimarães; LBRP 3490 (2), Grumixama Beach, 14th January 1996, R. Z. P. Guimarães and A. C. L. H. de Bacellar; LBRP 3504 (1), Itapinhoacanga Inlet, 24th December 1995, R. Z. P. Guimarães; LBRP 3937 (1), Ilha dos Macacos, 8th December 1996, R. Z. P. Guimarães; LBRP 5076 (1), Ilha Comprida, 25th July 1997, R. Z. P. Guimarães, A. C. L. H. de Bacellar and C. A. Rangel; MCZ 151299 (1), Freguesia de Santana, 20th October 1996, R. Z. P. Guimarães. São Paulo State: MZUSP 51603 (1), Ubatuba, July 1970, J. L. de Figueiredo; ZUEC 743-745 (3), tide-pool at Saco da Ribeira, Ubatuba, 17th October 1982, I. Sazima and O. C. de Oliveira; ZUEC 4076 (2), Saco da Ribeira, Ubatuba, 17th October 1982, I. Sazima; ZUEC 4389 (1), Praia da Fortaleza, Ubatuba, 9th July 1997, I. Sazima, C. Sazima and J. L. Gasparini. Santa Catarina State: MNRJ 15877 (2), tide-pool SE of Bombinhas Beach, February 1986, G. W. Nunan, D Moraes Jr. and W. Bandeira. Non-types: Rio de Janeiro State: MZUSP 46169 (6), MZUSP 46546 (3), LBRP 3148 (1), LBRP 3432 (3), LBRP 3522 (1), Ilha Grande Bay; São Paulo State: MZUSP 46219 (5), MZUSP 46239 (1), São Sebastião.

Diagnosis.-First two dorsal-fin spines much longer than remaining ones; distance between third and fourth dorsal-fin spines greater than orbit diameter; pelvic fins I-3; last dorsal-fin element segmented; opercular spine flattened and triangular; segmented anal-fin elements usually 19-20; body elongated (mean body depth 21.7 % SL in adult males); wide predorsal area (mean 22.6 % SL in adult males).

Description.-Frequency distributions of fin-element counts are given in Table 1. Dorsal-fin elements XXVII - XXIX,1 (XXVIII,1); anal-fin elements II, 18 - 20 (19); pectoral-fin rays 13; segmented caudal-fin rays 12 – 13 (13); pelvic-fin elements I, 3; lateral-line scales 33 - 36 (35). Branchiostegal rays 6, vertebrae 34. First two dorsal-fin spines longer than all others, with membranes of first two interspinal spaces projecting well beyond the spines. Distance between third and fourth dorsal-fin spines 5.6 - 8.0 % SL in adult specimens, distance greater than orbit diameter (two interneural spaces vacant between 3rd and 4th dorsal proximal radials); pectoral-fin base with 2-3 vertical rows of scales. Opercular spine flattened and triangular, rarely serrated at tip in large specimens. Area around anterior portion of dorsal-fin scaled, scales extending to level of first dorsal spine (Fig. 2B). A large species, reaching at least 51.9 mm SL; smallest ripe female 37 mm SL. See Table 2 for additional measurements of the species.

Sexual dimorphism.-Adult females with greater pelvic to anal-fin distance, adult males with longer maxilla and wider head.

Coloration.-Preserved specimens with light-brown body including 5-7 dark-brown bars, bars varying in width and shape. Dorsal fin with 7-8 dark bars, these usually triangular in shape; anal fin with 6 dark bars; one bar at caudal-fin base. Dark stripe from posteroventral margin of orbit to posterior maxillary tip. Juveniles and females with distinct bars on body, dorsal and anal fins; dark striae on pelvic, pectoral and distal portion of caudal fin. Adult males with bars less pronounced to absent, pelvic and pectoral fins uniformly dusky gray. Some adult males with longitudinal dark stripe along distal portion of anal fin. In life, brown markings and background color may vary from reddish to grayish, reddish specimens most often taken from areas richly covered by algae (*Sargassum* sp.), grayish specimens most often taken from naked rock piles. One or two (rarely three) ocellated spots on dorsal fin; anteriormost spot, when present, usually located on 15th to 16th spines, intermediate spot rarely present and posteriormost spot always present on 23rd to 25th dorsal-fin spines.

Remarks.-This species has been misidentified as *P. nigripinnis* in Brazilian collections, although it shares features with *P. marmoratus* Steindachner such as elongation of the first two dorsal-fin spines and a wider distance between the 3rd and 4th dorsal-fin spines, which are absent in *P. nigripinnis*. *Paraclinus marmoratus* is known from many localities throughout the Caribbean (Greenfield and Johnson, 1981; Guitart, 1985; Springer, 1954) and differs from *P. spectator* in having typically 29 dorsal-fin spines (vs. 28 in *P. spectator*, Table 1), typically 20 anal-fin rays (vs. 19 in *P. spectator*, Table 1), a sharply pointed opercular spine (vs. opercular spine flattened and triangular in *P. spectator*) a shorter predorsal distance (mean 19.8 % SL in adult males vs. 22.6 % SL in adult *P. spectator* males) and a markedly deeper body (mean body depth 26.4 % SL in adult males vs. 21.7 % SL in adult *P. spectator* males).

Etymology.-From the Latin *spectator*, meaning observer, an allusion to the fact that when closely approached underwater, this fish usually relies on its camouflaged coloration and observes the diver and its surroundings.

Distribution and habitat.-We have examined material from the Ilha Grande Bay, Rio de Janeiro state (ca. 23 S°) south to Bombinhas beach, Santa Catarina state (ca. 27 S°) (Fig. 4). In the continental portion of the Ilha Grande Bay it is the commonest of all *Paraclinus*, where it prefers shallow rocky-reefs (from 1-7 m deep). In some portions of that bay, *P. spectator* lives syntopically with *P. arcanus* and *P. rubicundus*.

2.6 Discussion

Paraclinus comprises small fishes found on reefs and in marine vegetation which have a limited capacity for dispersal. Females lay eggs in nests guarded by males and larvae have a very short, if any, planktonic phase (Breder, 1941). Taxa with these attributes can be expected to exhibit geographic variation in characters as a result of being split into small subpopulations throughout their geographic ranges (Rosenblatt, 1963). Geographic variation of characters has already been recognized in some *Paraclinus* species by Hubbs (1952) and Springer (1954), as well as in other labrisomids (e.g., Springer and Gomon, 1975). Because of that, we were concerned with the possibility that *P. arcanus*, *P. rubicundus* and *P. spectator* as recognized in this study are mere geographic extremes of supposed wide-ranging western Atlantic forms, namely *P. fasciatus*, *P. nigripinnis* and *P. marmoratus*, respectively. This possibility is refuted by the sharp morphologic differences found between specimens from Brazil and the Caribbean; by the absence of intergrades, and by the wide gap separating the geographic ranges of each pair (smaller distance equals 3,000 km along northeastern coast of South America). The fact that many faunistic surveys have failed to observe the presence of any *Paraclinus* between Cape São Roque, Brazil and Venezuela (e.g., Barthem, 1985; Collette and Rützler, 1970; Eskinazi and Lima, 1968), suggests that this gap is real rather than a collecting artifact. Such evidence indicates there is allopatric replacement within each supposed sister species pair (but see discussion under Phylogeny below).

Phylogenetic positions of the new species.-Monophyly and relationships of the Labrisomidae are unstudied cladistically (Springer, 1993). Relationships of some labrisomid genera have been phenetically hypothesized by Hubbs (1952: Fig. 2), who included *Paraclinus*, *Exerpes* Jordan and Evermann and *Auchenistius* Evermann and Marsh in the tribe Paraclinini Hubbs. *Auchenistius* is a junior synonym of *Stathmonotus* Bean and its affinities lie within the Chaenopsidae rather than the Labrisomidae (Hastings and Springer, 1994). Stepien et al. (1993: Figs. 2-3) recognized a sister-group relationship between *Paraclinus* and *Exerpes*. Available hypotheses on the relationships among species of *Paraclinus* are those of Hubbs (1952), Rosenblatt and Parr (1969) and Springer (1954), which are limited statements of groups of closely related species based on shared similarities. Assuming *Exerpes* is the outgroup for *Paraclinus*, then a sister-group relationship can be indicated for two of the three supposed Caribbean-Brazil species pairs. *Paraclinus arcanus* shares with *P. fasciatus* a pelvic fin with I,2 elements (typically I,3 in *Exerpes* and some other *Paraclinus*), a continuous dorsal fin (separated in two fins in *Exerpes* and deeply notched in some other *Paraclinus*) and an orbital cirrus with the outermost tip longest (orbital cirrus absent in *Exerpes* and apparently never asymmetric in other *Paraclinus*). *Paraclinus rubicundus* and *P. nigripinnis* share the complex condition of the opercular spine, although a similar condition (spine split into two or three points) is sometimes found in the Eastern Pacific *P. integripinnis* and *P. walkeri* (Rosenblatt and Parr, 1969). The position of *P. spectator* is less clear. It shares with the Caribbean *P. marmoratus* and the Eastern Pacific *P. altivelis* and *P. sini* diagnostic features such as an elongated first dorsal-fin spine, the crowding of the bases of the first three dorsal-fin spines, a large size (to 50 mm SL at least) and the pelvic fins with I,3 elements, but all these states are also present in *Exerpes*. A possible indication of a closer relationship between *Paraclinus spectator* and *P. sini* is provided by the flattened and triangular condition of the opercular spine, which is sharply pointed in *Exerpes* as well as in many other *Paraclinus*.

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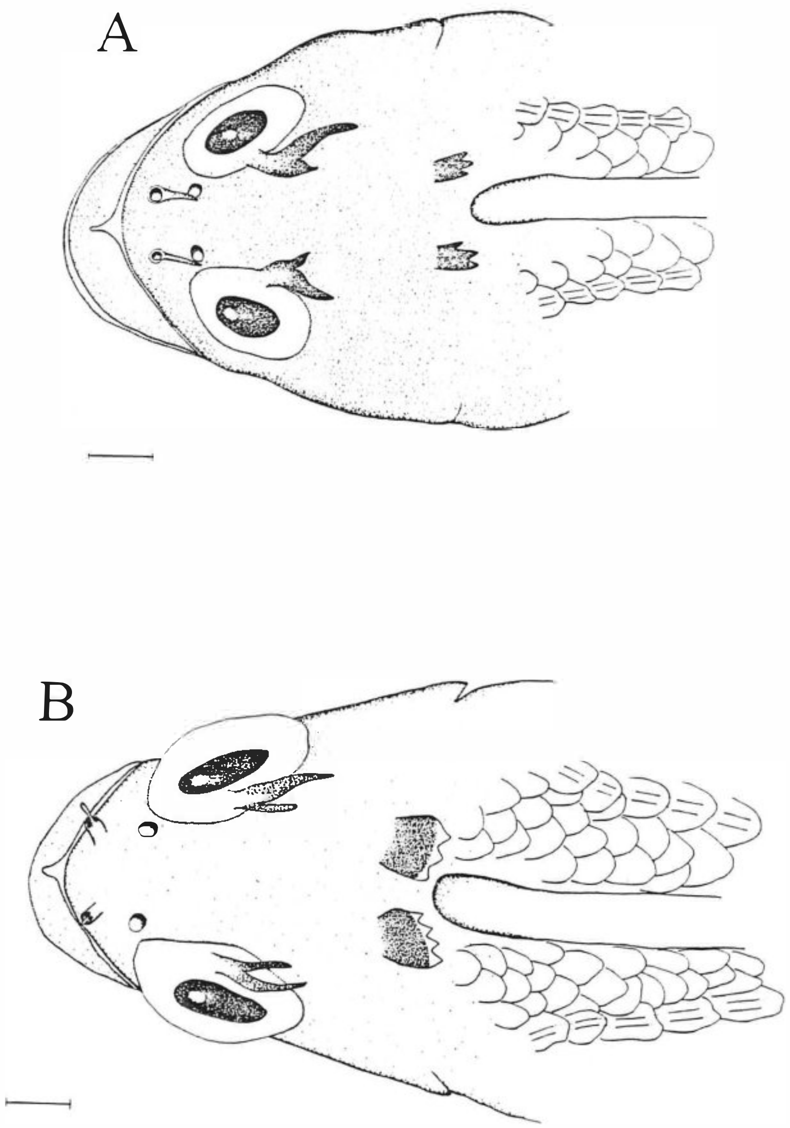

Figure 1. Dorsal view of head, scale bar equals 1 mm. A) *Paraclinus arcanus*, 29.5 mm SL, male, holotype, MNRJ 15900, Ilha Grande Bay, RJ, Brazil; B) *P. fasciatus*, 29.3 mm SL, female, MZUSP 50197, Florida, USA.

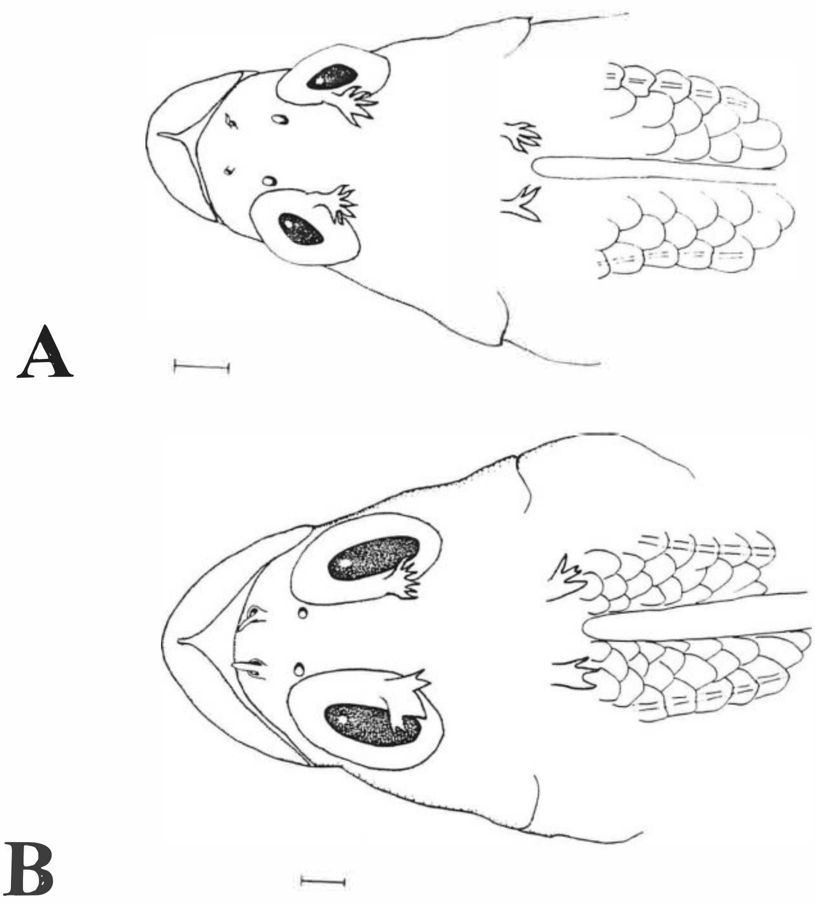

Figure 2. Dorsal view of head, scale bar equals 1 mm: A) *Paraclinus rubicundus*, female, 38.6 mm SL, MNRJ 15881, Nova Viçosa, Bahia, Brazil; B) *P. spectator*, young, 27.2 mm SL, paratype, LBRP 3432, Ilha Grande Bay, RJ, Brazil.

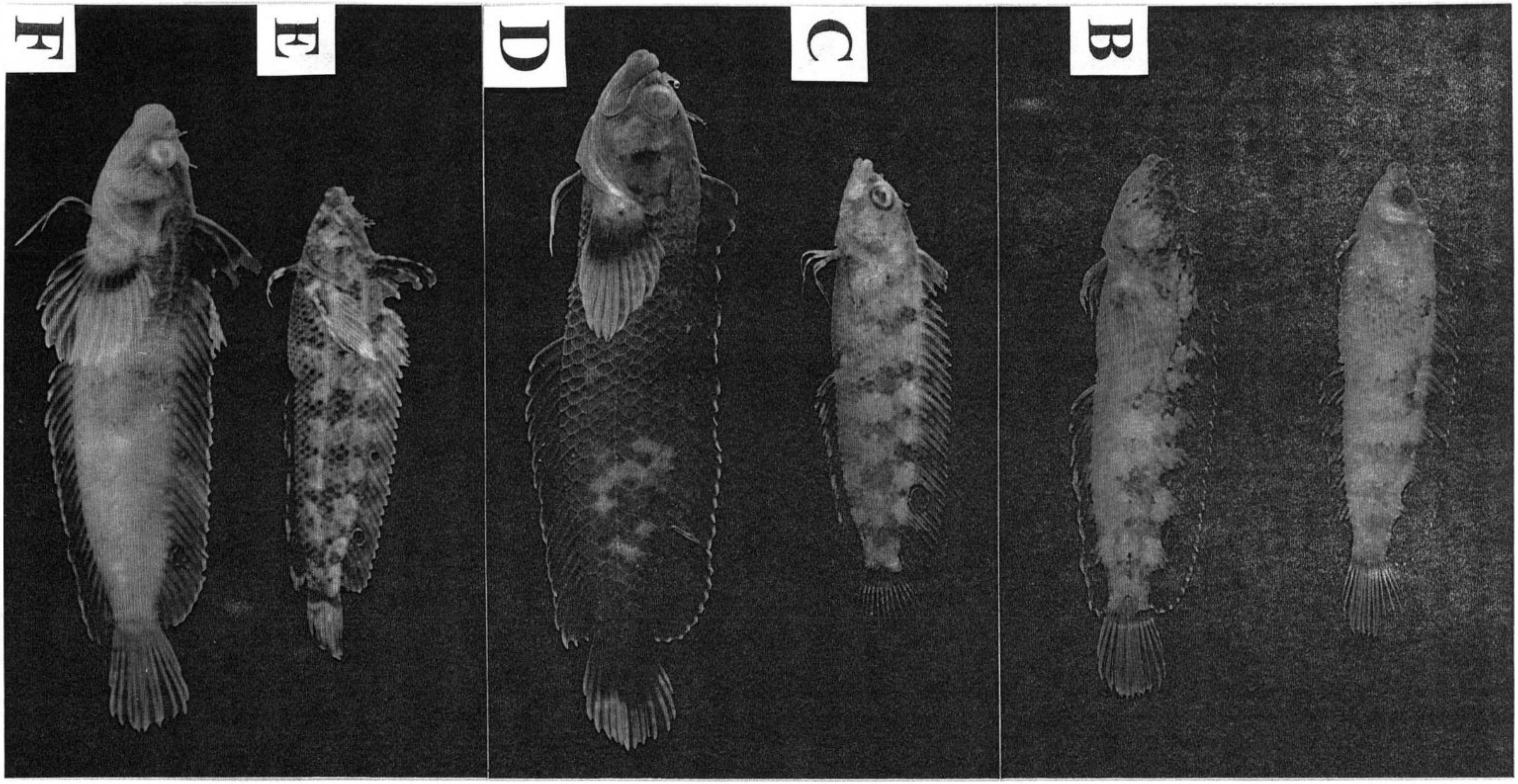

Figure 3: Brazilian species of *Paraclinus* - A) *Paraclinus arcanus* sp. n, , adult female, 23.5 mm SL, MNRJ 14577, paratype, Nova Viçosa Reef, BA; B) *P. arcaus*, adult male, 26.2 mm SL, LBRP 3431, paratype, Ilha Grande Bay, RJ; C) *Paraclinus rubicundus* Starks, adult female, 35.7 mm SL, LBRP 5013, Ilha Grande Bay, RJ; D) *P. rubicundus*, adult male, 40.6 mm SL, LBRP 5013, Ilha Grande Bay, RJ; E) *Paraclinus spectator* sp. n., adult female, 39.9 mm SL, LBRP 3504, paratype, Ilha Grande Bay, RJ; F) *P. spectator*, adult male, 51.4 mm SL, LBRP 3937, paratype, Ilha Grande Bay, RJ.

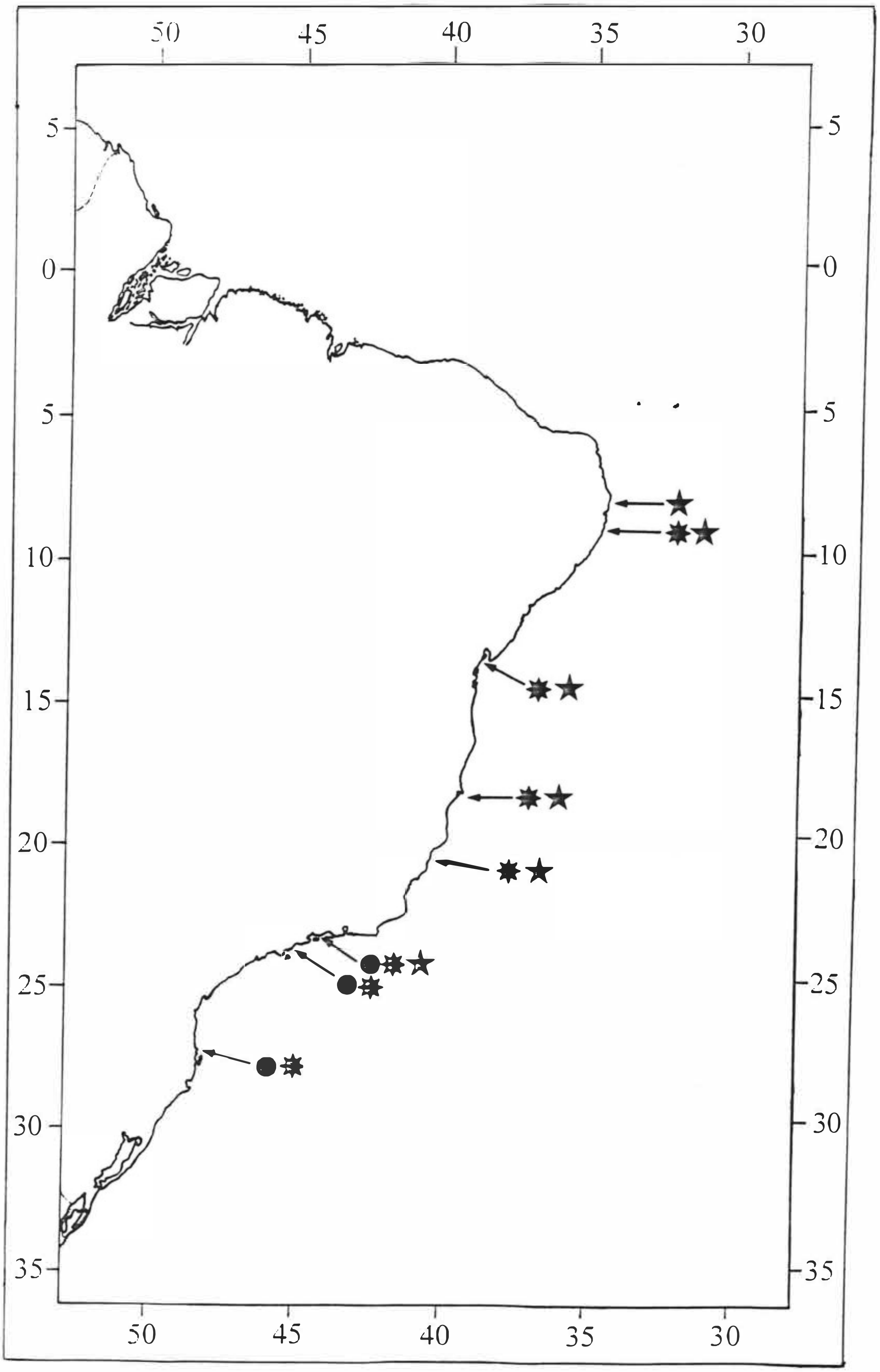

Figure 4. Distribution of *Paraclinus arcanus* (five-tip stars), *P. spectator* (circles) and *P. rubicundus* (eight-tip stars) based on examined material.

Table 1. Frequency distribution of dorsal-fin spines and anal-fin segmented rays in six Atlantic species of *Paraclinus* (data for *P. fasciatus* and *P. nigripinnis* based on Springer, 1954; for *P. marmoratus* based on Springer, 1954 and additional examined material).

	Dorsal-fin spines							Segmented anal-fin rays							
	27	28	29	30	31	32	mean	15	16	17	18	19	20	21	mean
P. nigripinnis			32	79	3		29.7	1	2	56	51	1			17.4
P. rubicundus		1	17	6			29.2		1	17	6				17.2
P. fasciatus		4	106	41	2		29.3			3	40	97	10		18.8
P. arcanus				8	27	1	30.8				3	20	13		19.3
P. marmoratus	3	52	99	4			28.7		1			49	94	7	19.7
P. spectator	1	19	11				28.3				1	20	10		19.3

Table 2. Selected morphometric characters of adults of *Paraclinus arcanus* n. sp. and *P. spectator* n. sp. expressed as percent standard length.

	Paraclinus arcanus				*Paraclinus spectator*			
	males (n= 6)		females (n= 6)		males (n= 6)		females (n= 6)	
	range	mean	range	mean	range	mean	range	mean
standard length (mm)	27.8 - 32.2	29.8	23.1 - 26.9	25.0	37.2 - 51.9	47.1	37.7 - 42.7	40.7
head length	29.5 - 31.7	30.7	30.1 - 32.0	31.0	28.8 - 31.7	30.3	27.3 - 30.4	29.1
head width	14.9 - 18.3	16.5	15.0 - 16.9	15.9	16.5 - 20.5	18.5	14.3 - 18.2	16.6
snout length	5.7 - 7.9	7.0	5.1 - 8.9	7.1	5.4 - 8.3	7.2	5.9 - 7.5	6.9
maxillary length	14.4 - 15.8	14.9	10.9 - 12.9	11.8	12.7 - 15.4	14.4	10.4 - 11.5	11.0
predorsal distance	23.0 - 25.1	24.0	23.3 - 26.7	25.0	20.1 - 24.0	22.6	18.1 - 23.3	21.6
preanal distance	48.7 - 52.9	50.9	51.2 - 55.4	53.6	48.3 - 53.6	50.6	50.1 - 52.0	51.0
length of anal-fin base	45.9 - 53.0	50.0	44.4 - 50.4	46.9	47.5 - 55.6	50.8	45.6 - 50.1	47.7
length of dorsal-fin base	76.7 - 80.3	78.3	77.0 - 82.7	79.6	77.9 - 82.7	80.7	68.4 - 85.7	80.0
pelvic to anal	26.6 - 29.2	27.8	29.4 - 33.4	31.6	26.5 - 29.9	28.0	29.2 - 32.0	30.1
body depth at anal-fin origin	20.9 - 22.5	21.7	20.1 - 23.8	21.7	20.0 - 23.6	21.7	18.3 - 22.6	19.7
caudal peduncle depth	8.4 - 9.2	8.8	7.8 - 9.5	8.8	8.7 - 10.2	9.1	8.2 - 9.5	8.7
orbit diameter	6.4 - 7.3	6.8	6.3 - 7.9	7.0	5.3 - 7.7	6.4	5.9 - 7.5	6.6
interorbital width	2.9 - 4.8	3.7	2.6 - 4.5	3.3	3.0 - 4.8	3.8	1.6 - 4.3	3.0
length 1st dorsal spine	5.1 - 9.0	7.1	8.9 - 10.7	9.4	12.9 - 16.2	14.3	10.6 - 16.0	13.6
length 10th dorsal spine	10.2 - 11.9	11.0	9.8 - 11.9	10.7	9.7 - 12.2	11.3	10.7 - 11.9	11.3
length 5th from last dorsal spine	10.4 - 11.8	11.2	10.7 - 12.3	11.7	9.4 - 12.3	11.4	10.7 - 12.7	11.6
dist. bet. 3rd and 4th dor. spines	3.9 - 4.8	4.4	2.6 - 4.9	3.8	5.6 - 7.7	6.9	6.9 - 8.0	7.6

Artigo II

Geographic variation in reef-fish assemblages along the Brazilian coast

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3.1- Abstract

The species composition of reef-fish assemblages from nine Brazilian major coastal sites and four oceanic islands are compared. Canonical Correspondence Analysis (CCA) was utilised to identify groups of sites based on similarity of composition, and correlate environmental trends with such groups. Five distinct groups of sites were recognised: (1) the South and South-eastern coastal reefs (from Guarapari Islands to Santa Catarina, the southernmost Brazilian reefs); (2) the North-eastern coast (extending from the Manuel Luis Reefs to Abrolhos Archipelago); (3) Trindade Island; (4) Fernando de Noronha and Atol das Rocas; and (5) St. Paul's Rocks. Water temperature, coral richness, distance from mainland, primary production and shelf width strongly correlated with the diversity and composition of the reef sites.

3.2- Introduction

The tropical fish fauna of the western Atlantic ranges from about 35°N to 28°S (Robins, 1971; Nunan, 1992; and present study), and a considerable part of this region (4°N to 28°S) is included in Brazilian waters. Although the reef ichthyofauna of the western North Atlantic has been subject to substantial study the reef fishes of the Brazilian coast and its oceanic islands have remained poorly known. This lack of information on species distributions and assemblages composition has left a significant gap in the understanding of the biogeography of the tropical Atlantic, specially that of the western South Atlantic (Sale, 1991; Briggs, 1995).

A significant increase in sampling effort on Brazilian waters occurred only after the mid-1990s, when the growing use of SCUBA by Brazilian ichthyologists led to the extension of the known geographical range of many species (e.g. Nunan, 1992; Guimarães, 1996a,b; Moura *et al.*, 1999), the description of new species (e.g. Sazima *et al.*, 1997, 1998; Gasparini *et al.*, 1999; Rocha, 1999a), and the first representative collections from major reef areas (e.g. Nunan, 1992; Rocha *et al.*, 1998; Rocha, 1999b; Gasparini & Floeter, *in press*).

Large-scale patterns in the composition of reef fish assemblages have distinct causes: (1) evolutionary histories of different regions, (2) dispersal processes, and (3) underlying environmental gradients. The latter is the central element addressed in this study. The Brazilian coast extends through *c.* 9500 km and is under the influence of a diverse set of oceanographic and ecological conditions. Locally, areas may be under continuous influence of the oligotrophic tropical waters of the Brazilian Current, or seasonally affected by upwelling of cold, nutrient-rich waters (cf. Castro & Miranda, 1998; Ekau & Knoppers, 1999). The nature of the substrate varies from rocky (cf. Maida & Ferreira, 1997) to considerable coral cover (cf. Leão *et al.*, 1988). A further item to consider is the enormous sediment and freshwater input from the Amazon and other Rivers (e.g. São Francisco and Doce River). Hypothetically, the fish faunas of the major Brazilian reefs vary according to these factors.

For the first time the opportunity arises to examine some aspects of the distributional patterns of the Brazilian reef fishes. In this paper, we will focus on the variation of fish assemblages among nine Brazilian coastal reef sites and four oceanic islands (Fig. 1), investigating distinctive environmental factors that possibly shaped the observed patterns.

<u>STUDY SITES.-</u> Thirteen reef complexes were studied, encompassing the whole area of occurrence of reef-associated fishes in the western Atlantic south of the Amazon River mouth (Fig. 1 and Table 1). Nine sites are located in the continental shelf. Four on the North-eastern coast: Manuel Luis Reefs (**ML**), the northernmost Brazilian reef formation, consisting of coralline algal crusts over a rocky substrate, sparsely covered with hermatypic and fire corals; Zumbi Reefs (**ZR**), a rocky formation dominated by sponges and calcareous algae; Paraíba Coast (**PA**), where several calcareous algae reefs grow parallel to the shoreline, mainly over a sandstone base; and Abrolhos Archipelago (**AB**), the largest and more diverse coral reef complex in the South Atlantic, with large isolated "mushroom shaped" pinnacles and wide platform-bank reefs. Five on the South-eastern and Southern coast: Guarapari Islands (**GI**), a rocky insular complex scattered with corals, milleporines, octocorals, and calcareous algae beds; Arraial do Cabo (**AC**), which consists of rocky shores with a veneer of corals, and depicts the southern limit of the distribution of fire corals; Ilha Grande Bay (**IG**) and São Paulo Coast (**SP**), with rocky habitats overgrown with macrobenthos (e.g. zoanthids, sponges); and Santa Catarina Coast (**SC**), the southernmost limit of reef-fish occurrence in the Brazilian Province, with rocky shore habitats covered with algae

and sponges. The other four sites included are the Brazilian oceanic islands: Atol das Rocas (**AR**), an atoll constructed mainly by coralline algae and vermetids, with a veneer of hermatypic corals; Fernando de Noronha (**FN**), a volcanic formation covered with calcareous algae, vermetids, and corals; St. Paul's Rocks (**SR**), a small isolated rocky archipelago overgrown with algae and zoanthids; and Trindade Island (**TR**), with volcanic rocky reefs covered with coralline algae.

3.3- Methods

This study was based on the tropical teleost species primarily associated with hard substrates in the continental shelf and oceanic islands, here referred as 'reef fishes'. To minimise potential bias due to taxonomic problems and misidentification, we included ten of the most characteristic reef-associated families (Muraenidae, Holocentridae, Serranidae, Haemulidae, Chaetodontidae, Pomacanthidae, Pomacentridae, Labridae, Scaridae, Acanthuridae). These families were chosen for the following reasons: (1) they are taxonomically well documented; (2) they are conspicuous and relatively easy to identify underwater; (3) most of these families are consistently among the 10 most speciose in the Western and Central Atlantic (Floeter & Gasparini, 2000).

The composition and species distribution of the reef ichthyofauna has been determined primarily through original field studies in the 13 reef sites (Fig. 1) by the authors and colleagues, as well as by compilation of data from the literature (e.g. Figueiredo & Menezes, 1978; 1980; Menezes & Figueiredo, 1980; 1985; Lubbock & Edwards, 1981; Nunan, 1992; Bölhke & Chaplin, 1993; Randall, 1996; Rosa & Moura, 1997; Carvalho-Filho, 1999) and museum collections [Museu Nacional Rio de Janeiro (MNRJ), Laboratório de Biodiversidade de Recursos Pesqueiros da Universidade

Federal do Rio de Janeiro (LBRP), Museu de Zoologia da Universidade de São Paulo (MZUSP), Universidade Federal da Paraíba (UFPB), Museu de Biologia Professor Mello Leitão (MBML), British Museum Natural History (BMNH), Universidade Federal do Espírito Santo (UFES), Laboratório de Ictiologia da Universidade Estadual de Feira de Santana (LIUEFS), Museu de Zoologia da Universidade Estadual de Campinas (ZUEC)].

STATISTICAL ANALYSIS.- Canonical Correspondence Analysis (CCA) was utilised to identify the main groups of sites and describe the relationships between reef-fish species and environmental factors (ter Braak & Verdonschat, 1995). With this intent, we ran together the binary data matrix of reef-fish and a matrix of environmental and oceanographical data including distance from mainland, number of coral species, mean surface water temperature, primary production [i.e. phytoplankton production ($gC \cdot m^{-2} \cdot d^{-1}$)] and shelf width (distance from the coast to the 100 m isobath). The main characteristics of the studied sites including all environmental data used in the CCA analysis are presented in Table 1. The explanatory variables in the output are represented by vectors pointing towards the maximum change in the value of the associated variable. The length of an environmental line indicates a variable's relative importance. In order to improve the robustness of the conclusions, classical cluster analysis (the sites were clustered according to Sorensen's similarity coefficient using complete linkage, although varying the clustering routine had no effect on the grouping of sites) was also performed.

3.4- Results

DISTRIBUTION PATTERNS AND RELATED ENVIRONMENTAL FACTORS.- In the CCA ordination, the 13 sites are represented by points and the environmental variables by arrows (Fig. 2). Together, they account for 71.4 % of the variance in the weighted averages. Five major groups are identified in the analysis: (**1**) SE coastal reefs (GI, AC, IG, SP and SC); (**2**) the NE coast (ML; PA, ZR, and AB); (**3**) Trindade Island (TR); (**4**) Fernando de Noronha and Atol das Rocas (FN and AR); and (**5**) St. Paul's Rocks (SR). The same five groups are also formed in cluster analysis.

In the CCA biplot, the first axis approximates a gradient of fish species richness, which is highly influenced by distance from mainland (.813), shelf width (-.787), water temperature (.765), and primary production (.707). Group 1, which includes all rocky-shore sites of the South and SE coast, is placed at one extreme of the temperature vector due to their lower mean annual water temperature. These sites also show relatively higher primary production and large shelf width. On the other hand, the oceanic islands (TR, FN, AR and SR), are characterised by relatively oligotrophic warmer water, narrower shelf width, and greater isolation. Along the second ordination axis, the sites are distributed as a function of the gradient of coral richness (-.762). Group 2, which includes the sites of the NE, is characterised by its relatively warm waters and high diversity of coral species. Both TR and SR sustain low coral species richness and are in the opposite extreme.

COMPOSITION AND GEOGRAPHIC RANGES.- The most speciose families among those included in this study are: Serranidae (25 spp.), Labridae (16), Pomacentridae (13), and Haemulidae (11). Although there is considerable homogeneity in the composition of the reef-fish fauna along the Brazilian coastal reefs (Table 2), slight differences were found in some families. The haemulids and labrids are richer in the

NE sites, scarids and serranids in the SE, and muraenids in the oceanic islands, particularly FN and AR. The coastal areas sustain richer fish assemblages when compared to the oceanic islands, as expected. However, the rocky shores and rocky reefs of the SE exhibit the most diverse assemblages.

Approximately 20% of the reef ichthyofauna occurring in all the study sites are restricted to the SW Atlantic (Table 3). Species that possess wider distribution (Pan-Atlantic + Western Atlantic and Mid-Atlantic) represent a greater fraction of offshore assemblages. As expected, the coastal reefs presented a higher rate of western Atlantic continental margin species. Only St. Paul's Rocks holds species restricted to the Mid-Atlantic Ridge islands (St. Paul's Rocks + Ascension + St. Helena).

3.5- Discussion

NE COASTAL REEFS.- The NE reef-fish assemblages are influenced by the warm and oligotrophic South Equatorial Current (SEC) and the relatively high coral diversity. The SEC impinges the Brazilian coast between 7° and 17° S, further dividing into two branches, the north-westward flowing North Brazil Current, and the south-eastward flowing Brazil Current (Evans *et al.*, 1985). Maximum shelf widths are attained off the Abrolhos bank (245 km). In contrast, the majority of the NE shelf is only 20–50 km wide.

The NE Brazilian assemblages are characterised by the dominance of tropical species. Many of these occur in the Caribbean and did not expand their distributions southwards [e.g. the serranid *Serranus annularis* (Günther); the Haemulid *Haemulon melanurum* (Linnaeus); the chaetodontid *Chaetodon ocellatus* Bloch; and the labrids *Xyrichtys splendens* (Castelnau) and *X.* cf. *martinicensis* (Cuvier)]. Haemulids and labrids are richer and more abundant in the NE (Ferreira & Maida, 1995) than in the

SE sites, indicating that water temperature is a constraint in these two typical tropical families.

The largest coral reefs of the South Atlantic are located in the Abrolhos Archipelago (Leão, 1988, 1996) and, as a consequence, the greatest reef-fish species richness was expected to occur in this area (Moura *et al*., 1999). However, its fish assemblage is poorer in species than those of the SE sites (Table 2).

Some conspicuous reef fishes [e.g. *Holacanthus tricolor* (Bloch), *Myripristis jacobus* Cuvier, and many zooplanktivores] are notably missing in the Abrolhos Archipelago. The reasons for this gaps are yet to be determined, but certainly some 'filters' could be acting in the region (e.g. particulate suspension matter, the São Francisco and Doce River freshwater and sediment barriers).

SOUTH AND SE COASTAL REEFS.- No true coral reefs are found in the SE coast, where rocky shores represent the main habitat for reef fishes. Rocky reefs occur with minor interruptions from the State of Espírito Santo to about 28° S, in Santa Catarina Coast. Nevertheless, the reef-fish fauna living in this area appears to be the richest of Brazil (Table II), due to the mix of tropical and subtropical elements. The Abrolhos reefs and the Vitória-Trindade Ridge form a topographical barrier to the Brazil Current, inducing fundamental changes and spatial variability in physical, chemical, and biological features over the SE shelf, which is generally larger than in the NE (Castro & Miranda, 1998; Schmid *et al*., 1995). The SE reefs are subjected to a relatively intense seasonal upwelling promoted by the South Atlantic Central Water (SACW), bringing low temperature (<18° C) and nutrient rich waters close to the coastline (Ekau & Knoppers, 1999).

Serranids and scarids reach their peak diversity in the SE sites. Interestingly, a considerable number of Caribbean reef fishes found in this region are absent from the NE sites [e.g. the serranids *Epinephelus niveatus* (Valenciennes), *Mycteroperca microlepis* (Goode & Bean), *M. tigris* (Valenciennes), *Serranus phoebe* Poey, and the scarid *Sparisoma atomarium* (Poey)]. However, a gradual faunal impoverishment is observed southwards of São Paulo, with Santa Catarina (28° S) being the southern limit of rocky reef bottoms under influence of the warm Brazil Current (Evans *et al.*, 1985; Stramma, 1989) and consequently of tropical reef fish species. In Santa Catarina, shallow sheltered bays are little affected by seasonal intrusions of subtropical waters from the south and provide habitat for about half of the reef-fish species known from the Brazilian continental shelf.

OFFSHORE ISLANDS.- Oceanic sites experience extreme isolation and relatively small shallow water area, thus diminishing the chances of larval input from the continental margins as well as limiting the offer of suitable habitats for the adults. The number of species decline impressively (Table 3). Haemulidae and Scaridae although consistently speciose in the Brazilian coastal reefs, are poorly or not represented in the oceanic sites. The larger scraper parrotfishes of the genus *Scarus*, which occur at oceanic sites in the Indo-Pacific and North Atlantic (Smith-Vaniz, 1999; L. Rocha, pers. obs.), are absent from the South Atlantic oceanic islands. On the other hand, members of the genus *Sparisoma* are present on the offshore islands, possibly reflecting the broader feeding habits of this genus, which includes not just algae but sponges as well (Deloach, 1999).

The two insular groups within the Fernando de Noronha Ridge, Atol das Rocas and Fernando de Noronha, have very similar fish faunas, with five shared endemic species. In contrast, St. Paul's Rocks and Trindade Island are very isolated (>1000 km from mainland) and sustain poorer assemblages, aside from harbouring a considerable number of endemic species (Floeter & Gasparini, 2000).

Some intriguing distribution patterns were found in the offshore islands. Of special interest is the absence of the family Acanthuridae from St. Paul's Rocks, probably the only tropical island in the world missing this conspicuous reef-associated family. In addition, the wide ranging banded butterflyfish *Chaetodon striatus* Linnaeus has never been recorded at Atol das Rocas. The pomacanthids, *Holacanthus ciliaris* (Linnaeus) and *Pomacanthus paru* (Bloch) are common in the Caribbean, the Brazilian coast, Atol das Rocas, Fernando de Noronha and St. Paul's Rocks. Surprisingly, both species are missing in Trindade Island, where *Holacanthus tricolor* and *Centropyge aurantonota* Burgess are known to occur (Gasparini & Floeter, *in press*). *Holacanthus ciliaris* and *P. paru* are common at Fernando de Noronha, where only a few vagrant juveniles of *H. tricolor* and *C. aurantonota* were recorded.

Theoretically all these pelagic-spawning species do not have larval dispersal restrictions, since Acanthurids, *C. striatus* and *P. paru* had successfully colonised very isolated sites such as Ascension and Bermuda. We therefore assume that ecological factors such as food availability, competition for space, temperature, or requirements for proper larval development are influencing these disjunct patterns of distribution.

In summary, the geographic variation in fish assemblages among the Brazilian reefs is strongly correlated with some general environmental variables. Actually, the same analysis were ran including about 250 fish species belonging to 55 families known to occur in the Brazilian reefs, and the same pattern of site association was found. Despite these results, other specific variables should be investigated (e.g. particulate suspension matter, freshwater input, habitat complexity) avoiding misinterpretation of local-specific patterns. Future studies focusing on quantitative aspects of the fish fauna on a coastal gradient, will certainly reveal a more detailed distributional patterns.

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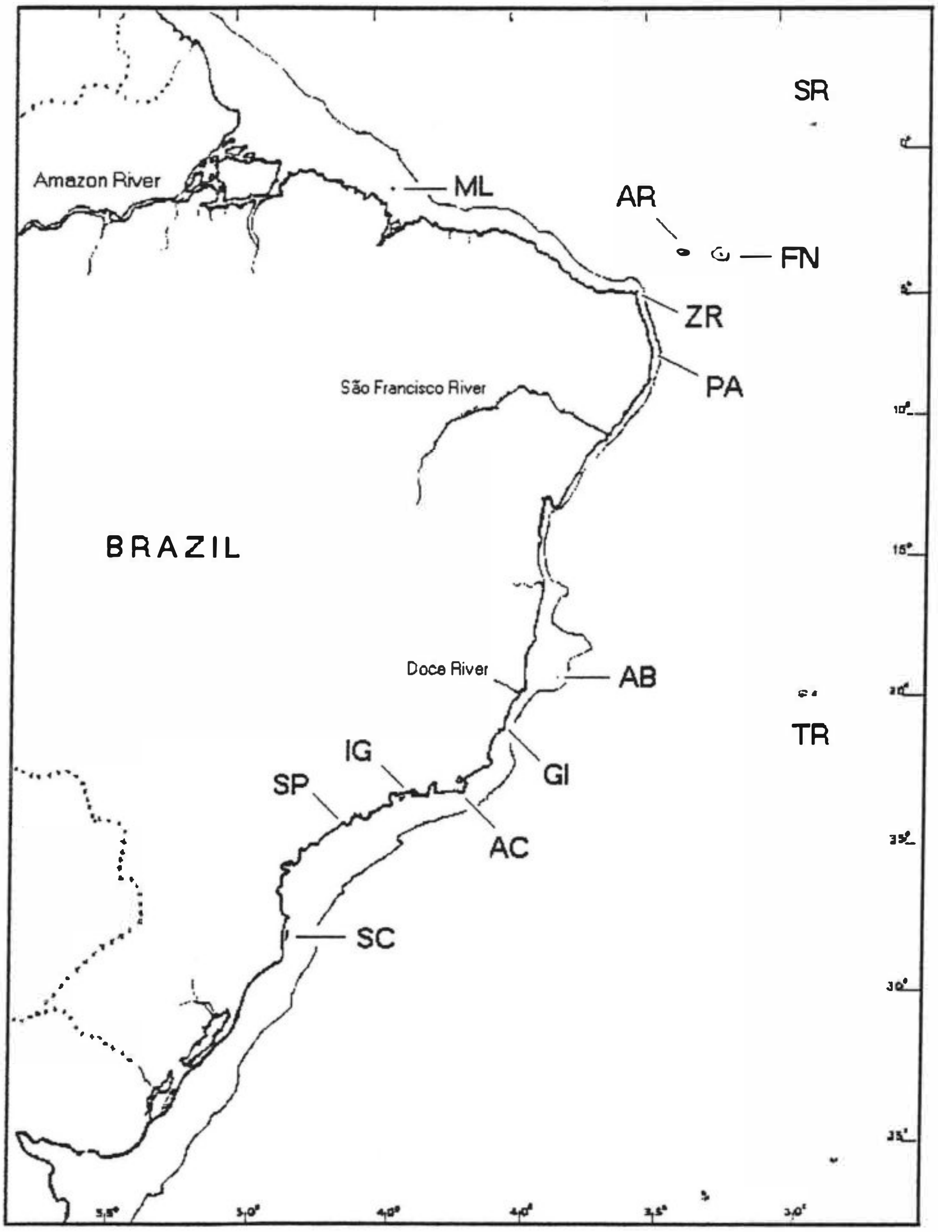

Fig. 1. Location of the 13 Brazilian reef sites. Legend: ML = Manuel Luis Reefs, AR = Atol das Rocas, FN = Fernando de Noronha, SR = St. Paul's Rocks, ZR = Zumbi Reefs, PA = Paraíba, AB = Abrolhos Archipelago, TR = Trindade Is., GI = Guarapari Is., AC = Arraial do Cabo, IG = Ilha Grande Bay, SP = São Paulo, and SC = Santa Catarina. The 100 m isobath is included.

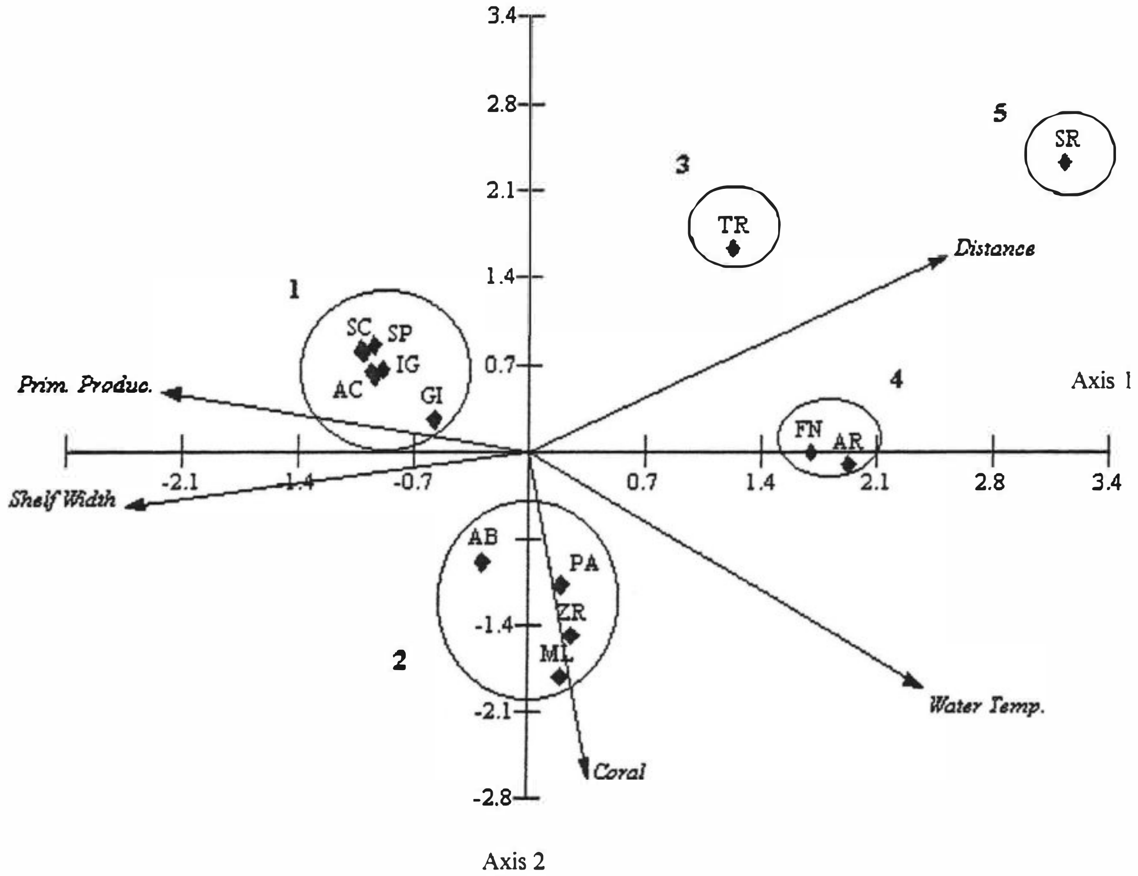

Fig. 2. CCA ordination diagram with reef sites (points) and environmental variables (arrows). Sites: (**1**) SC = Santa Catarina, SP = São Paulo, IG = Ilha Grande Bay, AC = Arraial do Cabo, GI = Guarapari Is.; (**2**) AB = Abrolhos Archipelago, PA = Paraíba, ZR = Zumbi Reefs, ML = Manuel Luis Reefs; (**3**) TR = Trindade Is.; (**4**) FN = Fernando de Noronha, AR = Atol das Rocas; (**5**) SR = St. Paul's Rocks.

Table 1. Characteristic features of the major Brazilian reef sites. SWT = Surface Water Temperature; NBC = North Brazil Current; SEC = South Equatorial Current; BC = Brazil Current; SACW = South Atlantic Central Water.

Reef site (Coordinates)	Distance from the coast (km)	Coral species[1,2] (Scleractinian + Hydrocorals)	SWT[1,3] (°C) winter-summer	Water regime[4]	Primary production[3] ($gC{\cdot}m^{-2}{\cdot}d^{-1}$)	Shelf width[3] (km)
Northeastern Brazil						
Manuel Luis Reefs (0°52'S; 44°15'W)	86	16	26 – 28	NBC	0.3 – 0.8	~130
Zumbi Reefs (5°S; 35°W)	10	8	26 – 28	NBC and SEC	0.02 – 0.2	~35
Paraiba Coast (7°S; 34°50W)	–	11	25 – 28	SEC	0.02 – 0.2	~35
Abrolhos Archipelago (17° 20'S; 39°W)	50	16	22 – 27	BC	0.3 – 1.1	~180
Southeastern Brazil						
Guarapari Islands (20°40'S; 40°22'W)	5	13	19 – 24	BC and SACW	0.3 – 1.1	~50
Arraial do Cabo (23°S; 42°W)	–	5	18 – 23	BC and SACW	0.3 – 1.3	~120
Ilha Grande Bay (23°05'S; 44°20'W)	–	2	18 – 23	BC and SACW	0.3 – 1.3	~150
São Paulo Coast (24°30'S; 46°W)	–	2	18 – 22	BC and SACW	0.1 – 0.5	~170
Santa Catarina Coast (27°30'S; 48°W)	–	1	17 – 21	BC and SACW	0.1 – 0.5	~150
Oceanic Islands						
Atol das Rocas (3°50'S; 33°49'W)	267	8	25 – 28	SEC	0.02 – 0.2	~10
Fernando de Noronha (3°51'S; 32°26'W)	345	10	24 – 25	SEC	0.02 – 0.2	~15
St. Paul's Rocks (0°55'N; 29°21'W)	1000	2	26	SEC	0.02 – 0.2	~1.5
Trindade Island (20°30'S; 29°20'W)	1160	4	25	BC	0.02 – 0.5?	~3

Sources: 1) Maida & Ferreira, 1997; 2) Belém *et al.*, 1986; and C.B. Castro, pers. com.; 3) Ekau & Knoppers, 1999; 4) Castro & Miranda, 1998.

Table 2. Number of species in each of the ten most characteristic Brazilian reef-fish families in the five reef complexes determined by CCA (see Methods).

	SE Brazil					NE Brazil				Trindade Island	F. de Noronha Ridge		St. Paul's Rocks
Families (Total number of spp.)	Santa Catarina	São Paulo	I. Grande Bay	Arraial do Cabo	Guarapari Islands	Abrolhos Reefs	Paraiba	Zumbi Reefs	Manuel Luis Reefs		Atol das Rocas	F. de Noronha	
ACANTHURIDAE (3)	2	3	3	3	3	3	3	3	3	2	3	3	0
CHAETODONTIDAE (6)	2	4	4	4	3	2	3	2	3	2	1	2	2
HAEMULIDAE (11)	6	6	6	6	8	8	9	8	6	1	3	4	0
HOLOCENTRIDAE (4)	2	3	3	4	4	1	3	3	2	2	2	3	2
LABRIDAE (16)	6	9	9	10	10	9	12	9	11	7	5	7	4
MURAENIDAE (8)	3	3	3	4	5	3	7	3	3	4	7	8	5
POMACANTHIDAE (5)	4	4	5	5	5	3	5	4	3	2	2	3	2
POMACENTRIDAE (13)	6	7	7	7	7	6	8	6	6	4	4	4	3
SCARIDAE (9)	4	9	9	9	9	7	7	6	8	3	3	3	3
SERRANIDAE (25)	15	18	18	20	22	13	12	8	9	8	5	6	2
Total (100)	**50**	**66**	**67**	**72**	**76**	**55**	**69**	**52**	**54**	**35**	**35**	**43**	**23**

Table 3. Geographic range of the species within the ten most characteristic reef-fish families in the five reef complexes determined by CCA (see Methods). Numbers refer to percentage of fish species.

	SE Brazil					NE Brazil				Trindade Island	F. de Noronha Ridge		St. Paul's Rocks
Geographic Range	Santa Catarina	São Paulo	I. Grande Bay	Arraial do Cabo	Guarapari Islands	Abrolhos Reefs	Paraiba	Zumbi Reefs	Manuel Luis Reefs		Atol das Rocas	F. de Noronha	
Pan Atlantic + Circumtropical	23.5	20.9	22	21.9	21.8	23.2	21.4	20.8	21.4	28.6	34.3	27.9	36.2
Western + Mid-Atlantic	7.8	7.5	7.4	6.8	6.5	8.9	8.6	9.4	8.9	11.4	17.1	16.3	15.8
Mid-Atlantic[1]	–	–	–	–	–	–	–	–	–	–	–	–	4.2
Western Atlantic Margin	51	50.7	50	52.1	53.8	46.5	48.6	47.2	51.8	42.9	25.7	37.2	11.8
Southwestern Atlantic[2]	17.7	20.9	20.6	19.2	17.9	21.4	21.4	22.6	17.9	17.1	22.9	18.6	32

[1] = St. Paul's Rocks + Ascension + St. Helena. [2] = Continental margin + Oceanic islands.

Artigo III

Pleistocenic glaciations and the high levels of diversity and endemism in Brazilian reef fishes

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Abstract

Aim The aim of this paper is to provide a review of the composition and distribution of the non-planktonic egg-laying Acanthopterygian fish-fauna endemic to Brazilian tropical reefs, to map and analyse the hierarchy of the resulting zones of superimposed endemism and to investigate the association of the observed hierarchical patterns with previously known Earth's history phenomena.

Location Shallow reefs along the Brazilian continental shelf were studied from Parcel Manoel Luís, Maranhão, south to the rocky reefs of São Paulo, as well as in three oceanic insular-complexes: St. Paul's Rocks, Fernando de Noronha Archipelago - Rocas Atoll and Trindade - Martin Vaz Islands.

Methods Locality records were obtained from field, institutional and personal sources and included only obligatory reef-resident Acanthopterygii, which do not release planktonic eggs and present a geographic distribution restricted to Brazilian shallow (up to about 50 m) territorial waters. A Parsimony Analysis of Endemicity (PAE) was performed upon a binary matrix of presence/absence of species, with the aid of HENNIG86's "ie" algorithm and within a TREE GARDENER environment.

Results Thirty four species were listed, some yet to be formally described. Six principal zones of endemism were recognised, which are related according to the following area cladogram: Trindade Island (St. Paul's Rocks (Fernando de Noronha Archipelago (Brazilian continental shelf))).

Main conclusions Within Brazilian territorial waters, the wide "bellow the Amazon mouth" Brazilian Province indicated in previous studies is among the weakest areas of endemism regarding reef fishes. Origins of smaller and better defined areas within Brazilian waters are related to the habitat fracturing-rejoining processes that resulted from Pleistocene glacial cycles.

Key-words

Reef fishes, historical biogeography, parsimony analysis of endemicity, eustatic events, glacial cycles, Brazil.

Introduction

Although the Brazilian reef-fish fauna has been subject to scientific investigation since pre-Linnean times, only after the introduction of SCUBA diving techniques that a significant number of species was discovered (Guimarães *et al.*, 2001). Since the earlier biogeography textbooks by Ekman (1953) and Briggs (1974) suggested the existence of an endemic component of the Brazilian shore fauna, it has been shown that such component is much more significant. From large conspicuous dasyatid rays (*e. g.* Gomes *et al.* 2000) to small secretive scaled-blennies (*e. g.* Guimarães & Bacellar, 2002), the list of Brazilian shallow-reef endemics is rapidly growing, some restricted to different segments of the Brazilian continental shelf, some endemic to each of the three insular complexes within Brazilian waters, and some distributed in a combination of two or more of these areas. In this study, the endemic component of the Brazilian shallow-reef ichthyofauna is reviewed, the existence of areas of superimposed endemism is indicated and possible vicariant scenarios underlying their origins are suggested.

Methods

A parsimony analysis of endemicity - PAE (Morrone & Crisci, 1995) was performed with the "*ie*" command of HENNIG86 software, based on the binary matrix of species occurrence (Table 1), within a TREE GARDENER software environment (Ramos, 1996). The PAE analysis generates area cladograms based on shared presence of endemic taxa, and, when performed with the "*ie*" command of HENNIG86, exhausts all possible tree topologies (Farris, 1988). Only the obligatory reef-resident species which have a geographic distribution restricted to Brazilian territorial waters and a bathymetric distribution of up to 50 m were considered for analysis. The target group was further restricted to include only the small, benthic Acanthopterygii which do not release eggs in open water during reproduction. Thus, the analysed group includes the mouth-brooders of the families Apogonidae and Opistognathidae, the marsupium-brooders of the family Syngnathidae, and the nesters of the families Pomacentridae, Gobiidae, Blenniidae, Labrisomidae, Chaenopsidae and Tripterygiidae (Thresher, 1984; Leis, 1991). Table 1 shows results from specimens' examination, personal field observations, personal communications provided by Liana F. Mendes, Carlos E. L. Ferreira, Bertran M. Feitoza, João L. Gasparini, Alfredo Carvalho Filho, and records published in the following studies: Carvalho-Filho, 1999; Ferreira *et al.*, 1995; Figueiredo & Menezes, 1980; Gasparini & Floeter, 2001; Gasparini *et al*, 1999; 2001; Guimarães & Bacellar, 2002; Koike & Guedes, 1981; Lubbock & Edwards, 1981; Menezes & Figueiredo, 1985; Moura, 1995; Novelli *et al.*, 2000; Nunan, 1992; Ramos, 1994; Rocha *et al.*, 1998; 2000; Rocha & Rosa, 2000; Rosa & Moura, 1997; Sazima *et al.*, 1997; 1998.

Results

A single, fully resolved tree (Fig. 1), length 46, consistency index 73 and retention index 84, resulted from the PAE analysis. Only one species (*i.e.*, the cardinalfish *Apogon americanus* Castelnau which was recorded in all studied sites) supports Brigg's (1974) "below the Amazon mouth" concept of a Brazilian zoogeographical province. Within this area, six principal zones of endemism were indicated by the occurrence of endemic species. Each of the three insular complexes studied, *i.e.*, Trindade Island / Martin-Vaz Island, Fernando de Noronha Archipelago / Rocas Atoll and St. Paul's Rocks, represent areas of endemism, defined by the presence of 5, 2 and 2 endemic species respectively. A fourth area is weakly defined by the presence of an undescribed species of *Starksia*, which includes all sites except Trindade. Included in this area is another one defined by the co-occurrence of the pomacentrid *Stegastes pictus* (Castelnau), the labrisomid *Starksia brasiliensis* (Gilbert) and the gobiids *Lythrypnus brasiliensis* Greenfield and *Priolepis dawsoni* Greenfield, which is composed by all localities except Trindade and St. Paul's Rocks. The Brazilian continental shelf is also a zone of endemism, defined by the presence of the dart-fish *Ptereleotris randalli* Gasparini, Rocha & Floeter, the gobiid *Elacatinus figaro* Sazima, Moura & Rosa and two undescribed species: one triple-fin of the genus *Enneanectes* and one scaled-blenny of the genus *Malacoctenus*.

Discussion

Briggs (1974) carved the term "Brazilian Province" based on the observation that Brazilian waters are inhabited by shore organisms found nowhere else in the Atlantic Ocean. Since then, the term has been inadvertently used to refer either to reef fishes endemic to the Brazilian continental shelf as well as to those endemic to oceanic islands like Trindade or Fernando de Noronha or to a combination of two or more of these areas (*e.g.*, Briggs, 1995; Greenfield, 1988;1989; Joyeux *et al.*, 2001).

Examination of the patterns of geographical distribution of 34 reef fishes (Table 1) supports the existence of six principal areas of endemism within Brazilian territorial waters. These areas are related according to an inclusive hierarchy (Fig. 1), which indicates a temporal sequence of biotic interchange breaks (Morrone & Crisci, 1995). In such perspective, the results suggest that fauna of Trindade was the first one to become isolated, followed by St. Paul's Rocks and so on.

Likelihood of the proposed sequence is reinforced when some of its nodes, especially nodes 1-3, are hypothetically coupled with some of the Earth's history phenomena (*sensu* Rosen, 1990) known to date, especially the Pleistocenic eustatic events described for the western south Atlantic.

Glacial cycles and eustatic events in Brazil: The western south Atlantic has been subject to considerable fluctuations in sea level and termohaline circulation patterns (Kousmann & Costa, 1979; Suguio *et al.*, 1985; Arz *et al.*, 1999). Although data on ancient eustatic events is scarce, transgressions and regressions are reported to have occurred in Brazil since the early Cretaceous (*e.g.*, Ponte & Asmus, 1978; Urien & Martins, 1979). Quaternary fluctuations along the Brazilian coast have been studied in better detail, when two phases have been recognised: a phase of rapid regression during the Last Glacial Maximum (16,000 - 14,000 yr. B. P.), and a subsequent phase of transgression (Flandrian Transgression), which occurred from about 14,000 to 7,000 yr B. P., and was interrupted by several short term cooling events (Arz *et al.*, 1999). During the regression, the sea level dropped to at least 130 m below the present level, exposing most of the recent continental shelf, except for its southern margin. As a result, a drainage system has developed over the continental shelf (Kousmann & Costa, 1979; Vicalvi *et al.*, 1978), an event that altered considerably the topography of the shelf. During the Flandrian Transgression, the sea level rose gradually to near its present level, with reported short term stabilisations of -110 m at 13,000 yr. B. P., and -

60 m at 11,000 yr. B. P. The episodic release of melt water that took place between each short term stabilisation led to disruptions of the global thermohaline circulation (THC) (Arz et al., 1999). The Flandrian Transgression ended about 7,000 yr. B. P., when the rates of sea-level rise decreased considerably (Suguio *et al.*, 1985). At about 6,000 yr. B. P., the sea level along the continental shelf was oscillating close to the present level (from 4.7 m above to 1.5 m below), with the shelf entirely submerged (Suguio *et al.*, 1985).

Eustatic events and speciation in Brazilian reef-fishes: Eustatic phenomena have been previously associated to cladogenetic events that originated areas of endemism for several different taxa around the world (*e.g.*, Fernandes *et al.*, 1995; Nelson, 2000). Considering the limited dispersal abilities of non-planktonic egg-laying reef-fishes and their physiological and ecological thresholds, it is likely to suppose that sea-level fluctuations and disruptions in THC that took place in Brazilian waters during the Pleistocene had a major impact on the distribution of that fauna. For instance, examination of the seafloor topography of the studied area suggests that nodes 1 and 3 in Figure 1 could be associated to those fluctuations. That is so because both Trindade - Martin Vaz and F. Noronha - Rocas insular complexes are outposts of a series of seamounts which were aerially exposed in the Last Glacial Maximum (LGM) (Figs. 2-5) (Kousmann & Costa, 1979; Vicalvi *et al.*, 1978). If one accept the idea that such configuration permitted gene flow among populations in each island in a "stepping-stone" manner (cf. McArthur & Wilson, 2001), then it is equally likely that this flow ended when the subsequent rising of the sea level (Flandrian Transgression) extinguished populations in the intermediate seamounts. As a result, the continental and the outposts populations gave rise to distinguished sister-group species. In fact, sister-group relationship has been suggested to occur among some Trindade / Continental Brazil species-pairs (Gasparini *et al.*, 1999; Gasparini & Floeter, 2001).

Geographic distances among sister-group areas support the proposed sequence of cladofaunal events: The proposed sequence of faunal interchange break indicated in nodes 1-3 is supported by the decreasing geographic distances among each pair of sister-group areas nested in the cladogram. Thus, the first area to became hypothetically isolated, *i.e.* Trindade Island, stands as the most isolated area among all others (smaller distance from any other location is some 1.160 km from the Brazilian coast). The subsequent areas that became isolated according to the proposed theory are Saint Paul's Rocks, which lies some 630 km from its closest locality (Fernando de Noronha), and Fernando de Noronha itself, which lies 330 km off the Brazilian continental margin.

Cladofaunal events in nodes 4 - 10: Nodes 4-10 indicate relationships among sub-areas located along the Brazilian continental shelf, where inclusiveness of localities follow a general southward trend, *i.e.,* southern localities share the largest number of endemic species. Unlike nodes 1-3, nodes 4-10 are best interpreted as different histories of dispersion, as there are no hypothesised sister-group species within any two sister-group areas.

Conclusions

There are 34 species of non-planktonic egg-laying acanthopterygian fishes endemic to Brazilian tropical reefs.

Patterns of geographic distribution of these species indicate the existence of six principal areas of superimposed endemism, organised according to the following cladogram: Trindade Island (St. Paul's Rocks (Fernando de Noronha Archipelago (Brazilian continental shelf))).

In a temporal perspective, this cladogram indicates that the fauna of Trindade Island was the first one to become isolated, followed by St. Paul's and so on. Such sequence is supported by the decreasing geographic distances among each pair of sister-group areas inclusively nested in the cladogram.

Within possible vicariant scenarios involving Brazilian reef ichthyofauna are the habitat fracturing-rejoining processes that took place during the Quaternary, when significant sea-level oscillations and changes in water-mass physical parameters occurred.

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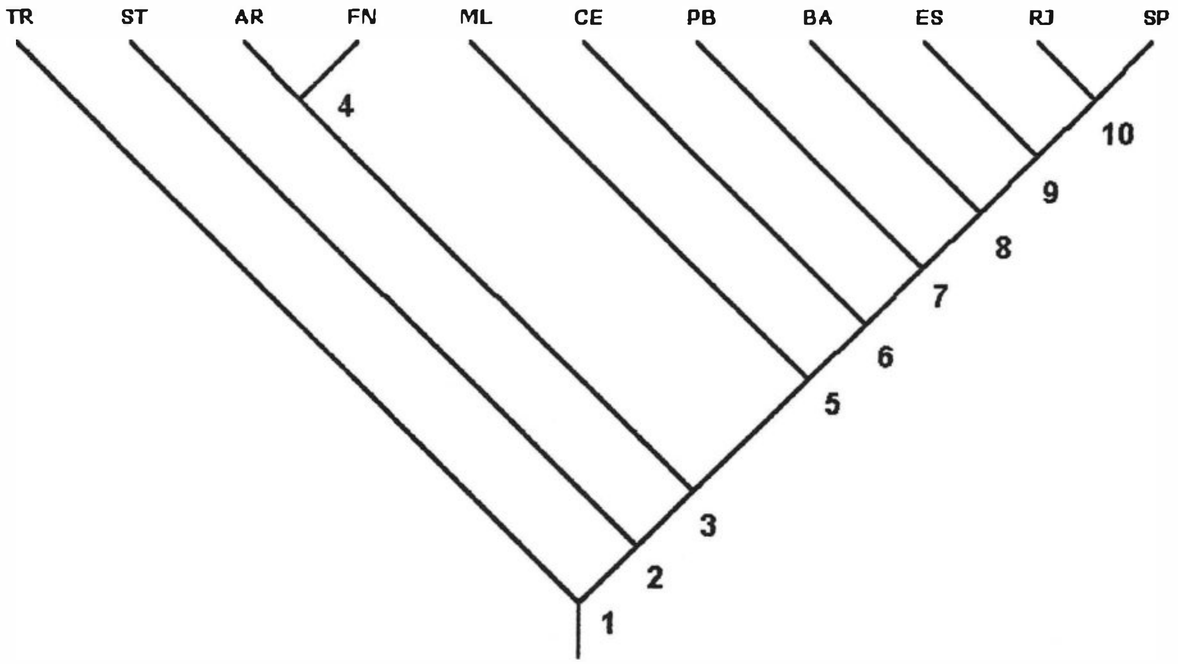

Fig. 1) Area cladogram resulting from Parsimony Analysis of Endemicity of Brazilian shallow-reef fishes. Length 46, Consistency Index 73, Retention Index 84.

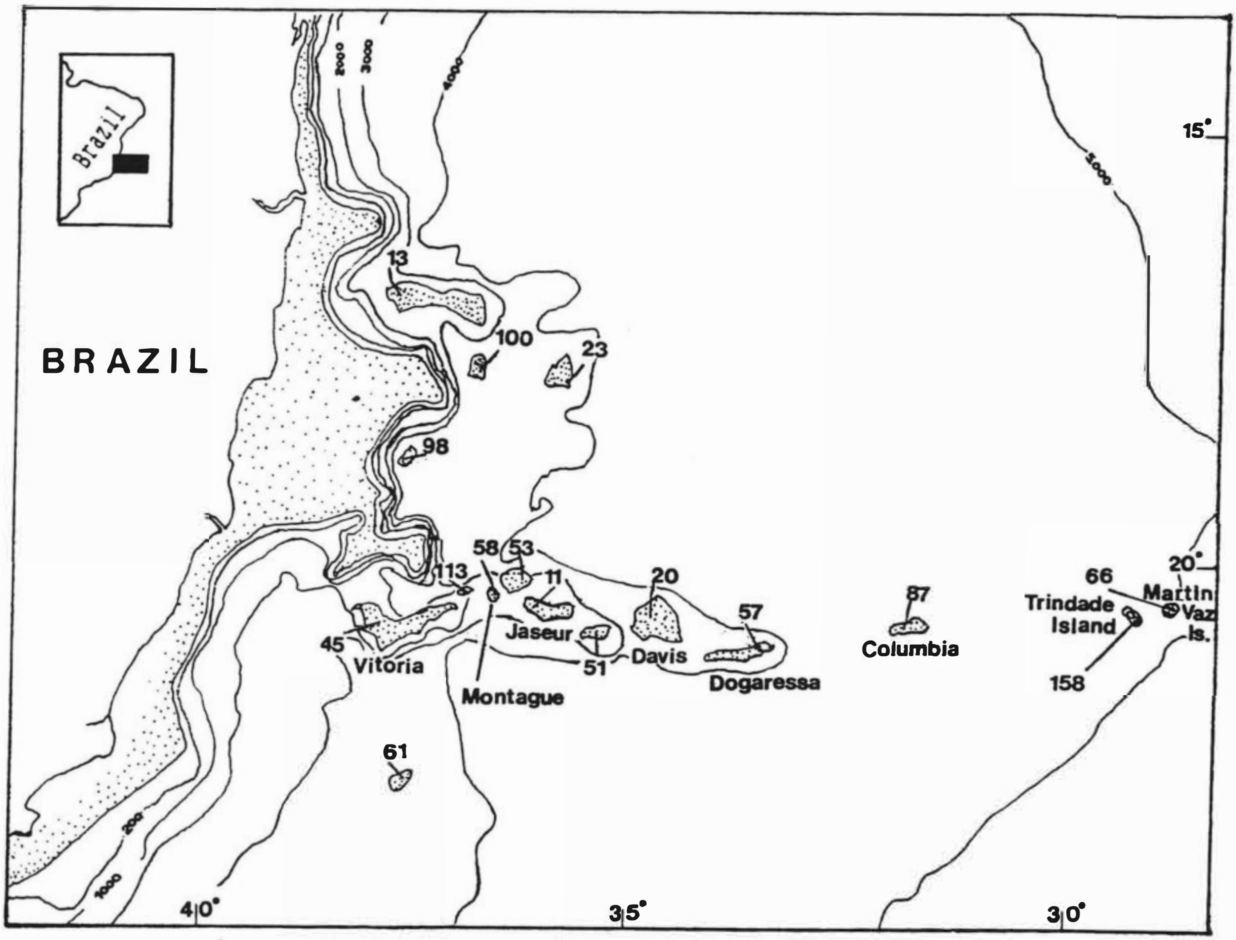

Fig. 2) General bathymetry of the Trindade-Vitória Seamount Chain. Depths of each seamount summit are indicated and doted areas correspond to those that were aerially exposed during the Late Pleistocene Regression (16,000 - 14,000 yr. B. P.) (after Nunan, 1992).

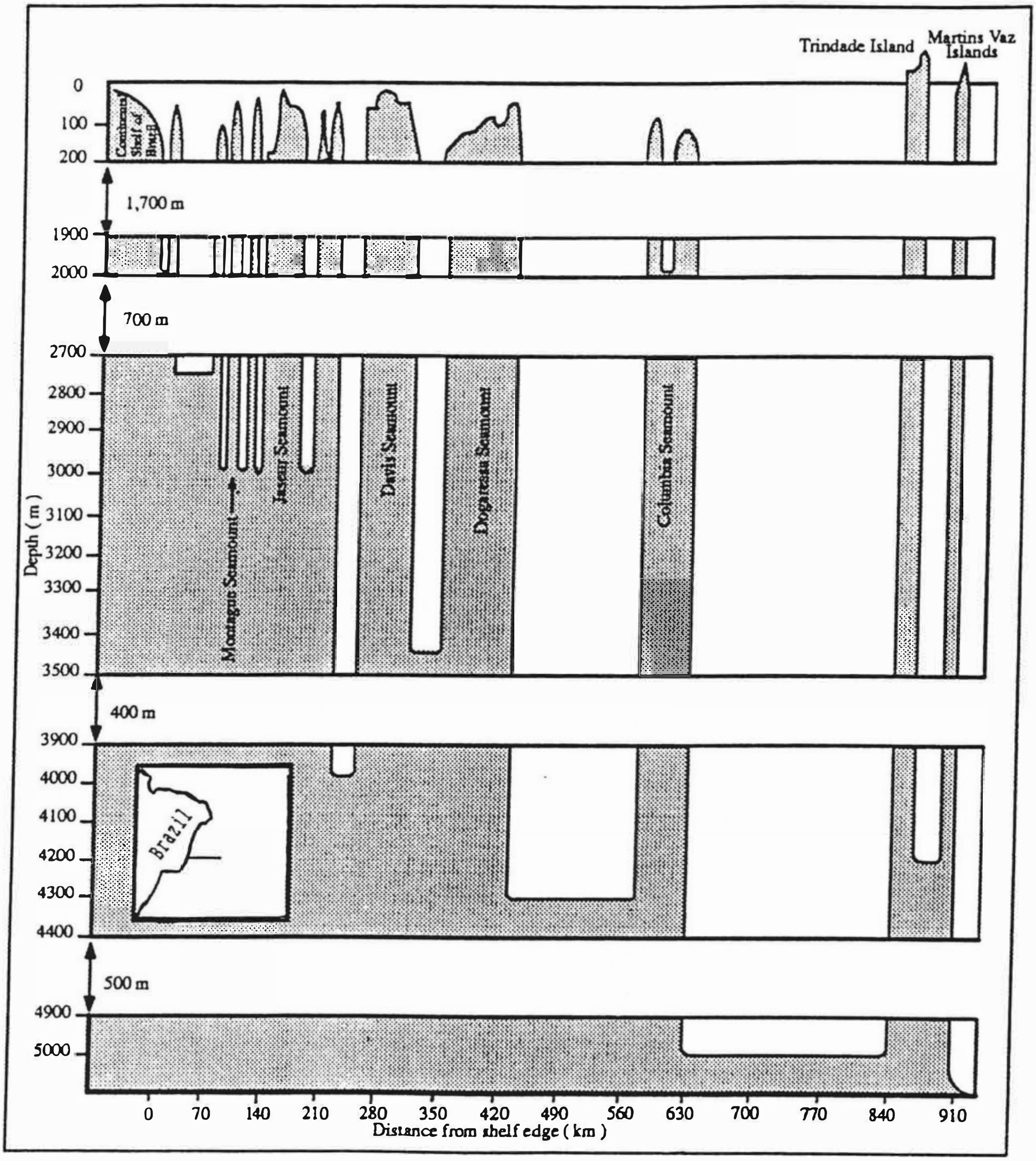

Fig. 3) Profile of the Vitória-Trindade Seamount-Chain (Vertical exaggeration of x 320) (after Nunan, 1992).

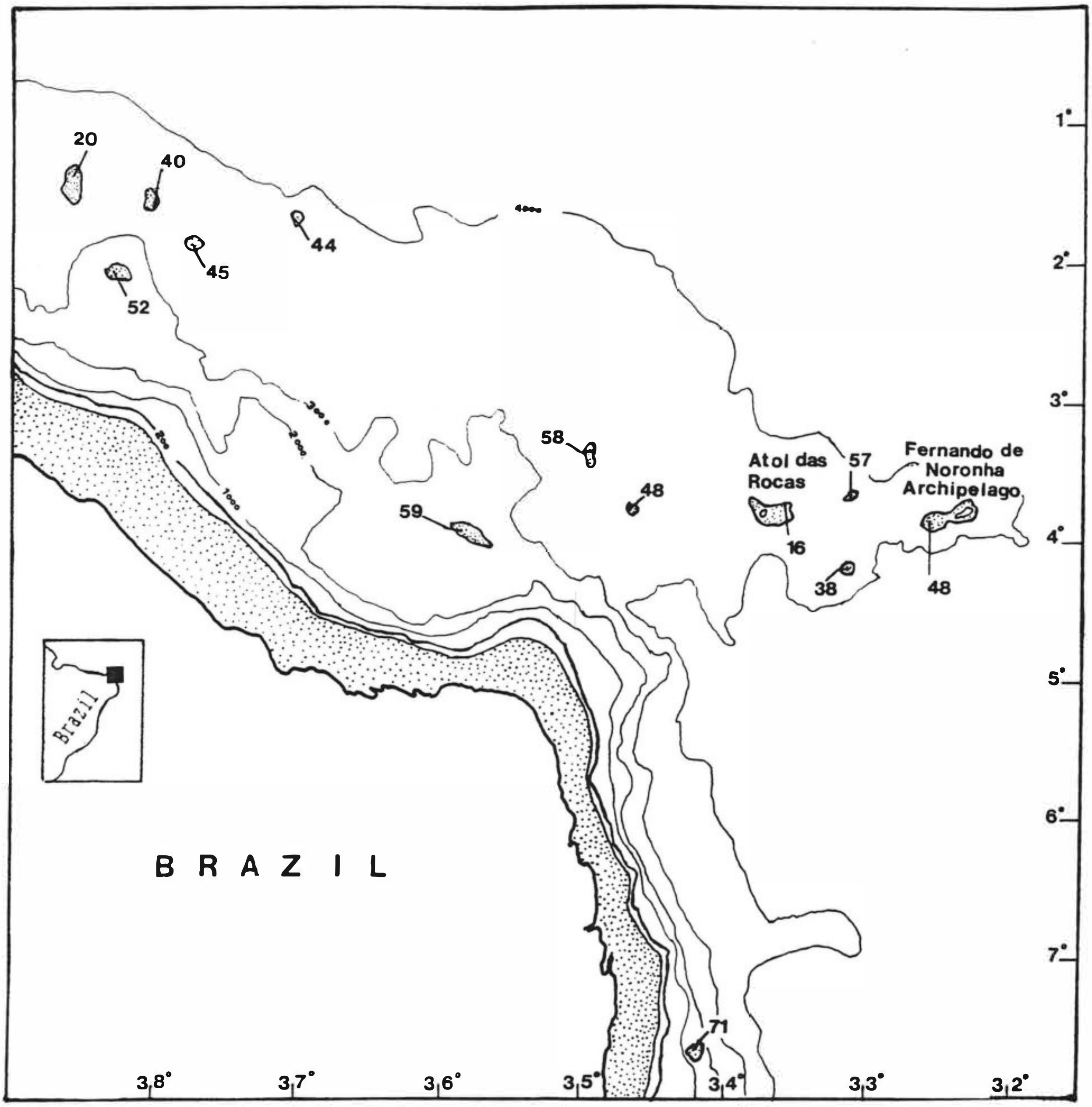

Fig. 4) General bathymetry of the Fernando de Noronha Seamount Chain. Depths of each seamount summit are indicated and doted areas correspond to those that were aerially exposed during the Late Pleistocene Regression (16,000 - 14,000 yr. B. P.) (after Nunan, 1992).

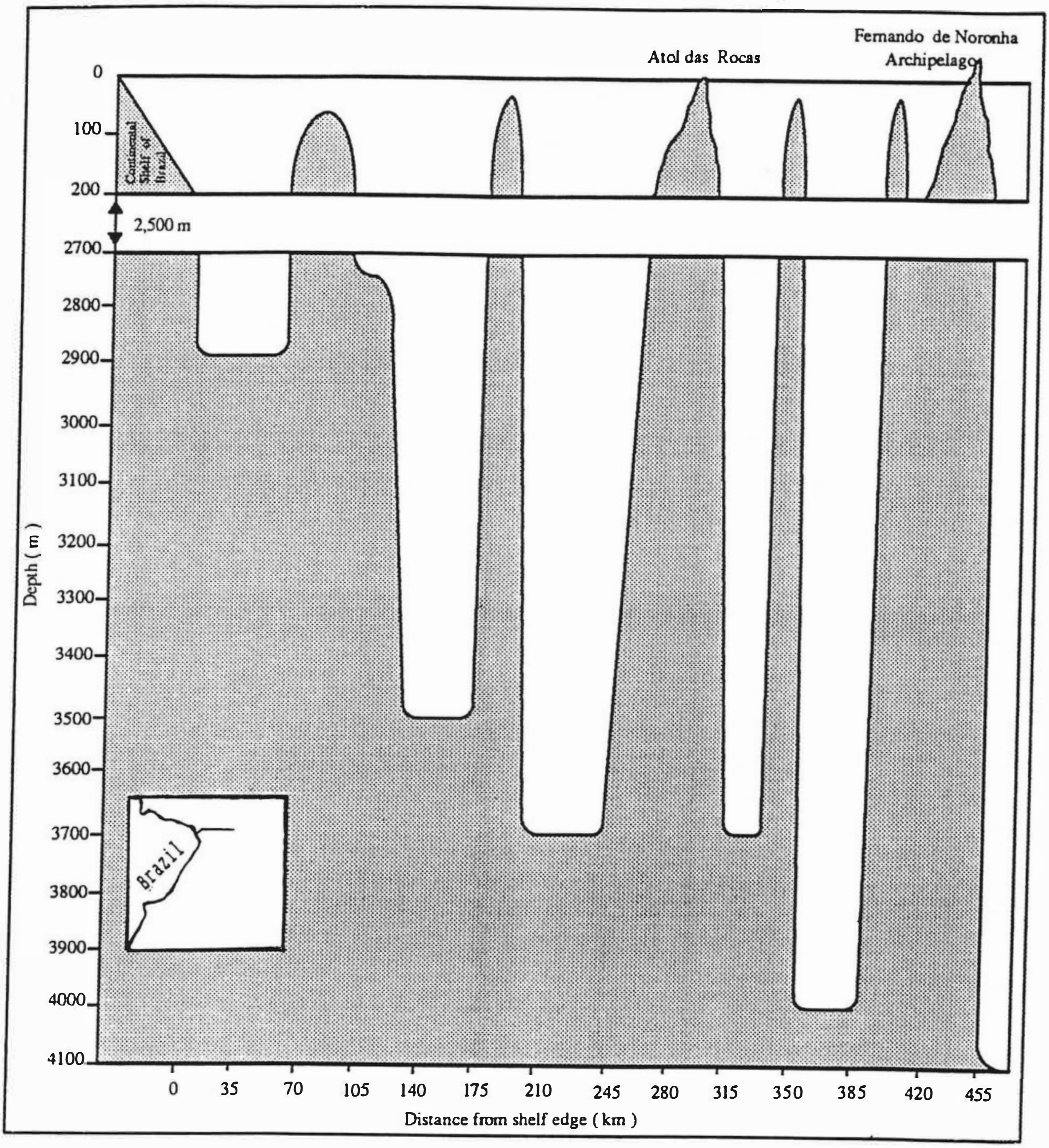

Fig. 5) Profile of the Fernando de Noronha Seamount-Chain (Vertical exaggeration x 175) (after Nunan, 1992).

Table 1: Binary matrix of endemic species occurrence in Brazilian shallow-reefs (out: outgroup; TR: Trindade Island; ST: Saint Paul's Rocks; AR: Atol das Rocas; FN: Fernando de Noronha Archipelago; ML: Manoel Luis Reef; CE: Ceará State; PB: Paraíba State, BA: Bahia State, ES: Espírito Santo State, RJ: Rio de Janeiro State; SP: São Paulo State.

		out	TR	ST	AR	FN	ML	CE	PB/P	BA	ES	RJ	SP
1.	*Bryx* sp.	0	0	0	0	0	0	0	1	1	1	1	1
2.	*Micrognathus erugatus* Herald & Dawson	0	0	0	0	0	0	0	0	1	0	0	0
3.	*Gramma brasiliensis* Sazima, Gasparini & Moura	0	0	0	0	1	1	1	1	1	1	1	0
4.	*Apogon americanus* Castelnau	0	1	1	1	1	1	1	1	1	1	1	1
5.	*Chromis jubauna* Moura	0	0	0	0	0	0	0	0	0	1	1	1
6.	*Stegastes fuscus* (Cuvier)	0	0	0	0	0	0	1	1	1	1	1	1
7.	*Stegastes pictus* (Castelnau)	0	0	0	1	1	1	1	1	1	1	1	1
8.	*Stegastes rocasensis* (Emery)	0	0	0	1	1	0	0	0	0	0	0	0
9.	*Stegastes sanctipauli* Lubbock & Edwards	0	0	1	0	0	0	0	0	0	0	0	0
10.	*Stegastes trindadensis* Gasparini, Moura & Sazima	0	1	0	0	0	0	0	0	0	0	0	0
11.	*Stegastes uenfi* Novelli, Nunan & Lima	0	0	0	0	0	0	0	1	1	1	1	0
12.	*Opistognathus* sp.	0	1	0	0	0	1	0	1	1	1	1	1
13.	*Opistognathus cuvieri* Valenciennes	0	0	0	0	0	0	0	0	0	1	1	1
14.	*Enneanectes* sp.	0	0	0	0	0	1	1	1	1	1	1	1
15.	*Enneanectes smithi* Lubbock & Edwards	0	0	1	0	0	0	0	0	0	0	0	0
16.	*Labrisomus* sp.	0	0	0	0	0	0	0	0	1	1	1	1
17.	*Malacoctenus* sp. 1	0	0	0	0	0	1	1	1	1	1	1	0
18.	*Malacoctenus* sp. 2	0	1	0	0	0	0	0	0	0	0	0	0
19.	*Paraclinus arcanus* Guimarães & Bacellar	0	0	0	0	0	0	0	1	1	1	1	0
20.	*Paraclinus spectator* Guimarães & Bacellar	0	0	0	0	0	0	0	0	0	0	1	1
21.	*Paraclinus rubicundus* (Starks)	0	0	0	0	0	0	0	1	1	1	1	1
22.	*Starksia brasiliensis* (Gilbert)	0	0	0	1	1	1	1	1	1	1	1	1
23.	*Starksia* sp.	0	0	1	0	1	1	1	0	0	0	0	0
24.	*Coralliozetus signifer* (Ginsburg)	0	0	0	0	0	0	0	0	1	1	1	1
25.	*Entomacrodus vomerinus* (Valenciennes)	0	0	1	1	1	0	0	1	1	1	0	0
26.	*Entomacrodus* sp.	0	1	0	0	0	0	0	0	0	0	0	0
27.	*Scartella* sp. 1	0	1	0	0	0	0	0	0	0	0	0	0
28.	*Scartella* sp. 2	0	0	0	0	0	0	1	1	1	1	1	1
29.	*Scartella* sp. 3	0	0	0	1	1	0	0	0	0	0	0	0
30.	*Elacatinus figaro* Sazima, Moura & Rosa	0	0	0	0	0	0	1	1	1	1	1	1
31.	*Elacatinus* sp.	0	1	0	0	0	0	0	0	0	0	0	0
32.	*Lythrypnus brasiliensis* Greenfield	0	0	0	1	1	1	1	1	1	1	1	1
33.	*Priolepis dawsoni* Greenfield	0	0	0	1	1	1	1	1	1	1	1	1
34.	*Ptereleotris randalli* Gasparini, Rocha & Floeter	0	0	0	0	0	1	1	1	1	1	1	1

5- Discussão Geral

Neste estudo foram apresentadas três publicações científicas focando aspectos relativos à diversidade e ao endemismo da fauna de peixes associada a ambientes recifais brasileiros.

A primeira publicação trata de uma revisão taxonômica que demonstra que as espécies de peixes de ambientes recifais rasos e de ovos não-pelágicos do gênero *Paraclinus* que ocorrem na costa brasileira são três e não duas como previamente se supunha, e que todas são endêmicas do Brasil e não de ampla distribuição no Oceano Atlântico Ocidental como antes considerado (Guimarães e Bacellar, 2002).

Assim como evidenciado no estudo supracitado, estudos sobre a taxonomia de outros grupos de peixes recifais brasileiros têm revelado descobertas similares, principalmente em trabalhos publicados na última década (Guimarães *et al.*, 2001). Neste período foram publicados estudos registrando a presença de diversas espécies antes desconhecidas em vários pontos da costa e ilhas oceânicas do país (*e.g.* Guimarães 1996A, 1996B; 1999A; 1999B; Moura *et al.*, 1999; Rocha *et al.*, 2001) e descrições de espécies de águas brasileiras antes desconhecidas pela ciência (*e.g.* Sazima *et al.*, 1997; 1998; Guimarães e Nunan, 1999; Rocha e Rosa, 1999; Guimarães *et al.*, 2000; Rangel e Guimarães, 2000; Gasparini *et al.*, 1999; 2001; Moura *et al.*, 2001).

A partir destas adições ao conhecimento sobre a composição ictiológica dos ambientes recifais brasileiros, emergiu um quadro geral onde são reconhecidos níveis de diversidade mais altos e zonas de endemismo mais refinadas do que o sugerido em estudos anteriores.

Considerando-se, por exemplo, apenas as dez famílias com maior número de representantes recifais obrigatórios no Brasil (*i.e.*, Apogonidae, Serranidae, Lutjanidae, Haemulidae, Pomacentridae, Labridae, Scaridae, Labrisomidae, Blenniidae e Gobiidae), vemos a seguinte evolução: Enquanto Greenfield (1988) reconhece apenas duas formas endêmicas na plataforma continental brasileira, Nunan (1992) indica três e Guimarães e Nunan (submetido) dez. Na Ilha da Trindade, Briggs (1974) indica a presença de duas espécies endêmicas (estas atualmente consideradas de distribuição não restrita a Trindade), Nunan (1992) uma e Guimarães e Nunan (submetido) cinco.

Considerando-se somente as famílias com desova não-pelágica, hoje são reconhecidas 69 espécies em águas territoriais brasileiras, das quais aproximadamente 50% são endêmicas destas águas ou de sub-regiões nelas contidas (Tabela 1).

Tabela 1: Matriz de ocorrência de espécies de ambientes recifais tropicais rasos no Brasil, cujos ovos não são pelágicos. Legenda: *Cb*: Caribe; *Trin*: Complexo Ilha da Trindade / Martin Vaz; *Pen*: Penedos de São Pedro e São Paulo; *FN*: Complexo Fernando de Noronha / Atol da Rocas; *NE*: Zona costeira da região nordeste do Brasil; *SE*: Zona costeira da região sudeste do Brasil; *Uru*: Uruguay. Dados obtidos de observações pessoais, comunicações pessoais e das seguintes publicações: Carvalho-Filho, 1999; Ferreira *et al.*, 1995; Figueiredo & Menezes, 1980; Gasparini e Floeter, 2001; Gasparini *et al*, 1999; 2001; Guimarães & Bacellar, 2002; Koike & Guedes, 1981; Lubbock & Edwards, 1981; Menezes & Figueiredo, 1985; Moura, 1995; Novelli *et al.*, 2000; Nunan, 1992; Ramos, 1994; Rocha *et al.*, 1998; Rocha & Rosa, 2000; Rosa & Moura, 1997; Sazima *et al.*, 1997; 1998.

Família	**Espécie**	**Cb**	**Tri**	**Pen**	**FN**	**NE**	**SE**	**Uru**
Syngnathidae	1. *Bryx* sp.	0	0	0	0	1	1	0
	2. *Micrognathus erugatus* Herald & Dawson	0	0	0	0	1	0	0
	3. *Halicampus crinitus* (Jenyns)	1	0	0	1	1	1	0
	4. *Hippocampus erectus* Perry	1	0	0	0	1	1	1
	5. *Hippocampus reidi* Ginsburg	1	0	0	0	1	1	1
Grammatidae	6. *Gramma brasiliensis* Sazima, Gasparini & Moura	0	0	0	1	1	1	0
Apogonidae	7. *Apogon americanus* Castelnau	0	1	1	1	1	1	0
	8. *Apogon planifrons* Longley & Hildebrand	1	0	0	0	1	1	0
	9. *Apogon pseudomaculatus* Longley	1	0	0	0	1	1	0
	10. *Apogon quadrisquamatus* Longley	1	0	0	0	1	1	0
	11. *Astrapogon stellatus* Cope	1	0	0	0	1	1	0
	12. *Phaeoptyx pigmentaria* Poey	1	0	0	0	1	1	0
Pomacentridae	13. *Abudefduf saxatilis* (Linnaeus)	1	1	1	1	1	1	0
	14. *Chromis enchrysura* Jordan & Gilbert	1	0	0	0	1	1	0

	15. *Chromis flavicauda* Günther	1	0	0	0	0	1	0
	16. *Chromis jubauna* Moura	0	0	0	0	0	1	0
	17. *Chromis miltilineata* Guichenot	1	1	1	1	1	1	0
	18. *Chromis scotti* Emery	1	0	0	0	1	0	0
	19. *Microspathodon chrysurus* (Cuv. & Val.)	1	0	0	0	1	0	0
	20. *Stegastes fuscus* (Cuvier)	0	0	0	0	1	1	0
	21. *Stegastes pictus* (Castelnau)	0	0	0	1	1	1	0
	22. *Stegastes rocasensis* (Emery)	0	0	0	1	0	0	0
	23. *Stegastes sanctipauli* Lubbock & Edwards	0	0	1	0	0	0	0
	24. *Stegastes trindadensis* Gaspa, Moura & Sazima	0	1	0	0	0	0	0
	25. *Stegastes uenfi* Novelli, Nunan & Lima	0	0	0	0	1	1	0
	26. *Stegastes variabilis* (Castelnau)	1	0	0	0	1	0	0
Opistognathidae	27. *Opistognathus* sp.	0	1	0	0	1	1	0
	28. *Opistognathus cuvieri* Valenciennes	0	0	0	0	0	1	0
	29. *Opistognathus lonchurus* (Jordan & Gilbert)	1	0	0	0	0	1	0
Tripterygiidae	30. *Enneanectes* sp.	0	0	0	0	1	1	0
	31. *Enneanectes smithi* Lubbock & Edwards	0	0	1	0	0	0	0
Dactyloscopidae	32. *Storrsia olsoni* Dawson	0	0	0	1	0	0	0
Labrisomidae	33. *Labrisomus kalisherae* (Jordan)	1	0	0	0	1	1	0
	34. *Labrisomus nuchipinnis* (Quoy & Gaimard)	1	1	0	1	1	1	1
	35. *Labrisomus* sp.	0	0	0	0	1	1	0
	36. *Malacoctenus delalandei* (Valenciennes)	1	0	0	0	1	1	0
	37. *Malacoctenus* sp. 1	0	0	0	0	1	1	0
	38. *Malacoctenus* sp. 2	0	1	0	0	0	0	0
	39. *Paraclinus arcanus* Guimarães & Bacellar	0	0	0	0	1	1	0
	40. *Paraclinus spectator* Guimarães & Bacellar	0	0	0	0	0	1	0
	41. *Paraclinus rubicundus* (Starks)	0	0	0	0	1	1	0
	42. *Starksia brasiliensis* (Gilbert)	0	0	0	1	1	1	0
	43. *Starksia* sp.	0	0	1	1	0	0	0
Chaenopsidae	44. *Coralliozetus signifer* (Ginsburg)	0	0	0	0	1	1	1
Blenniidae	45. *Entomacrodus vomerinus* (Valenciennes)	0	0	1	1	1	0	0
	46. *Entomacrodus* sp.	0	1	0	0	0	0	0
	47. *Hypleurochilus fissicornis* (Quoy & Gaimard)	0	0	0	0	0	1	1
	48. *Hypleurochilus pseudoaequipinnis* Bath	1	1	0	0	1	1	0
	49. *Hypsoblennius invemar* Smith-Vaniz & Acero	1	0	0	0	0	1	0
	50. *Ophioblennius atlanticus* (Valenciennes)	1	1	1	1	1	0	0
	51. *Parablennius marmoreus* (Poey)	1	0	0	0	0	1	0
	52. *Parablennius pilicornis* (Cuvier)	0	0	0	0	1	1	1
	53. *Scartella cristata*	1	0	0	1	0	0	0
	54. *Scartella* sp. 1	0	1	0	0	0	0	0
	55. *Scartella* sp. 2	0	0	0	0	1	1	0
Gobiidae	56. *Barbulifer ceuthoecus* (Jordan & Gilbert)	1	0	0	0	1	1	0
	57. *Coryphopterus dicrus* Böhlke & Robins	1	0	0	0	1	1	0
	58. *Coryphopterus eidolon* Böhlke & Robins	1	0	0	0	1	0	0
	59. *Coryphopterus glaucofraenum* Gill	1	1	0	1	1	1	0
	60. *Coryphopterus thrix* Böhlke & Robins	1	0	0	0	1	1	0
	61. *Gnatholepis thompsoni*	1	1	0	0	1	1	0
	62. *Gobulus myersi* Ginsburg	1	0	0	0	1	1	0
	63. *Elacatinus figaro* Sazima, Moura & Rosa	0	0	0	0	1	1	0
	64. *Elacatinus randalli* Böhlke	1	0	0	1	0	0	0
	65. *Elacatinus* sp.	0	1	0	0	0	0	0
	66. *Lythrypnus brasiliensis* Greenfield	0	1	0	0	1	1	0
	67. *Microgobius carri* Fowler	1	0	0	0	1	1	0
	68. *Priolepis dawsoni* Greenfield	0	1	0	1	1	1	0
Microdesmidae	69. *Ptereleotris randalli* Gasparini, Rocha & Floeter	0	0	0	0	1	1	0

A partir deste novo quadro, foram conduzidas duas análises distintas sobre a composição da ictiofauna recifal brasileira:

A primeira, representada pelo segundo artigo, é uma análise sobre a variação geográfica da composição ictiofaunística presente em formações recifais brasileiras, com indicações sobre os principais fatores que mantém esta variação.

A segunda, representada pelo terceiro artigo, corresponde a uma reavaliação dos limites e das relações hierárquicas das zonas de endemismo da ictiofauna recifal brasileira, com indicação dos processos históricos que as originaram.

Os resultados obtidos no âmbito da primeira análise permitiram estabelecer correlações significativas entre os agrupamentos ("clusters") de zonas recifais obtidos a partir de suas similaridades ictiofaunísticas com alguns parâmetros ambientais documentados em literatura. Um agrupamento envolve todas as localidades da região nordeste da costa brasileira, o qual está associado principalmente à maior diversidade de corais presente naquela região. Um segundo grupo inclui todas as localidades da região sudeste do Brasil, estando principalmente associado aos índices mais elevados de produtividade primária da área. Os complexos insulares não chegam a formar um grupo claro, mas estiveram todos significativamente influenciados pela distância geográfica que apresentam entre si e as demais localidades (Floeter *et al.*, 2001).

Já a segunda análise sustenta e refina as zonas de endemismo previamente sugeridas por Briggs (1974) e Nunan (1992). Enquanto Briggs (1974) refere-se genericamente a uma grande área de endemismo, a "Província Brasileira", Nunan (1992) indica a presença de algumas sub-áreas de endemismo dentro desta grande província, entre elas os complexos insulares oceânicos.

Consideradas as recentes adições faunísticas supracitadas, são reconhecidas, na presente análise, seis sub-áreas principais de endemismo em ambiente recifais de águas territoriais brasileiras, cada uma delas definida pela presença compartilhada de pelo menos uma espécie endêmica. Entre estas áreas estão, além da Província Brasileira *sensu* Briggs, e dos complexos insulares oceânicos indicados por Nunan, outras que resultam da combinação de duas ou mais destas áreas.

No presente estudo são também reavaliadas as relações hierárquicas entre as sub-regiões de endemismo reconhecidas. Neste sentido, ao contrário do que indica Nunan (1992: Fig. 8.10), a presente análise apresenta evidências de que foi a fauna da Ilha da Trindade a primeira a isolar-se das demais (Guimarães e Nunan, submetido: Fig. 1), e não a dos Penedos de São Pedro e São Paulo.

Os processos históricos que deram origem às regiões de endemismo reconhecidas também foram abordados neste estudo. Além dos fenômenos apontados por Nunan (1992), *i.e.*, as oscilações no nível do mar ocorridos no período pleistocênico, é indicada no presente estudo a relevância das alterações nos padrões de circulação oceânica e da temperatura das massas d'água na formação destas zonas.

6 - Conclusões Gerais

1) Revisões taxonômicas recentes indicam que os níveis de diversidade e endemismo da fauna de peixes recifais brasileiros são mais altos do que previamente suposto.
2) Estes níveis são ainda mais significativos se considerados somente os grupos de postura não-planctônica, os quais estão representados em águas tropicais brasileiras por 69 espécies. Destas, 34 são endêmicas de águas brasileiras ou de sub-áreas incluídas. Em alguns destes grupos, há 100 % de endemismo em águas brasileiras, como no caso do gênero *Paraclinus* (Teleostei: Blennioidei), que está representado em águas brasileiras por três espécies endêmicas da faixa tropical continental do Brasil.
3) As composições específicas das ictiofaunas presentes nas formações recifais de águas tropicais brasileiras estão principalmente relacionadas com as características geomorfológicas destas formações e com as características físico-químicas das massas d'água sob cuja influência estas se encontram. Sob esta perspectiva, as formações recifais da plataforma continental brasileira formam dois grupos principais: Um na região nordeste, influenciada principalmente por águas quentes e oligotróficas e com maior diversidade de corais; e um na região sudeste, onde há intrusão marcante de águas frias e eutróficas e onde o desenvolvimento de corais não se dá em larga escala.

4) São reconhecidas seis principais zonas de endemismo para peixes de postura não-pelágica nos ambientes recifais de águas brasileiras, estas hierarquizadas de acordo com o seguinte cladograma de área: Ilha da Trindade (Penedos de São Pedro e São Paulo (Arquipélago de Fernando de Noronha (plataforma continental do Brasil))). Esta sequência hierárquica indica uma sequência temporal de eventos cladofaunísticos corroborada por um ordenamento onde as localidades mais remotas isolaram-se primeiro.

5) O surgimento dos atuais padrões de diversidade e endemismo observados na ictiofauna de ambientes recifais tropicais brasileiros está intimamente relacionado com fenômenos eustáticos ocorridos durante os ciclos glaciais do período Quaternário. Durante este período, processos de especiação alopátrica estiveram relacionados com as oscilações no nível do mar e com rupturas nos padrões de circulação de termo-halinas ocorridos no Oceano Atlântico Ocidental Sul.

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