

UNIVERSIDADE ESTADUAL DE CAMPINAS

INSTITUTO DE BIOLOGIA



OSMAR JOSÉ LUIZ JUNIOR

“COMPOSIÇÃO E ESTRUTURA DA COMUNIDADE DE PEIXES RECIFAIS
EM RELAÇÃO A QUATRO VARIÁVEIS AMBIENTAIS NO PARQUE
ESTADUAL MARINHO DA LAJE DE SANTOS, ESTADO DE SÃO PAULO”

Este exemplar corresponde à redação final
da tese defendida pelo(a) candidato (a)
Osman José Luiz Junior
Ivan Sazima
e aprovada pela Comissão Julgadora.

Dissertação apresentada ao Instituto de
Biologia para obtenção do Título de
Mestre em Ecologia.

Orientador: Prof. Dr. Ivan Sazima

Co-Orientador: Prof. Dr. Carlos Eduardo Leite Ferreira

Campinas, 2009

**FICHA CATALOGRÁFICA ELABORADA PELA
BIBLIOTECA DO INSTITUTO DE BIOLOGIA – UNICAMP**

L968c

Luiz Junior, Osmar José

Composição e estrutura da comunidade de peixes recifais em relação a quatro variáveis ambientais no Parque Estadual Marinho da Laje de Santos, Estado de São Paulo / Osmar José Luiz Junior. – Campinas, SP: [s.n.], 2009.

Orientadores: Ivan Sazima, Carlos Eduardo Leite Ferreira.

Dissertação (mestrado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Costões rochosos. 2. Comunidades animais. 3. Ressurgência (Oceanografia). 4. Habitat (Ecologia). 5. Peixe – Ecologia. I. Sazima, Ivan. II. Ferreira, Carlos Eduardo Leite. III. Universidade Estadual de Campinas. Instituto de Biologia. IV. Título.

(rcdt/ib)

Título em inglês: Composition and structure of reef fish community structure in relation to four environmental variables in the Laje de Santos Marine State Park, São Paulo State.

Palavras-chave em inglês: Rocky shore; Animal communities; Upwelling (Oceanography); Habitat (Ecology); Fish – Ecology.

Área de concentração: Ecologia.

Titulação: Mestrado em Ecologia.

Banca examinadora: Ivan Sazima, Sergio Ricardo Floeter, Ronaldo Bastos Francini-Filho.

Data da defesa: 06/05/2009.

Programa de Pós-Graduação: Ecologia.

Campinas, 06 de Maio de 2009

BANCA EXAMINADORA

Prof. Dr. Ivan Sazima (Orientador)



Assinatura

Prof. Dr. Ronaldo Bastos Francini-Filho



Assinatura

Prof. Dr. Sergio Ricardo Floeter



Assinatura

Prof. Dr. Paulo Sergio Oliveira

Assinatura

Prof. Dr. Carlos Augusto Rangel Gonçalves

Assinatura

“COMPOSIÇÃO E ESTRUTURA DA COMUNIDADE DE PEIXES RECIFAIS EM
RELAÇÃO A QUATRO VARIÁVEIS AMBIENTAIS NO PARQUE ESTADUAL
MARINHO DA LAJE DE SANTOS, ESTADO DE SÃO PAULO”

Dedico este trabalho ao meu filho, Pedro Henrique Sanches Luiz

e a minha esposa, Alessandra Sanches Luiz.

Um amor maior que o mar.

“To be a naturalist is better than to be a king”

William Beebe, 1893

AGRADECIMENTOS

A minha família, **Alessandra** e **Pedro Henrique**, pelo apoio e amor incondicional e por terem suportado os momentos em que estive ausente em decorrência deste trabalho.

Sergio Ricardo Floeter, **Carlos Eduardo Leite Ferreira** e **João Luiz Gasparini** por serem ao mesmo tempo amigos, professores, irmãos, mestres, companheiros e por serem os principais responsáveis por hoje eu seguir esta carreira, sou eternamente grato.

Ao Professor **Ivan Sazima** pela confiança, orientação e imenso apoio durante todas as etapas deste trabalho e de outros trabalhos realizados.

João Paulo Krajewski, **Angela Correa da Silva** e **Roberta Martini Bonaldo** pela imensa amizade e por me acolherem como um membro da família quando precisei de abrigo em Campinas.

Aos companheiros do Instituto Laje Viva: **Guilherme Kodja**, **Ana Paula Balboni Pinto**, **Ricardo Coelho**, **Paula Romano**, **Cristiane Morgado**, **Vilma Lira**, **José Eduardo Guariglia Filho**, **Andreia Gondim**, **Luis Fernando Waib**, **Big Paul**, **Lucia Silva** e **Rogério Brito** pela amizade, ajuda no campo e apoio logístico.

Ao amigo **Clóvis B. de Carvalho**, por ter me ensinado a amar a “Grande Pedra Mágica”.

Carlo Leopoldo B. Francini, **Luis Fernando Cassino**, **Maurício Andrade**, **Augusto Valente**, **Ivan Cavas**, **Armando de Luca Jr.**, **Alfredo Carvalho-Filho**, **Renata Linger**, **Lara Cheidde** e **Rafael Leite** pelas inúmeras fotografias cedidas para a utilização neste trabalho.

Alfredo Carvalho-Filho, **Luiz A. Rocha**, **Cláudio “Buia” Sampaio**, **João Pedro Barreiros**, **Carlos Augusto Rangel**, **Jean-Christophe Joyeux**, **Alasdair Edwards**, **Peter Wirtz**, **Áthila B. Andrade**, **Leonardo Machado**, **Raphael Macieira**, **José Policarpo Mendonça Neto**, **Diego Barneche Rosado**, **Marcelo Silveira**, **Bertran Feitoza**, **Werther Khroling**, **Ramon Noguchi**, **Carlos “Guga” Ferreira**,

Leopoldo Gerhandinger, Maurício Hostim-Silva e demais colegas da ictiologia pela constante troca de idéias, companheirismo e discussões sobre a vida dos peixes.

Aos Professores **Paulo Sergio Oliveira, Thomas M. Lewinsohn** e **Wooldruff W. Benson** pela dedicação e excelentes aulas no programa de pós-graduação em ecologia da UNICAMP.

Maria Célia Duarte Pio pela excelência dos serviços prestados a frente da secretaria da pós-graduação em ecologia da UNICAMP.

Julio Vellardi, atual diretor e **Mabel Augustowski**, ex-diretora do Parque Estadual Marinho da Laje de Santos, por apoiarem e incentivarem a pesquisa científica no Parque.

CONTEÚDO

Resumo	07
Abstract	09
Introdução	11
Capítulo 1. The reef fish assemblage of the Laje de Santos Marine State Park, Southwestern Atlantic: annotated checklist with comments on abundance, distribution, trophic structure, symbiotic associations, and conservation	14
Capítulo 2. Community structure of fishes in a mid-shelf rocky reef in the southwestern Atlantic: The influence of depth, habitat complexity, and wave exposure	51
Capítulo 3. Upwelling effects upon reef fish community structure	89
Conclusões	119
Referências (Introdução e Conclusões)	121
Anexo 1. <i>Halichoeres sazimai</i> , a new species of wrasse (Perciformes: Labridae) from the Western South Atlantic	124
Anexo 2. Seasonal occurrences of <i>Manta birostris</i> (Chondrichthyes: Mobulidae) on southeastern Brazil	142

RESUMO

O Parque Estadual Marinho da Laje de Santos localiza-se na costa sudeste do Brasil a 36 km da cidade de Santos, Estado de São Paulo. O Parque consiste uma pequena ilha (Laje de Santos) com vários parcéis rochosos submersos. O substrato é composto por rochas graníticas cobertas por algas e várias espécies de invertebrados. Desde 1993, foi declarada como área de proteção marinha e desde então o local é de particular interesse, pois é a única área totalmente fechada para a pesca na região mais povoada e desenvolvida do país. Uma lista com 196 espécies de peixes recifais registradas é apresentada para o Parque Estadual Marinho da Laje de Santos. A maioria das espécies tem ocorrência comum a todo o Atlântico Ocidental tropical ou ocorre nos dois lados do Oceano Atlântico. Uma parte menor das espécies tem distribuição em comum com os recifes rochosos temperados da Patagônia ou é endêmica ao Sudeste do Brasil. *Moringua edwardsi*, *Antennarius multiocellatus*, *Scorpaena dispar*, *Aulostomus strigosus*, *Lutjanus buccanella*, *Mulloidichthys martinicus* and *Halichoeres penrosei* tem aqui seu limite meridional de distribuição estendido ao Estado de São Paulo. Há uma clara diferença na contribuição dos fatores abióticos para a estruturação da comunidade de peixes recifais. A profundidade foi o fator que mais influenciou a riqueza de espécies e abundância de indivíduos, apresentação uma clara distinção ambiental entre raso e fundo, com um decréscimo da riqueza e abundância conforme o aumento da profundidade. A complexidade do habitat também foi um fator de influência na comunidade, sendo a riqueza e abundância correlacionada com maior complexidade. Entretanto, esta relação só foi significativa na menor profundidade avaliada. A exposição às ondas não se correlacionou com nenhum dos descritores da comunidade utilizados neste estudo. Aparentemente os efeitos do hidrodinamismo em recifes rochosos se manifesta em escalas espaciais maiores entre a costa e ilhas com diferentes distâncias da costa. Espécies de diferentes categorias tróficas não respondem da mesma maneira a estes fatores. Herbívoros vagueadores são afetados pela profundidade, herbívoros territoriais pela complexidade e pela exposição a ondas, enquanto que planctívoros são afetados pela complexidade do habitat e em menor extensão pela

profundidade. Análises de espécies filogeneticamente relacionadas sugerem que ocorre partição de nicho, aparentemente mediada pela capacidade de natação em resposta ao grande dinamismo que ocorre nas zonas rasas. A água fria oriunda de eventos de ressurgência foi um fator de redução da abundância e número de espécies capazes de estender sua distribuição batimétrica para as zonas mais profundas, desencadeando respostas comportamentais específicas em algumas espécies como a formação de densos cardumes na camada superficial durante os eventos de ressurgência. Herbívoros vageadores e onívoros foram os grupos tróficos que foram particularmente afetados pela intrusão de água fria. Em geral, espécies com alta capacidade de mobilidade evitam a camada de água fria abaixo da termoclina durante o verão e espécies de pequena capacidade de mobilidade ou extremamente territoriais não alteram sua abundância em resposta a estes eventos.

Palavras Chave: Recifes Rochosos, Subtropical, Ressurgência, Profundidade, Estrutura do Habitat, Hidrodinamismo.

ABSTRACT

The Laje de Santos State Marine Park is located on the southeastern coast of Brazil, 36 km off the city of Santos, São Paulo State. It consists of an uninhabited islet and several sparse rocky reefs with extensive sand bottoms in between. The subtidal substrate is composed of granitic boulders of varying sizes and shapes. The rocky substrate is mainly covered with patches of algae and several species of sessile invertebrates. Since 1993 the Laje de Santos Island was declared a protected area. The area is of particular interest as this is the only Marine Protected Area totally closed to fishing in the most populated and developed region of Brazil. A check-list containing 196 species of reef fishes recorded at the Laje de Santos Marine State Park is presented. Most of them occur along the tropical western Atlantic or occur on both sides of the Atlantic Ocean. A minor part ranges to the temperate rocky reefs of Patagonia or are endemics to southeastern Brazil. *Moringua edwardsi*, *Antennarius multiocellatus*, *Scorpaena dispar*, *Aulostomus strigosus*, *Lutjanus buccanella*, *Mulloidichthys martinicus* and *Halichoeres penrosei* have here their ranges extended southward to the São Paulo coast. There is a clear difference among the contributions of each abiotic factors analyzed in the reef fish community structure. Depth was the most influent factor on species richness and abundance, presenting a clear distinction between shallow and deep zones with a decrease of both factors with depth increase. Habitat complexity also had an influence in the community, being species richness and abundance correlated with higher complexity. However, this relationship was significant on the shallower evaluated depth only. Exposition to wave surge does not correlate with any of the community descriptors used in this study. Apparently, hydrodynamics effects on rocky reefs manifest only at larger spatial scales like between the shore and islands. Species on different trophic categories do not respond the same way to these factors. Vagrant herbivores are affected by depth; territorial herbivores by habitat complexity and marginally by exposition, and planktivorous are affected mostly by habitat complexity and in less extension by depth. Analyses of phylogenetically related species suggest that niche partitioning occur, apparently mediated by swimming capacity in response to higher

hydrodynamic forces occurring in shallow water. Cold water derived from upwelling events was a further factor reducing species richness and abundance, triggering specific behavioral responses in some species such as the formation of tight packed schools in the surface layer during upwelling. Vagrant herbivores and omnivores were the trophic groups most affected by upwelling. In general, species with high mobility capacity avoid the cold-water layer below the thermocline during summer and species with limited mobility capacity do not change their abundance in response to these events.

Keywords: Rocky shore, Subtropical, Upwelling, Depth, Habitat Structure, Hydrodynamics

INTRODUÇÃO

Peixe recifal é um termo utilizado para designar espécies que vivem associadas a ambientes marinhos caracterizados por substrato rígido e consolidado, que na língua portuguesa são usualmente denominados de recifes, parcéis, laje, lajedo, rochedos, penedos, costões, entre outros nomes. Estes substratos proporcionam, aos peixes, refúgios contra predadores e oportunidades de forrageamento, pois sua estrutura física muitas vezes é composta por cavidades, frestas e interstícios onde os peixes podem se abrigar além de servir de base para o crescimento de uma grande diversidade de algas e invertebrados marinhos dos quais os peixes se alimentam (Choat & Bellwood 1991). A grande maioria dos estudos sobre a ecologia de peixes recifais foi realizada em recifes de corais tropicais, particularmente no Caribe e na Grande Barreira de Corais da Austrália (Sale 1991, 2002). A fauna de peixes recifais, entretanto, não é restrita a recifes de corais. Diversos ambientes tropicais e subtropicais nos quais as condições ambientais particulares restringem o crescimento de recifes coralíneos também abrigam comunidades de peixes recifais, que não se distinguem taxonomicamente das comunidades de recifes de corais (Robertson 1998). Estes ambientes são denominados de recifes rochosos tropicais (Robertson 1998, Aburto-Oropeza & Balart 2001, Ferreira et al. 2001, Floeter et al. 2001, Pondella et al. 2005, Dominici-Arosemena & Wolff 2006). Porém, ao mesmo tempo, são muito distintos dos recifes rochosos temperados (Jones 1988, Ebeling & Hixon 1991) por apresentarem temperaturas mais amenas, não possuírem “florestas de algas” (‘kelps’) e por terem uma parcela considerável da sua fauna composta por representantes em comum com os recifes de corais próximos. Desta forma, as espécies de peixes recifais que estendem sua distribuição a recifes rochosos estão sujeitas às condições ambientais que impedem o crescimento de recifes de corais, como turbidez e baixa temperatura da água (Perry & Larcombe 2003). Apesar da grande diversidade de espécies encontrada entre os peixes recifais, é notável a homogeneidade taxonômica nos níveis de família e de gênero nos ambientes recifais tropicais e subtropicais ao redor do mundo (Thresher 1991, Floeter &

Gasparini 2000). Entretanto, apesar da crescente literatura a respeito das respostas das comunidades de corais a estas condições sub-ótimas, muito pouco se sabe se estes fatores afetam, e como, comunidades de peixes de recifes rochosos tropicais e subtropicais.

Um grande número de espécies de peixes recifais que ocorre por todo o Atlântico Oeste Tropical tem seus limites meridionais de distribuição nos recifes rochosos da costa sudeste e sul do Brasil (Randall 1996, Carvalho-Filho 1999, Moura et al. 1999, Floeter et al. 2001, Humann & DeLoach 2002, Menezes et al. 2003). Apesar de possuir uma significativa proporção de endemismo, mais da metade das espécies que ocorrem nos recifes rochosos subtropicais do Brasil são espécies com ampla distribuição nos recifes tropicais do Caribe (Ferreira et al. 2001, Floeter & Gasparini 2000, Luiz Jr et al. 2008) representando uma ótima oportunidade de avaliar se e como distintas condições ambientais e diferentes tipos de estruturas recifais afetam a estruturação das comunidades de peixes que aí vivem.

O presente estudo tem como objetivo geral descrever a relação de variáveis abióticas com a comunidade de peixes recifais do Parque Estadual Marinho da Laje de Santos. Para esta finalidade, os seguintes objetivos específicos foram determinados: a) Determinar a composição de espécies que compõem a comunidade de peixes recifais do Parque Estadual Marinho da Laje de Santos; b) Avaliar a influência da profundidade, complexidade estrutural do substrato e batimento de ondas na composição e abundância de espécies de grupos tróficos e c) Avaliar a influência sazonal da água fria oriunda de eventos de ressurgência sobre a comunidade de peixes recifais.

As características do local deste estudo (Parque Estadual Marinho da Laje de Santos, Estado de São Paulo) são apresentadas em detalhes nos capítulos subseqüentes, mas basicamente trata-se de recifes rochosos localizados distante da costa, mas ainda sobre a plataforma continental. Sua localização em mar aberto o distingue dos recifes rochosos costeiros e litorâneos (costões rochosos) principalmente pelo nível de exposição a intempéries e hidrodinamismo, incluindo o batimento de ondas e correntes marinhas. Além disso, sua posição intermediária na plataforma continental torna o local de estudo também sujeito a

periódicas intrusões de água fria oriunda de eventos de ressurgência na borda da plataforma, com diversas implicações ecológicas sobre suas comunidades.

O conhecimento da composição de espécies da comunidade a ser estudada é fundamental para formar uma base de dados pelos quais se inicia a busca pelo conhecimento ecológico (Agardy 2000). Desta forma, no **Capítulo 1** é apresentada a primeira lista de espécies de peixes recifais que ocorrem no local de estudo, assim como algumas características biológicas destas espécies.

No **Capítulo 2** são verificados os efeitos de três variáveis ambientais sobre a comunidade de peixes. Estas variáveis, especificamente, profundidade, complexidade do habitat e exposição ao batimento de ondas; foram amplamente estudadas em recifes de corais, mas muito pouco avaliadas em recifes rochosos. Devido a grandes diferenças na estrutura física e zonação entre recifes de corais e os rochosos, seria esperado que as comunidades de peixes apresentem diferentes respostas a estes fatores.

Baixa temperatura é um fator com efeitos importantes na definição da distribuição geográfica de peixes tropicais (Bohnsack 1983, Mora & Ospina 2002, Kimball et al. 2004; Eme & Bennett 2008). O local de estudo é caracterizado por uma ressurgência sazonal, que traz água fria afetando as áreas mais fundas e cujo efeito é analisado no **capítulo 3**.

CAPÍTULO 1

THE REEF FISH ASSEMBLAGE OF THE LAJE DE SANTOS MARINE STATE PARK, SOUTHWESTERN ATLANTIC: ANNOTATED CHECKLIST WITH COMMENTS ON ABUNDANCE, DISTRIBUTION, TROPHIC STRUCTURE, SYMBIOTIC ASSOCIATIONS, AND CONSERVATION *

OSMAR J. LUIZ JR.^{1,2}, ALFREDO CARVALHO-FILHO^{2,3}, CARLOS E. L. FERREIRA⁴,
SERGIO R. FLOETER⁵, JOÃO L. GASPARINI⁶ & IVAN SAZIMA¹

¹ *Depto. de Zoologia e Museu de História Natural, Universidade Estadual de Campinas, Campinas, SP, Brasil.*

² *Instituto Laje Viva, www.lajeviva.org.br. Santos, SP, Brasil.*

³ *Fish Bizz Ltda. Rua Moncorvo Filho 51, São Paulo, SP, Brasil.*

⁴ *Depto. de Biologia Marinha, Universidade Federal Fluminense, Niterói, RJ, Brasil.*

⁵ *Lab. de Macroecologia e Biogeografia Marinha, Universidade Federal de Santa Catarina, Florianópolis, SC,
Brasil.*

⁶ *Depto. de Ecologia e Recursos Naturais, Universidade Federal do Espírito Santo, Av. Fernando Ferrari 514,
Vitória, ES, Brasil.*

*** Artigo publicado no Periódico Zootaxa**

Abstract: A check-list containing 196 species of reef fishes recorded at the Laje de Santos Marine State Park is presented. Most of them occur along the tropical western Atlantic or occur on both sides of the Atlantic Ocean. A minor part ranges to the temperate rocky reefs of Patagonia or are endemics to southeastern Brazil. *Moringua edwardsi*, *Antennarius multiocellatus*, *Scorpaena dispar*, *Aulostomus strigosus*, *Lutjanus buccanella*, *Mulloidichthys martinicus* and *Halichoeres penrosei* have here their ranges extended southward to the São Paulo coast. Basic data on species abundance at the study site, distribution of species between habitat types, trophic structures, symbiotic feeding associations and conservation are commented upon.

Resumo: Uma lista com 196 espécies de peixes recifais registradas é apresentada para o Parque Estadual Marinho da Laje de Santos. A maioria das espécies tem ocorrência comum a todo o Atlântico Ocidental tropical ou ocorre nos dois lados do Oceano Atlântico. Uma parte menor das espécies tem distribuição em comum com os recifes rochosos temperados da Patagônia ou é endêmica ao Sudeste do Brasil. *Moringua edwardsi*, *Antennarius multiocellatus*, *Scorpaena dispar*, *Aulostomus strigosus*, *Lutjanus buccanella*, *Mulloidichthys martinicus* and *Halichoeres penrosei* tem aqui seu limite meridional de distribuição estendido ao Estado de São Paulo. Informações básicas sobre abundância das espécies no local de estudo e sua distribuição entre os diferentes tipos de habitats, estrutura trófica, associações alimentares simbióticas e conservação, são aqui comentadas.

Key-words: Western South Atlantic, Brazil, Rocky Reefs, Reef Fishes, Species List and Distribution, Zoogeography, Conservation, Trophic Structure, Feeding Symbioses.

INTRODUCTION

The Laje de Santos State Marine Park (*Parque Estadual Marinho da Laje de Santos - PEMLS*) is located on the southeastern coast of Brazil (24°15'S; 46°10'W), 36 km off the city of Santos, São Paulo State (Fig. 1). It consists of an uninhabited islet and several sparse rocky reefs with extensive sand bottoms in between. The maximum depth is about 45 m. The subtidal substrate is composed of granitic boulders of varying sizes and shapes that delineate a steep profile (Fig. 2). The rocky substrate is mainly covered with patches of brown and red algae, the zoanthid *Palythoa caribeorum*, hydrozoans, ascidians, octocorals and sparse colonies of the scleractinian corals *Madracis decactis* and *Mussismilia hispida*. The local setting is a transitional tropical-subtropical environment that fits in the definition of a high latitude 'marginal' reef site (Perry & Larcombe 2003) where hard corals may occur only as isolated colonies on the exposed bedrock.

The area is of particular interest as this is the only Marine Protected Area totally closed to fishing in the most populated and developed region of Brazil, allowing researchers to evaluate fishing impacts on local rocky reefs (Floeter *et al.* 2006). Since 1993 a 5,000 ha area around the Laje de Santos Island was declared a protected area. After some years as a "paper park" with low or even inexistent effective enforcement, the study site is experiencing a great increase in the effort to eradicate fishing in the last four years. Since 2003, a new official government management policy and the rise of an active NGO dedicated to protect the Park brought new boats, equipment and several personnel (volunteer and staff) extensively engaged in the inspection of the Park boundaries. Recreational activities allowed in the Park include scuba diving and boating. Anchoring is not allowed anymore and mooring buoys have been used by dive boats.

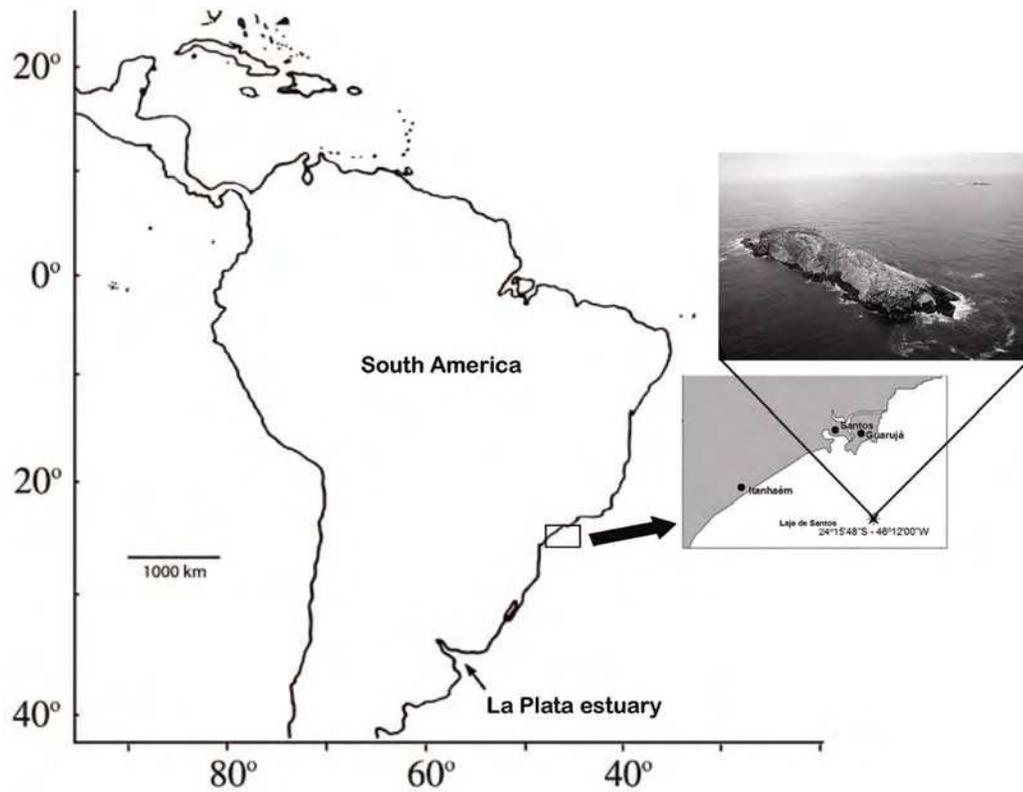


Figure 1. The Laje de Santos Marine State Park localization in western South Atlantic. Photo: C.L.B. Francini.

Despite a few recent publications on reef fish taxonomy (Moura 1995), behavior (Sazima *et al.* 2000) and a species list of benthic algae (Amado-Filho *et al.* 2006), the Laje de Santos remains largely unknown biologically and a comprehensive list of reef fish species occurring in the Marine Park is still lacking. The knowledge of the species composition of a community is instrumental to provide a baseline for future management and a starting point to produce scientific information needed for the process of designing and evaluating Marine Protected Areas, such as biomass, dispersal patterns, recruitment

dynamics, trophic interactions and habitat preferences of the resident organisms (Agardy 2000, Craig *et al.* 2004).

The present study provides the first comprehensive checklist of the reef fish species that occur at the Laje de Santos Marine State Park. In addition, patterns of species distribution, abundance, zoogeography, trophic types, representative feeding symbioses, and conservation issues are commented upon.

MATERIALS AND METHODS

The species list results from fishes observed, photographed, and collected by the authors, as well as museums vouchers and reliable literature records. Bony fishes are listed in the phylogenetic order of families following Nelson (2006); elasmobranchs are listed following Compagno (1999). Within families, species are organized in alphabetical order. Recent changes in the classification of the Serranidae as proposed by Craig and Hastings (2007) and Smith and Craig (2007) are adopted. Among these are the resurrection of the family Epinephelidae as distinct from Serranidae; the placement of the genus *Paranthias* within *Cephalopholis*; the change from genus *Epinephelus* to *Mycteroperca* for *M. marginata* (formerly *E. marginatus*) and the genus change of deep-bodied groupers of the *Epinephelus niveatus* complex to the resurrected genus *Hyporthodus*. In the list, we included the following information for each species:

Abundance – an indicator of the relative abundance in the last five years, period when the first author started quantitative visual censuses of fishes in the study area and in more than thirty years of observations on fishes done by the second author; this indicator is based on a diver's likelihood of recording a species in its normal habitat and depth range on any given dive (modified from Humann & DeLoach 2002, Feitoza *et al.* 2003), where: AB = abundant (several sightings of many individuals – at least 50 – are expected on nearly every dive), VC = very common (several sightings are expected on

nearly every dive, but not necessarily of many individuals), CO = common (sights are frequent, but not necessarily expected on every dive), OC = occasional (sightings are not unusual, but are not expected on a regular basis), UN = unusual (sights occurs less than occasionally), and RA = rare (sights are exceptional);

Habitat and Distribution – the particular place where a species has usually been found; we arbitrarily stipulated different habitats types based on physiographic factors like substrate type and depth (fig. 2). These habitats apparently differ in the type of resources provided for the reef fishes, which, in turn, are more likely to be found in habitats that are more suitable for their specific needs, where: Sh = Shallow reef (rocky substrate from 0 to 12 m depth), RS = Reef slope (rocky substrate from 13 to 20 m depth), SB = Sand bottom (sandy substrate adjacent to the rocky reef slope), WC = Water column (pelagic environment from 0 to 10 m depth, immediately adjacent to the rocky reef but distant enough to be considered not-associated to the bottom), and DR = Deep reef (rocky substrate in the range of 30-45 meters depth).

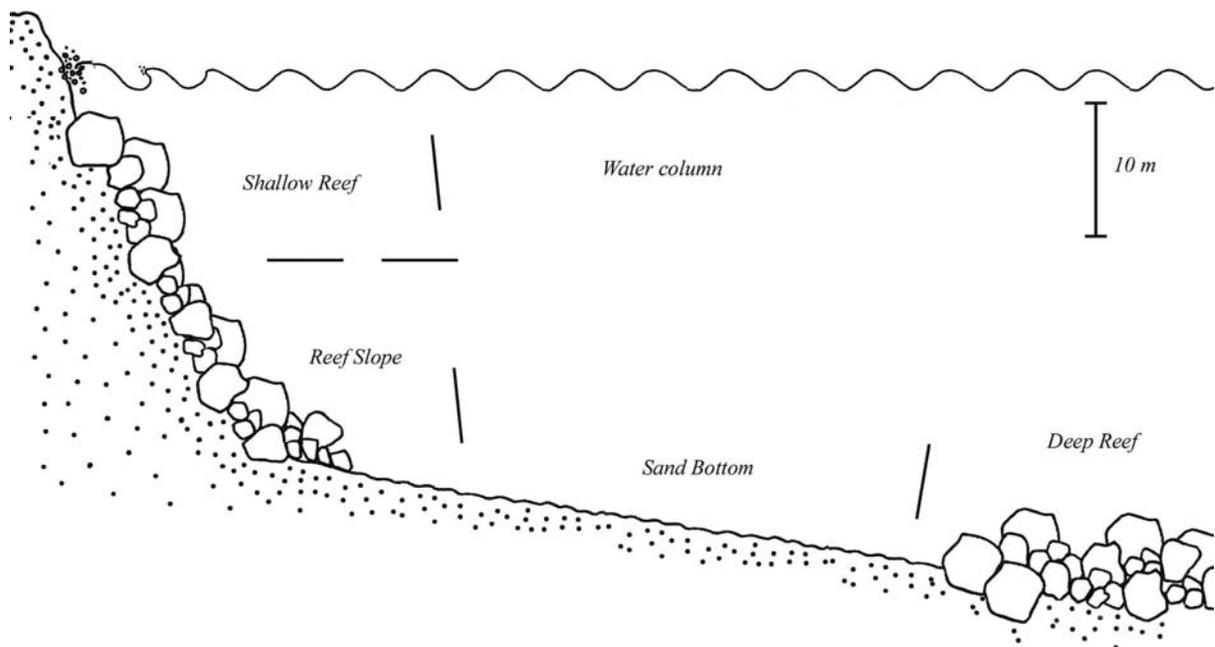


Figure 2. Habitat types found at the Laje de Santos Marine State Park.

Geographic range of the species – namely: Br = Brazilian province (*sensu* Briggs 1974), CE = Central Atlantic (Islands of St. Helena and Ascension), CT = Circumtropical, EA= Eastern Atlantic, Pat = Patagonian (occur primarily in the temperate rocky reefs south to Argentina), SCa = Southern Caribbean (Coast of Venezuela, Trinidad and Tobago and other islands of the low lesser Antilles), SE = Southeastern Brazil (endemic from the region that encompass 20°S to 27S° in the Western Atlantic), TA = Trans-Atlantic (occur at both sides of the Atlantic Ocean), and WA = Western Atlantic (occur in Northern and Southern West Atlantic).

Trophic category – assessed from direct behavioral observations and from the literature (Randall 1967, 1996, Carvalho-Filho 1999, Ferreira *et al.* 2004), where: CAR = Carnivores (eat a variety of mobile organisms, including invertebrates and fishes), MIF = Mobile invertebrate feeders (feed primarily on small benthic mobile invertebrates like mollusks, crustaceans, worms, etc. associated to the hard- or nearby soft-substrate), OMN = Omnivores (feed on variety of organisms, including animal and vegetal), PIS = Piscivores (feed only or mostly on live fishes), PLK = Planktivores (feed primarily on macro- and micro-zooplankton), ROVH = Roving herbivores (non-territorial, large herbivores which includes in their diet a rich mass of detritus, turf algae and macroalgae), SIF = Sessile invertebrate feeders (feeds on a array of sessile benthic invertebrates like cnidarians, bryozoans, ascidians and sponges that are most associated to hard substrata), and TERH = Territorial herbivores (with a diet composed mainly by turf algae farmed within a vigorously defended territory).

Record type – how the species was recorded, where: COL = Collected, MUS = Museum voucher, LIT = Literature, PHO = Photograph, and SIG = Sighting. For specimens deposited in museum collections, the institution and voucher number are provided in the appendix.

We define reef fishes here as those species that are primarily associated with hard substrata, and which depends on the reef or its immediately vicinity for shelter and food during any phase of its post-settlement life. We also consider as reef fishes the epipelagic species that regularly visit reefs in search for food, cleaning services, and reproduction. For the sake of convenience we based our list on Thresher

(1991) with the addition of characteristic subtropical families that were observed living on the rocky reefs at specific sites of the Laje de Santos.

For the purpose of describing the occurrence patterns of fish species in the different habitats, a cluster analysis based on a species matrix was performed. The Bray-Curtis dissimilarity index was used, and habitats were clustered according to the UPGMA method (Pielou 1984). This analysis accounts only for the presence or absence of a given species. The abundance patterns of reef fish in the different habitats, considering variables such as exposure degree, substrate complexity and depth will be presented elsewhere.

RESULTS AND DISCUSSION

Species composition

A total of 196 reef fish species in 124 genera in 66 families were recorded at the Laje de Santos (Table I). The most species rich families were Carangidae (16), Epinephelidae (12), Labridae (10), Pomacentridae (8) and Scaridae (8). *Caranx*, *Gymnothorax*, *Halichoeres*, *Mycteroperca* and *Sparisoma*, with 5 species each were the most species rich genera, followed by *Chromis*, *Haemulon*, and *Seriola* with 4 species. Twelve species were abundant (6%) (fig. 3), 26 (13%) were very common, 45 (23%) were common, 61 (32%) were occasional, 14 (7%) were unusual and 38 (19%) were rare.

Table 1. List of families and species, habitat, abundance, geographic range, trophic category and record status of the reef fishes recorded at the Laje de Santos Marine State Park. Families of elasmobranchs are arranged following Compagno (1999) and bony fishes are arranged according to Nelson (2006); genera and species are arranged in alphabetical order. **Habitat:** DR = Deep Reef; RS = Reef Slope; SB = Sand Bottom; SH = Shallow Reef; WC = Water Column. **Occurrence:** AB = Abundant; CO = Common; OC = Occasional; RA = Rare; UN = Unusual; VC = Very Common. **Geographic Range:** Br = Brazilian Province; CE = Central Atlantic; CT = Circumtropical. EA = Eastern Atlantic; SCa = Southern Caribbean; SE = Southeastern Brazil; TA = Trans-Atlantic; WA = Western Atlantic. **Trophic Category:** CAR = Carnivore; MIF = Mobile Invertebrate Feeder; OMN = Omnivore; PIS =

Piscivore; PLK = Planktivore; ROVH = Roving Herbivore; SIF = Sessile Invertebrate Feeder; TERH = Territorial Herbivore. **Record Type:** COL = Collected; MUS = Museum Voucher; PHO = Photograph; SIG = Sighting.

Family and species	Habitat	Occurrence	Geog. Range	Trophic Category	Record Type
ODONTASPIDIDAE					
<i>Carcharias taurus</i> Rafinesque, 1810	DR	UN	CT	PIS	SIG
ALOPIIDAE					
<i>Alopias vulpinus</i> (Bonaterre, 1788)	WC	RA	CT	PIS	SIG
CARCHARHINIDAE					
<i>Carcharhinus brevipinna</i> (Muller & Henle, 1839)	WC	RA	CT	PIS	COL, PHO
<i>Carcharhinus falciformis</i> (Bibron, 1839)	WC	RA	CT	PIS	COL, PHO
<i>Carcharhinus limbatus</i> (Muller & Henle, 1839)	WC	RA	CT	PIS	COL, PHO
<i>Carcharhinus longimanus</i> (Poey, 1861)	WC	RA	CT	PIS	PHO
RHINOBATIDAE					
<i>Zapteryx brevirostris</i> (Müller & Henle 1841)	SB	RA	WA	MIF	SIG
GYMNURIDAE					
<i>Gymnura altavela</i> (L. 1758)	RS, SB	RA	TA	MIF	PHO
DASYATIDAE					
<i>Dasyatis centroura</i> (Mitchill, 1815)	RS, SB	OC	TA	MIF	PHO
<i>Dasyatis hypostigma</i> Santos & Carvalho 2004	RS, SB	RA	SE	MIF	PHO
MYLIOBATIDAE					
<i>Aetobatus narinari</i> (Euphrasen, 1790)	WC	CO	CT	MIF	PHO
MOBULIDAE					
<i>Manta birostris</i> (Walbaum, 1792)	WC	OC	CT	PLK	PHO
<i>Mobula hypostoma</i> (Bancroft, 1831)	WC	RA	CT	PLK	MUS, SIG
<i>Mobula japonica</i> (Muller & Henle, 1841)	WC	RA	CT	PLK	SIG
<i>Mobula tarapacana</i> (Philippi, 1892) * Gadig & Sampaio, 2002	WC	RA	CT	PLK	LIT*
MORINGUIDAE					
<i>Moringua edwardsi</i> (Jordan & Bollman, 1889)	SH, RS	UN	WA	MIF	PHO
MURAENIDAE					
<i>Gymnothorax funebris</i> Ranzani, 1839	SH, RS	OC	WA	CAR	MUS, PHO
<i>Gymnothorax miliaris</i> (Kaup, 1856)	SH, RS	CO	TA	CAR	COL, PHO
<i>Gymnothorax moringa</i> (Cuvier, 1829)	SH, RS	CO	WA+CE	CAR	COL, PHO

<i>Gymnothorax ocellatus</i> Agassiz, 1831	SB	RA	WA	CAR	PHO
<i>Gymnothorax vicinus</i> (Castelnaul, 1855)	SH, RS	CO	TA	CAR	COL, PHO
<i>Muraena retifera</i> Goode & Bean, 1882	RS, DR	OC	WA	CAR	COL, PHO
OPHICHTHIDAE					
<i>Ahlia egmontis</i> (Jordan, 1884)	SH, RS	UN	WA	MIF	COL, PHO
<i>Myrichthys ocellatus</i> (LeSueur, 1825)	SH	CO	WA	MIF	PHO
<i>Myrichthys breviceps</i> (Richardson, 1848)	SH, RS	RA	WA	MIF	PHO
<i>Ophichthus ophis</i> (L., 1758)	SB	RA	TA	PIS	MUS
CLUPEIDAE					
<i>Harengula clupeola</i> (Cuvier, 1829)	WC	OC	WA	PLK	COL
<i>Sardinella janeiro</i> (Eingenmann, 1894)	WC	OC	WA	PLK	MUS
SYNODONTIDAE					
<i>Synodus foetens</i> (L., 1776)	SH, RS, SB	UN	WA	PIS	MUS
<i>Synodus intermedius</i> (Spix & Agassiz, 1829)	SH, RS, SB	VC	WA	PIS	MUS, COL, PHO
<i>Synodus synodus</i> (L., 1758)	SH, RS, SB	CO	TA	PIS	COL, PHO
BATRACHOIDIDAE					
<i>Porichthys porosissimus</i> (Cuvier, 1829)	SB	RA	SE+Pa	CAR	MUS
ANTENNARIIDAE					
<i>Antennarius multiocellatus</i> (Valenciennes, 1837)	SH	UN	WA	CAR	PHO
OGCOCEPHALIDAE					
<i>Ogcocephalus vespertilio</i> (L., 1758)	RS, SB	UN	WA	CAR	PHO
BELONIDAE					
<i>Tylosurus acus</i> (Lacepede, 1803)	WC	OC	CT	PIS	MUS, PHO
HEMIRAMPHIDAE					
<i>Hemiramphus balao</i> (Lesueur, 1821)	WC	OC	TA	OMN	SIG
<i>Hemiramphus brasiliensis</i> (L., 1758)	WC	OC	TA	OMN	SIG
HOLOCENTRIDAE					
<i>Holocentrus adscensionis</i> (Osbeck, 1765)	SH, RS	VC	TA	MIF	MUS, COL, PHO
<i>Myripristis jacobus</i> Cuvier, 1829	SH	CO	TA	PLK	MUS, COL, PHO
SYNGNATHIDAE					
<i>Hippocampus reidi</i> Ginsburg, 1933	RS	RA	WA	PLK	PHO
<i>Micrognathus crinitus</i> (Jenyns, 1842)	RS	OC	WA	PLK	PHO
AULOSTOMIDAE					
<i>Aulostomus strigosus</i>	SH	RA	TA	CAR	PHO

Wheeler, 1955						
FISTULARIDAE						
<i>Fistularia tabacaria</i> L., 1758	RS, SB	OC	TA	PIS	SIG	
DACTYLOPTERIDAE						
<i>Dactylopterus volitans</i> L., 1758	RS, SB	CO	TA	MIF	MUS, COL, PHO	
SCORPAENIDAE						
<i>Scorpaena dispar</i> Longley & Hildebrand, 1940	SH, RS, DR	OC	WA	CAR	PHO	
<i>Scorpaena isthmensis</i> Meek & Hildebrand, 1928	?	RA	WA	CAR	MUS	
<i>Scorpaena plumieri</i> Bloch, 1789	SH, RS, DR	OC	WA+CA	CAR	COL, PHO	
<i>Scorpaenodes tredecimspinosus</i> (Metzelaar, 1919)	SH, RS	CO	WA	CAR	COL, PHO	
SERRANIDAE						
<i>Acanthistius brasilianus</i> (Cuvier, 1828)	RS, DR	CO	SE+Pat	CAR	MUS, COL, PHO	
<i>Acanthistius patachonicus</i> (Jenyns, 1840)	DR	RA	SE+Pat	CAR	COL, PHO	
<i>Diplectrum formosum</i> (L., 1766)	SB	UN	WA	CAR	PHO	
<i>Dules auriga</i> Cuvier, 1829	DR	CO	SE+Pat	CAR	COL, PHO	
<i>Pronotogrammus martinicensis</i> (Guichenot, 1868)	DR	UN	WA	PLK	SIG	
<i>Serranus baldwini</i> (Evermann & Marsh, 1899)	SH, RS	CO	WA	CAR	MUS, PHO	
EPINEPHELIDAE						
<i>Cephalopholis fulva</i> (L., 1758)	?	RA	WA	CAR	MUS	
<i>Cephalopholis furcifer</i> (Valenciennes, 1828)	WC	CO	TA	PLK	MUS, COL, PHO	
<i>Epinephelus adscensionis</i> (Osbeck, 1765)	SH, RS	RA	TA	CAR	MUS, COL, PHO	
<i>Epinephelus itajara</i> Lichtenstein, 1822	SH, RS	OC	TA	CAR	PHO	
<i>Epinephelus morio</i> (Valenciennes, 1828)	RS	UN	WA	CAR	COL, PHO	
<i>Hyporthodus flavolimbatus</i> (Poey, 1865)	DR	OC	WA	CAR	COL, PHO	
<i>Hyporthodus niveatus</i> (Valenciennes, 1828)	SH, RS, DR	CO	WA	CAR	MUS, COL, PHO	
<i>Mycteroperca acutirostris</i> (Valenciennes, 1828)	SH, RS	VC	WA	PIS	MUS, COL, PHO	
<i>Mycteroperca bonaci</i> (Poey, 1860)	SH, RS	RA	WA	PIS	COL, PHO	
<i>Mycteroperca interstitialis</i> (Poey, 1860)	SH, RS	CO	WA	PIS	MUS, COL, PHO	
<i>Mycteroperca marginata</i> (Lowe, 1834)	SH, SB, RS, DR	VC	SE+Pat+E A	CAR	MUS, COL, PHO	
<i>Mycteroperca venenosa</i> (L., 1758)	SH, RS, DR	RA	WA	PIS	COL, PHO	

PRIACANTIDAE						
<i>Cookeolus japonicus</i> (Cuvier, 1829)	DR	OC	CT	PLK	COL, PHO	
<i>Heteropriacanthus cruentatus</i> (Lacepède 1801)	SH, RS	OC	CT	PLK	COL, PHO	
<i>Priacanthus arenatus</i> Cuvier, 1829	SH, RS, DR	OC	TA	MIF	COL, PHO	
APOGONIDAE						
<i>Apogon americanus</i> Castelnau, 1855	SH, RS	CO	Br	PLK	MUS, COL, PHO	
<i>Apogon pseudomaculatus</i> Longley, 1932	SH, RS	CO	TA	PLK	MUS, COL, PHO	
MALACANTHIDAE						
<i>Caulolatilus chrysops</i> (Valenciennes, 1833)	SB	RA	WA	CAR	MUS	
<i>Malacanthus plumieri</i> (Bloch, 1786)	SB	CO	WA+CE	CAR	MUS, PHO	
POMATOMIDAE						
<i>Pomatomus saltatrix</i> (L., 1766)	WC	OC	CT	CAR	COL, PHO	
ECHENEIDIDAE						
<i>Echeneis naucrates</i> (L., 1758)	WC	OC	CT	CAR	COL, PHO	
<i>Remora albescens</i> (Temminck & Schlegel, 1845)	WC	OC	CT	CAR	PHO	
<i>Remora remora</i> (L., 1758)	WC	OC	CT	MIF	PHO	
RACHYCENTRIDAE						
<i>Rachycentron canadum</i> (L., 1766)	SB	OC	CT	CAR	COL, PHO	
CORYPHAENIDAE						
<i>Coryphaena hippurus</i> L., 1758	WC	RA	CT CT	CAR	COL	
CARANGIDAE						
<i>Alectis ciliaris</i> (Bloch, 1787)	WC	CO	CT	CAR	COL, PHO	
<i>Caranx bartholomaei</i> (Cuvier, 1833)	WC	OC	WA	PIS	COL, PHO	
<i>Caranx crysos</i> (Mitchill, 1815)	WC	OC	TA	CAR	COL, PHO	
<i>Caranx hippos</i> (L., 1766)	WC	RA	TA	CAR	COL, PHO	
<i>Caranx latus</i> Agassiz 1831	WC	OC	TA	CAR	MUS, PHO	
<i>Caranx ruber</i> (Bloch, 1793)	WC	OC	WA	CAR	PHO	
<i>Decapterus macarellus</i> (Cuvier, 1833)	WC	OC	CT	PLK	COL, PHO	
<i>Decapterus punctatus</i> (Cuvier, 1829)	WC	UN	TA	PLK	COL, PHO	
<i>Pseudocaranx dentex</i> (Bloch & Schneider 1801)	WC, SH, RS, SB, DR	VC	CT	MIF, PLK	MUS, COL, PHO	
<i>Seriola dumerilli</i> (Risso 1810)	WC	CO	CT	CAR	MUS, COL, PHO	
<i>Seriola fasciata</i>	WC	UN	TA	CAR	COL, PHO	

(Bloch, 1793)						
<i>Seriola lalandi</i> Valenciennes, 1833	WC	OC	CT	CAR	COL, PHO	
<i>Seriola rivoliana</i> (Valenciennes, 1833)	WC	OC	CT	PIS	COL, PHO	
<i>Trachinotus falcatus</i> (L., 1758)	WC	OC	WA	CAR	PHO	
<i>Trachinotus goodei</i> Jordan & Evermann, 1896	WC	VC	WA	CAR	PHO	
<i>Uraspis secunda</i> (Poey, 1860)	WC	OC	CT	CAR	COL, PHO	
LUTJANIDAE						
<i>Lutjanus analis</i> (Cuvier 1828)	SH, RS	VC	WA	CAR	PHO	
<i>Lutjanus bucanella</i> (Cuvier, 1828)	DR	RA	WA	CAR	COL, PHO	
<i>Lutjanus cyanopterus</i> (Cuvier, 1828)	SH, RS, DR	OC	WA	CAR	PHO	
<i>Ocyurus chrysurus</i> (Bloch, 1791)	WC	RA	WA	CAR	COL, PHO	
<i>Pristipomoides aquilonaris</i> Goode & Bean, 1896)	DR	OC	WA	PIS	COL, PHO	
<i>Rhomboplites aurorubens</i> (Cuvier, 1829)	WC	CO	WA	CAR, PLK	MUS, COL, PHO	
LOBOTIDAE						
<i>Lobotes surinamensis</i> (Bloch, 1790)	WC	OC	CT	CAR	COL, PHO	
HAEMULIDAE						
<i>Anisotremus surinamensis</i> (Bloch, 1791)	SH, RS	VC	WA	MIF	COL, PHO	
<i>Anisotremus virginicus</i> (L., 1758)	SH, RS, WC, DR	AB	WA	MIF	COL, PHO	
<i>Haemulon aurolineatum</i> Cuvier, 1830	SH, RS, WC, DR	AB	WA	MIF	COL, PHO	
<i>Haemulon parra</i> (Desmarest, 1823)	RS	OC	WA	MIF	COL, PHO	
<i>Haemulon plumierii</i> (Lacepède, 1801)	RS	CO	WA	MIF	COL, PHO	
<i>Haemulon steindachneri</i> (Jordan & Gilbert 1882)	RS	CO	WA	MIF	COL, PHO	
SPARIDAE						
<i>Calamus bajonado</i> (Bloch & Schneider, 1801)	RS	RA	WA	MIF	COL, PHO	
<i>Calamus mu</i> Randall & Caldwell, 1966	RS, SB	RA	SE	MIF	MUS	
<i>Calamus pennatula</i> Guichenot, 1868	SB	CO	WA	MIF	COL, PHO	
<i>Diplodus argenteus</i> (Valenciennes, 1830)	WC, SH, RS	AB	WA	OMN	COL, PHO	
<i>Pagrus pagrus</i> (L., 1758)	SB, DR	VC	TA	MIF	MUS, COL, PHO	
SCIAENIDAE						
<i>Odontoscion dentex</i> (Cuvier, 1830)	SH, RS	CO	WA	CAR	PHO	

<i>Pareques acuminatus</i> (Bloch & Schneider, 1801)	SH, RS	CO	WA	CAR	MUS, PHO
MULLIDAE					
<i>Mulloidichthys martinicus</i> (Cuvier, 1829)	RS, SB	RA	TA	MIF	PHO
<i>Pseudupeneus maculatus</i> (Bloch, 1793)	RS, SB	VC	WA	MIF	MUS, COL, PHO
PEMPHERIDAE					
<i>Pempheris schomburgki</i> Müller & Troschel, 1848	SH	VC	WA	PLK	MUS, PHO
CHAETODONTIDAE					
<i>Chaetodon sedentarius</i> Poey, 1860	SH, RS	UN	WA	MIF	MUS, PHO
<i>Chaetodon striatus</i> L., 1758	SH, RS	VC	WA	SIF	MUS, PHO
<i>Prognathodes brasiliensis</i> Burgess, 2001	DR	OC	Br	MIF	PHO
<i>Prognathodes guyanensis</i> (Durand, 1960)	DR	RA	WA	MIF	PHO
POMACANTHIDAE					
<i>Centropyge aurantonotus</i> Burgess, 1974	SH, RS	OC	TA	TERH	SIG
<i>Holacanthus ciliaris</i> (L., 1758)	SH, RS	OC	WA	SIF	PHO
<i>Holacanthus tricolor</i> (Bloch, 1795)	SH	OC	WA	SIF	PHO
<i>Pomacanthus paru</i> (Bloch, 1787)	SH, RS, WC	VC	WA	OMN	PHO
KYPHOSIDAE					
<i>Kyphosus incisor</i> (Cuvier, 1831)	SH, RS, WC	AB	TA	ROVH	MUS, COL, PHO
<i>Kyphosus sectator</i> (L., 1766)	SH, RS, WC	AB	TA	ROVH	COL, PHO
POMACENTRIDAE					
<i>Abudefduf saxatilis</i> (L., 1758)	SH, WC	AB	CT	OMN	COL, PHO
<i>Chromis cf. enchrysur</i> Jordan & Gilbert, 1882	RS, DR	OC	WA	MIF	PHO
<i>Chromis flavicauda</i> (Günther, 1880)	RS	CO	Br	PLK	MUS, COL, PHO
<i>Chromis jubauna</i> Moura, 1995	RS, DR	AB	Br+SCa	PLK	MUS, COL, PHO
<i>Chromis multilineata</i> (Guichenot, 1853)	WC, SH	AB	TA	PLK	MUS, COL, PHO
<i>Stegastes fuscus</i> (Cuvier, 1830)	SH, RS	AB	Br	TERH	COL, PHO
<i>Stegastes pictus</i> (Castelnau, 1855)	RS	CO	Br+SCa	TERH	COL, PHO
<i>Stegastes cf. variabilis</i> (Castelnau, 1855)	SH, RS	CO	WA	TERH	COL, PHO
LABRIDAE					
<i>Bodianus pulchellus</i>	SH, RS, DR	VC	TA	MIF	MUS, COL,

(Poey 1860)					PHO
<i>Bodianus rufus</i>	SH, RS	VC	WA	MIF	MUS, COL, PHO
(L., 1758)					
<i>Clepticus brasiliensis</i> Heiser, Moura & Robertson, 2000	WC	OC	Br	PLK	MUS, COL, PHO
<i>Doratonotus megalepis</i> Günther, 1862	RS	RA	TA	MIF	PHO
<i>Halichoeres</i> sp n.	SB, DR	CO	SE	MIF	COL, PHO
<i>Halichoeres brasiliensis</i> (Bloch, 1791)	SH, RS, SB	CO	Br	MIF	COL, PHO
<i>Halichoeres dimidiatus</i> (Agassiz, 1831)	RS	VC	Br	MIF	COL, PHO
<i>Halichoeres penrosei</i> (Starks, 1913)	SH, RS	OC	Br	MIF	SIG
<i>Halichoeres poeyi</i> (Steindachner, 1867)	SH, RS	AB	WA	MIF	MUS, COL, PHO
<i>Thalassoma noronhanum</i> (Boulenger, 1890)	WC, Sh	OC	Br	PLK	MUS, PHO
SCARIDAE					
<i>Cryptotomus roseus</i> Cope, 1871	RS	CO	WA	ROVH	PHO
<i>Scarus trispinosus</i> Valenciennes, 1840	SH	RA	Br	ROVH	PHO
<i>Scarus zelindae</i> Moura, Figueiredo & Sazima, 2001	SH, RS	CO	Br	ROVH	PHO
<i>Sparisoma amplum</i> (Ranzani, 1842)	SH, RS	CO	Br	ROVH	PHO
<i>Sparisoma axillare</i> (Steindachner, 1878)	SH, RS	VC	Br	ROVH	COL, PHO
<i>Sparisoma frondosum</i> (Agassiz 1831)	SH, RS	VC	Br+SCa	ROVH	PHO
<i>Sparisoma radians</i> (Valenciennes, 1840)	RS	CO	WA	ROVH	MUS, SIG
<i>Sparisoma tuiupiranga</i> Gasparini, Joyeux & Floeter, 2003	RS	VC	SE	ROVH	PHO
PINGUIPEDIDAE					
<i>Pinguipes brasilianus</i> Cuvier, 1829	DR	OC	SE+Pat	CAR	PHO
TRIPTERYGIIDAE					
<i>Enneanectes altivelis</i> Rosenblatt, 1960	SH, RS	CO	WA	MIF	COL
LABRISOMIDAE					
<i>Labrisomus nuchipinnis</i> (Quoy & Gaimard, 1824)	SH	VC	TA	MIF	MUS, COL, PHO
<i>Labrisomus kalisheræ</i> (Jordan, 1904)	SH	OC	WA	MIF	PHO
<i>Malaccoctenus delalandii</i> (Valenciennes, 1836)	SH	CO	WA	MIF	PHO
<i>Starksia brasiliensis</i> (Gilbert, 1900)	SH	CO	Br	MIF	PHO
CHAENOPSIDAE					
<i>Emblemariopsis signifera</i> (Ginsburg, 1942)	SH, RS	VC	WA	MIF	MUS, COL, PHO

BLENNIDAE

<i>Hypleurochilus fissicornis</i> (Quoy & Gaimard, 1824)	SH	OC	Br	MIF	PHO
<i>Hypsoblennius invemar</i> Smith- Vaniz & Acero 1980	SH	CO	WA	MIF	PHO
<i>Ophioblennius trinitatis</i> Miranda-Ribeiro, 1919	SH	RA	Br	TERH	MUS, SIG
<i>Parablennius marmoreus</i> (Poey, 1876)	SH	VC	WA	MIF	PHO
<i>Parablennius pilicornis</i> (Cuvier 1829)	SH, RS, DR	AB	TA	MIF	MUS, COL, PHO
<i>Scartella cristata</i> (L., 1758)	SH	OC	CT	TERH	MUS, COL, PHO

CALLYONIMIDAE

<i>Callionymus bairdi</i> Jordan, 1887	SH,, RS	CO	WA	MIF	COL
---	---------	----	----	-----	-----

GOBIIDAE

<i>Coryphopterus glaucofraenum</i> Gill, 1863	RS, SB	VC	WA	OMN	COL, PHO
<i>Ctenogobius saepepallens</i> (Gilbert & Randall, 1968)	RS, SB	OC	WA	OMN	SIG
<i>Elacatinus figaro</i> Sazima, Moura & Rosa, 1997	SH, RS	VC	Br	MIF	COL, PHO
<i>Gnatholepis thompsoni</i> Jordan, 1902	RS, SB	OC	TA	OMN	SIG

MICRODESMIDAE

<i>Ptereleotris randalli</i> Gasparini, Rocha & Floeter, 2001	SB	CO	Br+SCa	MIF	PHO
--	----	----	--------	-----	-----

EPHIPPIDAE

<i>Chaetodipterus faber</i> (Broussonet, 1782)	WC	CO	WA	SIF	COL, PHO
---	----	----	----	-----	----------

ACANTHURIDAE

<i>Acanthurus bahianus</i> Castelnau, 1855	SH	CO	WA	ROVH	COL, PHO
<i>Acanthurus coeruleus</i> Bloch & Schneider, 1801	SH	RA	WA	ROVH	PHO
<i>Acanthurus chirurgus</i> (Bloch, 1787)	SH, RS	AB	TA	ROVH	COL, PHO
<i>Acanthurus monroviae</i> Steindachner, 1876	SH, RS	OC	SE+EA	ROVH	PHO

SPHYRAENIDAE

<i>Sphyraena barracuda</i> (Edwards, 1771)	WC	RA	CT	PIS	PHO
<i>Sphyraena tome</i> Fowler, 1903	WC	OC	SE	PIS	PHO

SCOMBRIDAE

<i>Euthynnus alleteratus</i> (Rafinesque, 1810)	WC	OC	TA	CAR	PHO
--	----	----	----	-----	-----

BOTHIDAE

<i>Bothus maculiferus</i> (Poey, 1860)	SB	OC	WA	CAR	PHO
<i>Bothus ocellatus</i> (Agassiz, 1831)	SB	CO	WA	CAR	PHO

BALISTIDAE

<i>Balistes vetula</i>	SH, RS	OC	TA	MIF	PHO
------------------------	--------	----	----	-----	-----

L.1758	WC	RA	CT	OMN	SIG
<i>Melichthys niger</i> (Bloch, 1786)					
MONACANTHIDAE					
<i>Aluterus monoceros</i> (L., 1758)	SH, RS, WC	UN	CT	CAR	PHO
<i>Aluterus scriptus</i> (Osbeck, 1765)	SH, RS	OC	CT	SIF	SIG
<i>Cantherhines macrocerus</i> (Hollard, 1853)	SH, RS	OC	WA	SIF	PHO
<i>Cantherhines pullus</i> (Ranzani, 1842)	SH	UN	TA	OMN	MUS, SIG
<i>Stephanolepis hispidus</i> (L., 1766)	SH, RS	UN	TA	MIF	SIG
OSTRACIDAE					
<i>Acanthostracion polygonius</i> Poey, 1876	RS	CO	WA	SIF	PHO
TETRAODONTIDAE					
<i>Canthigaster figueiredoi</i> Moura & Castro, 2002	SH, RS	VC	Br+SCa	MIF	MUS, PHO
<i>Sphoeroides spengleri</i> (Bloch, 1785)	SH, RS	VC	WA	MIF	MUS, COL, PHO
DIODONTIDAE					
<i>Chilomycterus spinosus</i> (L., 1758)	SH, RS	OC	WA	MIF	MUS, SIG
<i>Diodon hystrix</i> L., 1758	RS	OC	CT	MIF	SIG
MOLIDAE					
<i>Mola mola</i> (L., 1758)	WC	RA	CT	CAR	PHO



Figure 3. Some abundant fish species at the Laje de Santos Marine State Park. The tomtate grunt *Haemulon aurolineatum* (a); adult and juvenile sergeant major *Abudefduf saxatilis* (b); the brown damselfish *Chromis multilineata* (c); juvenile dusky damselfish *Stegastes fuscus* (d); intermediate individual of the jubauna reef fish *Chromis jubauna* (e); the silver porgy *Diplodus argenteus* (f); juvenile porkfish *Anisotremus virginicus* (g); the ringneck blenny *Parablennius pilicornis* (h). Photos: O.J. Luiz Jr, except (e) by L.F. Cassino.

Geographical Distributions and Zoogeography

The relative proportion of geographic distributions types is shown on Fig.4. Forty two percent (86 species) occur in the entire Western Atlantic, 19% (40) are trans-Atlantic, 18% (37) are circumtropical, and 12% (22) are endemic to the Brazilian coast (Fig. 5), 3% (6) are distributed southwards to temperate Patagonia, 2% (3) are found in Western Atlantic plus the islands of the mid-Atlantic (Ascension and Sta. Helena) and 1% (2) are found in the eastern Atlantic and southeastern coast of Brazil but neither reach northern sites of Brazil and the Northwestern Atlantic. Five species (3% of the grand total of species) presents a curious distribution pattern: they occur along the Brazilian coast but are limited to Southern Caribbean in the Northwest Atlantic (coast of Venezuela, Trinidad & Tobago, Barbados and Curacao). It has been hypothesized that these latter species are supposed to have a Brazilian origin and only recently crossed to the north of the Amazon Barrier (Joyeux *et al.* 2001, Rocha 2003).

Despite the position of the study site at subtropical latitudes, the local reef fish fauna resembles more closely that of the tropical Western Atlantic and Northeastern Brazilian coast than that of the southern temperate reefs (Floeter *et al.* 2008). Due to the prevailing Brazil Current, which flows southwards from low latitudes, superficial warm waters continuously reach the Laje de Santos Marine Park, providing larval supply and a suitable thermal range for tropical reef species. Colder waters are also present at the study site due to a seasonal upwelling that brings cold (14-18°C) deep waters from the shelf slope (Campos *et al.* 1995). Although these cold waters could sometimes reach depths of 7-10 m, they are usually restricted to the deepest parts of the reefs, providing a suitable environment for temperate species (fig. 6). In fact, the few temperate species that range south to Patagonia and the subtropical endemics were observed mostly, or are even restricted, to the deep reefs at our study site.

The mixture of different conditions in ecological transitional areas is regarded as a major factor for a high diversity in SE Brazilian reef systems (Floeter *et al.* 2001). Why such a discrepancy among the relative richness ratio of tropical and subtropical/temperate species occurs is a subject of inquires and future research. One possible cause is that the deep reefs were poorly sampled and an increase in the

sampling effort could result in additional new records of cold water species for the region. This is possibly true, but only to some extent. Indeed, few studies with the use of SCUBA were done by biologists at depths greater than 30 m, but on the other hand commercial and recreational fisheries was present for many decades in the surrounding areas of the study site, providing a fairly good assessment of fish species from all depths over the study area. Thus, we could expect some new findings in the deep reefs that could only be assessed by SCUBA and not by conventional fishing gear, but this is not expected to significantly change the proportion of the zoogeographical affinities presented here.

An alternative explanation to poor sampling may be that the larval input from the southern temperate reefs is limited. Waters from Patagonia are known to reach the southeastern coast of Brazil through the Malvinas current, which flows northward from the coast of Argentina and can carry larvae from temperate reefs to the study site (Pereira 1989, Campos *et al.* 1996). However, dispersal via Malvinas Current may be restricted to species with some tolerance to low salinity waters. The high freshwater outflow from La Plata River and Patos Lake may extend for a great distance offshore (Piola *et al.* 2000, Pimenta *et al.* 2005) and can act as a barrier to larval dispersal in the same way as the Amazon River do between the Caribbean and Brazil (Floeter & Gasparini 2000, Rocha *et al.* 2003).

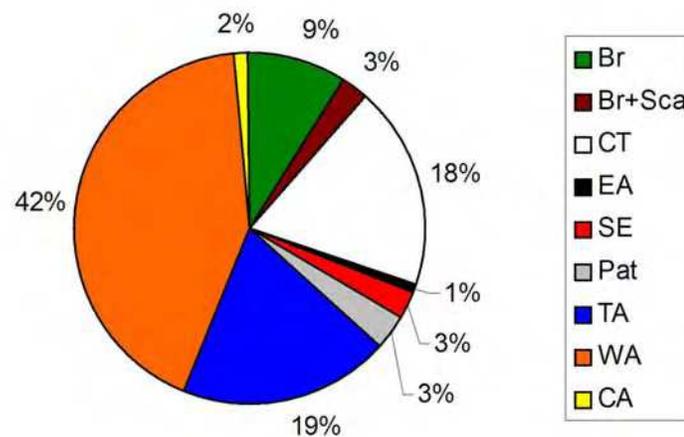


Figure 4. Relative proportions of types of geographic distributions of the species observed at the Laje de Santos Marine State Park. Br = Brazilian Province; CE = Central Atlantic; CT = Circumtropical. EA = Eastern Atlantic; Sca = Southern Caribbean; SE = Southeastern Brazil; TA = Trans-Atlantic; WA = Western Atlantic.



Figure 5. Selected Brazilian endemic reef fish species that occur at the Laje de Santos Marine State Park. The barber goby *Elacatinus figaro* (a); the Brazilian yellowcheek wrasse *Halichoeres dimidiatus*, initial phase (b); the Brazilian wrasse *Halichoeres brasiliensis*, intermediate phase (c); the noronha wrasse *Thalassoma noronhanum*, terminal male (d); the red parrotfish *Sparisoma tuiupiranga*, initial phase (e); the Zelinda's parrotfish *Scarus zelindae*, initial phase (f); the Brazilian parrotfish *Sparisoma amplum*, initial phase (g); the redeye parrotfish *Sparisoma axillare*, terminal male (h). Photos: O.J. Luiz Jr, except (d) by I. Cavas.

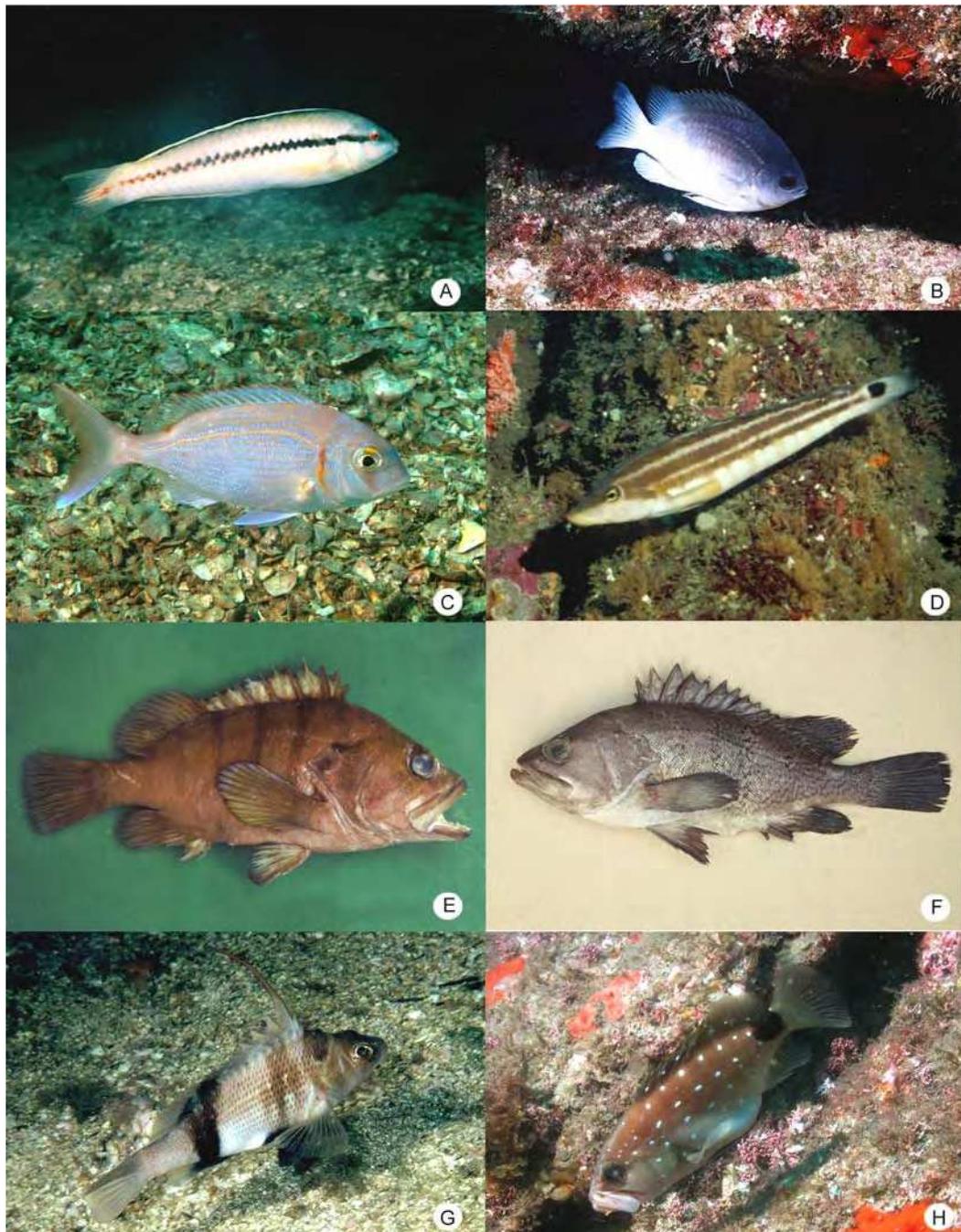


Figure 6. Selected fish species that dwell in the deep reef (30-45 m) community at the Laje de Santos Marine State Park. The deep-reef wrasse *Halichoeres* sp.n. (a); the reef fish *Chromis* cf. *enchrysurus* (b); the red porgy *Pagrus pagrus* (c); the Brazilian sandperch *Pinguipes brasilianus* (d); the sea basses *Acanthistius brasilianus* (e), *A. patachonicus* (f) and *Dules auriga* (g); the snowy grouper *Hyporthodus niveatus* (h). The former species (a) are probably a Brazilian endemic, closely related to the Northwestern Atlantic species *H. bathyphilus*. The distinctive status from its sister species is supported by molecular mtDNA analysis (L.A. Rocha pers. comm.), the last six species (c-h) ranges southward to temperate Patagonian rocky reefs. Photos: A. Carvalho-Filho (e-g); O.J. Luiz Jr. (a-d, h).

Range Extensions

We consider here only species previously unrecorded for the coast of the São Paulo State. We use this unnatural, political division because most books and species accounts of fishes in Brazil usually determine the limits of species ranges this way. Additionally, we feel that species whose recorded range limits lie only a few kilometers north or south of our study site do not represent an actual range increase. Thus, the Laje de Santos Marine Park position, about in the middle of the São Paulo State coast, distant 171 km from Rio de Janeiro State to the north and 215 km from Paraná State to the south, provides a convenient ‘buffer’ distance for both possible northern and southern occurrences. Perhaps the most surprising and unexpected finding at the Laje de Santos Marine State Park was the occurrence of *Acanthurus monroviae* individuals (fig. 7a), a surgeonfish thought to be restricted to the Eastern Atlantic, a record dealt with in detail by Luiz Jr. *et al.* (2004). Additional species which ranges are extended in this paper are listed below.

Moringua edwardsi: Previously recorded for Trindade Island (Gasparini & Floeter 2001) and on the continental coast south to the State of Bahia (Menezes *et al.* 2003). Our record is based on a photograph made in July 2006 by Armando de Luca Jr. (fig. 7b).

Antennarius multiocellatus: Previous southernmost record is the Arraial do Cabo, Rio de Janeiro State (Carvalho-Filho 1999, Ferreira *et al.* 2001). Our record is based on a photograph made in November 2004 by Robson Leite (fig. 7c).

Scorpaena dispar: Southernmost occurrence previously recorded for the State of Rio de Janeiro (Menezes *et al.* 2003). Our record is based on a photograph made in July 2001 by Osmar J. Luiz Jr. (fig. 7d).

Aulostomus strigosus: Previous southernmost record is the state of Rio de Janeiro (Carvalho-Filho 1999). Our record is based on a photograph made in January 2004 by Renata Linger (fig. 7e).

Lutjanus buccanella: Previous southernmost record is Ilhéus, State of Bahia (Carvalho-Filho 1999, Menezes *et al.* 2003). Our record is based on a specimen 42 cm SL collected in October 1987 by Alfredo Carvalho-Filho (fig. 7f).

Mulloidichthys martinicus: Previous southernmost record is the state of Rio de Janeiro (Carvalho-Filho 1999, Menezes *et al.* 2003). Our record is based on a photograph made in June 2002 by Osmar J. Luiz Jr. (fig. 7g).

Halichoeres penrosei: Previous southernmost record is the state of Rio de Janeiro (Carvalho-Filho 1999, Menezes *et al.* 2003). Our record of this characteristic species is based on sighting of several individuals in January 2006 and 2007 by Alfredo Carvalho-Filho.

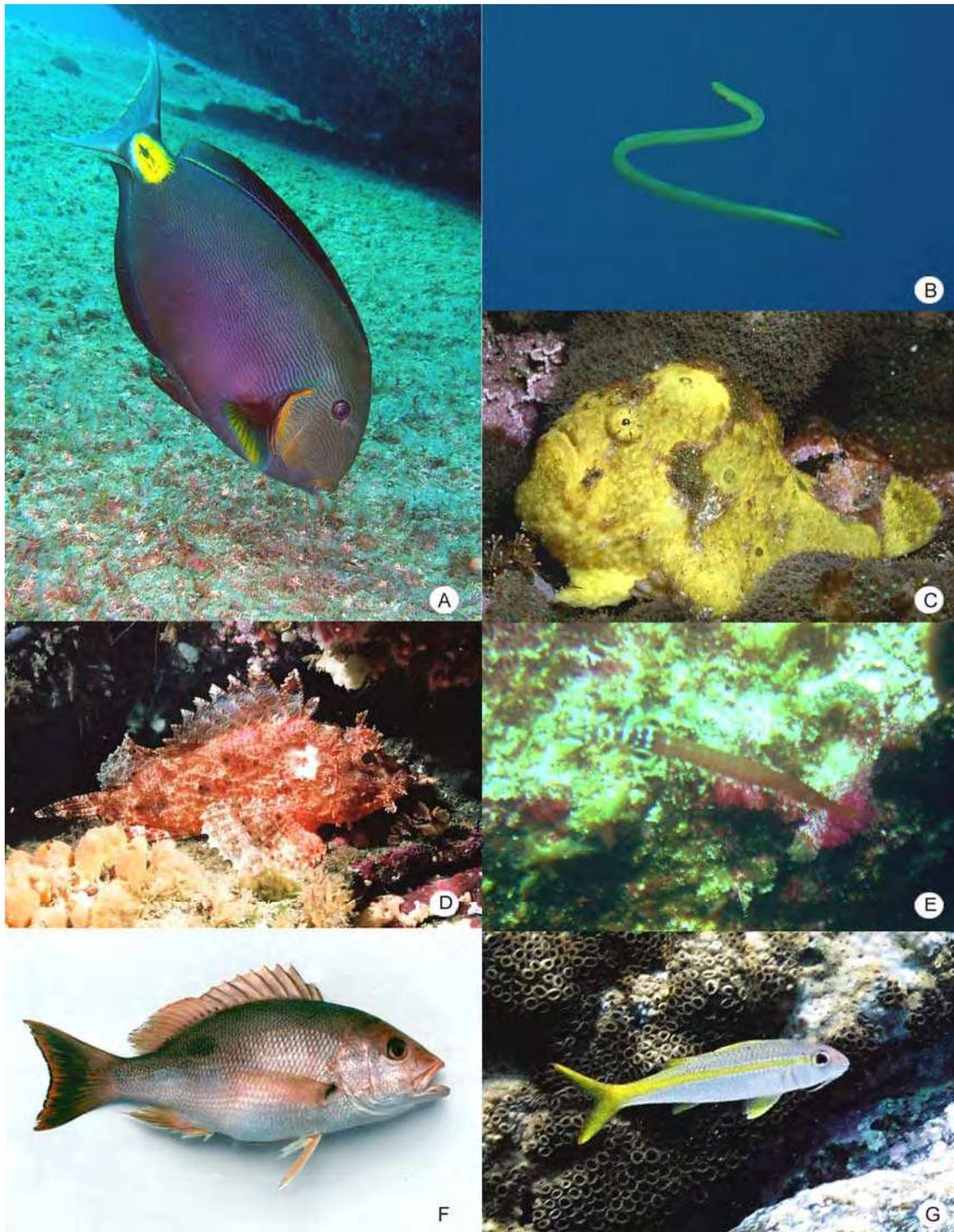


Figure 7. Reef fish species previously unrecorded for the State of São Paulo. The African surgeonfish *Acanthurus monroviae* (a), which record was dealt in details by Luiz Jr. *et al.* (2004); the eel *Moringua edwardsi* (b); the frogfish *Antennarius multiocellatus* (c); the scorpionfish *Scorpaena dispar* (d); the trumpetfish *Aulostomus strigosus* (e); the blackfin snapper *Lutjanus buccanella* (f); the yellow goatfish *Mulloidichthys martinicus* (g). Except for (a), all records are southward extensions for these species' ranges in the West Atlantic. Photos: A. Carvalho-Filho (f); R. Leite (c); R. Linger (e); A. de Luca Jr. (a, b); O.J. Luiz Jr. (d, g).

Trophic Structure

Considering the whole reef fish assemblage, more than a half of the species are carnivores and mobile invertebrate feeders pooled, 28% of the species belonging in each category, followed by planktivores (13%), piscivores (11%), roving herbivores (8%), omnivores (5%), sessile invertebrate feeders (4%), and territorial herbivores (3%). Mobile invertebrate feeders are expected to be the most speciose trophic category on reef fish assemblages along the Brazilian coast due mostly to their ecomorphological features and prey types diversity (Ferreira *et al.* 2004). Carnivores are most epinephelids, carangids and muraenids, three speciose families at the study site. The relatively high proportion of planktivores and piscivores may be accounted to the offshore, relatively mid-shelf location of the study site. Distance from the coast is regarded as a good predictor for the occurrence and abundance of planktivorous reef fishes in southwestern Atlantic rocky reef system (Floeter *et al.* 2007). The Piscivores are varied species from several epipelagic families (carangids, scombrids, pomatomids, sphyraenids) that usually are found far offshore, but this category also includes many species that dwell on sandy bottom, an extensive habitat at the study site. These patterns, however, were not consistent between the different zones of the study site. Variations in habitat specific trophic structure were reflected in the similarity of clusters of species recorded for each habitat (fig. 8). The shallow reef and reef slope zones were almost identical and matched best for the whole assemblage at the study site. However, as would be expected, in the water column zone there is an increasing relative richness of the planktivore and carnivore categories. The deep reef and the sand bottom habitats were similar in trophic structure patterns; both have no herbivores and no sessile invertebrate feeders, probably a result of the reduced algal coverage due to low light levels in the deep reef, and the lack of suitable substrate for attachment of algae.

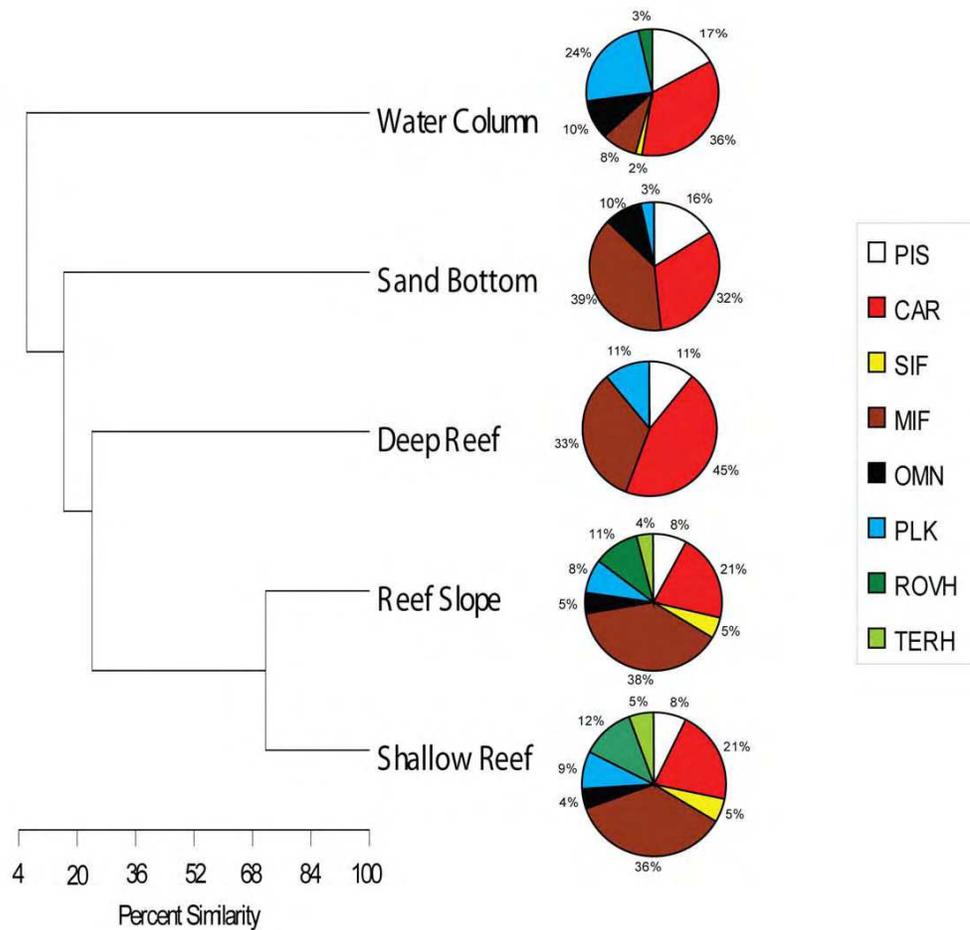


Figure 8. Cluster analysis of habitat types at the Laje de Santos Marine State Park based on the similarity of species composition. The relative distribution of trophic categories in each habitat is shown in the graphs. CAR = Carnivore; MIF = Mobile Invertebrate Feeder; OMN = Omnivore; PIS = Piscivore; PLK = Planktivore; ROVH = Roving Herbivore; SIF = Sessile Invertebrate Feeder; TERH = Territorial Herbivore.

Symbiotic feeding associations

As most if not all reef assemblages in tropical or temperate regions (e.g., Fricke 1975, Strand 1988, Côté 2000, Grutter 2005, Sazima *et al.* 2007), the Laje de Santos has its share of symbiotic feeding relationships. One such feeding association is cleaning symbiosis, in which a fish species (the cleaner) remove parasites, necrotic tissue, and mucus from a variety of fishes (the clients) that seek the cleaner's

services (reviews in Côté 2000, Grutter 2005). An obligate cleaner recorded at our study site is the barber goby *Elacatinus figaro*, which maintains well defined cleaning stations on prominent points of the reef and services a diverse and species-rich fish assemblage (see Sazima *et al.* 2000). The goby is a bottom-dweller but moves towards mid-water clients that hovers near the cleaning station (fig. 9a). Since cleaning symbiosis between fishes is a strictly diurnal activity, nocturnal species leave their shelters to seek cleaning (fig. 9b). Other cleaners recorded at the Laje de Santos are facultative and clean mostly as juveniles (Côté 2000), such as the spotfin hogfish *Bodianus pulchellus* (fig. 9c), which, however, occasionally cleans as a small adult (fig. 9d). Another conspicuous symbiotic association in reef assemblages is following behavior (revision in Sazima *et al.* 2007). In this association type, a zoobenthivorous species (the nuclear) attracts other, opportunistic and mostly carnivorous species (the followers) during its feeding activity. Small animals exposed by the substrate-disturbing activity of the nuclear fish and not taken by it may be preyed on by the follower fish. Zoobenthivores that dig into sandy substrates are very prone to attract followers, as the sediment clouds are a clue to the latter (see Sazima *et al.* 2006). The best known and studied example is that of goatfishes, Mullidae, which are regarded as nuclear fishes par excellence (Sazima *et al.* 2006). Less studied in the following symbiosis is the role of jacks, Carangidae, which are able to fill the zoobenthivorous role as well (Sazima 1988) and may act both as nuclear and followers (Sazima *et al.* 2007). At our study site, the white trewally *Pseudocaranx dentex* (fig. 9e) acts as a nuclear species and attracts mostly wrasses, which are known for their follower role (Sazima *et al.* 2007). Morays and other eels are another fish group that is readily followed during foraging activity (Diamant & Shpigel 1985, Gerhardinger *et al.* 2006), and attracts mostly groupers (fig. 9f). Less important are several fishes that forage on sandy bottoms but need not raise sediment to attract followers. One such example is the flying gurnard *Dactylopterus volitans* (fig. 9g) whose moving close to the bottom disturb small fishes and other animals that are preyed on by the followers (Sazima & Grossman 2005). The hitch-hiking remoras (Echeneididae) exemplify another type of feeding symbiosis. Although widely known as hitch-hikers on larger fishes and other animals, and feeding on scraps left by their hosts or

cleaning them of parasites (review in O'Toole 2002), there is a less known feeding activity of remoras on their hosts. While attached near the mouth of a filter-feeding, large fish such as the Atlantic manta (fig. 9h) or a whale shark, the remoras engage in filter-feeding (Clarke & Nelson 1997).

Conservation Remarks

With 196 species recorded, the reef fish assemblage of the Laje de Santos Marine State Park has a relative high richness as compared with other localities on the Brazilian coast. Despite situated at higher latitudes (*i.e.*, subtropical), our study site has an equal or even a larger number of species than similarly-sized tropical biogenic reefs of the Northeastern Brazil (Rosa & Moura 1997, Feitoza 2001, Ferreira & Cava 2001, Rocha & Rosa 2001, Souza *et al.* 2007). This is probably due to the co-occurrence of tropical and subtropical/temperate species on Brazil's southeastern coast. Additionally, there are more species at the Laje de Santos than at other similarly-sized coastal reef sites in southeastern and south Brazil (Ferreira *et al.* 2001, Hostim-Silva *et al.* 2006, Rangel *et al.* 2007), which could be explained by the off-shore, mid-shelf location of the Laje de Santos reefs and the consequent occurrence of a relatively large number of epipelagic species. Unlike coral reefs, rocky reefs are highly restricted to the shores of continents and islands (Ebeling & Hixon 1991) with few patchily distributed rocky bottoms at the mid-shelf. Thus, the Laje de Santos Marine State Park is to be regarded as an important biodiversity hot-spot for Brazilian reef fishes. Some species that are targeted and highly prized by spear-fishers occasionally attain large sizes at the Laje de Santos (fig. 10). However, it would be premature to say that the occurrence of these endangered species is directly related with the protection conferred to the Laje de Santos without further investigation.



Figure 9. Selected examples of symbiotic associations between reef fishes recorded at the Laje de Santos Marine State Park. The barber goby *Elacatinus figaro* cleans the head of the jubauna reeffish *Chromis jubauna* hovering close to the goby's cleaning station (a); the same cleaner species inspects the back of the nocturnal squirrelfish *Holocentrus adscensionis* that approached its cleaning station (b); juvenile spotfin hogfish *Bodianus pulchellus* cleans the mouth of the spotted moray *Gymnothorax moringa* (c); adult of the same hogfish species cleans the head of the jubauna reeffish (d); the wrasse *Halichoeres* sp. n. follows a group of the white trewallly *Pseudocaranx dentex*, which stir sediment clouds while feeding on the sandy bottom (e); the dusky grouper *Mycteroperca marginata* closely follows the goldspotted snake eel *Myrichthys ocellatus* that nudges its head in rocky crevices (f); the spotfin hogfish follows the flying gurnard *Dactylopterus volitans* moving close to the bottom (g); two diskfish *Remora remora* attached near the mouth of the Atlantic manta *Manta birostris* (h). Photos: M. Andrade (h); A. Carvalho Filho (e-f); J. P. Krajewski (a); O.J. Luiz Jr. (c-d, g); A. de Luca Jr. (b).

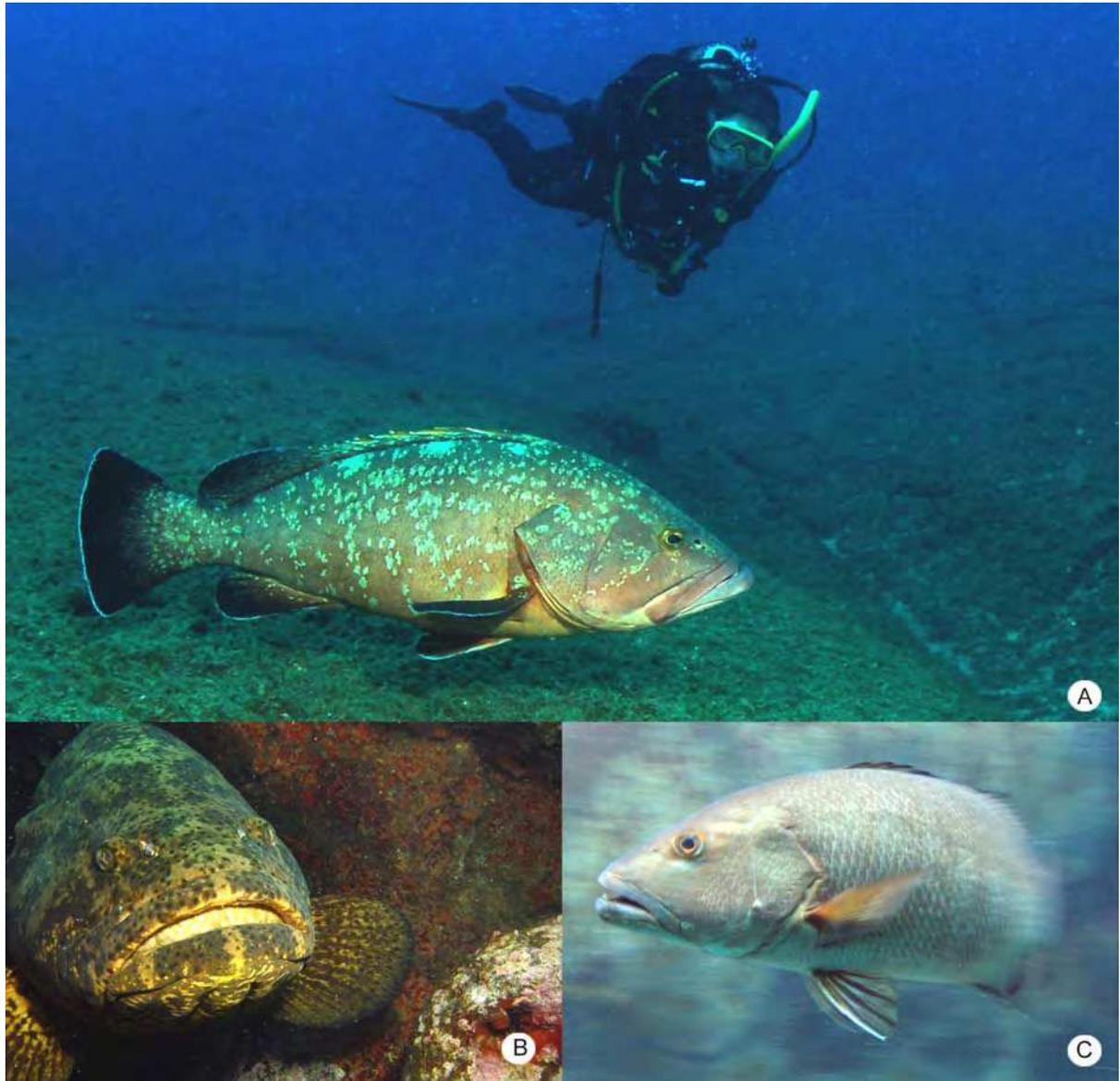


Fig.10. Targeted and endangered top-predators reef fishes recorded at the Laje de Santos Marine State Park. The dusky groupers *Mycteroperca marginata* are very common in the area, but attain unusual large size and are largely unafraid of divers, contrary to which happens at other sites on southeastern coast of Brazil (a); the giant grouper *Epinephelus itajara* (b) and the cubera snapper *Lutjanus cyanopterus* (c). Several individuals of these two large species have been seen at in the Laje de Santos in the last two years, after a period of more than ten years over which they remained unrecorded at the site. Photos: A. Carvalho-Filho (c); L. Cheidde (b); A. Valente (a).

LITERATURE CITED

- Agardy, T. (2000) Information needs for marine protected areas: scientific and societal. *Bulletin of Marine Science* 66(3): 875-888.
- Amado-Filho, G.M., Horta, P.A., Brasileiro, P.S., Barros-Barreto, M.B. & Fujii, M.T. (2006) Subtidal benthic marine algae of the marine state park of Laje de Santos (São Paulo, Brazil). *Brazilian Journal of Oceanography* 54(4): 224-234.
- Campos, E.J.D., Miller, J.L., Müller, T.J. & Peterson, R.G. (1995) Physical oceanography of the Southwest Atlantic Ocean. *Oceanography* 8(3): 87-91.
- Campos, E.J.D., Lorenzetti, J.A., Stevenson, M.R., Stech, J.L. & Souza, R.B. (1996) Penetration of waters from the Brazil-Malvinas confluence region along the South American Continental Shelf up to 23°S. *Anais da Academia Brasileira de Ciências*, 68(supl.1): 49-58.
- Carvalho-Filho, A. (1999) *Peixes: Costa Brasileira*. 3rd ed. Ed. Marca D'água, São Paulo, Brazil, 320 pp.
- Clarke, E. & Nelson, D.R. (1997) Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. *Environmental Biology of Fishes* 50: 63-73.
- Compagno, L.J.V. (1999) Checklist of living elasmobranches. In: Hamlett, W.C. (Ed.), *Sharks, skates and rays: the biology of elasmobranch fishes*. John Hopkins University Press, Baltimore, pp.471-498.
- Craig, M.T. & Hastings, P.A. (2007) A molecular phylogeny of the groupers of the subfamily Epinephelinae (Serranidae) with a revised classification of Epinephelini. *Ichthyological Research* 54: 1-17.
- Craig, M.T., Fodrie, F.J. & Hastings, P.A. (2004) The nearshore fish assemblage of the Scripps Coastal Reserve, San Diego, California. *Coastal Management* 32: 341-351.

- Diamant, A. & Shpigel, M. (1985) Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Aqaba). *Environmental Biology of Fishes* 13: 153-159.
- Ebeling, A.W. & Hixon, M.A. (1991) Tropical and temperate reef fishes: comparison of community structures. In: Sale, P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, pp. 509-563.
- Feitoza, B.M. (2001) *Composição e estrutura da comunidade de peixes recifais da Risca do Zumbi, Rio Grande do Norte*. Unpublished MSc. Thesis, Universidade Federal da Paraíba, 156 pp.
- Feitoza, B.M., Rocha, L.A., Luiz Jr, O.J., Floeter, S.R. & Gasparini, J.L. (2003) Reef fishes of St. Paul's Rocks: new records and notes in biology and zoogeography. *Aqua, Journal of Ichthyology and Aquatic Biology* 7(2): 61-82.
- Ferreira, B.P. & Cava, F. (2001) Ictiofauna marinha da APA Costa dos Corais: Lista de espécies através de levantamento da pesca e observações subaquáticas. *Boletim Técnico Científico do CEPENE, Tamandaré* 9(1): 167-180.
- Ferreira, C.E.L., Gonçalves, J.E.A. & Coutinho, R. (2001) Community structure of fishes and habitat complexity on a tropical rocky shore. *Environmental Biology of Fishes* 61: 353-369.
- Ferreira, C.E.L., Floeter, S.R., Gasparini, J.L., Ferreira, B.P. & Joyeux, J.-C. (2004) Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *Journal of Biogeography* 31: 1093-1106.
- Floeter, S.R. & Gasparini, J.L. (2000) The south-western Atlantic reef fish fauna: composition and zoogeographic patterns. *Journal of Fish Biology* 56: 1099-1114.
- Floeter, S.R., Guimarães, R.Z.P., Rocha, L.A., Ferreira, C.E.L., Rangel, C.A. & Gasparini, J.L. (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecology and Biogeography* 10: 423-431.

- Floeter, S.R., Halpern, B.S. & Ferreira, C.E.L. (2006) Effects of fishing and protection on Brazilian reefs. *Biological Conservation* 128: 391-402.
- Floeter, S.R., Kröhling, W., Gasparini, J.L., Ferreira, C.E.L. & Zalmon, I. (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and cover. *Environmental Biology of Fishes* 78: 147-160.
- Floeter, S.R., Rocha, L.A., Robertson, D.R., Joyeux, J.-C., Smith-Vaniz, W.F., Wirtz, P., Edwards, A.J., Barreiros, J.P., Ferreira, C.E.L., Gasparini, J.L., Brito, A., Falcón, J.M., Bowen, B.W. & Bernardi, G. (2008) Atlantic reef fish biogeography and evolution. *Journal of Biogeography* 35: 22-47.
- Fricke, H. W. (1975) The role of behaviour in marine symbiotic animals. *Symposia of the Society of Experimental Biology* 1975: 581-594.
- Gadig, O.B.F. & Sampaio, C.L.S. (2002) Occurrence of *Mobula japonica* in the Western Atlantic Ocean and *Mobula tarapacana* in Brazil, with comments on the diversity of devil rays (Chondrichthyes, Mobulidae) in Brazil. *Arquivos de Ciências do Mar* 35: 33-37 (in Portuguese).
- Gasparini, J.L. & Floeter, S.R. (2001). The shore fishes of Trindade Island, Western South Atlantic. *Journal of Natural History* 35: 1639-1656.
- Gerhardinger, L.C., Hostim-Silva, M., Samagaia, R. & Barreiros, J.P. (2006) A following association between juvenile *Epinephelus marginatus* (Serranidae) and *Myrichthys ocellatus* (Ophichthidae). *Cybium* 30(1): 82-84.
- Grutter, A.S. (2005) Cleaning mutualism in the sea. In: Rohde, K. (ed.), *Marine parasitology*, CSIRO Publishing, Collingwood, pp. 264-278.
- Hostim-Silva, M., Andrade, A.B., Machado, L.F., Gerhardinger, L.C., Daros, F.A., Barreiros, J.P. & Godoy, E.A.S. (2006) *Peixes de costão rochoso de Santa Catarina: I. Arvoredo*. Ed. Universidade do Vale do Itajaí, 134 pp.

- Humann, P. & DeLoach, N. (2002) *Reef fish identification: Florida, Caribbean, Bahamas*. 3rd ed. New World Publications, Jacksonville, USA, 481 pp.
- Joyeux, J.-C., Floeter, S.R., Ferreira, C.E.L. & Gasparini, J.L. (2001) Biogeography of tropical reef fishes: the South Atlantic puzzle. *Journal of Biogeography* 28: 831-841.
- Luiz Jr., O.J., Floeter, S.R., Ferreira, C.E.L., Gasparini, J.L. & Wirtz, P. (2004) The occurrence of *Acanthurus monroviae* (Perciformes: Acanthuridae) in the southwestern Atlantic, with comments on other eastern Atlantic reef fishes occurring in Brazil. *Journal of Fish Biology* 65: 1173–1179.
- Moura, R.L. (1995) A new species of *Chromis* (Perciformes: Pomacentridae) from the southeastern coast of Brazil, with comments on other species of the genus. *Revue Française d’Aquariologie* 21: 91-96.
- Nelson, J.S. (2006) *Fishes of the world*. 4th ed. John Wiley & Sons, New Jersey, 601 pp.
- O’Toole, B. (2002) Phylogeny of the species of the superfamily Echeneoidea (Perciformes: Carangoidei: Echeneidae, Rachycentridae, and Coryphaenidae), with an interpretation of echeneid hitchhiking behaviour. *Canadian Journal of Zoology* 80: 596-623.
- Pereira, C.S. (1989) Seasonal variability in the coastal circulation on the Brazilian continental shelf (29°S-35°S). *Continental Shelf Research* 9(3): 285-299.
- Perry, C.T. & Larcombe, P. (2003) Marginal and non-reef-building coral environments. *Coral Reefs* 22: 427-432.
- Pielou, E.C. (1984) *The interpretation of ecological data: a primer on classification and ordination*. John Wiley and Sons Inc, New York, 288 pp.
- Pimenta, F.M., Campos, E.J.D., Miller, J.L. & Piola, A.R. (2005) A numerical study of the Plata River plume along the southeastern South American continental shelf. *Brazilian Journal of Oceanography* 53: 129-146.

- Piola, A.R., Campos, E.J.D., Möller Jr, O.O., Charo, M. & Martinez, C. (2000) The subtropical shelf front off eastern South America. *Journal of Geophysical Research* 105: 6565-6578.
- Randall, J.E. (1967) Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* 5: 665-847.
- Randall, J.E. (1996) *Caribbean Reef Fishes*. 3rd ed. TFH Publications, Hong Kong, 368 pp.
- Rangel, C.A., Chaves, L.C.T. & Monteiro-Neto, C. (2007) Baseline assessment of the reef fish assemblage from Cagaras Archipelago, Rio de Janeiro, Southeastern Brazil. *Brazilian Journal of Oceanography* 55(1): 7-17.
- Rocha, L.A. (2003) Patterns of distribution and processes of speciation in Brazilian reef fishes. *Journal of Biogeography* 30: 1161-1171.
- Rocha, L.A. & Rosa, I.L. (2001) Baseline assessment of reef fish assemblages of Parcel Manuel Luiz State Park, Maranhão, North-east Brazil. *Journal of Fish Biology* 58: 985-998.
- Rosa, R.S. & Moura, R.L. (1997) Visual assessment of reef fish community structure in the Atol das Rocas Biological Reserve, off Northeastern Brazil. *Proceedings of the 8th International Coral Reef Symposium 1*: 983-986.
- Sazima, C. & Grossman, A. (2005) A non-digging zoobenthivorous fish attracts two opportunistic predatory fish associates. *Neotropical Ichthyology* 3: 445-448.
- Sazima, C., Krajewski, J.P., Bonaldo, R.M. & Guimarães Jr., P.R. (2006) The goatfish *Pseudupeneus maculatus* and its follower fishes at an oceanic island in the tropical west Atlantic. *Journal of Fish Biology* 69: 883-891.
- Sazima, C., Krajewski, J.P., Bonaldo, R.M. & Sazima, I. (2007) Nuclear-follower foraging associations of reef fishes and other animals at an oceanic island. *Environmental Biology of Fishes* 80: 351-361.

- Sazima, I. (1998) Field evidence for suspension feeding in *Pseudocaranx dentex*, with comments on ram filtering in other jacks (Carangidae). *Environmental Biology of Fishes* 53: 225-229.
- Sazima, I., Sazima, C., Francini-Filho, R.B. & Moura, R.L. (2000) Daily cleaning activity and diversity of clients of the barber goby, *Elacatinus figaro*, on rocky reefs in southeastern Brazil. *Environmental Biology of Fishes* 59: 69-77.
- Smith, W.L. & Craig, M.T. (2007) Casting the Percomorph net widely: the importance of broad taxonomic sampling in the search for the placement of the serranid and percoid fishes. *Copeia* 2007(1): 35-55.
- Souza, A.T., Ilarri, M.I., Medeiros, P.R., Gempel, R.G., Rosa, R.S. & Sampaio, C.L.S. (2007). Fishes (Elasmobranchii and Actinopterygii) of Picãozinho reef, northeastern Brazil, with notes on their conservation status. *Zootaxa* 1608: 11-19.
- Strand, S. (1988) Following behavior: interspecific foraging association among Gulf of California reef fishes. *Copeia* 1988: 351-357.
- Thresher, R.E. (1991) Geographic variability in the ecology of coral reef fishes: evidence, evolution and possible implications. In: Sale, P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, pp. 401-436.

Appendix

Museum vouchers of specimens from the Laje de Santos Marine State Park. Species arranged in alphabetical order. Institutions names and acronyms are the follow: California Academy of Sciences (CAS); Museu de Zoologia, Universidade de São Paulo (MZUSP); National Museum of Natural History, Smithsonian Institution (USNM); Museu de História Natural, Universidade Estadual de Campinas (ZUEC).

Abudefduf saxatilis - MZUSP 50989; *Acanthistius brasiliensis* - MZUSP 14890, 70738, 70743; *Acanthurus bahianus* - MZUSP 45659; *Acanthurus chirurgus* - MZUSP 45661; *Anisotrenus virginicus* - MZUSP 45662, 67870, 67873; *Apogon americanus* - MZUSP 45641; *Apogon pseudomaculatus* - MZUSP 45635, 45643; *Bodianus pulchellus* - MZUSP 44589, 66230, 66238, 66242; ZUEC 3394, 4255,

4427; *Bodianus rufus* – MZUSP 44596, 66240; *Calamus mu* – MZUSP 69958, 70039; *Calamus penna* - MZUSP 14891, 14892; *Cantherhines pullus* – MZUSP 44658, 44660, 72924; *Canthigaster figueiredoi* – MZUSP 44594 (paratype), 44595; USNM 357498 (paratype); *Caranx latus* - MZUSP 43487; *Caulolatilus chrysops* - MZUSP 14878, 44650; *Cephalopholis fulva* – MZUSP 47436; *Chaetodon sedentarius* – MZUSP 45654; *Chaetodon striatus* – MZUSP 45644, 45649; *Chilomycterus spinosus* – MZUSP 5246, 5247, 5248, 5249, 71370; *Chromis flavicauda* MZUSP 44624, 44625, 44626; *Chromis jubauna* – MZUSP 44631 (holotype), 44632- 44635 (paratypes); ZUEC 4331, 4426; *Chromis multilineata* – MZUSP 44619, 44620; ZUEC 3916, 6310; *Clepticus brasiliensis* – CAS 99821-99822 (paratypes); MZUSP 44590, 44644, 44657, 47151 (paratype), 53271, 99821-99822 (paratypes); *Dactylopterus volitans* – MZUSP 46986; *Diplodus argenteus* – MZUSP 45651; *Dules auriga* – MZUSP 70845; *Elacatinus figaro* – ZUEC 3898, 3902, 3903, 3911, 3912, 3914, 3915; *Emblemariopsis signifera* – MZUSP 44608; *Epinephelus adscensionis* – MZUSP 47440; *Epinephelus morio* – MZUSP 71106; *Gymnothorax funebris* - MZUSP 14877; *Halichoeres* sp n. – MZUSP 46825, 47152; *Halichoeres poeyi* – MZUSP 44584, 44585, 44586, 47435; *Halichoeres brasiliensis* – MZUSP 47437, 47438, 47441; *Holocentrus adscensionis* - MZUSP 43489, 47434, 45657, 47434; *Hyporthodus niveatus* – MZUSP 43490, 70937, 70949; *Kyphosus incisor* – 43495, 44656; *Labrisomus nuchipinnis* – MZUSP 44614, 44615, 44616, 44617, 44618, 66796; ZUEC 6309; *Lobotes surinamensis* – MZUSP 72733; *Malacanthus plumieri* – MZUSP 14870; *Mobula hypostoma* – 13402 (head); *Mycteroperca acutirostris* – MZUSP 43494; *Mycteroperca interstitialis* – MZUSP 43497; 47150, 70975, 70976; *Mycteroperca marginata* – MZUSP 43491, 51248, 70913; *Myripristis jacobus* - MZUSP 43488, 44645; *Ophichthus ophis* – MZUSP 44649; *Ophioblennius trinitatis* – MZUSP 44607; *Pagrus pagrus* – MZUSP 45647, 70094; *Parablennius pilicornis* – MZUSP 44599, 44601, 63869; *Paranthias furcifer* – MZUSP 43496, 71045, 71046; *Pareques acuminatus* – MZUSP 43493, 44647; *Pempheris schomburgki* – MZUSP 43492, 45645; *Porichthys porosissimus* – MZUSP 44651; *Priacanthus arenatus* – MZUSP 69931; *Pseudocaranx dentex* – MZUSP 14871, 45655; *Pseudupeneus maculatus* – MZUSP 41992, 43486; *Remora albescens* - MZUSP 69754; *Rhomboplites aurorubens* – MZUSP 44582; *Sardinella janeiro* - MZUSP 11411; *Scartella cristata* – MZUSP 44602; *Scarus zelindae* – USNM 357500 (paratype); *Scorpaena isthmensis* - MZUSP 43481; *Serranus baldwini* - MZUSP 43478, 43479; *Seriola dumerili* - MZUSP 14880, 46989; *Seriola fasciata* – MZUSP 46990; *Sparisoma amplum* – MZUSP 46444; *Sparisoma axillare* – MZUSP 46817; *Sparisoma frondosum* – MZUSP 46802, 46818; *Sparisoma radians* – MZUSP 46440; *Sparisoma tuipiranga* – MZUSP 46441, 46442, 46443; *Sphoeroides spengleri* – MZUSP 44579; *Stegastes fuscus* – MZUSP 45775, 45780, 45782, 45784, 45787, 45789, 49065; ZUEC 6309; *Stegastes pictus* – MZUSP 45786; *Stegastes variabilis* – MZUSP 45776, 45779, 45781, 45783, 45791; *Synodus foetens* – MZUSP 43483; *Synodus intermedius* – MZUSP 43484; *Thalassoma noronhanum* – MZUSP 45633, 45639; ZUEC 3146; *Tylosurus acus*- MZUSP 14879; *Uraspis secunda* – MZUSP 65901.

CAPÍTULO 2

COMMUNITY STRUCTURE OF FISHES IN A MID-SHELF ROCKY REEF IN THE SOUTHWESTERN ATLANTIC: THE INFLUENCE OF DEPTH, HABITAT COMPLEXITY, AND WAVE EXPOSURE

OSMAR J. LUIZ JR.¹, SERGIO R. FLOETER², CARLOS E. L. FERREIRA³, IVAN SAZIMA¹

¹ *Depto. de Zoologia e Museu de História Natural, Universidade Estadual de Campinas, Campinas, SP, Brasil.*

² *Lab. de Macroecologia e Biogeografia Marinha, Universidade Federal de Santa. Catarina, Florianópolis, SC, Brasil.*

³ *Depto. de Biologia Marinha, Universidade Federal Fluminense, Niterói, RJ, Brasil.*

ABSTRACT: The effects of depth, habitat complexity and wave exposure on the reef fish community structure of a mid-shelf rocky reef system off southeastern Brazil were assessed. There were clear differences of physical factors analyzed in this study and the contribution of each one to the structuring of the fish community. Depth was the factor that influenced most the species distribution, presenting a pattern in which species richness and abundance decreased as the depth increased. Habitat structure was also a good predictor for community structure, species richness and abundance being correlated with higher complexity. However, the effects of this relationship were significant only at the shallowest depth category. Wave exposure was not correlated with any of the community descriptors used in this study and the effects of wave surge and water motion in rocky reefs were thus likely to be detected on larger scale comparisons, such as those among coastal shores and islands with different distances from the shore. Fish species of different trophic categories did not respond similarly to these abiotic factors. Roving herbivores were affected by depth, territorial herbivores were affected by habitat complexity and wave exposure, and planktivores were mostly affected by habitat structure and to a lesser extent by depth. Within-family analyses showed that niche partitioning is present and seems to be mediated mainly by swimming performance in response to a greater hydrodynamics in the shallow zone as well as diet plasticity.

Key words: Brazil, subtropical reefs, Laje de Santos Marine State Park, abiotic factors, reef fish community

INTRODUCTION

Reef fish species are not randomly distributed along available habitats. Several biotic and abiotic factors drive patterns of differential distribution among and within reefs (Williams 1991). These factors were particularly well studied on coral reefs, where the great morphological diversity of reef corals coupled with oceanographic processes promote a high environmental heterogeneity for reef dwellers (Done 1982, Paulay 1997). The kind of associations that reef fishes would establish with habitat structure is, therefore, expected to be scale dependent. For example, it is known that distinct reef fish assemblages inhabit reefs with variable sizes, physiographic characteristics and distance from the coast (Williams 1982, Russ 1984a, Bellwood & Wainwright 2001, Chittaro 2002, Nuñez-Lara et al. 2005) and, at smaller scales, fish assemblages also vary among distinct zones on a coral reef, e.g. lagoon, back reef, reef crest, reef slope (Clarke 1977, Thresher 1983, Russ 1984b, Alevizon et al. 1985, Nuñez-Lara & Arias-González 1998).

In tropical and subtropical rocky shores and reefs there are few recent studies on patterns and processes on the distribution of fish assemblages (Aburto-Oropeza & Balart 2001, Ferreira et al. 2001, Dominici-Arosemena & Wolff 2006, Floeter et al. 2007). Localized at the limits of coral reef distribution, tropical and subtropical rocky reefs are subjected to environmental conditions that stunt the development of a coral reef framework (cold water intrusions, turbidity, sediment resuspension) albeit some hard corals may be present, if any, only as scattered colonies over the bedrock (Perry & Larcombe 2003). Although the taxonomic structure of fish communities on these ‘marginal’ rocky reefs are essentially similar to that found on coral reefs (Robertson 1998), and sometimes share a great number of species (Luiz Jr et al. 2008) the hard bottom physiography is significantly distinct from those found on coral reefs (Ebeling & Hixon 1991). For instance, rocky reefs lack the high convoluted profile characteristic of coral reef frame and are usually restricted to a thin strip at the shore of continents and islands. Several physiographic

features of coral reef systems are absent in rocky reefs, such as a back reef lagoon to mention one of them. Thus, the patterns observed from early studies on coral reefs may be not replicable there.

Among the physical factors of reefs that determine distribution patterns of fishes, very little attention was paid by researchers to the effects of depth. Gosline (1965) made the first attempt to establish patterns of vertical zonation in a coral reef in Hawaii. In his baseline report, he noted that some species were replaced by congeners in different depths and, within a genus, some species were restricted to a particular depth whereas others were found along a wider depth range. The vertical zonation of fishes was, however, affected by the degree of wave exposure. Apart from some studies focused specifically on herbivores fishes (Russ 1984a,b, Fox & Bellwood 2007) the influence of the depth gradient on the community structure of tropical reef fishes was addressed by McGhee (1994) who found significant differences between assemblages in shallower and deeper parts of the forereef in Caribbean coral reefs. She argued that the effects of depth act in conjunction with other correlated environmental gradients, such as substrate complexity and water motion (McGhee 1994), a relation that have been supported by subsequent research (Srinivasan 2003, Brokovich et al. 2008).

On the other hand, the effects of habitat structure were extensively studied and considered as a main factor structuring local fish assemblages in coral reefs (Luckhurst & Luckhurst 1978, Friedlander & Parrish 1998, Gratwicke & Speight 2005). The high bottom complexity supplied by hard corals provides fishes with a refuge against predation (Caley & St John 1996, Beukers & Jones 1997, Almany 2004), besides a hard substrate to forage on algae, sessile animals and other small prey types (Russ 1984 a, b, McCormick 1995, Eagle et al. 2001). More recently, a new function for habitat complexity as a refuge from high water flow and surge was described (Johansen et al. 2007, Johansen et al. 2008). Reef fish richness and abundance were then considered as positively correlated with a high habitat complexity due to several ecological benefits thus provided (Gratwicke & Speight 2005, Friedlander et al. 2007, Lindsay et al. 2008) although studies yielded distinct and debatable results, most of which due to different approaches and definitions of habitat complexity (Roberts & Ormond 1987, Rilov et al. 2007, Mattila et

al. 2008). There are distinct measures of habitat complexity (McCormick 1994, Clua et al. 2006, Wilding et al. 2007) most of them being usually time expensive and requiring cumbersome equipment in the field, albeit Wilson et al. (2007) present a reliable and efficient method of visual assessment that correlate positively with most of previously used techniques.

Water motion and wave surge has long been recognized as an important factor that structure intertidal and shallow subtidal communities (Lewis 1968, Little & Kitching 1996, Denny 2006). Due its shallow waters, the topography of coral reefs is highly structured by wave energy (Bradbury & Young 1982) although the extent to which biotic communities are influenced by the degree of wave exposure is a complex and non-linear indirect relationship. McGhee (1994) and Gust (2002) suggested that wave motion is the main physical factor structuring fish communities. Living in the shallow surge zone would be an important strategy to avoid predation, but there are morphological constraints affecting the species that are able to explore this environment (Fulton & Bellwood 2005, Fulton et al. 2005). Other authors, however, state that wave exposure does not overcome the effects of habitat complexity (Friedlander et al. 2003).

Brazilian reefs harbor a distinct reef fish fauna (10.5% of endemism) but yet with many species shared with Caribbean coral reefs (Floeter & Gasparini 2000, Moura & Sazima 2003, Floeter et al. 2008, Luiz Jr. et al. 2008). The reef fish assemblages along the Brazilian coast, however, are exposed to a wide range of environmental conditions, from warm water coral reefs in the northeast to upwelling-influenced rocky reefs in the southeast and south (Maida & Ferreira 1997, Floeter et al. 2001, Luiz Jr. & Ferreira, this volume chapter 3). The extent to what different abiotic conditions affect reef fish distribution, and ultimately their evolution, has been the focus of great interest and speculation (Bellwood 1996, Bellwood 1998, Robertson 1998, Dominici-Arosemena & Wolff 2006). Thus, Brazilian reefs provide excellent study cases for these effects due to the taxonomic homogeneity of fish assemblages living on well defined and distinct environmental conditions.

The fish assemblages of Brazil's southeastern rocky reefs recently received a considerable attention although all quantitative studies are restricted to continental rocky shores and coastal islands very close to mainland (Ferreira et al. 2001, Floeter et al. 2007, Mendonça-Neto et al. 2008). Variability among fish assemblages in reefs arranged in a cross-shelf gradient is well described for coral reefs (Williams 1982, Williams 1991, Gust 2002) but is rarely studied in rocky reefs because the latter is most often restricted to continental shore and coastal islands (Ebeling & Hixon 1991). The Brazilian continental shelf is very narrow in most of its extension (Maida & Ferreira 1997) but reaches considerable width at the Abrolhos banks, where the mid-shelf Abrolhos National Marine Park and adjacent coral reefs have been studied (Ferreira & Gonçalves 2006, Francini-Filho & Moura 2008). On the southeastern coast, where there are scattered rocky reefs arranged in a mid-shelf position, the continental shelf is wide as well (Maida & Ferreira 1997). In the present study we present the first assessment of a reef fish community in a subtropical mid-shelf rocky reef and its relation with selected abiotic factors, namely depth, habitat complexity, and wave exposure. We gathered data for answer the following three basic questions: Is the fish community influenced by one or more of the above mentioned physical attributes? If yes, what is the preponderant factor structuring leading the observed patterns? Are there fish species with distinct attributes varying their abundances among environmental zones on rocky reefs?

MATERIALS AND METHODS

Study Site and habitat structure

The study was conducted at the Laje de Santos Marine State Park (24°15'S; 46°10'W) at 36 km off the city of Santos, São Paulo, southeastern Brazil (Fig. 1). This marine park is an uninhabited rocky islet, an emerged rocky outcrop, and several sparse underwater rocky ledges with extensive intervening sand bottoms. The subtidal substrate is composed of granitic boulders of varying sizes and shapes that delineate a steep profile, covered mainly with turf algae and patches of brown and red algae, the zoanthid

Palythoa caribeorum, hydrozoans, ascidians, octocorals and sparse colonies of the scleractinian corals *Madracis decactis* and *Mussismilia hispida*. The local setting is a transitional tropical-subtropical environment that fits in the definition of a high latitude ‘marginal’ reef site (Perry & Larcombe 2003) where hard corals occur only as isolated colonies on the exposed bedrock. Seven sampled sites were classified in terms of exposure to wave surge, habitat complexity and depth (Table 1). The selection of the study sites was based on a previous survey aimed at identifying zones of different but characteristic environmental conditions of the study area.

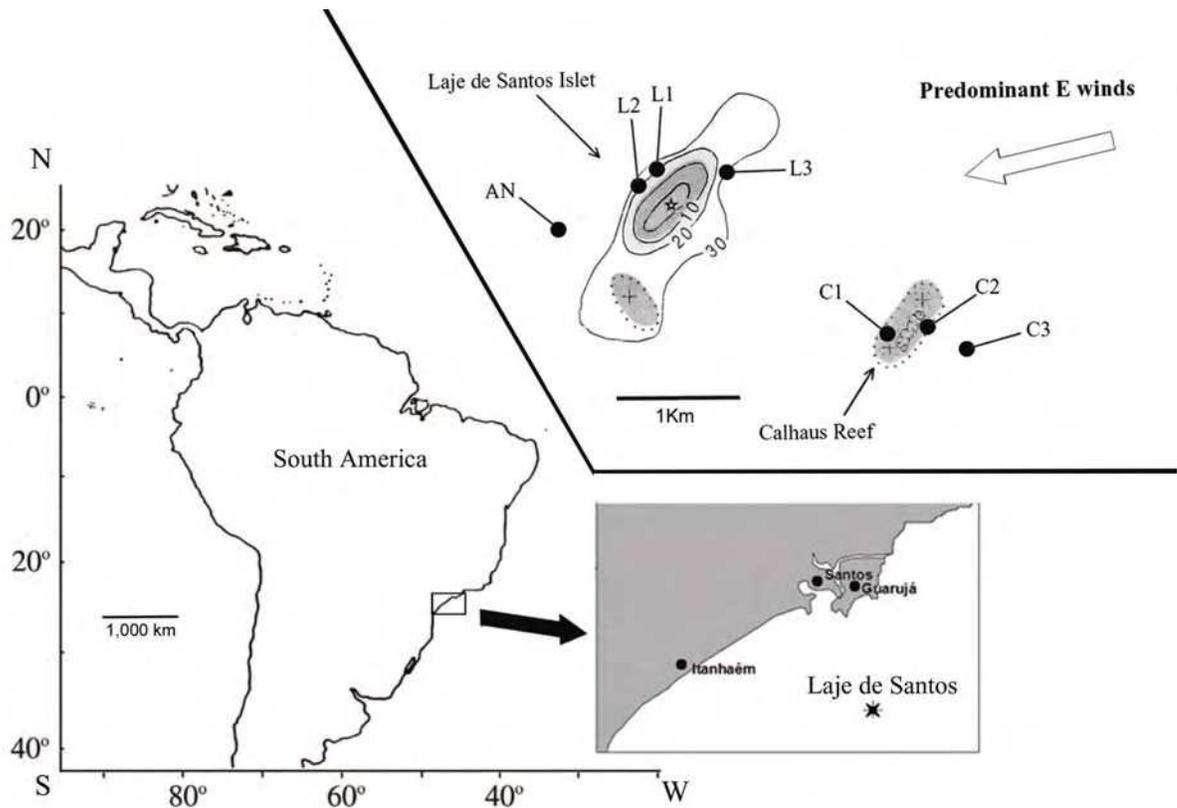


Figure 1. The Laje de Santos Marine State Park localization in western South Atlantic and sampled sites. (see Table 1 for site names and environmental characteristics).

The study area is under constant influence of eastern trade winds and despite the offshore position of the reefs, a well defined windward and leeward faces are present. Both the above-water surface rocks (Laje de Santos islet and Calhaus Reef) are roughly aligned north-south, one mirroring the other, as if Calhaus reef were a smaller version of the Laje de Santos islet (Fig.1b). We thus considered the eastern faces (windward) of the two rocky reefs as exposed to wave surge and the western faces (leeward) as sheltered from wave surge (Table 1). It is important to stress that due to the offshore position of the study area, the leeward face is not strictly comparable to other sheltered sites on the coast (Ferreira et al. 2001, Floeter et al. 2007) but is relatively sheltered when compared to the windward face. The definitions used in the present study for sheltered and exposed apply only to discriminate the degree of wave surge among zones. The leeward face is not sheltered from high water flow that sometimes run over the entire study area but is definitively sheltered from wave surge, which is restricted to the windward side. Two sampling sites were located at greater depths than those at the shores of the above-water rocks and were not influenced by wave surge; thus, no exposure category was assigned to them (Table 1).

Table 1. Defining habitat characteristics of each site sampled at the Laje de Santos Marine Park. Depth categories: Shal = Shallow (1-6m); Mid = Mid-Slope (>6-12m); Inter = Interface Rock-Sand Bottom (>12-20m); Deep Reef (37-42m).

Site Name	Site Code	Censuses (<i>n</i>)	Degree Exposure	Habitat Complexity	Depth Categories
Laje1	L1	27	Sheltered	Low	Shal, Mid, Inter
Laje2	L2	43	Sheltered	High	Shal, Mid, Inter
Laje3	L3	33	Exposed	Low	Shal, Mid, Inter
Calhaus1	C1	38	Sheltered	High	Shal, Mid, Inter
Calhaus2	C2	22	Exposed	High	Shal, Mid, Inter
Calhaus3	C3	05	---	Low	Deep Reef
Âncoras	AN	10	---	High	Deep Reef

Habitat complexity can be considered as variation in topographic structure of a habitat and can be measured by relief, interstitial space and surface area (Wilson et al. 2007). Several techniques have been used to measure habitat complexity and several studies have compared their efficacy on coral reefs (review in McCormick 1994). Most of them were, however, positively correlated with a visual estimate technique described by Wilson et al. (2007) who considered such estimate a quick, reliable and effective way to assess habitat complexity of coral reefs, although affected to some degree by the subjectivity of observers. We thus used a visual estimate to assess habitat complexity in the study site based in the following assumptions: a) the complexity of rocky reefs is relatively simpler than that of coral reefs (Dominici-Arosemena & Wolff 2006) (lower micro-topography variability) and consequently have greater reliability in visual assessments; b) there is a low range in the variability of the bottom physical structure at the study site which, coupled with the small reef area, resulted in well defined differences among them; c) the subjectivity of the visual assessment was reduced to the fact that the determination of complexity categories on each sampled location was made by the same observer (OJLJr) and d) based in an ongoing study (M. Silveira & S. Floeter unpublished data), visual estimates of habitat complexity in rocky reefs were additionally correlated with several previously used techniques of habitat complexity assessments such as the ratio of developed length to linear length (Luckhurst & Luckhurst 1978) and the count of number of holes (Roberts & Ormond 1987). The two above-water surface rocks are each a very large single boulder (Fig. 1) surrounded by sand bottom. At places where they were adjoined by several piled up small boulders that formed a complex structure with several cavities among blocks and were thus considered as places with a high habitat complexity (Table 1). On the other hand, there are sites without adjoining small boulders and the subtidal substrate is essentially the continuity of the main rock through the sand bottom. At these sites there are a few shallow crevices but usually the hard bottom is an inclined and smooth face with no cavities. These latter sites were thus considered to have low habitat complexity (Table 1). Two locations were not immediately adjoined to the above-water main rocks (Fig. 1) and thus could not be included in any of the above descriptions. One of them, the Âncoras Reef (AN) is a complex

of boulders of varying sizes and shapes on a flat bottom about 50 m far from the Laje de Santos Islet. The structure of the habitat was similar to that recorded at sites with several boulders at the shore of Laje de Santos Islet, with several cavities among blocks, and thus AN was considered as a site with high habitat complexity. The other deep-reef location, Calhaus 3 (C3), is about 30 m far from the Calhaus Reef. It is a roughly flat bottom covered with pebbles, with minimal space for a fish living in the pebbles' interstices. Thus, C3 was considered as a site with low habitat complexity.

Data Acquisition

Surveys of the fish community structure were conducted from July 2006 to December 2007. Replicated visual transects using SCUBA diving were performed at each site and at each depth category. Transects were 20 m long and 2 m wide (40m²). During the surveys, the observer held a 20 m rolled-up tape from a randomly chosen point and the tape was unwound. All fishes within view were counted along the transect, except for cryptic species that were counted by carefully scanning the substrate when the diver turned back and started rolling-up the tape. This technique ensured that species prone to retreat due to observer's presence were the first ones to be counted (Floeter et al. 2007). Depth categories were standardized as follows. Shallow (Shal): depth 1-6m; Mid-Slope (Mid): >6-12 m; Interface (Inter): >12 to sand bottom; and Deep Reef (DR) 37-42m. In all locations adjacent to shore, censuses were performed in three depth categories (Shal, Mid, Inter). Reefs that are not adjacent to the shore of above-water rocks were located at greater depths and only one depth category (DR) was assessed. Fishes were grouped into major trophic categories following Randall (1967), Ferreira et al. (2004), and through direct behavioral observations (e.g. Sazima 1986).

Data Analysis

Fish abundance, species richness and proportion of trophic groups per transect were compared among depths and locations with distinct environmental categories. Due to the fact that for the two deep-

reef locations no exposure category was assigned, they were removed from the set of data used to perform a three-way analysis of variance (ANOVA) where the significance of exposure and its interaction with depth and habitat complexity on the parameters of fish community listed above were assessed. A second data set with the DR data included was used to perform a two-way ANOVA to assess the effects of depth and its interaction with habitat complexity. Locations L2 and C1 had the same environmental parameters (exposure, habitat complexity and range of depth categories, Table 1); as data from these locations were not significantly different (ANOVA $p = 0.49$, $F = 0.46$) they were pooled. When deemed necessary, data were log-transformed to stabilize variances (Underwood 1997). Additional Student-Newman-Keuls (SNK) multiple comparisons of means were performed as a post-hoc test (Zar 1999). Trophic comparisons were made based on percentual relative abundance among the analyzed factors. A principal component analysis (PCA) was performed to explore the patterns of distribution of species and trophic groups that contributed most for the differences found among different environmental conditions. For this multivariate technique, only the species whose abundances summed 85% of the total fish abundance (12 species, see Table 2) were included in the analysis. For trophic groups was included the total sum of each group that was count in each site (sites L2 and C1 pooled). Separate PCA's were performed to detect patterns of habitat use among members of two species rich and abundant families (Labridae and Pomacentridae). Parametric analyses were performed using Statistica 6.0 software and the multivariate analysis was performed with MVSP 3.1 software.

RESULTS

A total of 10,442 individuals of 83 teleost fish species belonging to 33 families was recorded throughout the study (Table 1). The sixteen most abundant species accounted for 90,4% of all fish recorded and the twelve species whose densities summed up 85% of all fish censused were included in the multivariate matrix (Table 1). Almost all species were identified during the census to species level (except species of the genera *Parablennius*, *Kyphosus* and *Scorpaena* that were not possible to identify visually

and thus were pooled at genus level). The majority of fishes counted was composed of mobile invertebrate feeders summing up 44.7%, followed by omnivores with 22.6%, planktivores with 17.7%, roving herbivorous with 8.6%, territorial herbivores with 4.0%, macrocarnivorous with 1.8% and sessile invertebrate feeders with 0.4%. Among the abiotic factors analyzed, depth and habitat complexity affected both richness (ANOVA $p < 0.0001$, $F = 11.53$; $p < 0.0001$, $F = 24.02$ respectively) and abundance ($p < 0.0001$, $F = 20.18$; $p < 0.01$, $F = 10.81$ respectively) of the reef fish assemblage at Laje de Santos Marine State Park (Table 3, 4; Figures 2, 3). The degree of wave exposure did not affect both richness ($p = 0.161$, $F = 0.118$) and abundance of reef fishes ($p = 0.118$, $F = 2.466$).

SNK homogenous groups showed a distinct partition among depths. For species richness, three groups were distinguishable; in one of them, shallow and mid-slope grouped together and were distinct from interface and deep-reef. For abundance the effect of depth is more subtle than for richness and only two groups were detected; one group formed by shallow and mid-slope was distinct from a second group formed by interface and deep-reef (Fig. 2). Habitat complexity was positively correlated with richness and abundance. Sites with a high bottom complexity harbored more species and individuals per transect. The analysis of the effect of habitat complexity within each depth category indicated, however, that this trend was driven by a positive relationship at the shallows (Fig. 2).

Table 2. Total composition of fish species in visual census at the study area at different sites and depths (see Table 1) and their distribution in trophic groups relative to reef fish species at the Laje de Santos Marine Park: Density per 40 m² (mean ± SE) per species. Species followed by (*) were included in the multivariate analysis. Families, genera, and species in alphabetical order. Abbreviations in trophic groups: Herbiv = herbivore; Invert = invertivore (feeds on invertebrates); Mob = mobile; Plankt = planktivore; Ter = territorial.

Family/Species	Troph. Gr.	Locations/Depths																
		L1			L2			L3			C1			C2			C3	AN
		Shal	Mid	Int	Shal	Mid	Int	Shal	Mid	Int	Shal	Mid	Int	Shal	Mid	Int	DR	DR
Acanthuridae																		
<i>Acanthurus bahianus</i>	Roving Herbivore	0.45 ± 0.25	–	–	0.26 ± 0.21	0.14 ± 0.10	–	0.10 ± 0.10	0.18 ± 0.18	–	0.75 ± 0.30	–	–	–	–	–	–	–
<i>Acanthurus chirurgus</i> *	Roving Herbivore	0.54 ± 0.21	0.33 ± 0.33	–	3.31 ± 1.85	1.07 ± 0.58	–	0.60 ± 0.40	2.11 ± 0.44	1.17 ± 0.52	1.17 ± 0.62	0.57 ± 0.43	0.50 ± 0.37	4.00 ± 1.93	1.25 ± 0.61	2.00 ± 0.75	–	–
<i>Acanthurus monroviae</i>	Roving Herbivore	–	–	–	–	–	–	–	0.09 ± 0.09	0.17 ± 0.11	–	–	–	–	–	–	–	–
Apogonidae																		
<i>Apogon pseudomaculatus</i>	Mobile. Invertivore	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.10 ± 0.10
Balistidae																		
<i>Balistes vetula</i>	Mobile. Invertivore	–	–	–	–	–	–	–	–	–	0.80 ± 0.80	–	–	–	0.12 ± 0.12	–	–	–
Blennidae																		
<i>Hypsoblennius invemar</i>	Mobile. Invertivore	–	–	–	0.26 ± 0.26	–	–	0.40 ± 0.30	–	–	0.08 ± 0.08	–	–	–	–	–	–	–
<i>Parablennius</i> spp.*	Omnivore	1.27 ± 1.01	0.44 ± 0.24	0.42 ± 0.30	2.10 ± 0.56	2.78 ± 0.99	1.28 ± 0.80	5.00 ± 1.34	7.66 ± 2.98	3.25 ± 1.18	2.75 ± 0.77	4.64 ± 1.04	1.87 ± 1.40	5.57 ± 1.92	6.5 ± 2.37	4.00 ± 1.79	4.80 ± 2.18	1.50 ± 0.60
Bothidae																		
<i>Bothus ocellatus</i>	Carnivore	–	–	0.14 ± 0.14	–	–	0.14 ± 0.10	–	–	–	–	–	–	–	–	–	–	–
Carangidae																		
<i>Caranx crysos</i>	Piscivore	–	–	–	–	–	–	–	–	–	0.83 ± 0.83	–	–	–	–	–	–	–

<i>Caranx latus</i>	Piscivore	0.09± 0.09	-	-	-	-	-	-	1.00 ± 1.00	-	-	-	-	-	-	-	-
<i>Pseudocaranx dentex</i>	Plankt./Mo b. Invert.	-	-	0.71 ± 0.71	0.05 ± 0.05	-	0.86 ± 0.71	0.20 ± 0.20	0.64 ± 0.64	-	-	0.43 ± 0.43	-	0.43 ± 0.30	-	-	-
<i>Seriola lalandi</i>	Piscivore	-	-	-	-	-	-	-	-	-	-	0.14 ± 0.14	-	-	-	-	-
<i>Seriola dumerili</i>	Piscivore	-	-	-	-	-	-	-	-	-	0.08 ± 0.08	-	-	-	-	-	-
<i>Trachinotus goodei</i>	Mobile. Invertivore	-	-	-	-	-	-	2.60 ± 2.02	-	-	-	-	-	-	-	-	-
Chaetodontidae																	
<i>Chaetodon striatus</i>	Sessile Invertivore	0.09 ± 0.09	-	-	0.31 ± 0.17	0.14 ± 0.14	0.28 ± 0.12	-	0.22 ± 0.18	0.17 ± 0.17	0.58 ± 0.26	0.50 ± 0.23	0.37 ± 0.26	0.14 ± 0.14	-	0.28 ± 0.28	-
Chaenopsidae																	
<i>Emblemariopsis signifera</i>	Mobile. Invertivore	0.18± 0.18	0.11 ± 0.11	-	0.26 ± 0.18	1.07 ± 0.93	0.14 ± 0.14	-	-	0.42 ± 0.42	0.83 ± 0.83	0.50 ± 0.43	-	-	-	-	-
Epinephalidae																	
<i>Cephalopholis furcifer</i>	Planktivore	-	-	-	0.10 ± 0.07	-	0.21 ± 0.21	-	1.81 ± 0.92	-	-	-	-	0.14 ± 0.14	0.12 ± 0.12	-	-
<i>Hyporthodus niveatus</i>	Carnivore	-	-	0.43 ± 0.30	-	-	0.07 ± 0.07	-	-	-	-	-	-	0.71 ± 0.47	-	-	0.20 ± 0.13
<i>Mycterperca acutirostris</i>	Piscivore	0.09 ± 0.09	0.11 ± 0.11	1.57 ± 0.92	0.16 ± 0.11	0.36 ± 0.22	0.36 ± 0.13	0.30 ± 0.21	0.77 ± 0.64	0.00 ± 0.00	0.08 ± 0.08	0.07 ± 0.07	0.25 ± 0.16	0.57 ± 0.43	0.37 ± 0.37	-	0.20 ± 0.13
<i>Mycterperca interstitialis</i>	Piscivore	-	-	-	-	-	-	-	-	-	-	-	-	-	0.12 ± 0.12	-	-
<i>Mycterperca marginata</i>	Carnivore	-	-	0.14 ± 0.14	0.42 ± 0.14	0.93 ± 0.40	0.14 ± 0.10	-	0.78 ± 0.45	0.42 ± 0.19	0.25 ± 0.13	0.14 ± 0.10	0.25 ± 0.16	-	0.25 ± 0.25	0.57 ± 0.30	0.50 ± 0.31
Gobiidae																	
<i>Coryphopterus glaucofraenum</i>	Omnivore	-	-	0.14 ± 0.14	-	-	0.14 ± 0.14	-	-	-	-	0.07 ± 0.07	-	-	-	-	-
<i>Elacatinus figaro</i>	Mobile. Invertivore	-	0.33 ± 0.23	-	0.26 ± 0.21	0.21 ± 0.11	0.28 ± 0.16	-	0.09 ± 0.09	-	-	0.57 ± 0.25	0.25 ± 0.25	-	0.12 ± 0.12	-	-
<i>Gnatholepis thompsoni</i>	Omnivore	-	-	-	-	0.07 ± 0.07	0.07 ± 0.07	-	-	-	-	-	-	-	-	-	-
Haemulidae																	
<i>Anisotremus surinamensis</i>	Mobile. Invertivore	0.45 ± 0.25	-	-	0.94 ± 0.32	0.07 ± 0.07	-	0.30 ± 0.30	0.11 ± 0.09	-	1.08 ± 0.60	-	0.12 ± 0.12	1.00 ± 0.38	-	-	-

<i>Anisotremus virginicus</i> *	Mobile. Invertivore	0.72 ± 0.24	0.22 ± 0.15	0.28 ± 0.28	3.00 ± 1.41	4.86 ± 2.86	1.00 ± 0.50	2.00 ± 0.61	29.11± 11.80	0.33 ± 0.26	2.75 ± 1.61	5.57 ± 4.32	0.37 ± 0.26	7.71 ± 5.42	17.75± 12.25	0.43 ± 0.43	0.00 ± 0.00	0.40 ± 0.40	
<i>Haemulon aurolineatum</i> *	Mob.Invert. / Plankt	11.82 ± 2.75	12.55 ± 4.03	11.42 ± 4.46	13.10± 5.77	18.28± 7.63	13.42± 3.97	2.50 ± 1.29	60.55± 13.83	7.66 ± 2.80	8.00 ± 4.92	12.14± 3.56	6.37 ± 1.73	9.42 ± 4.27	30.75± 11.69	13.14 ± 3.57	-	1.60 ± 1.02	
<i>Haemulon parrae</i>	Mob.Invert. / Plankt	-	-	-	-	-	0.07 ± 0.07	-	-	-	-	0.07 ± 0.07	-	-	-	-	-	-	
<i>Haemulon plumieri</i>	Mobile. Invertivore	0.09 ± 0.09	-	-	-	-	-	0.09 ± 0.09	-	-	-	-	-	-	-	-	-	-	
<i>Haemulon steindachneri</i>	Mob.Invert. / Plankt	-	-	-	0.05 ± 0.05	-	0.21 ± 0.11	-	-	-	-	-	-	-	-	-	-	-	
Holocentridae																			
<i>Holocentrus adscensionis</i> *	Mobile. Invertivore	0.91 ± 0.21	0.22 ± 0.15	0.28 ± 0.18	2.26 ± 1.55	1.64 ± 1.06	0.28 ± 0.12	0.60 ± 0.30	2.00 ± 1.07	0.33 ± 0.19	1.08 ± 0.26	0.14 ± 0.10	-	1.43 ± 0.43	1.12 ± 0.23	0.57 ± 0.30	1.40 ± 0.50	0.50 ± 0.22	
<i>Myripristis jacobus</i>	Planktivore	-	-	-	-	0.07 ± 0.07	-	-	-	-	-	-	-	-	-	-	-	-	
Kyphosidae																			
<i>Kyphosus</i> spp.*	Roving Herbivore	5.27 ± 2.51	0.22 ± 0.15	0.00 ± 0.00	4.21 ± 2.07	0.93 ± 0.42	-	5.30 ± 2.01	5.55 ± 3.56	0.08 ± 0.08	5.91 ± 1.92	0.07 ± 0.07	0.62 ± 0.32	13.57 ± 5.32	1.87 ± 1.04	-	-	-	
Labridae																			
<i>Bodianus pulchellus</i>	Mobile. Invertivore	0.36 ± 0.20	0.22 ± 0.15	-	0.42 ± 0.18	1.00 ± 0.23	0.57 ± 0.27	0.20 ± 0.13	1.22 ± 0.42	0.58 ± 0.36	0.17 ± 0.17	1.00 ± 0.38	0.37 ± 0.18	0.57 ± 0.30	1.87 ± 0.71	1.00 ± 0.58	-	0.80 ± 0.36	
<i>Bodianus rufus</i>	Mobile. Invertivore	0.36 ± 0.15	-	-	0.94 ± 0.26	0.07 ± 0.07	0.14 ± 0.10	1.50 ± 0.73	0.66 ± 0.31	0.16 ± 0.11	0.83 ± 0.24	0.57 ± 0.17	0.75 ± 0.36	2.86 ± 0.91	0.62 ± 0.32	0.28 ± 0.18	-	-	
<i>Halichoeres brasiliensis</i>	Mobile. Invertivore	0.09 ± 0.09	-	-	0.16 ± 0.08	-	-	0.00 ± 0.00	0.27 ± 0.19	-	0.08 ± 0.08	0.28 ± 0.12	0.12 ± 0.12	0.14 ± 0.14	-	-	-	-	
<i>Halichoeres dimidiatus</i>	Mobile. Invertivore	-	-	-	-	0.07 ± 0.07	-	-	-	-	-	-	-	-	-	-	-	0.10 ± 0.10	
<i>Halichoeres poeyi</i>	Mobile. Invertivore	0.09 ± 0.09	1.33 ± 1.21	-	0.05 ± 0.05	1.14 ± 0.34	0.93 ± 0.35	-	0.11 ± 0.09	0.17 ± 0.17	0.17 ± 0.11	0.86 ± 0.34	2.12 ± 0.29	0.14 ± 0.14	1.00 ± 0.46	0.28 ± 0.28	-	0.40 ± 0.22	
<i>Halichoeres sazimai</i>	Mobile. Invertivore	-	-	0.71 ± 0.42	-	-	0.28 ± 0.19	-	-	-	-	-	0.12 ± 0.12	-	-	-	0.45 ± 0.20	1.00 ± 0.52	
<i>Thalassoma noronhanum</i>	Planktivore	0.09 ± 0.09	-	-	0.05 ± 0.05	-	-	-	-	-	0.17 ± 0.11	-	-	-	0.12 ± 0.12	-	-	-	
Labrisomidae																			
<i>Labrisomus kalisherai</i>	Carnivore	-	-	-	-	-	-	0.20 ± 0.20	-	-	-	-	-	-	-	-	-	-	

<i>Labrisomus nuchipinnis</i>	Carnivore	0.18 ± 0.18	0.11 ± 0.11	0.14 ± 0.14	0.31 ± 0.15	0.07 ± 0.07	-	0.30 ± 0.20	-	-	0.33 ± 0.19	0.07 ± 0.07	-	1.57 ± 0.57	0.12 ± 0.12	-	-	-	
Lutjanidae																			
<i>Lutjanus analis</i>	Carnivore	0.18 ± 0.18	0.11 ± 0.11	-	0.10 ± 0.10	-	-	-	0.36 ± 0.28	-	0.08 ± 0.08	-	-	0.14 ± 0.14	0.25 ± 0.16	-	-	-	
<i>Lutjanus cyanopterus</i>	Carnivore	-	-	-	-	-	-	-	0.09 ± 0.09	-	-	0.07 ± 0.07	-	-	-	-	-	-	
Monacanthidae																			
<i>Cantherinus macrocerus</i>	Omnivore	-	-	-	0.05 ± 0.05	-	-	-	-	-	-	0.07 ± 0.07	-	-	-	-	-	-	
<i>Cantherinus pullus</i>	Omnivore	0.36 ± 0.24	-	-	-	0.28 ± 0.28	-	0.10 ± 0.10	-	-	0.33 ± 0.19	-	-	-	-	-	-	-	
Mullidae																			
<i>Pseudupeneus maculatus</i>	Mobile. Invertivore	-	-	-	-	0.07 ± 0.07	0.07 ± 0.07	-	0.09 ± 0.09	0.08 ± 0.08	0.25 ± 0.18	0.07 ± 0.07	0.25 ± 0.16	-	0.37 ± 0.26	0.14 ± 0.14	-	0.30 ± 0.15	
Muraenidae																			
<i>Gymnothorax vicinus</i>	Piscivore	-	-	-	-	0.07 ± 0.07	-	-	-	-	-	-	-	-	-	-	-	-	
Ogcocephalidae																			
<i>Ogcocephalus vespertilio</i>	Carnivore	-	-	-	-	-	0.07 ± 0.07	-	-	-	-	-	-	-	-	-	-	-	
Pempheridae																			
<i>Pempheris schomburgkii</i>	Planktivore	-	-	-	1.36 ± 1.06	0.07 ± 0.07	-	-	-	-	5.83 ± 4.99	1.64 ± 1.42	-	-	-	-	-	-	
Pinguipedidae																			
<i>Pinguipes brasilianus</i>	Mobile. Invertivore	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.20 ± 0.20	
Pomacanthidae																			
<i>Holacanthus ciliaris</i>	Sessile Invertivore	-	-	-	-	-	-	-	0.09 ± 0.09	-	-	-	-	-	0.12 ± 0.12	-	-	-	
<i>Holacanthus tricolor</i>	Sessile Invertivore	-	-	-	-	-	-	-	-	-	-	-	-	-	0.12 ± 0.12	-	-	-	
<i>Pomacanthus paru</i>	Omnivore	0.45 ± 0.25	0.22 ± 0.22	-	1.10 ± 0.73	0.57 ± 0.27	0.36 ± 0.20	0.50 ± 0.27	2.66 ± 0.86	1.08 ± 0.47	2.08 ± 1.55	1.43 ± 1.14	0.62 ± 0.42	0.57 ± 0.30	1.37 ± 0.70	1.86 ± 0.67	-	0.50 ± 1.58	

Pomacentridae																			
<i>Abudefduf saxatilis</i> *	Omnivore	8.73 ± 3.44	3.00 ± 0.88	–	26.63± 5.53	6.57 ± 4.42	0.07 ± 0.07	2.10 ± 1.41	6.55 ± 3.25	0.25 ± 0.25	18.5 ± 3.77	3.14 ± 1.18	0.25 ± 0.25	13.43± 8.20	1.75 ± 1.27	0.43 ± 0.43	–	–	
<i>Chromis flavicauda</i>	Planktivore	–	–	0.14 ± 0.14	–	0.14 ± 0.14	0.14 ± 0.10	–	–	–	–	–	–	–	–	–	–	–	
<i>Chromis jubauna</i> *	Planktivore	–	0.11 ± 0.11	1.71 ± 0.56	–	9.64 ± 3.51	1.64 ± 0.44	–	1.00 ± 1.04	3.33 ± 3.33	–	6.86 ± 2.96	5.50 ± 1.19	–	1.87 ± 1.87	5.71 ± 5.71	0.40 ± 0.24	1.60 ± 0.78	
<i>Chromis multilineata</i> *	Planktivore	4.72 ± 3.10	–	–	21.00± 6.27	3.14 ± 1.58	–	3.40 ± 1.80	14.44± 5.85	0.25 ± 0.25	19.75± 8.09	8.00 ± 3.90	0.25 ± 0.16	20.86± 13.48	26.00 ± 9.65	0.43 ± 0.43	–	0.00 ± 0.00	
<i>Stegastes fuscus</i> *	Ter. Herbiv.	2.09 ± 0.81	0.44 ± 0.34	–	9.26 ± 1.33	5.00 ± 1.20	0.43 ± 0.20	0.90 ± 0.55	0.89 ± 0.73	0.17 ± 0.11	7.25 ± 1.50	12.14 ± 2.00	3.37 ± 0.70	1.14 ± 0.46	0.37 ± 0.26	0.28 ± 0.18	–	–	
<i>Stegastes pictus</i>	Ter. Herbiv./ Plankt.	–	–	–	–	–	0.07 ± 0.07	–	–	0.42 ± 0.19	–	0.28 ± 0.19	0.50 ± 0.27	–	–	0.71 ± 0.28	–	–	
<i>Stegastes variabilis</i>	Ter. Herbiv.	0.27 ± 0.19	0.66 ± 0.37	–	0.63 ± 0.20	0.28 ± 0.16	–	0.20 ± 0.13	0.22 ± 0.18	0.17 ± 0.17	0.75 ± 0.46	0.14 ± 0.14	–	0.71 ± 0.28	1.12 ± 0.51	0.28 ± 0.28	–	–	
Priacanthidae																			
<i>Heteropriacanthus cruentatus</i>	Carnivore	–	–	–	0.10 ± 0.10	0.07 ± 0.07	–	–	–	–	–	–	–	–	–	–	–	–	
Scaridae																			
<i>Cryptotomus roseus</i>	Roving Herbivore	–	–	0.14 ± 0.14	–	0.43 ± 0.43	0.14 ± 0.14	–	–	–	–	–	0.25 ± 0.25	–	–	–	–	–	
<i>Scarus trispinosus</i>	Roving Herbivore	–	–	–	0.05 ± 0.05	–	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Scarus zelindae</i>	Roving Herbivore	–	–	–	0.05 ± 0.05	0.07 ± 0.07	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Sparisoma amplum</i>	Roving Herbivore	0.27 ± 0.19	0.22 ± 0.22	–	0.05 ± 0.05	0.07 ± 0.07	–	0.30 ± 0.20	–	–	0.08 ± 0.08	–	–	0.14± 0.14	–	–	–	–	
<i>Sparisoma axillare</i>	Roving Herbivore	0.18 ± 0.18	0.22 ± 0.22	–	0.37 ± 0.27	0.14 ± 0.10	–	–	–	–	0.83 ± 0.50	0.14 ± 0.10	–	1.28 ± 1.13	0.50 ± 0.33	–	–	–	
<i>Sparisoma frondosum</i>	Roving Herbivore	0.18 ± 0.12	0.22 ± 0.15	–	0.47 ± 0.22	0.43 ± 0.20	0.07 ± 0.07	0.50 ± 0.22	0.44 ± 0.28	0.33 ± 0.19	0.33 ± 0.14	0.64 ± 0.36	0.25 ± 0.25	1.00 ± 0.38	0.25 ± 0.16	0.43 ± 0.30	–	–	
<i>Sparisoma radians</i>	Roving Herbivore	0.18 ± 0.18	0.33 ± 0.33	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Sparisoma tuiupiranga</i>	Roving Herbivore	–	–	0.57 ± 0.43	–	0.21 ± 0.21	0.50 ± 0.25	–	–	–	–	–	0.25 ± 0.16	–	0.50 ± 0.50	–	0.20 ± 0.20	–	

Scienidae																		
<i>Odontoscion dentex</i>	Carnivore	-	-	-	-	1.14 ± 0.80	-	-	-	-	1.42 ± 0.87	-	-	0.25 ± 0.25	-	-		
<i>Pareques acuminatus</i>	Roving Herbivore	-	-	0.14 ± 0.14	-	-	0.07 ± 0.07	-	-	-	-	-	-	-	-	-		
Scombridae																		
<i>Euthynnus alletteratus</i>	Piscivore	-	-	-	-	0.50 ± 0.50	-	-	-	-	-	-	-	-	-	-		
Scorpaenidae																		
<i>Scorpaena</i> spp.	Carnivore	-	-	-	-	-	-	-	-	-	-	0.12 ± 0.12	-	-	-	-	0.50 ± 0.27	
Serranidae																		
<i>Acanthistius brasiliensis</i>	Carnivore	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.40 ± 0.24	0.60 ± 0.26	
<i>Dules auriga</i>	Carnivore	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.20 ± 0.20	0.10 ± 0.10	
<i>Serranus baldwini</i>	Mobile. Invertivore	-	-	0.28 ± 0.18	-	0.07 ± 0.07	0.28 ± 0.12	-	-	-	-	0.50 ± 0.27	-	0.12 ± 0.12	-	0.20 ± 0.20	-	
Sparidae																		
<i>Calamus pennatula</i>	Mobile. Invertivore	-	-	0.71 ± 0.56	-	-	1.07 ± 0.50	-	-	0.33 ± 0.22	-	-	-	-	0.28 ± 0.28	-	0.80 ± 0.80	
<i>Diplodus argenteus*</i>	Omnivore	5.36 ± 1.45	1.66 ± 1.03	3.57 ± 2.79	3.00 ± 1.20	1.00 ± 0.27	2.35 ± 1.42	3.00 ± 0.77	16.22 ± 4.00	0.92 ± 0.51	4.41 ± 2.39	0.43 ± 0.25	1.00 ± 0.53	4.57 ± 2.03	4.00 ± 2.43	1.57 ± 0.81	-	0.70 ± 0.39
<i>Pagrus pagrus*</i>	Carnivore	-	-	3.14 ± 1.31	-	-	1.00 ± 0.43	-	-	-	-	0.28 ± 0.28	1.12 ± 0.44	-	-	-	8.20 ± 0.97	8.00 ± 1.82
Synodontidae																		
<i>Synodus intermedius</i>	Piscivore	-	-	-	-	-	-	-	0.18 ± 0.18	-	-	-	-	0.25 ± 0.25	-	-	-	
Tetraodontidae																		
<i>Canthigaster figueiredoi</i>	Sessile Invertivore	-	-	-	-	0.36 ± 0.20	0.07 ± 0.07	-	0.09 ± 0.09	0.08 ± 0.08	-	0.36 ± 0.29	0.12 ± 0.12	-	0.12 ± 0.12	0.14 ± 0.14	-	-
<i>Spherooides spengleri</i>	Mobile. Invertivore	-	-	-	-	0.71 ± 0.40	-	-	-	-	-	-	-	-	-	-	-	

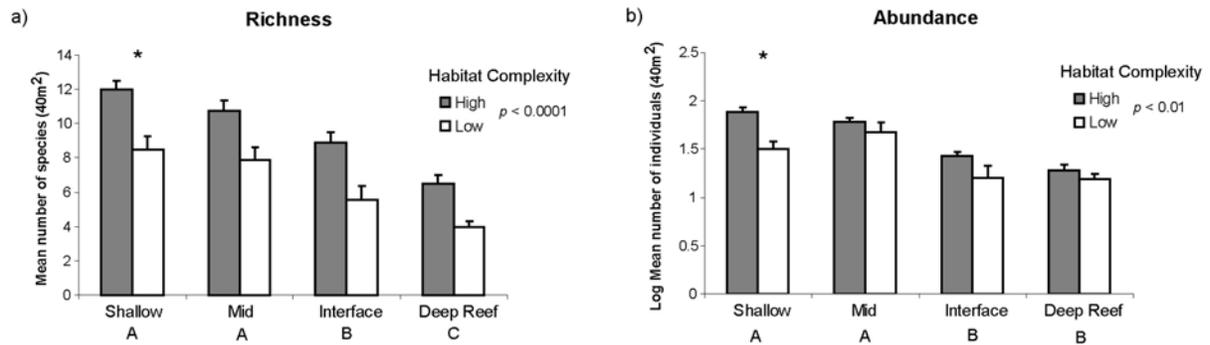


Figure 2. Mean species richness and log mean abundance (\pm SE) per transect of samples taken at different depth and habitat complexity categories for reef fish species at the Laje de Santos Marine Park. The p value in the graph resulted from the effect of habitat complexity. Letters below each depth category indicate homogenous groups for this factor extracted from SNK test. Compared pairs that differ significantly are marked by an asterisk.

Different trophic categories were not similarly affected by a depth gradient (Fig. 4a). Major changes in relative abundance were detected for roving herbivorous and planktivores, their participation largely reducing as depth increased. A more subtle trend of decrease with depth was recorded for territorial herbivores and omnivores, and an increase in the participation of macrocarnivores and mobile invertebrate feeders was detected as well (Fig. 4a). Wave exposure was again a poor descriptor of the community at the study area as only territorial herbivores were negatively affected by a high wave surge (Fig. 4b). Habitat complexity affected positively the relative abundance of territorial herbivores and planktivores (Fig. 4c).

Table 2. Summary of two-way ANOVA for species richness and fish abundance per transect with depth and habitat complexity as fixed factors relative to reef fish species at the Laje de Santos Marine Park. Significant values of p are in bold (<0.05). For those variables differing significantly among factors, homogenous subsets were extracted by Student-Newman-Keuls test (Zar 1999). See table 1 for depth codes.

Parameter	Factor	df	MS	F	P	SNK
Richness	Depth (1)	3	135.7	11.53	<0.0001	Shal = Mid > Inter > DR
	Habitat complexity (2)	1	277.0	24.02	<0.0001	High complex > Low complex

	1 x 2	3	1.670	0.144	0.932	
	Error	170	11.53			
Abundance	Depth (1)	3	2.201	20.180	<0.0001	Shal = Mid > Inter = DR
	Habitat complexity (2)	1	1.180	10.818	<0.01	High complex > Low complex
	1 x 2	3	0.185	1.699	0.169	
	Error	170	0.109			

The role of depth as a main factor structuring the community structure of reef fishes at the study site was confirmed by a principal component analysis (PCA) of the most abundant species in which samples sites were grouped mainly according to depth (Fig. 5). In the PCA ordination diagram axis 1 represents a depth gradient and explains 62% of the variance in the weighted averages (Fig. 5). Axis 2 accounts for other differences and was responsible for only 14% of the variability. Among the species that contributed mostly to the recorded variability, *Abudefduf saxatilis* and *Kyphosus* spp. formed a group highly associated with shallow waters. *Anisotremus virginicus*, *Diplodus argenteus* and *Haemulon aurolineatum* were highly characteristic for the mid-slope; *Chromis jubauna* was characteristic for interface and *Pagrus pagrus* for deep reefs. The same depth gradient was found in a PCA performed for trophic groups (Fig. 6). Principal component analyses in which sample sites were grouped according to the distribution of families, Labridae and Pomacentridae showed a strong depth partition among species within these families (Fig. 7).

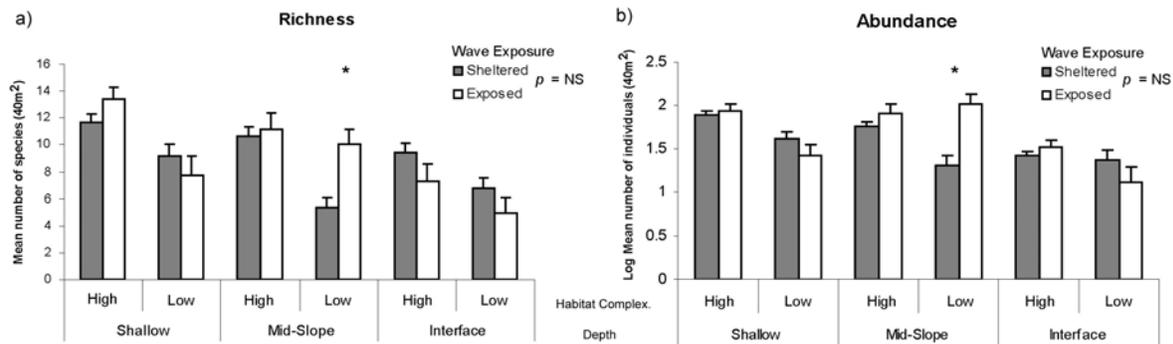


Figure 3. Mean species richness and log mean abundance (\pm SE) per transect of samples taken at different depth, wave exposure and habitat complexity categories for reef fish species at the Laje de Santos Marine Park. The p value in the graph resulted from the effect of wave exposure. Compared pairs that differ significantly are marked by an asterisk.

Table 3. Summary of three-way ANOVA for species richness and fish abundance per transect with depth, wave exposure and habitat complexity as fixed factors relative to reef fish species at the Laje de Santos Marine. Data from Deep Reefs (DR) were not included. Significant values of p are in bold (<0.05). For those variables differing significantly among factors, homogenous subsets were extracted by Student-Newman-Keuls test (Zar 1999). See table 1 for depth codes.

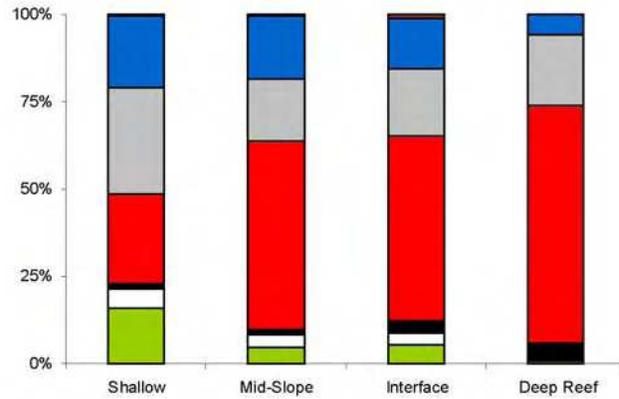
Parameter	Factor	df	MS	F	P	SNK
Richness	Depth (1)	2	122.1	10.49	<0.0001	Shal = Mid > Inter
	Wave exposure (2)	1	1.877	1.877	0.161	
	Habitat complexity (3)	1	341.35	29.31	<0.0001	High complex > Low complex
	1 x 2	2	53.331	4.580	0.01	See figure 3a
	1 x 3	2	6.623	0.568	0.567	
	2 x 3	1	1.500	0.128	0.720	
	1 x 2 x 3	2	37.449	3.216	<0.05	See figure 3a
	Error	151	11.643			
Abundance	Depth (1)	2	1.899	18.955	<0.0001	Shal = Mid > Inter
	Wave exposure (2)	1	0.247	2.466	0.118	
	Habitat complexity (3)	1	2.193	21.884	<0.0001	High complex > Low complex
	Error	151	11.643			

1 x 2	2	0.867	8.651	<0.001	See figure 3b
1 x 3	2	0.142	1.419	0.244	
2 x 3	1	0.0002	0.0024	0.960	
1 x 2 x 3	3	0.185	1.699	0.169	
Error	151	0.100			

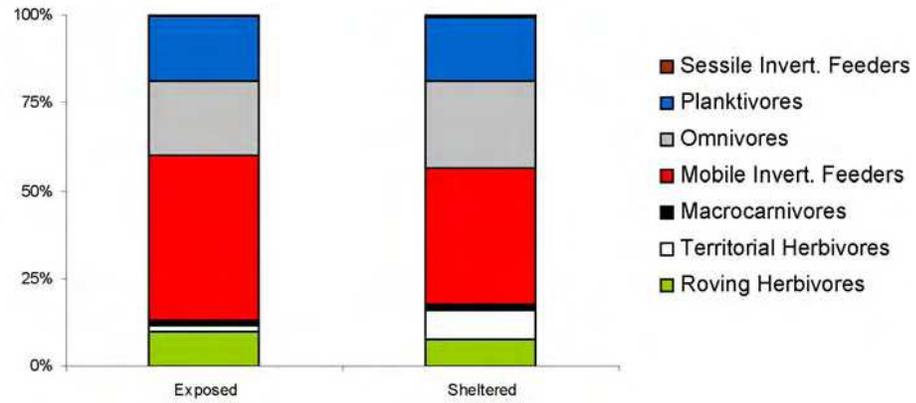
DISCUSSION

The reef fish community at the Laje de Santos Marine Park is characterized by few dominant species that are very abundant and widespread over the Atlantic Ocean. Of the 16 species that comprise 90% of all censused individuals, 14 are widely distributed in the West Atlantic and within these, eight are recorded from both sides of the Atlantic Ocean or at islands of the Mid-Atlantic ridge (Randall 1996, Carvalho-Filho 1999, Floeter et al. 2008). Exceptions were the Brazilian endemic damselfishes *Stegastes fuscus* and *Chromis jubauna*. The former is widespread (and abundant) along the Brazilian coast and the latter, in spite of sparse records on deep reefs in northeastern Brazil (Feitoza et al. 2005, C.L. Sampaio pers. comm.) and at the southern tip of the Caribbean (Rocha 2003, Floeter et al. 2008), is particularly abundant only at some coastal and offshore sites in southeastern Brazil. The fish community at Laje de Santos also seems to be dominated by species that are very versatile in their diet and habitat use. Omnivorous species, which can regularly shift from algae to animal feeding to cope with variable environmental conditions (Behrens & Lafferty 2007), are the second most abundant trophic group recorded at the harsh environment of the Laje de Santos as predicted by Floeter et al. (2004). Even among other trophic groups there are species that display wide habitat use and great feeding plasticity. Most abundant of all, the mobile invertebrate feeders, for example, have its pattern driven mainly by the tomtate *Haemulon aurolineatum*, a benthic invertebrate forager regularly recorded feeding on plankton at the study site.

a) Depth



b) Wave exposure



b) Habitat complexity

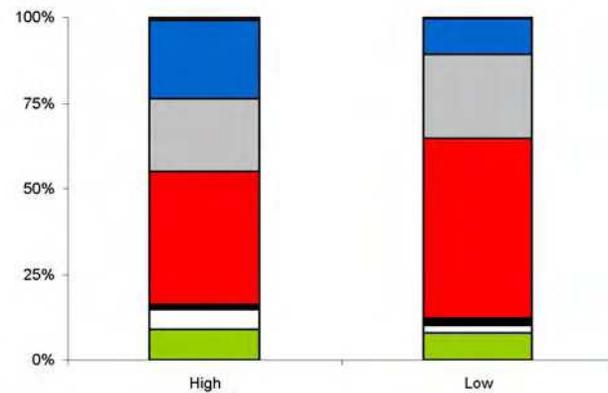


Figure 4. Relative abundance (%) of reef fish trophic groups at the Laje de Santos Marine Park relative to: a) depth; b) wave exposure; and c) habitat complexity categories.

Aside from being the most abundant species at the study site, *H. aurolineatum* was also the most frequent species, recorded in high numbers at almost all sampled sites. Among other species that dominated the fish community there were species considered the less specialized within their genera in the Atlantic, such as *Acanthurus chirurgus* and *Halichoeres poeyi* (Rocha et al. 2002, Rocha et al. 2005). These results agree with a recurring pattern of dominance of a few generalist species in areas with low species richness on the Brazilian coast and oceanic islands when compared with areas in the Caribbean centre of diversity (Ferreira et al. 2001, Floeter et al. 2007, Mendonça-Neto et al. 2008, authors' unpublished data).

Among the factors here studied, depth was the main driver of the reef fish community structure at the Laje de Santos. There was a steady decrease of species richness and abundance with depth increase, as well a clear partition between shallower and deeper depth categories. This result contrasts with studies that evaluate changes along a depth gradient in coral reefs, in which species richness (Edwards & Rosewell 1985) and abundance (Thresher & Colin 1986) increase as depth increase. This increase, however, is expected to reach a threshold. Indeed, Brokovich (2008) studied a depth gradient in Red Sea's coral reefs down to 65 m and found a peak of species richness at 30 m, from which on it started to decrease. Conversely, the depth structure recorded in the present study is similar to those found for Mediterranean temperate reefs (Bell 1983, Letourneur et al. 2003) and other subtropical rocky reefs (Aburto-Oropeza & Balart 2001), in which species richness and abundance peak at lesser depths and decrease as depth increases. A seasonal cold upwelling is known to occur at the study area but its influence is restricted to the deeper parts of the reefs (Luiz Jr. & Ferreira, chapter 3 of this volume). As the taxonomic structure of fish community at Laje de Santos Marine Park is mainly characterized by species with tropical affinities (Luiz Jr et al. 2008) the upwelling influence is probably leading this trend of depth-related community impoverishment. Cold water intrusions are one of a set of environmental conditions that may stunt the growth of healthy coral reefs in tropical and subtropical areas (Perry & Larcombe 2003). We predict that patterns of depth changes in fish species richness and abundance similar to those found in the present study will be recurrent as studies of environmentally similar areas advance.

Habitat structure was also a good predictor for community structure, as species richness and abundance were correlated with higher complexity. However, a detailed analysis of these relationships showed that the effects were significant only at the shallowest depth category, even if the differences between complexity categories were highly proportional within depths (Fig. 2). A probable explanation for the significant relationship of species richness and abundance with habitat complexity being detected only in the shallows is that fishes may be responding to an additional micro-topography generated by benthic invertebrates. These latter organisms occurs only at shallow sites at the study area (unpublished data), and elsewhere in subtropical and temperate systems several reef fish species are significantly associated with sea urchins (Hartney & Grorud 2002) and massive corals (Benfield et al. 2008) for shelter. However, this hypothesis is very unlikely for our study site due to the small size of sea urchins as compared to the study by Hartney and Grorud (2002) and to extremely low abundance of massive corals (unpublished data). Alternatively, the positive relationship of species richness and fish abundance with complexity in the shallows may indicate that rocky reefs present a finer physical structure relevant for fishes that was not detected in the visual assessment. Number and size of holes are considered as an important physiographic descriptor of the habitat that account for variability of reef fish richness and abundance (Roberts & Ormond 1987, Ferreira et al. 2001). Thus, it is possible that number and size range of holes and cavities were higher in shallow sites than on other depth categories and the visual assessment used in the present study failed to detect variations at this scale.

Wave exposure was not correlated with any of the community descriptors used in this study. This may be attributed to the small scale of the present survey and to particular characteristics of rocky reefs. For example, coral reefs (even distant atolls) with high exposed offshore have a zonation pattern that usually includes a back reef lagoon relatively sheltered to wave surge and water motion when compared to the outer reef. Conversely, in exposed rocky reefs the hard bottom is usually submerged or adjoined to the shore. Thus, in small offshore rocky islands such as the study area, even if there was a leeward face protected from wave surge, the effects of strong water motion derived by currents which were pervasive

over the reef may contribute to homogenize the hydrodynamics effects on the fish community. The effects of wave surge and water motion in rocky reefs are thus likely to be detected on larger scale comparisons, e.g. among coastal shores and islands that lie at variable distances from the mainland in which a gradient of exposure can be demonstrated (Floeter et al. 2007). This hierarchy of importance of factors in structuring the fish community at the Laje de Santos is confirmed by the dominant species (Fig. 5). There was some evidence of grouping by habitat structure in two depth categories: shallow and interface. Grouping by exposure was not evident.

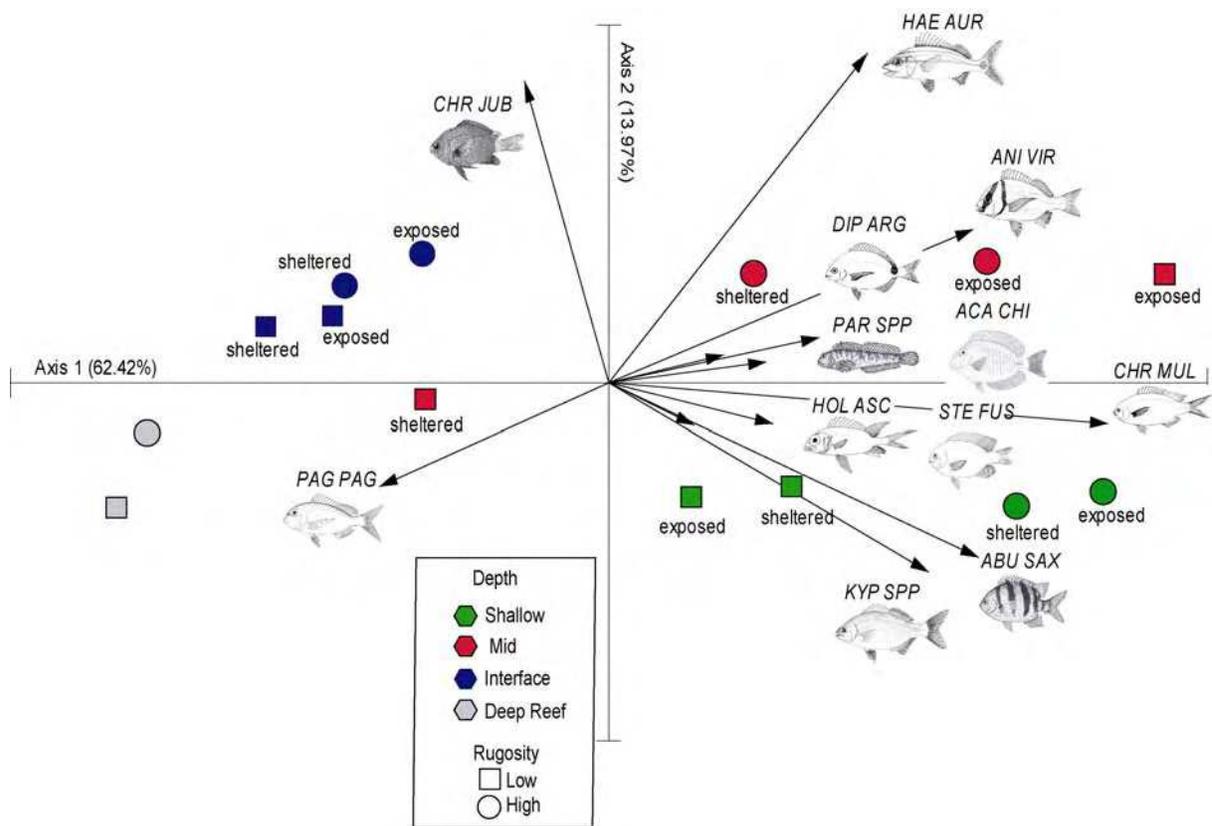


Figure 5. Principal component analyses ordination diagram performed for the most abundant 12 species of reef fishes at the Laje de Santos Marine Park. Samples taken in different depth categories are represented by different colors. Habitat complexity categories are represented by a circle (high complexity) and square (low complexity). Exposure categories are indicated below each point. Fish species are: abu sax (*Abudefduf saxatilis*), aca chi (*Acanthurus chirurgus*), ani vir (*Anisotremus virginicus*), chr jub (*Chromis jubauna*), chr mul (*Chromis multilineata*), dip arg (*Diplodus argenteus*), hae aur (*Haemulon aurolineatum*), hol asc (*Holocentrus ascencionis*), kyp spp (*Kyphosus* spp.), pag pag (*Pagrus pagrus*), par spp (*Parablennius* spp), ste fus (*Stegastes fuscus*).

Trophic groups were not similarly affected by the factors here analyzed. In spite of a general trend of decrease in richness and abundance with increasing depth, this tendency was much more pronounced in roving herbivores, followed by planktivores and, on a lesser scale, territorial herbivores. For herbivores this was an expected outcome, as studies conducted in coral reefs showed that herbivory is highly correlated with high turnover of algal turf (Russ 2003) that peaks in the shallows due to the maximum exposition to sunlight. Mobile invertebrate feeders and macrocarnivores increased their relative abundance with depth as connected to a lesser representation of other trophic categories (Fig. 5a). Territorial herbivores were highly susceptible to variations in habitat complexity and exposure (Fig. 5b,c) which may be explained by their strong site-attached characteristic (Bergman et al. 2000). Planktivores showed a tendency to occur in high complexity habitats, probably related to protection against predation (Almany 2004). Depth was here confirmed depth as the main factor structuring fish community, herbivores being highly associated with shallow reefs and macrocarnivores and mobile invertebrate feeders well represented in deeper reefs (Fig. 6).

The PCA ordination of figure 7 indicates that niche partitioning probably occurs among phylogenetically related species, as exemplified by the two of the most speciose and abundant families, Labridae and Pomacentridae. Depth was again the main factor structuring this partitioning, as congeners at the study area were associated with distinct depth categories. For example, within Labridae *Bodianus rufus* and *Halichoeres brasiliensis* were associated with shallows, whereas *B. pulchellus* and *H. poeyi* were most related to the mid-slope; additionally, *H. sazimai* was associated with the interface and deep reefs (Fig. 7a). Within Pomacentridae *Chromis multilineata* and *C. jubauna* were associated with shallow and mid-slope/interface respectively; *Stegastes fuscus* and *S. pictus* were associated to with mid-slope and interface respectively (Fig. 7b). It seems that swimming performance (sensu Fulton et al. 2005) influences the abundances of the aforementioned fishes in relation to the depth gradient, as found in other rocky reefs

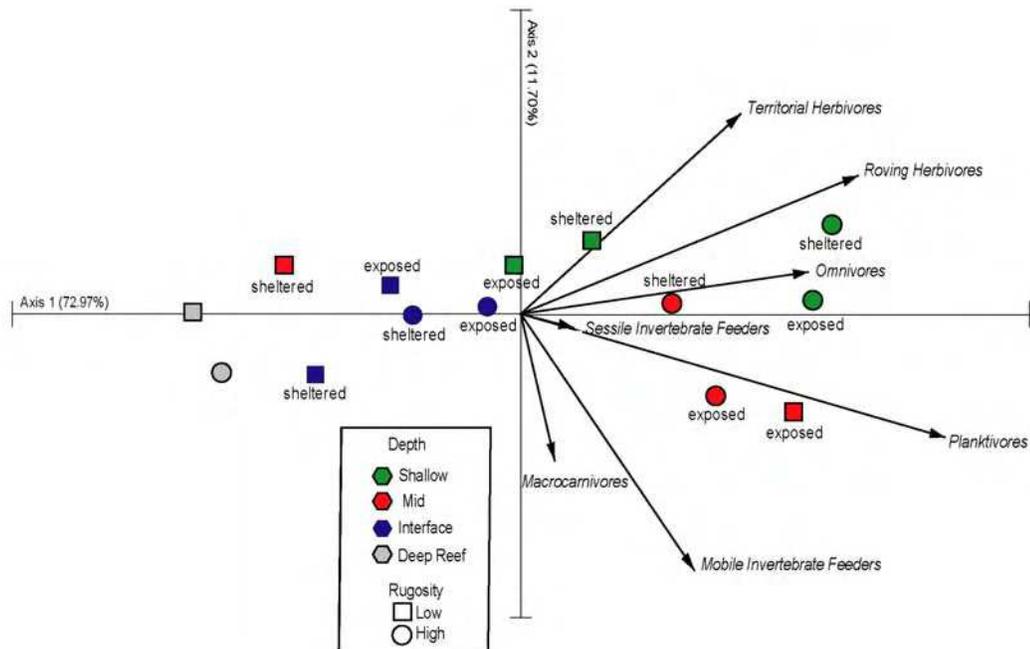


Figure 6. Principal component analyses ordination diagram performed for reef fish trophic categories at the Laje de Santos Marine Park. Samples taken in different depth categories are represented by different colors. Habitat complexity categories are represented by circles (high complexity) and squares (low complexity). Exposure categories are indicated below each point.

that are influenced by a high degree of exposition to hydrodynamic forces (Fulton & Bellwood 2004). For example, the labrid *Halichoeres brasiliensis* has a higher fin aspect ratio (a proxy for swimming performance) than *H. poeyi* (Wainwright et al. 2002) and this was reflected in their depth preferences (Fig. 7a). In a similar way, the pomacentrid *Chromis multilineata*, which has longer caudal fins than *C. jubauna* is found primarily in shallower sites whereas the latter is highly restricted to deeper sites (Fig. 7b). It is noteworthy that species that usually occur in shallow and sheltered coastal sites, such as *H. poeyi* and *Stegastes fuscus* (Ferreira et al. 2001) were found at mid-slope sites at the Laje de Santos; the latter distribution may be regarded as a response to the high hydrodynamics that characterize the study area. However, other factors than swimming performance may influence niche partitioning. For example, there

are no obvious differences in the aspect fin ratio between *Bodianus rufus* and *B. pulchellus* (Sazima & Gasparini 1999) or between *S. fuscus* and *S. pictus* (pers. obs.). In those cases further research is needed to elucidate whether different habitat preference among closely related species may be a result of competitive interactions whereby which one species dislodge the other to a sub-optimal habitat, or whether they simply have different habitat requirements.

In summary: (1) there is a clear difference of physical factors analyzed in this study and the contribution of each one relative to the structure of fish community. Depth is the factor that influenced most the species distribution, followed by habitat complexity and wave exposure; (2) Species of different trophic categories do not react similarly to these abiotic factors. Roving herbivores are affected by depth, territorial herbivores are influenced by habitat complexity and wave exposure and planktivores are affected by habitat structure and, to a lesser extent, by depth; (3) Within-family analyses indicate that there is niche partitioning among the species and that this partitioning seems to be mediated mainly by swimming performance (in response to a greater hydrodynamics in the shallow zone), as well by trophic plasticity.

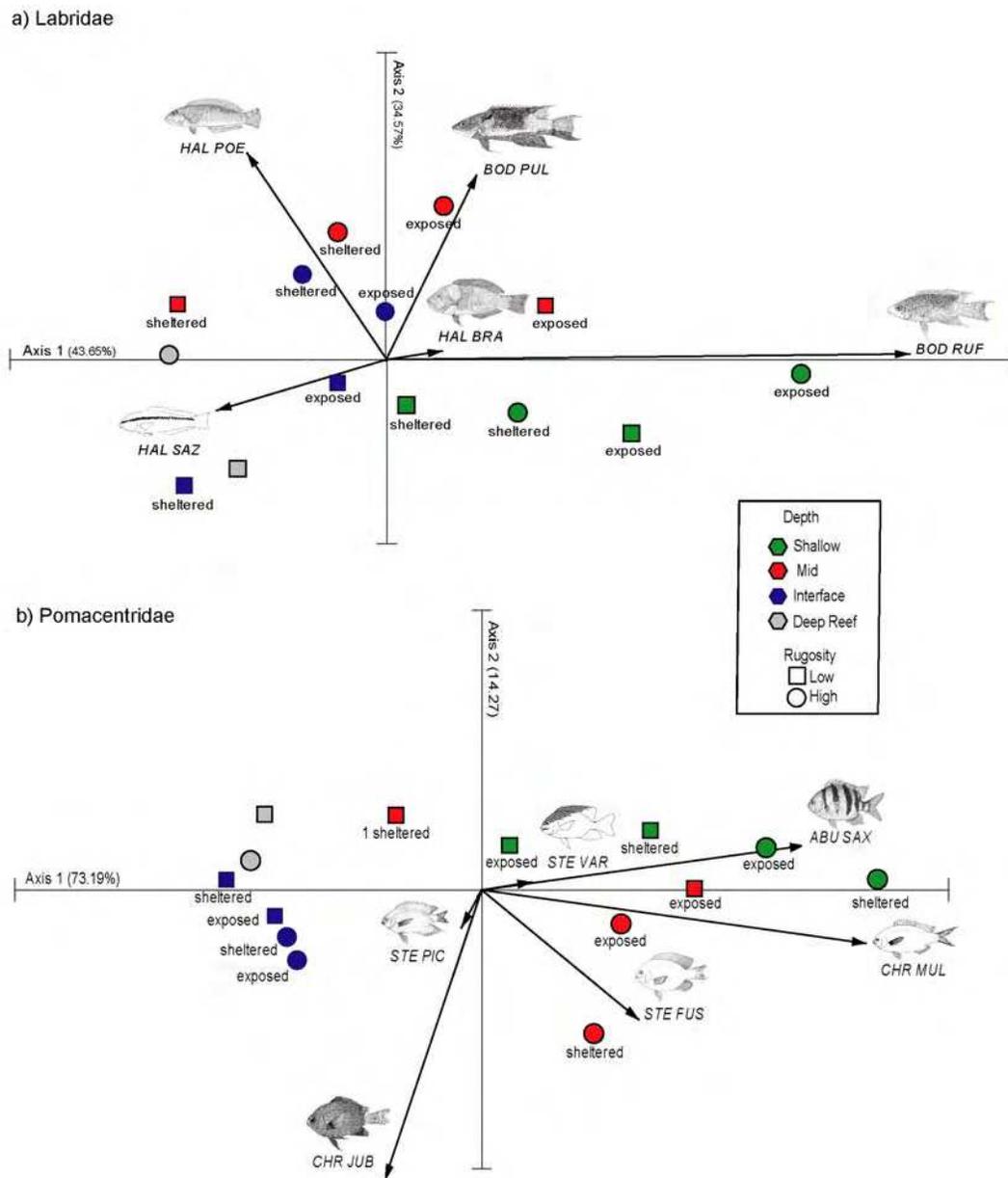


Figure 7. Principal component analyses ordination diagram performed for members of two species-rich and abundant families of reef fishes at Laje de Santos Marine Park. Samples taken in different depth categories are represented by different colors. Habitat complexity categories are represented by circles (high complexity) and squares (low complexity). Exposure categories are indicated below each point. Fish species are represented by arrows: abu sax (*Abudefduf saxatilis*), bod pul (*Bodianus pulchellus*), bod ruf (*Bodianus rufus*), chr jub (*Chromis jubauna*), chr mul (*Chromis multilineata*), hal bra (*Halichoeres brasiliensis*), hal poe (*Halichoeres poeyi*), hal saz (*Halichoeres sazimai*), ste fus (*Stegastes fuscus*), ste pic (*Stegastes pictus*) and ste var (*Stegastes variabilis*).

LITERATURE CITED

- Aburto-Oropeza O, Balart EF (2001) Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *Mar Ecol* 22:283–305
- Alevizon W, Richardson R, Pitts P, Serviss G (1985) Coral zonation and patterns of community structure in Bahamian reef fishes. *Bull Mar Sci* 36:304–318
- Almany GR (2004) Does increase habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106:275–284
- Behrens MD, Lafferty KD (2007) Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity gradient in herbivorous fishes. *Can J Fish Aquat Sci* 64:867–873
- Bell JD (1983) Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean Sea. *J App Ecol* 20:357–369
- Bellwood DR (1996) The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. *Coral Reefs* 15:11–19
- Bellwood DR (1998) What are reef fishes? – Comment on the report by D.R. Robertson. *Coral Reefs* 17:187–189
- Bellwood DR, Wainwright PC (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Greater Barrier Reef. *Coral Reefs* 20:139–150
- Benfield S, Baxter L, Guzman HM, Mair JM (2008) A comparison of coral reef and coral community fish assemblages in Pacific Panama and environmental factors governing their structure. *J Mar Biol Ass UK* 88:1331–1341

- Bergman KC, Öhman MC, Svensson S (2000) Influence of habitat structure on *Pomacentrus sulfurous*, a western Indian Ocean reef fish. *Environ Biol Fish* 59:243–252
- Beukers JS, Jones GP (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50–59
- Bradbury RH, Young PC (1981) The effects of a major forcing function, wave energy, on a coral reef ecosystem. *Mar Ecol Prog Ser* 5:229–241
- Brokovich E, Einbinder S, Shashar N, Kiflawi M, Kark S (2008) Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient. *Mar Ecol Prog Ser* 371:253–262
- Caley MJ, St John J (1996) Refuge availability structures assemblages of tropical reef fishes. *J Anim Ecol* 65:414–428
- Carvalho-Filho A (1999) Peixes: Costa Brasileira. Marca D'água, São Paulo
- Chittaro PM (2002) Species-area relationships for coral reef fish assemblages of St. Croix, US Virgin Islands. *Mar Ecol Prog Ser* 233: 253–261
- Clarke RD (1977) Habitat distribution and species diversity of Chaetodontid and Pomacentrid fishes near Bimini, Bahamas. *Mar Biol* 40:277–289
- Clua E, Legendre P, Vigliola L, Magron F, Kulbicki M, Sarramegna S, Labrosse P, Galzin R (2006) Medium scale approach (MSA) for improved assessment of coral reef fish habitat. *J Exp Mar Biol Ecol* 333: 219–230
- Denny MW (2006) Ocean waves, nearshore ecology, and natural selection. *Aquat Ecol* 40:439–461
- Dominici-Arosemena A, Wolff M (2006) Reef fish community structure in the tropical Eastern Pacific (Panamá): living on a relatively stable rocky reef environment. *Helgol Mar Res* 60:287–305

- Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1:95–107
- Eagle JV, Jones GP, McCormick MI (2001) A multi-scale study of the relationships between habitat use and the distribution and abundance patterns of three coral reef angelfishes (Pomacanthidae). *Mar Ecol Prog Ser* 214:253–265
- Edwards A, Rosewell J (1981) Vertical zonation of coral reef fishes in the Sudanese red Sea. *Hydrobiologia* 79:21–31
- Feitoza BM, Rosa RS, Rocha LA (2005) Ecology and zoogeography of deep-reef fishes in northeastern Brazil. *Bull Mar Sci* 76:727–742
- Ferreira CEL, Gonçalves JEA (2006) Community structure and diet of roving herbivorous reef fishes in the Abrolhos Archipelago, south-western Atlantic. *J Fish Biol* 69:1533–1551
- Ferreira CEL, Gonçalves JEA, Coutinho R (2001) Community structure of fishes and habitat complexity on a tropical rocky shore. *Environ Biol Fish* 61: 353–369
- Ferreira CEL, Floeter SR, Gasparini JL, Ferreira BP, Joyeux J-C (2004) Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *J Biogeogr* 31:1093–1106
- Floeter SR, Gasparini JL (2000) The south-western Atlantic reef fish fauna: composition and zoogeographic patterns. *J Fish Biol* 56:1099–1114
- Floeter SR, Guimarães RZP, Rocha LA, Ferreira CEL, Rangel CA, Gasparini JL (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecol Biogeogr* 10:423–431
- Floeter SR, Ferreira CEL, Dominici-Arosemena A, Zalmon IR (2004) Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. *J Fish Biol* 64:1680–1699

- Floeter SR, Khroling W, Gasparini JL, Ferreira CEL, Zalmon IR (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. *Environ Biol Fish* 10:423–431
- Floeter SR, Rocha LA, Robertson DR, Joyeux J-C, Smith-Vaniz WF, Wirtz P, Edwards AJ, Barreiros JP, Ferreira CEL, Gasparini JL, Brito A, Falcón JM, Bowen BW, Bernardi G (2008) Atlantic reef fish biogeography and evolution. *J Biogeogr* 35:22–47
- Fox R, Bellwood DR (2007) Quantifying herbivory across a coral reef depth gradient. *Mar Ecol Prog Ser* 339:49–59
- Francini-Filho RB, Moura RL (2008) Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil. *Aquatic Conserv: Mar Freshw Ecosyst* 18:1166–1179
- Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J Exp Mar Biol Ecol* 224:1–30
- Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22:291–305
- Friedlander AM, Brown E, Monaco ME (2007) Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. *Mar Ecol Prog Ser* 351:221–233
- Fulton CJ, Bellwood DR (2004) Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. *Mar Biol* 144:429–437
- Fulton CJ, Bellwood DR (2005) Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnol Oceanogr* 50:255–264

- Fulton CJ, Bellwood DR, Wainwright PC (2005) Wave energy and swimming performance shape coral reef fish assemblages. *Proc R Soc B* 272:827–832
- Gosline WA (1965) Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. *Ecology* 46:823–831
- Gratwicke B, Speight MR (2005) Effects of marine habitat complexity on Caribbean marine fish assemblages. *Mar Ecol Prog Ser* 292:301–310
- Gust N (2002) Scarid biomass on the northern Great Barrier Reef: the influence of exposure, depth and substrata. *Environ Biol Fish* 64:353–366
- Hartney KB, Grorud KA (2002) The effect of sea urchins as biogenic structures on the local abundance of a temperate reef fish. *Oecologia* 131:506–513
- Johansen JL, Fulton CJ, Bellwood DR (2007) Avoiding the flow: refuges expand the swimming potential of coral reef fishes. *Coral Reefs* 26:577–583
- Johansen JL, Bellwood DR, Fulton CJ (2008) Coral reef fishes exploit flow refuges in high-flow habitats. *Mar Ecol Prog Ser* 360:219–226
- Letourneur Y, Ruitton S, Sartoretto S (2003) Environmental and benthic habitat factors structuring the spatial distribution of a summer infralittoral fish assemblage in the north-western Mediterranean Sea. *J Mar Biol Ass UK* 83:193–204
- Lewis JR (1968) Water movements and their role in rocky shore ecology. *Sarsia* 34:13–36
- Lindsay MJ, Patterson HM, Swearer SE (2008) Habitat as a surrogate measure of reef fish diversity in the zoning of the Lord Howe Island Marine Park, Australia. *Mar Ecol Prog Ser* 353:265–273
- Little C, Kitching JA (1996) *The biology of rocky shores*. Oxford University Press, Oxford

- Luiz Jr OJ, Carvalho-Filho A, Ferreira CEL, Floeter SR, Gasparini JL, Sazima I (2008) The reef fish assemblage of the Laje de Santos Marine State Park, Southwestern Atlantic: annotated checklist with comments on abundance, distribution, trophic structure, symbiotic associations, and conservation. *Zootaxa* 1807:1–25
- Maida M, Ferreira BP (1997) Coral reefs of Brazil: an overview. *Proc 8th Int Coral Reef Symp* 1:263–274
- Mattila J, Heck Jr. KL, Millstein E, Miller E, Gustafsson C, Williams S, Byron D (2008) Increased habitat structure does not always provide increased refuge from predation. *Mar Ecol Prog Ser* 361:15–20
- McCormick MI (1994) Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Mar Ecol Prog Ser* 112:87–96
- McCormick MI (1995) Fish feeding on mobile benthic invertebrates: influence of spatial variability in habitat associations. *Mar Biol* 121:627–637
- McGhee MA (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Mar Ecol Prog Ser* 105:243–255
- Mendonça-Neto JP, Monteiro-Neto C, Moraes LE (2008) Reef fish community structure on three islands of Itaipu, Southeast Brazil. *Neotrop Ichthyol* 6:267–274
- Moura RL, Sazima I (2003) Species richness and endemism levels of the Brazilian reef fish fauna. *Proc 9th Int Coral Reef Symp, Bali, Indonesia* 1:956–959
- Nuñez-Lara E, Arias-González JE (1998) The relationship between reef fish community structure and environmental variables in the southern Mexican Caribbean. *J Fish Biol* 53(Suppl A):209–221
- Nuñez-Lara E, Arias-González JE, Legendre P (2005) Spatial patterns of Yucatan reef fish communities: testing models using a multi-scale survey design. *J Exp Mar Biol Ecol* 324:157–169

- Paulay G (1997) Diversity and distribution of reef organisms. In: Birkeland C (ed) Life and death of coral reefs. Chapman & Hall, New York
- Perry CT, Larcombe P (2003) Marginal and non-reef-building coral environments. *Coral Reefs* 22:427–432
- Randall JE (1996) Caribbean Reef Fishes. TFH Publications, Hong Kong
- Rilov G, Figueira WF, Lyman SJ, Crowder LB (2007) Complex habitats may not always benefit prey: linking visual field with reef fish behavior and distribution. *Mar Ecol Prog Ser* 329:225–238
- Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar Ecol Prog Ser* 41:1–8
- Robertson DR (1998) Do coral-reef fish faunas have a distinctive taxonomic structure? *Coral Reefs* 17:179–186
- Rocha LA, Bass AL, Robertson DR, Bowen BW (2002) Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). *Mol Ecol* 11:243–252
- Rocha LA (2003) Patterns of distribution and processes of speciation in Brazilian reef fishes. *J Biogeogr* 30:1161–1171
- Rocha LA, Robertson DR, Roman J, Bowen BW (2005) Ecological speciation in tropical reef fishes. *Proc R Soc B* 272:573–579
- Russ G (1984a) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar Ecol Prog Ser* 20:23–34
- Russ G (1984b) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. *Mar Ecol Prog Ser* 20:35–44

- Sazima I (1986) Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *J Fish Biol* 29:53–65
- Sazima I, Gasparini JL (1999) A presumed hybrid of the hogfishes *Bodianus pulchellus* and *Bodianus rufus* in the western South Atlantic (Perciformes: Labridae). *Aqua, J Ichthyol Aquat Biol* 3:89–92
- Srinivasan M (2003) Depth distributions of coral reef fishes: the influence of microhabitat structure, settlement, and post-settlement processes. *Oecologia* 137:76–84
- Thresher RE (1983) Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef lagoon. *Mar Ecol Prog Ser* 10:137–145
- Thresher RE, Colin P (1986) Trophic structure, diversity and abundance of fishes of the deep reef (30–300m) at Enewetak, Marshall Islands. *Bull Mar Sci* 38:253–272
- Underwood AJ (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge
- Wainwright PC, Bellwood DR, Westneat MW (2002) Ecomorphology of locomotion in labrid fishes. *Environ Biol Fish* 65:47–62
- Wilding TA, Rose CA, Downie MJ (2007) A novel approach to measuring subtidal habitat complexity. *J Exp Mar Biol Ecol* 353:279–286
- Williams DMcB (1982) Patterns in the distribution of fish communities across the central Greater Barrier Reef. *Coral Reefs* 1:35–43.
- Williams DMcB (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego.
- Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Mar Biol* 151:1069–1076
- Zar JH (1999) *Biostatistical analysis*. Prentice Hall, New Jersey

CAPÍTULO 3

UPWELLING EFFECTS UPON REEF FISH COMMUNITY STRUCTURE

OSMAR J. LUIZ JR. ¹, CARLOS EDUARDO L. FERREIRA ²

¹ *Depto. de Zoologia, Universidade Estadual de Campinas, 13083-970, Campinas, SP, Brasil*

² *Depto. de Biologia Marinha, Universidade Federal Fluminense, 24001-970, Niterói, RJ, Brasil*

ABSTRACT: The effects of cold water intrusion during upwelling events in the community structure of reef fishes were examined at the Laje de Santos Marine State Park, southeastern Brazil. Upwelling events at the study site occurs only in the austral summer and its influence is restricted to the deeper reef slope, usually below 10m depth. Species richness and abundance of individuals were quantified in shallow and deep areas within periods with and without upwelling influence. The cold water derived from upwelling was a contributing factor reducing the total fish abundance and the main factor reducing the number of species that were able to extend their depth ranges to the deeper parts of the study site, triggering specific behavioral responses as it was noted that some fish species formed large and tight-packed schools in the upper warmer layer. Roving herbivores and omnivores were the trophic groups whose abundances were particularly affected by upwelling. Change in abundance of territorial herbivores was driven mainly by depth and was not influenced by cold water. Individual species presents distinctive responses to the presence of cold water. In general, fishes with high mobility avoid the deep cold layer, being restricted to shallow waters during summer and species that are strongly site-attached and with limited mobility did not change their abundances due the presence of cold water. Species that are associated with deep reefs (>30m) were favored by upwelling influence to reach shallower areas. The effects of upwelling on reef fish communities are largely understudied, further research is needed on this topic, and in particular regarding behavior consequences of species is response to changes in species richness and abundance during such events.

Key words: Rocky Reefs, Brazil, Subtropical, Oceanography, South Western Atlantic

INTRODUCTION

Tropical reef fishes are acknowledged to maintain diverse and complex structured communities in coral reef systems (Sale 1991, 2002). Although the evolution of this distinctive assemblage of fishes is often associated with the rise of modern coral reefs (Bellwood 1996, Bellwood & Wainwright 2002) they can also thrive and establish healthy populations in places where environmental conditions stunt or prevent the formation of a coral reef framework (Robertson 1998). These places were previously defined by Kleypas et al. (1999) and Perry and Larcombe (2003) as ‘marginal’ reefs, i.e. geographically located at the periphery of coral reefs; where hard corals may be present only as isolated colonies scattered over the exposed bedrock. These are usually referred in the literature as tropical or subtropical ‘rocky reef’ systems (Robertson 1998, Aburto-Oropeza & Balart 2001, Ferreira et al. 2001, Floeter et al. 2001, Pondella et al. 2005, Dominici-Arosemena & Wolff 2006). However, they are very distinct from temperate rocky reefs (*sensu* Ebeling & Hixon 1991, Andrew & Francis 2003) mainly by displaying usually mild temperatures when compared to temperate reefs; a lack of extensive kelp forests; and a high component of their biota being composed of tropical species that are also found in the adjacent tropical coral reefs. The tropical reef fishes that extend their range into these ‘marginal’ sites should, therefore, deal with the same environmental factors that are supposed to prevent coral reef growth like turbid water conditions and/or periodic cold water intrusions (Perry & Larcombe 2003). However, despite a growing literature on the response of corals to these sub-optimal conditions, it is not yet clear the extension to which tropical reef fishes are affected by these factors.

The rocky reefs of the southeastern and southern Brazilian coast are the limit of a wide range of Western Atlantic tropical reef fish species (Randall 1996, Carvalho-Filho 1999, Moura et al. 1999, Floeter et al. 2001, Humann & DeLoach 2002, Menezes et al. 2003) and, despite a significant proportion of Brazilian endemics, more than a half of their assemblages is composed of species that are widespread over the Caribbean coral reefs (Ferreira et al. 2001, Floeter & Gasparini 2000, Luiz Jr et al. 2008). The marine

environment in the southeastern coast of Brazil is seasonally affected by an upwelling that brings cold waters during the austral summer and set down the sea surface temperature (SST) to values below than of the minimum in the SST's normal range of tropical coral reefs (Campos et al. 1994, Castro & Miranda 1998). Water temperature and primary production are the most variable environmental factors during upwelling events (Bakun 1996), which have important ecological effects on a wide diversity of taxa; from benthic organisms (Ventura et al. 1997, Sumida et al. 2005) to zooplankton and pelagic fish (Lopes et al. 1999, Andrade 2003). However, the effects of the upwelling on the relatively site attached tropical reef fish assemblages are yet to be determined in the southwestern Atlantic.

Low temperature is recognized as an important factor defining geographic ranges of tropical fishes, as evidenced by mass mortalities which occur during anomalous low SST's (Thomson & Lehner 1976, Bohnsack 1983, Mora & Ospina 2002, Hsieh et al. 2008) and as biogeographic barriers like cold water masses preventing optimal conditions for larvae development and dispersion of tropical fish species (Briggs 1974, Bowen et al. 2001, Pondella et al. 2005, Floeter et al. 2008). These factors notwithstanding, there are some species which are equally wide ranging over tropical and subtropical seas. More recently, low temperatures were shown to impose limits on the northward expansion of invasive tropical reef fishes in the Western Atlantic (Kimball et al. 2004; Eme & Bennett 2008). Low temperature can affect fish behaviour and fitness, reducing the rate of food acquisition and digestive capabilities (Ferreira et al. 1998a, Floeter et al. 2004, Floeter et al. 2005, Behrens & Lafferty 2007, Smith 2008). Cold water also was reported to reduce the growth rate of larvae and condition at settlement (McCormick & Molony 1995, Meekan et al. 2003) while providing fishes to live longer and attain larger sizes (Choat & Robertson 2002).

The northern limits of occurrence of most Western Atlantic tropical reef fishes are suggested to be defined by a decrease in the mean annual SST (McBride & Able 1998, Love & Chase 2007) and the same process is likely to occur on the southern boundary of Western Atlantic reef fish distribution. To gain a better understanding of the thresholds for reef fish occurrence driven by changes in temperature regime,

we investigated how some community parameters, namely, species richness, abundance, trophic structure and depth distribution of fishes are affected by periodic cold water intrusions driven by local upwelling in a rocky reef in the southeastern Brazilian shelf. Data was gathered for answer the following three basic questions: Does the cold water intrusion of upwelling events affect the species richness and abundance patterns at the rocky reef? Which species are more or less affected, if any? Are there common attributes shared by the affected species, like trophic category or mobility?

MATERIALS AND METHODS

Study Site

The study was conducted at the Laje de Santos Marine State Park (24°15'S; 46°10'W), located 36 km off the city of Santos, São Paulo State, Southeastern Brazil (Fig. 1). It consists of an uninhabited rocky islet and several sparse rocky reefs with extensive intervening sand bottoms. The subtidal substrate is composed of granitic boulders of varying sizes and shapes that delineate a steep profile, mainly covered by turf algae with patches of brown and red algae, the zoanthid *Palythoa caribaeorum*, hydrozoans, ascidians, octocorals and sparse colonies of the scleractinian corals *Madracis decactis* and *Mussismilia hispida*. The SE Brazilian Bight (SBB, 23°S to 28°S) is influenced by three water masses: the Tropical Water (TW, $T > 20^{\circ}\text{C}$ and $S > 36.4$), which is carried southward from the tropics by the Brazil Current; the South Atlantic Central Water (SACW, $T < 18^{\circ}\text{C}$ and $S < 36.4$) which is confined to the shelf slope during most part of the year but carried by the upwelling to inner shelf during the summer when it reaches the study site; and the Coastal Water (CW), a low salinity water resulting from the dilution of oceanic water by continental freshwater input (Campos et al. 1994, Castro & Miranda 1998, Sumida et al. 2005). In the summer, the Brazil Current intensifies forming meanders and eddies that promote the upwelling and intrusion of SACW in SBB (Castro & Miranda 1998). The interaction of the warm TW and the cold SACW produces a sharp thermocline with a variable depth but usually seems at 10-12m depth at high

summer in the study site (Fig. 2). Based on experience of more than 10 years of diving at the study site by the first author, it appears that the thermocline reaching depths shallower than 10 m is a very rare event, and it is very unlikely that it reaches the surface. The TW carried by the Brazil Current corresponds to the upper layer of the thermocline and has a SST usually warmer than 24°C (range 24-28°C); the immediately lower layer is formed by the cold SAWC, with water temperature usually less than 18°C (range 14-18°C). During the austral winter, the Brazil Current loses strength, the SACW retreats towards the shelf slope and the TW mixes with cool CW carried northwards by southern cold fronts (S-SW winds) (Pereira 1989). During this period the SST at the study site is maintained within a range of 19°C - 22°C from the surface to at least 20 m depth and no shallow thermocline is recorded during wintertime (Fig. 2).

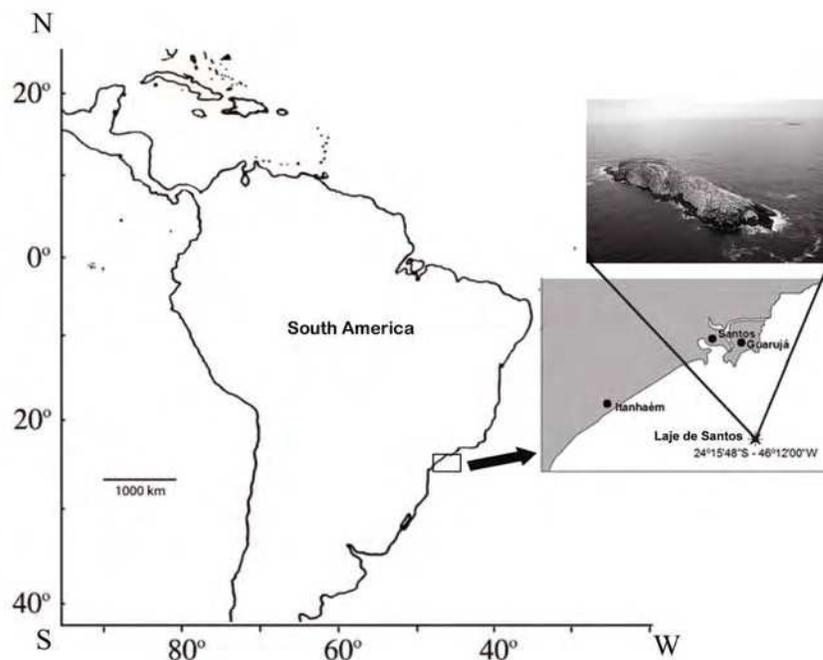


Figure1. The Laje de Santos Marine State Park localization in western South Atlantic.

Photo: C.L.B. Francini.

Data Acquisition

Surveys of the fish community structure were conducted in January/February and in July/August of 2003 and 2004, during the austral summer and winter respectively. Eighty-five replicated underwater visual censuses were performed using strip transect ($20 \times 2\text{m} = 40\text{m}^2$) and SCUBA in the leeward side of the study site at both seasons and within two depth categories: (2-10m and 10-18m), the two categories hereafter called shallow and deep. These depth intervals were arbitrarily determined to suit censuses carried above and below the thermocline in the summer and to provide replicate samples at the same depth interval in a non-thermocline condition during the winter. As the thermocline boundary was not always at the same depth, summer censuses were based on the position of the thermocline as determined by the abrupt change on temperature. All fishes were counted along the transect, except for cryptic species that were counted with use of careful scanning of the substrate when the diver turned back and started wounding the tape. This method ensured that the species more likely to swim away due to the observer are the first ones to be counted and that underestimation of cryptic species numbers would be minimized. To standardize observations, data was collected on SCUBA in a single area with no variation in slope and benthic complexity (site called 'Portinho'). Water temperature during the censuses was determined by calibrated thermometers. Fishes were grouped into major trophic categories following Randall (1967), Ferreira et al. (2004) and also through direct behavioral observations.

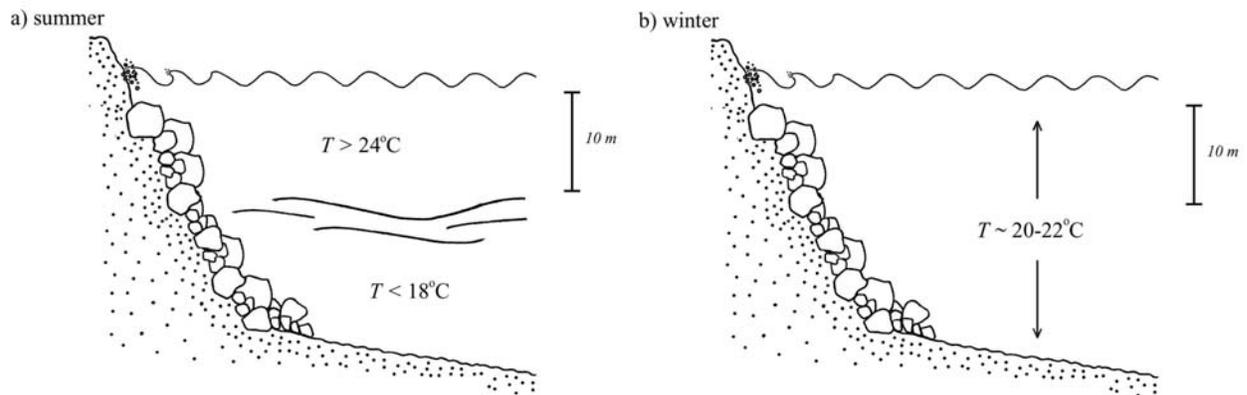


Figure 2. Temperatures usually recorded at the study site in summer **a)** and winter **b)**. The bold lines in the water column in summer **a)** indicate the usual depth which thermocline was recorded.

Data Analysis

Fish abundance, species richness and proportion of trophic groups per transect were compared among depth categories and seasons with and without thermocline (summer and winter respectively) using two-way analysis of variance (ANOVA). When necessary, data were log-transformed to stabilize variances (Underwood 1997). Additional Student-Newman-Keuls (SNK) multiple comparisons of means were performed as a post-hoc test (Zar 1999). A principal component analysis (PCA) was performed to explore the patterns of distribution of species that contributed most for the differences found among depths and seasons. For this multivariate technique, only the species with a total abundance higher than 0.5 individuals per transect was considered in the analysis ($n=36$). The abundance of each of these species was then pairwise compared between seasons within each depth category using Student t-test. As the cold water of the upwelling affects only the deeper part of the study site, species whose abundances in the deep category differed significantly between seasons were considered negatively affected by the cold water if their abundances were higher at winter and positively affected by the cold water if their abundances were higher at summer. Parametric analyses were performed using Statistica 6.0 software and the multivariate analysis was performed with MVSP 3.1 software.

RESULTS

A total of 5,711 individuals of 74 teleost fish species belonging to 29 families were recorded throughout the study (Table 1). Thirty six species whose densities were higher than 0.5 individuals per transect correspond to 97.5% of the total censused fishes, and were included in the multivariate matrix (Table 1). Almost all species were identified during the census to species level (except species of the genera *Parablennius*, *Kyphosus* and *Scorpaena* that were not possible to identify visually and thus were pooled at the genus level).

The recorded cold water intrusion altered the reef fish community structure at the study site and affected the assemblage of fishes at the deeper part of the rocky reef in summer months (Fig.3, Table 2), period when the thermocline generated by the seasonal upwelling reaches its maximum level at the Laje de Santos Marine State Park. The species richness was significantly lower at the deep during summertime ($p < 0.001$, $F = 22.849$) (Fig. 3a) but did not change in the shallow between summer and winter and neither in the winter between shallow and deep (Fig. 3a, Table 2), which indicate that the cold water was the main factor reducing the number of species that were able to extend their depth ranges to the deeper parts of the study site. The total abundance of fish decreased with depth independently of temperature ($p < 0.001$, $F= 62.727$), but the decrease was significantly higher in summer than in winter ($p = 0.001$, $F= 10.507$) (Fig. 3b, Table 2) indicating low temperature as a contributing factor reducing the total fish abundance.

Table 1. Total composition of fish species in visual census at the study site at different depth and seasons, plus presence of thermocline: Density per 40 m² (mean ± SE) per species and percent of total observed. Species followed by (*) were included in the multivariate analysis. Families, genera, and species in alphabetical order.

Family/Species	Trophic Group	Summer (with thermocline)		Winter (without thermocline)	
		Shallow (<10m; ≥24°C)	Deep (>10m; ≤18°C)	Shallow (<10m; ~20°C)	Deep (>10m; ~20°C)
		Density	Density	Density	Density
Acanthuridae					
<i>Acanthurus bahianus</i>	Rov. Herbivore	0.24 ± 0.14	–	0.14 ± 0.10	–
<i>Acanthurus chirurgus</i> *	Rov. Herbivore	2.33 ± 1.04	–	2.57 ± 1.43	1.40 ± 0.43
<i>Acanthurus monroviae</i>	Rov. Herbivore	–	–	0.05 ± 0.05	0.05 ± 0.05
Balistidae					
<i>Balistes vetula</i>	Mob. Invert.	0.05 ± 0.05	–	–	0.05 ± 0.05
Blennidae					
<i>Parablennius spp.</i> *	Omnivore	4.48 ± 1.72	2.13 ± 0.70	3.57 ± 0.82	2.80 ± 0.85
Bothidae					
<i>Bothus ocellatus</i>	Carnivore	–	0.04 ± 0.04	–	0.10 ± 0.10
Carangidae					
<i>Caranx crysos</i>	Piscivore	–	–	0.48 ± 0.48	–
<i>Pseudocaranx dentex</i> *	Plankt./Mob. Invert.	0.05 ± 0.05	0.96 ± 0.53	0.04 ± 0.04	0.10 ± 0.07
Chaetodontidae					
<i>Chaetodon striatus</i> *	Sessile Invert.	0.52 ± 0.21	0.04 ± 0.04	0.48 ± 0.17	0.55 ± 0.18
Chaenopsidae					
<i>Emblemariopsis signifera</i> *	Mob. Invert.	0.95 ± 0.36	0.39 ± 0.22	0.47 ± 0.21	0.50 ± 0.22
Epinephalidae					
<i>Cephalopholis furcifer</i>	Planktivore	–	–	0.52 ± 0.47	0.15 ± 0.15
<i>Hyporthodus niveatus</i>	Carnivore	–	0.13 ± 0.10	–	–
<i>Mycterperca acutirostris</i> *	Piscivore	0.29 ± 0.14	0.30 ± 0.10	0.62 ± 0.37	0.30 ± 0.16
<i>Mycterperca interstitialis</i>	Piscivore	–	–	–	0.05 ± 0.05
<i>Mycterperca marginata</i> *	Carnivore	0.29 ± 0.12	0.26 ± 0.09	0.71 ± 0.27	0.35 ± 0.15
Gobiidae					
<i>Coryphopterus glaucofraenum</i>	Omnivore	–	0.13 ± 0.07	–	0.20 ± 0.12
<i>Elacatinus figaro</i> *	Mob. Invert.	0.43 ± 0.20	0.13 ± 0.10	0.33 ± 0.23	0.65 ± 0.21
<i>Gnatholepis thompsoni</i>	Omnivore	–	–	–	0.05 ± 0.03
Haemulidae					
<i>Anisotremus surinamensis</i> *	Mob. Invert.	1.14 ± 0.51	–	0.90 ± 0.38	–
<i>Anisotremus virginicus</i> *	Mob. Invert.	5.90 ± 2.35	1.04 ± 0.67	6.19 ± 2.82	2.10 ± 0.77
<i>Haemulon aurolineatum</i> *	Mob. Invert./ Plankt	11.95 ±5.31	11.22 ± 2.18	12.29 ±3.19	11.30 ± 2.33

<i>Haemulon parrae</i>	Mob. Invert./ Plankt	–	–	0.05 ± 0.05	0.05 ± 0.05
<i>Haemulon steindachneri</i>	Mob. Invert./ Plankt	0.05 ± 0.05	0.09 ± 0.09	–	0.15 ± 0.11
Holocentridae					
<i>Holocentrus adscensionis</i> *	Mob. Invert.	2.67 ± 1.48	0.43 ± 0.12	0.95 ± 0.22	0.35 ± 0.13
Kyphosidae					
<i>Kyphosus</i> spp.*	Rov. Herbiv.	3.90 ± 1.38	0.04 ± 0.04	4.23 ± 1.32	1.65 ± 0.40
Labridae					
<i>Bodianus pulchellus</i> *	Mob. Invert.	0.76 ± 0.28	0.57 ± 0.20	0.71 ± 0.32	0.65 ± 0.17
<i>Bodianus rufus</i> *	Mob. Invert.	0.67 ± .027	0.17 ± 0.08	1.19 ± 0.22	0.60 ± 0.20
<i>Halichoeres brasiliensis</i> *	Mob. Invert.	0.19 ± 0.09	–	0.19 ± 0.09	0.20 ± 0.09
<i>Halichoeres poeyi</i> *	Mob. Invert.	0.10 ± 0.10	0.83 ± 0.21	0.29 ± 0.10	1.80 ± 0.31
<i>Halichoeres sazimai</i> *	Mob. Invert.	–	0.65 ± 0.26	–	–
<i>Thalassoma noronhanum</i>	Planktivore	0.10 ± 0.07	–	–	–
Labrisomidae					
<i>Labrisomus nuchipinnis</i> *	Carnivore	0.29 ± 0.12	0.09 ± 0.06	0.52 ± 0.24	0.05 ± 0.05
Lutjanidae					
<i>Lutjanus analis</i>	Carnivore	0.05 ± 0.05	–	0.05 ± 0.05	–
<i>Lutjanus cyanopterus</i>	Carnivore	–	–	0.05 ± 0.05	–
Monacanthidae					
<i>Cantherinus macrocerus</i>	Omnivore	–	–	0.05 ± 0.05	–
<i>Cantherinus pullus</i>	Omnivore	–	–	0.14 ± 0.10	–
<i>Stephanolepis hispidus</i>	Omnivore	–	–	0.05 ± 0.05	–
Mullidae					
<i>Pseudupeneus maculatus</i>	Mob. Invert.	0.14 ± 0.10	0.09 ± 0.06	–	0.25 ± 0.10
Muraenidae					
<i>Gymnothorax miliaris</i>	Piscivore	0.05 ± 0.05	–	–	–
<i>Gymnothorax vicinus</i>	Piscivore	0.05 ± 0.05	–	–	0.05 ± 0.05
Ogcocephalidae					
<i>Ogcocephalus vespertilio</i>	Carnivore	–	–	–	0.05 ± 0.05
Pomacanthidae					
<i>Pomacanthus paru</i> *	Omnivore	1.86 ± 0.97	0.22 ± 0.13	0.90 ± 0.48	1.40 ± 0.53
Pomacentridae					
<i>Abudefduf saxatilis</i> *	Omnivore	22.81 ±4.42	0.26 ± 0.16	14.71 ±3.32	2.20 ± 0.79
<i>Chromis flavicauda</i>	Planktivore	–	0.09 ± 0.06	–	–
<i>Chromis jubauna</i> *	Planktivore	2.38 ± 1.94	3.61 ± 1.55	2.24 ± 1.33	4.15 ± 2.02
<i>Chromis multilineata</i> *	Planktivore	24.05 ±5.23	–	12.43 ±5.07	4.95 ± 1.69
<i>Stegastes fuscus</i> *	Ter. Herbiv.	9.90 ± 2.29	2.70 ± 0.61	8.19 ± 1.40	3.60 ± 1.13
<i>Stegastes pictus</i> *	Ter. Herbiv./	–	0.26 ± 0.13	–	0.40 ± 0.15

	Plankt.				
<i>Stegastes variabilis</i> *	Ter. Herbiv.	1.24 ± 0.44	–	0.24 ± 0.15	0.30 ± 0.15
Priacanthidae					
<i>Heteropriacanthus cruentatus</i>	Carnivore	0.10 ± 0.10	–	0.47 ± 0.47	0.05 ± 0.053
Scaridae					
<i>Cryptotomus roseus</i>	Rov. Herbiv.	0.05 ± 0.05	0.09 ± 0.09	–	0.15 ± 0.11
<i>Scarus trispinosus</i>	Rov. Herbiv.	–	–	0.05 ± 0.05	–
<i>Scarus zelindae</i>	Rov. Herbiv.	–	–	0.05 ± 0.05	–
<i>Sparisoma amplum</i>	Rov. Herbiv.	–	–	0.33 ± 0.16	–
<i>Sparisoma axillare</i> *	Rov. Herbiv.	0.57 ± 0.13	–	0.14 ± 0.04	0.35 ± 0.07
<i>Sparisoma frondosum</i> *	Rov. Herbiv.	0.95 ± 0.29	0.04 ± 0.04	0.90 ± 0.28	0.75 ± 0.16
<i>Sparisoma tuiupiranga</i> *	Rov. Herbiv.	–	0.30 ± 0.15	–	0.25 ± 0.14
Scienidae					
<i>Odontoscion dentex</i> *	Carnivore	0.57 ± 0.48	–	0.86 ± 0.60	0.10 ± 0.10
<i>Pareques acuminatus</i>	Mob. Invert.	0.05 ± 0.05	0.04 ± 0.04	–	–
Scorpaenidae					
<i>Scorpaena</i> spp.	Carnivore	–	0.04 ± 0.04	–	–
Serranidae					
<i>Serranus baldwini</i>	Mob. Invert.	–	0.22 ± 0.11	–	0.25 ± 0.12
Sparidae					
<i>Calamus pennatula</i> *	Mob. Invert.	–	0.57 ± 0.28	–	–
<i>Diplodus argenteus</i> *	Omnivore	3.90 ± 2.21	1.39 ± 0.52	3.86 ± 1.30	1.75 ± 0.42
<i>Pagrus pagrus</i> *	Carnivore	–	2.26 ± 0.98	–	0.15 ± 0.11
Synodontidae					
<i>Synodus intermedius</i>	Piscivore	–	0.04 ± 0.04	–	0.10 ± 0.07
Tetraodontidae					
<i>Canthigaster figueiredoi</i> *	Sessile Invert.	–	0.30 ± 0.18	–	0.25 ± 0.12
<i>Sphoeroides spengleri</i>	Mob. Invert.	–	–	–	0.20 ± 0.14

Different trophic categories were not similarly affected by cold water (Table 3, Fig. 4). Although macrocarnivores, mobile invertebrate feeders and sessile invertebrate feeders did not show significant differences between factors, other categories did. Territorial herbivores differed significantly only between depths, with a higher mean abundance in the shallow ($p < 0.0001$, $F = 21.535$), but not between seasons or among interactions indicating that this trophic group did not show differences in abundance related to cold water. Planktivorous fishes also were more abundant in shallow water ($p = 0.002$, $F = 10.263$) and did not differ significantly between seasons. Omnivorous fishes differed significantly between depths and were

more abundant in the shallow ($p < 0.0001$, $F = 68.776$). However, their abundance was significantly different between seasons within deep samples, being lower in summer than winter ($p = 0.002$, $F = 9.628$), which indicates again low temperature as a contributing factor reducing abundance. The abundance of roving herbivores decreased significantly only at the deep during summer ($p = 0.0001$, $F = 16.611$). Thus, one could suggest that only omnivores and roving herbivores were affected by cold water (Fig. 4).

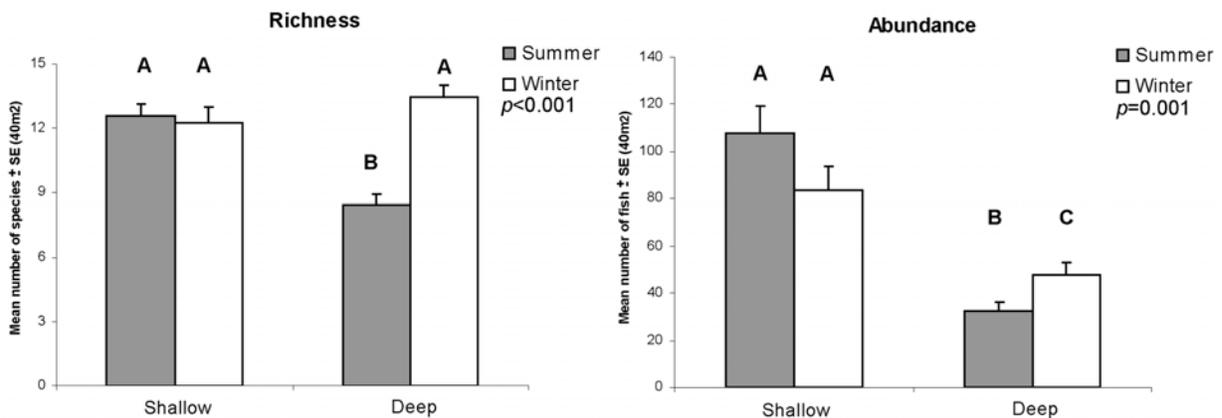


Figure 3. Mean abundance and species richness (\pm SE) per transect of samples taken at different depth categories and seasons. The p value resulted from the interaction among factors. Letter above bar indicate homogenous groups extracted from SNK test.

Table 2. Summary of two-way ANOVA for species richness and fish abundance per transect. Significant values of p are in bold (<0.05). For those variables differing significantly among factors, homogenous subsets were extracted by Student-Newman-Keuls test (Zar 1999).

Parameter	Factor	df	MS	F	P	SNK
Richness	Depth	1	0.089	7.355	0.008	Shallow > Deep
	Season	1	0.194	16.055	<0.001	Winter > Summer
	Depth x Season	1	0.277	22.849	<0.001	Deep Summer < all other combinations
	Error	81	0.012			
Abundance	Depth	1	3.063	62.727	<0.001	Shallow > Deep
	Season	1	0.022	0.463	0.497	
	Depth x Season	1	0.513	10.507	0.001	Deep Summer < Deep Winter < Shallow Winter, Shallow Summer
	Error	81	0.048			

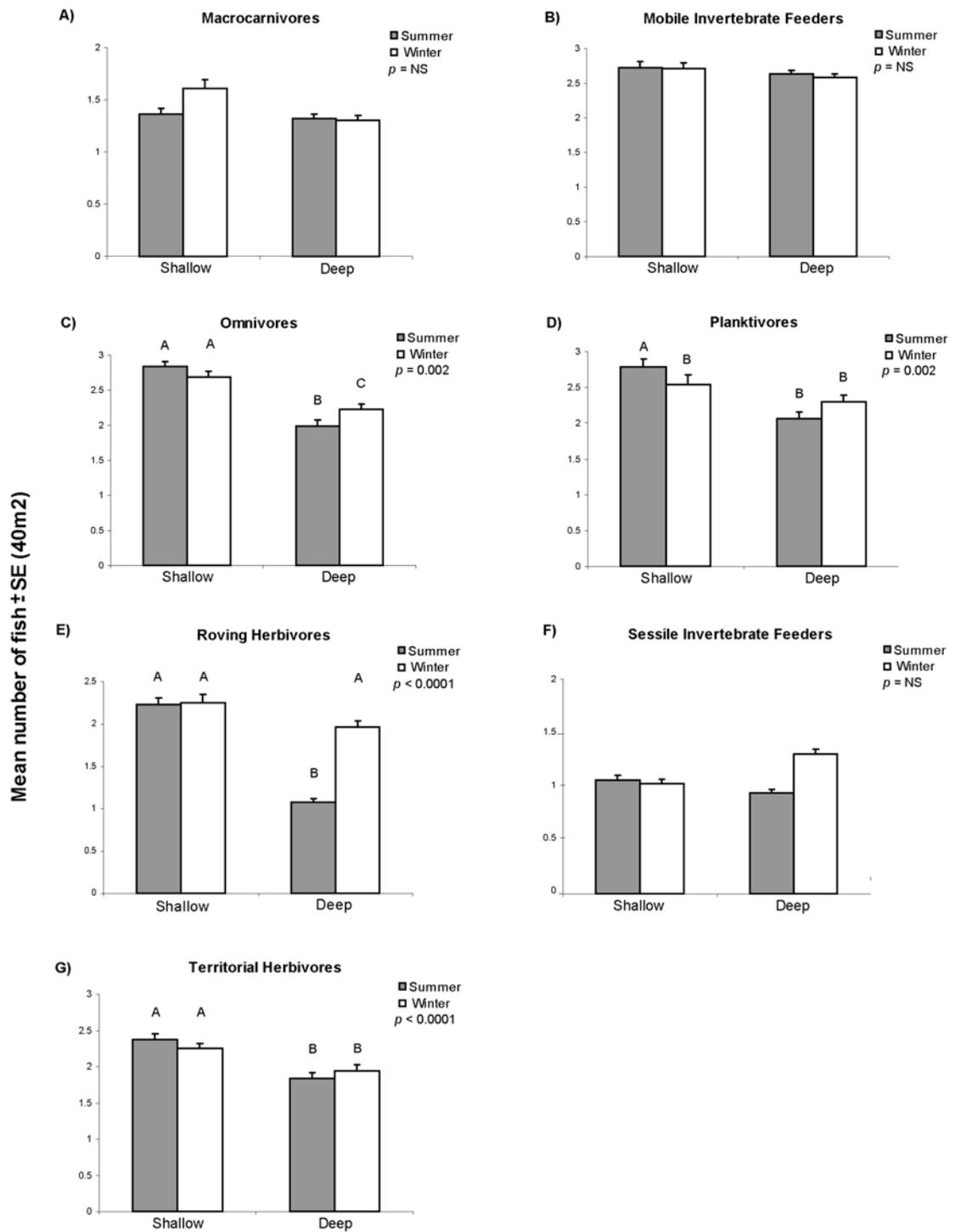


Figure 4. Mean abundance of trophic groups (\pm SE) per transect of samples taken at different depth categories and seasons. The p value resulted from the interaction among factors. The homogenous subsets were extracted for the interaction effects by student-Newman-Keuls test.

Table 3. Summary of two-way ANOVA for trophic categories abundances per transect. Factors included depth (shallow and deep) and season (summer and winter). Significant values of p are in bold (<0.05). For those variables differing significantly among factors, homogenous subsets were extracted by Student-Newman-Keuls test (Zar 1999).

Trophic Category	Factor	df	MS	F	P	SNK
Macrocarnivore	Depth	1	0.004	0.063	0.802	
	Season	1	0.017	0.236	0.628	
	Depth x Season	1	0.008	0.122	0.727	
	Error	81	0.072			
Mobile Invertebrate Feeder	Depth	1	0.001	0.014	0.904	
	Season	1	0.026	0.219	0.640	
	Depth x Season	1	0.001	0.014	0.903	
	Error	81	0.121			
Omnivore	Depth	1	9.292	68.776	<0.0001	Shallow > Deep
	Season	1	0.141	1.049	0.308	
	Depth x Season	1	1.300	9.628	0.002	Deep Summer < Deep Winter < Shallow Winter , Shallow Summer
	Error	81	0.135			
Planktivore	Depth	1	2.678	10.263	0.002	Shallow > Deep
	Season	1	0.048	0.187	0.665	
	Depth x Season	1	2.561	9.816	0.002	Shallow Summer > All other combinations
	Error	81	0.260			
Roving Herbivore	Depth	1	3.027	24.618	<0.0001	Shallow > Deep
	Season	1	1.378	11.210	0.001	Winter > Summer
	Depth x Season	1	2.043	16.611	0.0001	Deep Summer < All other combinations
	Error	81	0.122			

Sessile Invertebrate Feeder	Depth	1	0.037	0.914	0.341	
	Season	1	0.132	3.194	0.077	
	Depth x Season	1	0.144	3.484	0.065	
Territorial Herbivore	Depth	1	3.258	21.535	<0.0001	Shallow > Deep
	Season	1	0.012	0.085	0.770	
	Depth x Season	1	0.155	1.029	0.313	
	Error	81	0.151			

The distinctiveness of samples taken from colder water were confirmed by a principal component analysis (PCA) in which seasons related to ‘deep’ were positioned very apart each other on the graph, whereas in the case of shallow, both seasons clustered together (Fig. 5). As depicted on the abundance graph (Fig. 3b), also in the PCA, three groups are clearly distinguished. In the PCA ordination diagram axis 1 represents a gradient in depth and explains 88% of the variance in the weighted averages (Fig. 5). Axis 2 accounts for other differences and was responsible just for 7% of the variability. Among the species that most contributed for the recorded variability *Pagrus pagrus*, *Calamus pennatula*, *Halichoeres sazimai* and *Pseudocaranx dentex* formed a group associated with the deep summer samples and thus to the cold waters from the upwelling. Positioned very opposite to them on the PCA plot were a group of species which occur at the deep in winter but whose abundances were significantly lower or were even absent in summer (*Pomacanthus paru*, *Chaetodon striatus*, *Acanthurus chirurgus*, *Kyphosus* spp., *Sparisoma frondosum*, *Elacatinus figaro* and *Chromis multilineata*). The pairwise comparisons of species revealed the effects of the cold water at species level (Fig. 6). As we were interested in the effects of the seasonal cold water intrusion and it only affect the deeper part of the reef, comparisons were held between seasons within depths. In the shallow, the species analyzed did not present any significant differences

DISCUSSION

The environmental variability promoted by upwelling mirrors in part the variability associated with high latitudes settings (Perry & Larcombe 2003). Such increases on the range of temperature values and presence of a defined seasonal component are clearly more characteristic of temperate than tropical latitudes (McGuinness 1990, Ebeling & Hixon 1991). Coral communities under the influence of seasonal upwelling within the tropical belt have their structure altered by the effect of cold water intrusion. Constraints include prevention of carbonate accretion and growth of reef framework, shifts in species' relative abundances and diversity loss (Glynn 1993, Benzoni et al. 2003) in a way that this set of features was previously defined as a 'pseudo-high-latitude' effect (Benzoni et al. 2003). Thus, it is not surprising that reef fish communities respond to upwelling in a way similar to the above mentioned patterns as they change with latitude. Data presented here showed a decrease in species richness and total abundance associated with the presence of cold water. Decrease in species richness from the tropics toward temperate areas is a well known pattern of latitudinal gradients in terrestrial and marine communities (Willig et al. 2003, Hillebrand 2004) and was extensively reported for a wide range of organism's assemblages including reef fishes (Ebeling & Hixon 1991, Floeter et al. 2004, Mora & Robertson 2005). Factors that regulate abundance of fishes on reefs have produced a lively discussion over the last thirty years and apparently there is not a clear pattern of variation in abundance that could be attributed to environmental differences between tropical and temperate assemblages (Ebeling & Hixon 1991). Upwelling areas are thought to increase productivity and to sustain low diversity plus high fish biomass, in comparatively short food webs (Bakun 1996). However, due to tropical affinities of most species in the studied community here, fishes may actively select an appropriate 'thermal niche' to optimize physiological, ecological and reproductive performance (Coutant 1987) by avoiding the deeper layer in the upwelling period and thus occupying shallower, warm waters. In fact, during the present study it was noted that some fish species formed large and tight-packed schools in the upper warmer layer actively avoiding the cold water in the

stratification period (Fig. 7). This behavior was previously recorded for other areas subjected to upwelling and even species whose abundance are not sensitive to low temperature are known to concentrate at the top of reefs that protrude above the thermocline boundary when a warm water layer is available (Buxton & Smale 1989; CEL Ferreira pers. obs. for other sites of the southeastern Brazilian coast).

Trophic categories were differentially affected by the presence of cold water and again the changes in part reflect, in part, patterns recorded for latitudinal gradients. Ferreira et al. (2004) analyzed the latitudinal variation in reef fish trophic structure among different sites along the Brazilian coast. Trophic categories that rely on high caloric food like mobile invertebrate feeders and carnivores did not show any changes in relative abundance despite latitudinal variation and the same was found in our study despite the presence of cold water. Relative abundance of sessile invertebrate feeders also neither changed with latitude nor with the presence of cold water. Roving herbivore was one of the categories in which a decrease in abundance was recorded due to cold water from the upwelling. Herbivorous fishes are thought to be particularly sensitive to low temperature due to physiological constraints related to energetic demands and algae digestion in cold waters (Floeter et al. 2005). In fact, the decrease of roving herbivores with increasing latitude (by a decrease in mean SST) was one of the most consistent patterns of latitudinal variation of reef fish communities (Meekan & Choat 1997, Ferreira et al. 2004, Floeter et al. 2004, Floeter et al. 2005). Despite physiological constraints on herbivory, territorial herbivores did not change their abundance in presence of cold water. This pattern was clearly related to their restricted mobility as compared to roving herbivores. Abundance of omnivorous fishes was also significantly influenced by cold water in the present study, although the high density of *Abudefduf saxatilis* at the study site led mainly this pattern. Omnivorous fishes have plasticity to change their diets from algal to animal material or to explore a wide set of animal material (from sessile to mobile invertebrates) to circumvent physiological constraints and survive in harsh conditions, including cold water (Behrens & Lafferty 2007). Although the relative abundance of omnivorous fishes, and particularly of *A. saxatilis*, increases with latitude along the

Brazilian coast (Ferreira et al. 2004) it seems that, despite its capacity to inhabit high latitude reefs, in a local scale of data collected *A. saxatilis* exert an avoidance for colder water.

Individual species present distinctive responses to the presence of cold water as would be expected. With the exception of *Sparisoma tuiupiranga*, all roving herbivores included in the analysis significantly reduced their abundance in colder water (Fig. 6b). The Tuiupiranga parrotfish does not present any evident characteristics that would distinguish it from its congeners, beyond being smaller (Ferreira et al. 1998, Gasparini et al 2003) and basal in the phylogenetic tree (Robertson et al. 2006). However, this parrotfish frequently establishes territories and forages on macroalgae beds, which are mainly restricted to deeper sites in the study area. This behavior could be related to the high density of territorial damselfishes in the shallow waters. The influence of mobility and affinities to warm-temperate conditions is also consistent for the roving *Kyphosus* spp. This genus are considered to be well represented in mid and high latitude reefs and classified as a true herbivore, holding a distinct digestive mechanism with high rates of fermentation and presence of microbial symbionts (Choat & Clements 1995, Ferreira et al. 2004). However, we found that its high mobility allows them to avoid the colder lower layer of the thermocline when this option is available.

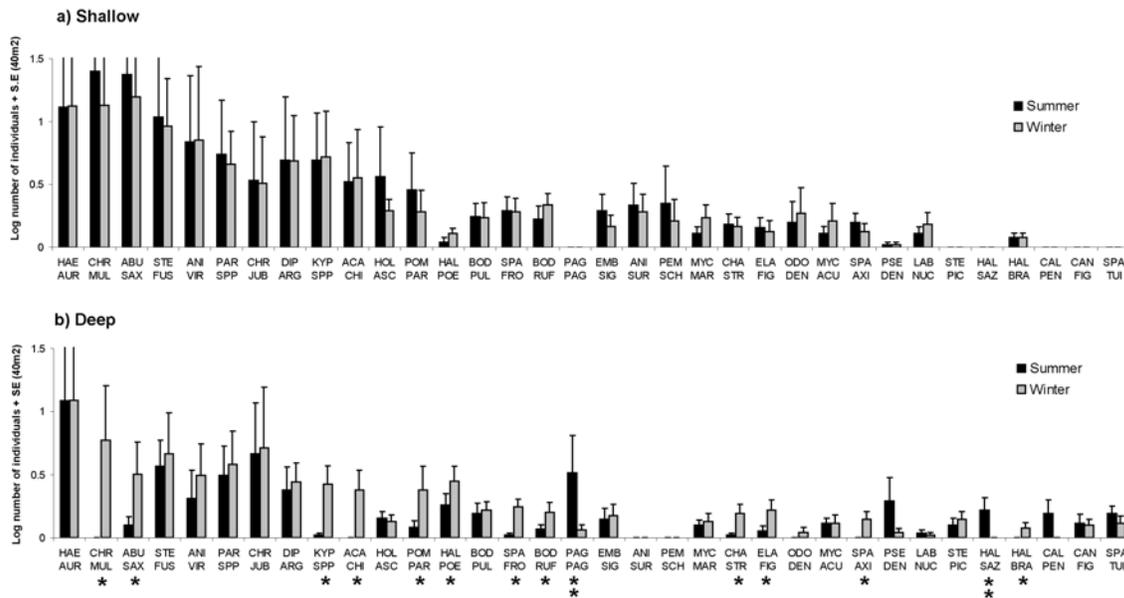


Figure 6. Pairwise t-tests of the 34 most abundant species between seasons within depths. Species whose abundances decrease significantly in summer are marked with (*) and species which abundances increase significantly in winter are marked with (**). All other comparisons were not statistically significant. Code for species in same order of appearance on the graphs: hal aur (*Haemulon aurolineatum*), chr mul (*Chromis multilineata*), abu sax (*Abudefduf saxatilis*), ste fus (*Stegastes fuscus*), ani vir (*Anisotremus virginicus*), par spp (*Parablennius* spp.), chr jub (*Chromis jubauna*), dip arg (*Diplodus argenteus*), kyp spp (*Kyphosus* spp.), aca chi (*Acanthurus chirurgus*), hol asc (*Holocentrus ascensionis*), pom par (*Pomacanthus paru*), hal poe (*Halichoeres poeyi*), bod pul (*Bodianus pulchellus*), spa fro (*Sparisoma frondosum*), bod ruf (*Bodianus rufus*), pag pag (*Pagrus pagrus*), emb sig (*Emblemariopsis signifera*), ani sur (*Anisotremus surinamensis*), pem sch (*Pempheris schomburgkii*), myc mar (*Mycteroperca marginata*), cha str (*Chaetodon striatus*), ela fig (*Elacatinus figaro*), odo den (*Odontoscion dentex*), myc acu (*Mycteroperca acutirostris*), spa axi (*Sparisoma axillare*), pse den (*Pseudocaranx dentex*), lab nuc (*Labrisomus nuchipinnis*), ste pic (*Stegastes pictus*), hal saz (*Halichoeres sazimai*), hal bra (*H. brasiliensis*), cal pen (*Calamus pennatula*), can fig (*Canthigaster figuiredoi*), spa tui (*Sparisoma tuipiranga*).

In general, fishes with high mobility avoid the deep cold layer, being restricted to shallow waters during summer. Noteworthy exceptions include *Diplodus argenteus* (Sparidae), *Anisotremus virginicus* and *Haemulon aurolineatum* (Haemulidae) and *Bodianus pulchellus* (Labridae). The Sparidae and Haemulidae are not typical coral reef families and are thought to derive from temperate groups (Bellwood & Wainwright 2000) and thus this unresponsiveness to cold water may be a result of their affinities with species of cold waters. *Bodianus pulchellus* is associated with deeper areas in Caribbean coral reefs, being

seldom seen in shallow waters (Randall 1996) and the Southern Atlantic populations seems to conform to this trend.

Species that are strongly site-attached and with limited mobility, in general did not change their abundances due the presence of cold water. However, the barber goby *Elacatinus figaro*, a small species that tends fixed cleaning stations, was less abundant during the upwelling period (Fig. 6b). Some of the small species with limited mobility could reach a state of torpor and immobility in cold waters in order to reduce their metabolic rate and consequently also reduce their energetic requirements (Thomson & Lehner 1976). Thus, because cleaning stations frequently have crevices that provide shelter, these fishes may retreat within these during upwelling period and consequently are underestimated in visual assessments.

The above pattern is clearly represented among the Pomacentridae, in which highly-mobile species such *Abudefduf saxatilis* and the midwater planktivore *Chromis multilineata* restrict their bathymetric distribution to shallow areas during the period of upwelling influence. On the other hand, highly site-attached or territorial species such *Chromis jubauna*, *Stegastes fuscus* and *S. pictus* did not change their mean abundance in deeper areas during the same period (Fig. 6b). Two species, *Halichoeres sazimai* and *Pagrus pagrus*, had a positive association (were more abundant) in the presence of the upwelling. *Pagrus pagrus* is a typical target of deep fisheries along southeastern and southern Brazilian coast (Cegole & Rossi-Wongtschowski 2002) and its distribution extends to Argentina (Carvalho-Filho 1999). Both *Halichoeres sazimai* and *P. pagrus* are known to characteristically inhabit reefs deeper than 30 meters and the adjacent unconsolidated bottoms at the study site (Luiz Jr. et al. 2008, Luiz Jr. et al. 2009) and other subtropical reefs along the coast (Ferreira et al. 2001). Both species favored relatively shallower bottoms when the cold water was present.

Very little is known about the way community characteristics (richness and abundance of organisms) influences behavior. Further research in this topic should include specific behavioral changes that may be induced by upwelling. For instance, the Caribbean damselfish *Stegastes planifrons* is known to alter the time spent for agonistic behavior by detecting changes in abundance of potential competitors

instead of changes in total species richness and/or abundance (Abrey 2005). One, thus, could hypothesize that *S. fuscus* also spend lesser effort in territorial defense when its territory is under upwelling influence and the abundance and diversity of roving herbivores are negatively affected, albeit *S. fuscus* reduces its feeding frequency during this period (Ferreira et al. 1998). Another behaviorally mediated interaction among reef fishes which are known to be influenced by community characteristics is cleaning symbiosis (Floeter et al. 2007). Sazima et al. (2000) suggested that seasonality in the SST (sea surface temperature) in southeastern Brazilian coast may influence temporal patterns of daily activity of the barber goby *E. figaro*. Thus, it would be instructive to study to what extent reduction in species richness and abundance of some of its habitual client fishes would affect the frequency of daily cleaning interactions of *E. figaro* during upwelling period.

All around the coast and islands off southeastern and southern Brazil there are sites influenced directly or indirectly by seasonal or periodical upwelling events, with waters at 18°C or below that. At some sites the cold water has direct influence over shallow reef zones (Ferreira et al. 2001) and in others, as herein demonstrated, only deep reef zones. These events are triggered by differential oceanographic, meteorological, geological, but most frequently, by a coupling of one or more of these processes (Valentin et al. 1987, Campos et al. 2000). The most frequently reported changes in environment conditions from upwelling events are anomalies in the distribution of oceanographic properties that provide a great amount of nutrients to the euphotic zone and a consequent increase in primary net productivity (Daly & Smith Jr., 1993). Seasonally the water masses of shallow and deeper reefs may be separated by a thermocline that influences nutrient circulation and detritus path. If cold water upwelling provides clear constraints to reef fishes and possibly for other reef organisms, the overall benthic community is taking profit of an important source of nutrients. The bottom up processes are in that way incremented and culminate in high rates of primary production and microbial looping, which will further provide food for herbivorous fishes and invertebrates as well (Gonzalez-Rodriguez et al. 1992, Sumida et al. 2005). Presently, however, our

knowledge of the influence of local upwelling upon trophic web chain and communities of these subtropical systems are understudied.



Figure 7. Usually found alone or in pairs at the Laje de Santos, the French Angelfish (*Pomacanthus paru*) aggregates in densely packed schools restricted to the upper warmer layer during upwelling events.

Photo: A. Carvalho-Filho.

LITERATURE CITED

- Abrey CA (2005) The effect of community on the territorial behavior of the threespot damselfish. *Environ Biol Fish* 73:163–170
- Aburto-Oropeza O, Balart EF (2001) Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *Mar Ecol* 22:283–305
- Andrade HA (2003) The relationship between the skipjack tuna (*Katsuwonus pelamis*) fishery and seasonal temperature variability in the south-western Atlantic. *Fish Oceanogr* 12:10–18

- Andrew N, Francis M (2003) The living reef: the ecology of New Zealand rocky reefs. Craig Potton, Nelson, NZ
- Bakun A (1996) Patterns in the ocean: ocean processes and marine population dynamics. California Sea Grant/NOAA
- Behrens MD, Lafferty KD (2007) Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity gradient in herbivorous fishes. *Can J Fish Aquat Sci* 64:867–873
- Bellwood DR (1996) The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. *Coral Reefs* 15:11–19
- Bellwood DR, Wainwright PC (2002) The history and biogeography of fishes on coral reefs. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego
- Benzoni F, Bianchi CN, Morri C (2003) Coral communities of the northwestern Gulf of Aden (Yemen): variation in framework building related to environmental factors and biotic conditions. *Coral Reefs* 22:475–484
- Bohnsack JA (1983) Resiliency of reef fish communities in the Florida Keys following a January 1977 hypothermal fish kill. *Environ Biol Fish* 9:41–53
- Bowen BW, Bass AL, Rocha LA, Grant WS, Robertson DR (2001) Phylogeography of the trumpetfishes (*Aulostomus*): ring species complex on a global scale. *Evolution* 55:1029–1039
- Briggs, JC (1974) *Marine Zoogeography*. McGraw-Hill, New York
- Buxton CD, Smale MJ (1989) Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the southern Cape Coast. *J App Ecol* 26:441–451
- Campos EJD, Godoi SS, Ikeda Y, Nonato LV, Gonçalves JE (1994) Summertime thermohaline structure of the Brazil Current Region between Santos (SP) and Rio de Janeiro (RJ). *Bolm Inst Oceanogr* 42:1–18

- Campos EJD, Velhote D, Silveira ICA (2000) Shelf break upwelling driven by Brazil Current cyclonic meanders. *Geophys Res Lett* 27:751–754
- Carvalho-Filho A (1999) Peixes: Costa Brasileira. Marca D'água, São Paulo
- Castro BM, Miranda LB (1998) Physical oceanography of the western Atlantic continental shelf located between 4°N and 34°S. In: Robinson AR, Brink KH (eds) *The Sea*, Volume 11. John Wiley and Sons, New York
- Cegole MC, Rossi-Wongtschowski CLDB (2002) Análise das principais pescarias comerciais do sudeste-sul do Brasil. Vol. 1. Dinâmica das frotas pesqueiras. Levantamento dos recursos vivos da zona econômica exclusiva, Programa REVIZEE/Score-Sul. Ministério do Meio Ambiente, dos Recursos Hídricos e da Amazônia Legal, Brasília
- Choat JH, Clements KD (1998) Vertebrate herbivores in marine and terrestrial environments: a nutritional perspective. *Ann Rev Ecol Syst Evol* 29:375–403
- Choat JH, Robertson DR (2002) Age-based studies. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego
- Coutant CC (1987) Thermal preference: when does an asset become a liability? *Environ Biol Fish* 18:161–172
- Daly KL, Smith Jr, WO (1993) Physical-biological interactions influencing marine plankton production. *Ann Rev Ecol Evol Syst* 24:555–585
- Dominici-Arosemena A, Wolff M (2006) Reef fish community structure in the tropical Eastern Pacific (Panamá): living on a relatively stable rocky reef environment. *Helgol Mar Res* 60:287–305
- Ebeling AW, Hixon MA (1991) Tropical and temperate reef fishes: comparison of community structures. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego
- Eme J, Bennett WA (2008) Low temperature as a limiting factor for introduction and distribution of Indo-Pacific damselfishes in the eastern United States. *J Thermal Biol* 33:62–66

- Ferreira CEL, Peret AC, Coutinho R (1998) Seasonal grazing rates and food processing by tropical herbivorous fishes. *J Fish Biol* 53(Suppl A):222–235
- Ferreira CEL, Gonçalves JEA, Coutinho R (2001) Community structure of fishes and habitat complexity on a tropical rocky shore. *Environ Biol Fish* 61: 353–369
- Ferreira CEL, Floeter SR, Gasparini JL, Ferreira BP, Joyeux J-C (2004) Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *J Biogeogr* 31:1093–1106
- Floeter SR, Gasparini JL (2000) The south-western Atlantic reef fish fauna: composition and zoogeographic patterns. *J Fish Biol* 56:1099–1114
- Floeter SR, Guimarães RZP, Rocha LA, Ferreira CEL, Rangel CA, Gasparini JL (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecol Biogeogr* 10:423–431
- Floeter SR, Ferreira CEL, Dominici-Arosemena A, Zalmon IR (2004) Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. *J Fish Biol* 64:1680–1699
- Floeter SR, Behrens MD, Ferreira CEL, Paddock MJ, Horn MH (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. *Mar Biol* 147:1435–1447
- Floeter SR, Vázquez DP, Grutter AS (2007) The macroecology of marine cleaning mutualisms. *J Anim Ecol* 76:105–111
- Floeter SR, Rocha LA, Robertson DR, Joyeux J-C, Smith-Vaniz WF, Wirtz P, Edwards AJ, Barreiros JP, Ferreira CEL, Gasparini JL, Brito A, Falcón JM, Bowen BW, Bernardi G (2008) Atlantic reef fish biogeography and evolution. *J Biogeogr* 35:22–47
- Gasparini JL, Joyeux J-C, Floeter SR (2003) *Sparisoma tuiupiranga*, a new species of parrotfish (Perciformes: Labroidei: Scaridae) from Brazil, with comments on the evolution of the genus. *Zootaxa* 384:1–14
- Glynn PW (1993) Monsoonal upwelling and episodic *Acanthaster* predation as probable controls of coral reef distribution and community structure in Oman, Indian Ocean. *Atoll Res Bull* 379:1–66

- Gonzalez-Rodriguez E, Valentin JL, André DL, Jacob AS (1992) Upwelling and downwelling at Cabo Frio (Brazil): comparisons of biomass and primary production responses. *J Plank Res* 14:289–306
- Hillebrand H (2004) Strength, slope and variability of marine latitudinal gradients. *Mar Ecol Prog Ser* 273:251–267
- Hsieh HJ, Hsien YL, Tsai WS, Chen CA, Su WC, Jeng MS (2008) Tropical fishes killed by the cold. *Coral Reefs* 27:599
- Humann P, DeLoach N (2002) Reef fish identification: Florida, Caribbean, Bahamas. New World Publications, Jacksonville
- Kimball ME, Miller JM, Whitfield PE, Hare JA (2004) Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. *Mar Ecol Prog Ser* 283:269–278
- Kleypas JA, McManus JW, Meñez LAB (1999) Environmental limits to coral reef development: where do we draw the line? *Amer Zool* 39:146–159
- Lopes RM, Brandini F, Gaeta SA (1999) Distribution patterns of epipelagic copepods off Rio de Janeiro (SE Brazil) in summer 1991/1992 and winter 1992. *Hydrobiologia* 411:161–174
- Love JW, Chase PD (2007) Marine fish diversity and composition in the Mid-Atlantic and South Atlantic Bights. *Southeastern Naturalist* 6(4):705–714
- Luiz Jr OJ, Carvalho-Filho A, Ferreira CEL, Floeter SR, Gasparini JL, Sazima I (2008) The reef fish assemblage of the Laje de Santos Marine State Park, Southwestern Atlantic: annotated checklist with comments on abundance, distribution, trophic structure, symbiotic associations, and conservation. *Zootaxa* 1807:1–25
- Luiz Jr OJ, Ferreira CEL, Rocha LA (2009) *Halichoeres sazimai*, a new species of wrasse (Perciformes: Labridae) from the Western South Atlantic. *Zootaxa* in press
- McBride RS, Able KW (1998) Ecology and fate of butterflyfishes, *Chaetodon* spp., in the temperate, western North Atlantic. *Bull Mar Sci* 63:401–416

- McCormick MI, Molony BW (1995) Influence of water temperature during the larval stage on size, age and body condition of a tropical reef fish at settlement. *Mar Ecol Prog Ser* 118:59–68
- McGuinness KA (1990) Physical variability, diversity gradients and the ecology of temperate and tropical reefs. *Austral J Ecol* 15:465–476
- Meekan MG, Choat JH (1997) Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical reefs. *Mar Biol* 128:373–383
- Meekan MG, Carleton JH, McKinnon AD, Flynn K, Furnas M (2003) What determines the growth of tropical reef fish larvae in the plankton: food or temperature. *Mar Ecol Prog Ser* 256:193–204
- Menezes NA, Buckup PA, Figueiredo JL, Moura RL (2003) Catálogo das espécies de peixes marinhos do Brasil. Museu de Zoologia USP, São Paulo
- Mora C, Ospina AF (2002) Experimental effect of cold La Niña temperatures on the survival of reef fishes from Gorgona Island (eastern Pacific Ocean). *Mar Biol* 141:789–793
- Mora C, Robertson DR (2005) Causes of latitudinal gradients in species richness: a test with fishes of the tropical eastern Pacific. *Ecology* 86:1771–1782
- Moura RL, Gasparini JL, Sazima I (1999) New records and range extensions of reef fishes in the Western South Atlantic, with comments on reef fish distribution along the Brazilian coast. *Revta Bras Zool* 16:513–530
- Pereira CS (1989) Seasonal variability in the coastal circulation on the Brazilian continental shelf (29°S–35°S). *Cont Shelf Res* 9:285–299
- Perry CT, Larcombe P (2003) Marginal and non-reef-building coral environments. *Coral Reefs* 22:427–432
- Pondella II DJ, Gintert BE, Cobb JR, Allen LG (2005) Biogeography of the nearshore rocky-reef fishes at the southern and Baja California islands. *J Biogeogr* 32:187–201
- Randall JE (1967) Food habits of reef fishes of the West Indies. *Stud Trop Oceanogr* 5:665–847
- Randall JE (1996) *Caribbean Reef Fishes*. TFH Publications, Hong Kong

- Robertson DR (1998) Do coral-reef fish faunas have a distinctive taxonomic structure? *Coral Reefs* 17:179–186
- Robertson DR, Karg F, Moura RL, Victor BC, Bernardi G (2006) Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. *Mol Phylogenet Evol* 40:795–807
- Sale PF (1991) *The ecology of fishes on coral reefs*. Academic Press, San Diego.
- Sale PF (2002) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego
- Sazima I, Sazima C, Francini-Filho RB, Moura RL (2000) Daily cleaning activity and diversity of clients of the barber goby, *Elacatinus figaro*, on rocky reefs in southeastern Brazil. *Environ Biol Fish* 59:69–77
- Smith TB (2008) Temperature effects on herbivory for an Indo-Pacific parrotfish in Panamá: implications for coral–algal competition. *Coral Reefs* 27:397–405
- Sumida PYG, Yoshinaga MY, Ciotti AM, Gaeta SA (2005) Benthic responses to upwelling events off the SE Brazilian coast. *Mar Ecol Prog Ser* 291:35–42
- Thomson DA, Lehner CE (1976) Resilience of a rocky intertidal fish community in a physically unstable environment. *J Exp Mar Biol Ecol* 22:1–29
- Underwood AJ (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge
- Ventura CRR, Falcão APC, Santos JS, Fiori CS (1997) Reproductive cycle and feeding periodicity in the starfish *Astropecten brasiliensis* in the Cabo Frio upwelling ecosystem (Brazil). *Invertebr Reprod Dev* 31:135–141
- Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annu Rev Ecol Evol Syst* 34:273–309
- Zar JH (1999) *Biostatistical analysis*. Prentice Hall, New Jersey

CONCLUSÕES

A comunidade de peixes recifais do Parque Estadual Marinho da Laje de Santos é dominada por poucas espécies de ampla distribuição e grande abundância por todo o Oceano Atlântico Ocidental, além de espécies muito versáteis em relação à dieta e ao uso do habitat. Estes resultados estão de acordo com um padrão de dominância por poucas espécies generalistas em localidades com baixa riqueza de espécies na costa Brasileira e em ilhas oceânicas, quando comparadas com localidades recifais do Caribe.

Entre os fatores abióticos estudados, a profundidade foi o principal de estruturação da comunidade. Foi observado um decréscimo contínuo da riqueza de espécies e da abundância de indivíduos com o aumento da profundidade. Este resultado é diferente do padrão encontrado em alguns recifes de corais, onde um aumento da riqueza e da abundância é observado com o aumento da profundidade, geralmente alcançando um pico de riqueza em torno dos 30 metros (Brokovich 2008) e de abundância em torno de 90 metros (Thresher & Colin 1986). O padrão encontrado na Laje de Santos está mais próximo dos observados nos recifes rochosos temperados do Mediterrâneo (Bell 1983, Letourneur et al. 2003) e subtropicais no Pacífico Oriental (Aburto-Oropeza & Balart 2001), onde a riqueza de espécies e a abundância é máxima no raso e decresce de acordo com o aumento de profundidade.

O local de estudo é afetado sazonalmente por intrusões de águas frias oriundas de eventos de ressurgência em suas partes mais fundas. Como a estrutura taxonômica da comunidade de peixes recifais na Laje de Santos é composta em sua maior parte por espécies de afinidades tropicais (Luiz Jr. et al. 2008, capítulo 1 deste volume) a influência da ressurgência é provavelmente a causa desta tendência de “empobrecimento” da comunidade relacionado com o aumento da profundidade.

A complexidade do habitat é um fator positivamente correlacionado com a riqueza de espécies e a abundância de indivíduos. Entretanto, uma análise detalhada desta relação mostrou que o efeito só é significativo na zona mais rasa dos recifes. Este resultado indica uma possibilidade dos recifes rochosos

apresentarem uma escala de complexidade mais fina do que a detectada através de estimativa visual (método empregado no presente estudo). Variabilidade no tamanho de cavidades, assim como a sua quantidade, são considerados uma importante variável do habitat, correlacionada com a riqueza e a abundância de peixes (Roberts & Ormond 1987, Ferreira et al. 2001). Assim, é possível que a zona mais rasa do local de estudo tenha mais cavidades ou cavidades com maior variabilidade de tamanhos e o método de estimativa visual tenha sido falho em detectar a complexidade nesta escala.

A exposição ao batimento de ondas não está correlacionado a nenhum dos descritores da comunidade utilizados neste estudo. Isto pode ser atribuído a pequena escala do presente estudo ou a características específicas de recifes rochosos. Por exemplo, em recifes de corais, mesmo nos atóis mais expostos, há normalmente um padrão de zonação que inclui uma lagoa interna abrigada, a exposição às ondas (batimento) estando restrita ao lado externo do recife. Recifes rochosos localizados distantes na plataforma continental ou são totalmente submersos ou então adjacentes a costa de ilhas. Assim, em recifes pequenos e distantes da costa, como a Laje de Santos, mesmo quando um há uma face relativamente protegida do vento e conseqüentemente das ondas, isso não a torna abrigada da grande movimentação hidrodinâmica causada pelo efeito de correntes que influencia todo o local de estudo. O efeito da exposição ao hidrodinamismo em recifes rochosos, aparentemente, só é capaz de ser detectado em escalas espaciais maiores, como em comparações entre a costa continental e ilhas com distâncias variadas da costa onde um gradiente de exposição pode ser determinado (Floeter et al. 2007). É sugerido no presente estudo que há uma escala hierárquica de importância dos fatores físicos na estruturação da comunidade de peixes recifais no Parque Estadual Marinho da Laje de Santos.

REFERÊNCIAS

- Aburto-Oropeza O, Balart EF (2001) Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *Mar Ecol* 22:283–305
- Agardy, T. (2000) Information needs for marine protected areas: scientific and societal. *Bulletin of Marine Science* 66(3): 875-888
- Bell JD (1983) Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean Sea. *J App Ecol* 20:357–369
- Bohnsack JA (1983) Resiliency of reef fish communities in the Florida Keys following a January 1977 hypothermal fish kill. *Environ Biol Fish* 9:41–53
- Brokovich E, Einbinder S, Shashar N, Kiflawi M, Kark S (2008) Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient. *Mar Ecol Prog Ser* 371:253–262
- Carvalho-Filho A (1999) Peixes: Costa Brasileira. Marca D'água, São Paulo
- Choat JH, Bellwood DR (1991) Reef fishes: their history and evolution. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego
- Dominici-Arosemena A, Wolff M (2006) Reef fish community structure in the tropical Eastern Pacific (Panamá): living on a relatively stable rocky reef environment. *Helgol Mar Res* 60:287–305
- Ebeling AW, Hixon MA (1991) Tropical and temperate reef fishes: comparison of community structures. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego
- Eme J, Bennett WA (2008) Low temperature as a limiting factor for introduction and distribution of Indo-Pacific damselfishes in the eastern United States. *J Thermal Biol* 33:62–66

- Ferreira CEL, Gonçalves JEA, Coutinho R (2001) Community structure of fishes and habitat complexity on a tropical rocky shore. *Environ Biol Fish* 61: 353–369
- Floeter SR, Gasparini JL (2000) The south-western Atlantic reef fish fauna: composition and zoogeographic patterns. *J Fish Biol* 56:1099–1114
- Floeter SR, Guimarães RZP, Rocha LA, Ferreira CEL, Rangel CA, Gasparini JL (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecol Biogeogr* 10:423–431
- Floeter SR, Khroling W, Gasparini JL, Ferreira CEL, Zalmon IR (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. *Environ Biol Fish* 10:423–431
- Humann P, DeLoach N (2002) Reef fish identification: Florida, Caribbean, Bahamas. New World Publications, Jacksonville
- Jones, GP (1988) Ecology of rocky reef fishes of north-eastern New Zealand: a review. *New Zeal J Mar Fres Res* 22:445–462
- Kimball ME, Miller JM, Whitfield PE, Hare JA (2004) Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. *Mar Ecol Prog Ser* 283:269–278
- Letourneur Y, Ruitton S, Sartoretto S (2003) Environmental and benthic habitat factors structuring the spatial distribution of a summer infralittoral fish assemblage in the north-western Mediterranean Sea. *J Mar Biol Ass UK* 83:193–204
- Luiz Jr OJ, Carvalho-Filho A, Ferreira CEL, Floeter SR, Gasparini JL, Sazima I (2008) The reef fish assemblage of the Laje de Santos Marine State Park, Southwestern Atlantic: annotated checklist with comments on abundance, distribution, trophic structure, symbiotic associations, and conservation. *Zootaxa* 1807:1–25

- Mora C, Ospina AF (2002) Experimental effect of cold La Niña temperatures on the survival of reef fishes from Gorgona Island (eastern Pacific Ocean). *Mar Biol* 141:789–793
- Menezes NA, Buckup PA, Figueiredo JL, Moura RL (2003) Catálogo das espécies de peixes marinhos do Brasil. Museu de Zoologia USP, São Paulo
- Moura RL, Gasparini JL, Sazima I (1999) New records and range extensions of reef fishes in the Western South Atlantic, with comments on reef fish distribution along the Brazilian coast. *Revta Bras Zool* 16:513–530
- Perry CT, Larcombe P (2003) Marginal and non-reef-building coral environments. *Coral Reefs* 22:427–432
- Pondella II DJ, Gintert BE, Cobb JR, Allen LG (2005) Biogeography of the nearshore rocky-reef fishes at the southern and Baja California islands. *J Biogeogr* 32:187–201
- Randall JE (1996) *Caribbean Reef Fishes*. TFH Publications, Hong Kong
- Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar Ecol Prog Ser* 41:1–8
- Robertson DR (1998) Do coral-reef fish faunas have a distinctive taxonomic structure? *Coral Reefs* 17:179–186
- Sale PF (1991) *The ecology of fishes on coral reefs*. Academic Press, San Diego.
- Sale PF (2002) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego
- Thresher RE, Colin P (1986) Trophic structure, diversity and abundance of fishes of the deep reef (30–300m) at Enewetak, Marshall Islands. *Bull Mar Sci* 38:253–272
- Wood, R (1999) *Reef evolution*. Oxford University Press, Oxford

ANEXO 1

***HALICHOERES SAZIMAI*, A NEW SPECIES OF WRASSE (PERCIFORMES: LABRIDAE) FROM THE WESTERN SOUTH ATLANTIC ***

OSMAR J. LUIZ JR.¹, CARLOS E. L. FERREIRA² & LUIZ A. ROCHA³

¹ *Dept. de Zoologia e Museu de História Natural, Universidade Estadual de Campinas, Campinas, SP
13083-970, Brazil and Instituto Laje Viva, São Paulo, SP, Brasil*

² *Dept. de Biologia Marinha, Universidade Federal Fluminense, Caixa Postal 100644, Niterói, RJ 24001-
970, Brasil*

³ *Marine Science Institute, University of Texas at Austin, 750 Channel View Drive, Port Aransas, TX
78373-5015, USA*

*** Artigo aceito para publicação no periódico Zootaxa**

Abstract: *Halichoeres sazimai*, n. sp. is described from the Western South Atlantic. During many years it was misidentified as *H. bathyphilus* from the Northwestern Atlantic, but it can be distinguished from the later by striking color differences between the two species, with *H. sazimai* being characterized by a white body with a midline, zigzag patterned stripe on body, black and brownish in terminal males and yellow or golden in females and juveniles. Preserved specimens can also be distinguished by the visible mid-body stripe in *H. sazimai*, which disappears in *H. bathyphilus*. Diagnostic differences in the mitochondrial DNA cytochrome *b* gene separate *H. sazimai* from all other Western Atlantic labrids, with *H. bathyphilus* being its sister species. Individuals of *H. sazimai* were observed living on the deeper part (20-40 m) of rocky reefs and sand bottoms, apparently associated with water temperatures lower than 18°C. This species is currently known from the southeastern and southern coasts of Brazil, from Espírito Santo to Santa Catarina States.

Keywords: Taxonomy, Endemic Species, Brazilian Province, Rocky Reefs.

INTRODUCTION

Reef fishes of the genus *Halichoeres* occur throughout tropical and subtropical reefs of the world from shallow to deep reefs (Parenti & Randall 2000). Randall and Böhlke (1965) recognized nine species occurring in the Northwestern Atlantic, five of which ranging south to Brazil: *Halichoeres bivittatus*, *H. poeyi*, *H. cyanocephalus*, *H. maculipinna*, and *H. radiatus*. More recently, the latter three species had their Southern Atlantic populations revalidated as *H. dimidiatus*, *H. penrosei* and *H. brasiliensis* respectively and considered endemics to the Brazilian Province (Rocha & Rosa 2001; Rocha 2004) with the notable exception of *H. radiatus* from the Fernando de Noronha Archipelago, Atol das Rocas and St. Paul's Rocks whose population remain genetically linked with that of the Caribbean (Rocha *et al.* 2005). Additionally, two new species from the Northwestern Atlantic were described (Randall & Lobel 2003; Weaver & Rocha 2007), resulting in a total of fourteen species of *Halichoeres* in the Atlantic Ocean.

The deep-reef species *Halichoeres bathyphilus* was described from Bermuda, caught in depths over 150 meters (Beebe & Tee-Van 1932) and since then it was rarely collected or observed (Smith-Vaniz *et al.* 1999). It was further recorded in the Northwestern Atlantic from North Carolina, Florida, the Gulf of Mexico, Yucatan Peninsula and off Venezuela's coast, in depths of 27 to 118 meters (Randall & Böhlke 1965; Cervigón 1993). For nearly two decades, a wrasse from the subtropical coast of Brazil (from 20°S to 27°S) has been identified as *H. bathyphilus* (Menezes & Figueiredo 1985; Moura *et al.* 1999; Carvalho-Filho 1999). Despite its morphological similarity, striking color differences noted during underwater observations and photographs lead us to suspect that the wrasse from the rocky reefs off the Southeastern Brazilian coast was a new species of *Halichoeres*. Color patterns are usually a useful character for diagnosing reef fish species (Moura & Castro 2002), however, as Rocha *et al.* (2007) pointed out; species diagnosis based on color differences alone should be taken with caution, as they may represent within-species phenotypic variation. We therefore conducted a molecular mtDNA analysis of specimens of *H. bathyphilus* from populations in the North and South Western Atlantic, and re-analyzed

their morphological characters and color patterns in order to determine the distinctiveness of the Brazilian species.

MATERIALS AND METHODS

Morphology. Measurements follow Randall and Böhlke (1965) and Randall and Lobel (2003) and are expressed as percent standard length (SL) (Table 1). Measurements were done with dial calipers to the nearest 0.1 mm. Counts and measurements in the description are for the holotype followed, in parentheses, by the range of paratypes when different. Ratios of proportional measurements are rounded to the nearest 0.1. Institutional abbreviations follow Leviton *et al.* (1985) and Leviton and Gibbs (1988).

Genetics. DNA extraction, polymerase chain reaction, and sequencing followed the methods described in detail by Rocha (2004). PCR products were sequenced in the forward and reverse directions, and resulting mtDNA cytochrome *b* sequences are deposited at Genbank with accession number FJ800096. Sequences were aligned and edited with Sequencer version 3.0 (Gene Codes Corp., Ann Arbor, MI). In order to estimate corrected genetic distances between *H. sazimai* and *H. bathyphilus* the computer program MODELTEST version 3.06 (Posada & Crandall 1998) was used to determine the substitution model that best fit the data through a hierarchical likelihood ratio test (HLRT). The Tamura-Nei model (Tamura & Nei 1983) with gamma distribution shape parameter of 0.17 was chosen. A molecular clock for *Halichoeres* as proposed by Barber & Bellwood (2005) was used to estimate the distance of separation between the species analyzed.

Comparative material examined. *Halichoeres bathyphilus*: Bermuda: ANSP 133442, 3; ANSP 133443, 3; Florida: UF 122049; UF 203925; UF 204525; UF 209822.

***Halichoeres sazimai* sp. n.**

Figures 1, 2, 3; Table 1

Halichoeres bathyphilus, Menezes and Figueiredo 1985: 32, 92 fig. 32; Moura *et al.* 1999: 520; Carvalho-Filho 1999: 186, 314 fig. 164; Parenti and Randall 2000: 37; Joyeux *et al.* 2001: 832, 835; Rangel *et al.* 2007: 11.

Halichoeres sp., Moura & Sazima 2003: 482; Luiz Jr. *et al.* 2008: 9, 16 fig. 6a, 21 fig. 9e, 25.

Holotype: ZUEC 6323, male, 214 mm SL, Ilha de Cabo Frio, Arraial do Cabo, Rio de Janeiro State, South Eastern Brazil, 23°44'S, 42°00'W, interface rocky reef and sand bottom, 23 m, pole spear, 14 Jan 2002, C.E.L. Ferreira.

Paratypes: UF 172665, male, 192 mm SL, Laje de Santos, São Paulo State, South Eastern Brazil, 24°15'S, 46°10'W, interface rocky reef and sand bottom, 21 m, pole spear, 20 Feb 2004, O.J. Luiz Jr.; UF 171285, female, 155 mm SL, same locality as holotype, 30 Jan 2004, C.E.L. Ferreira; MZUSP 98973, 2, female, 150–176 mm SL, same data as holotype, C.E.L. Ferreira; ZUEC 6324, female, 171 mm SL, same locality as holotype, 06 Mar 2003, C.E.L. Ferreira.

Diagnosis. A species of *Halichoeres* as defined by Randall and Böhlke (1965) with the following combination of characters: dorsal rays IX, 11; anal rays III, 12; pectoral rays 13; caudal rays 14; lateral line scales 27. Distinct from other Atlantic Ocean congeners by coloration as follows: body white with a distinctive stripe running on midline of the body from the snout, through the eye to tail. The stripe is straight, broadest and continuous from the snout to the shoulder, when it turns into a line of close-set spots in a zigzag pattern on alternate scales of two adjoining rows. Terminal phase adults have the stripe entirely black or black at the first half becoming brownish, some with golden spots above and below scales, body darkened on the dorsum and the abdomen, becoming grayish or greenish in the area just

above the mid-body stripe to the base of the dorsal fin. In initial phase adults the stripe is brown on the first third of its length and yellow to golden on the last two thirds.

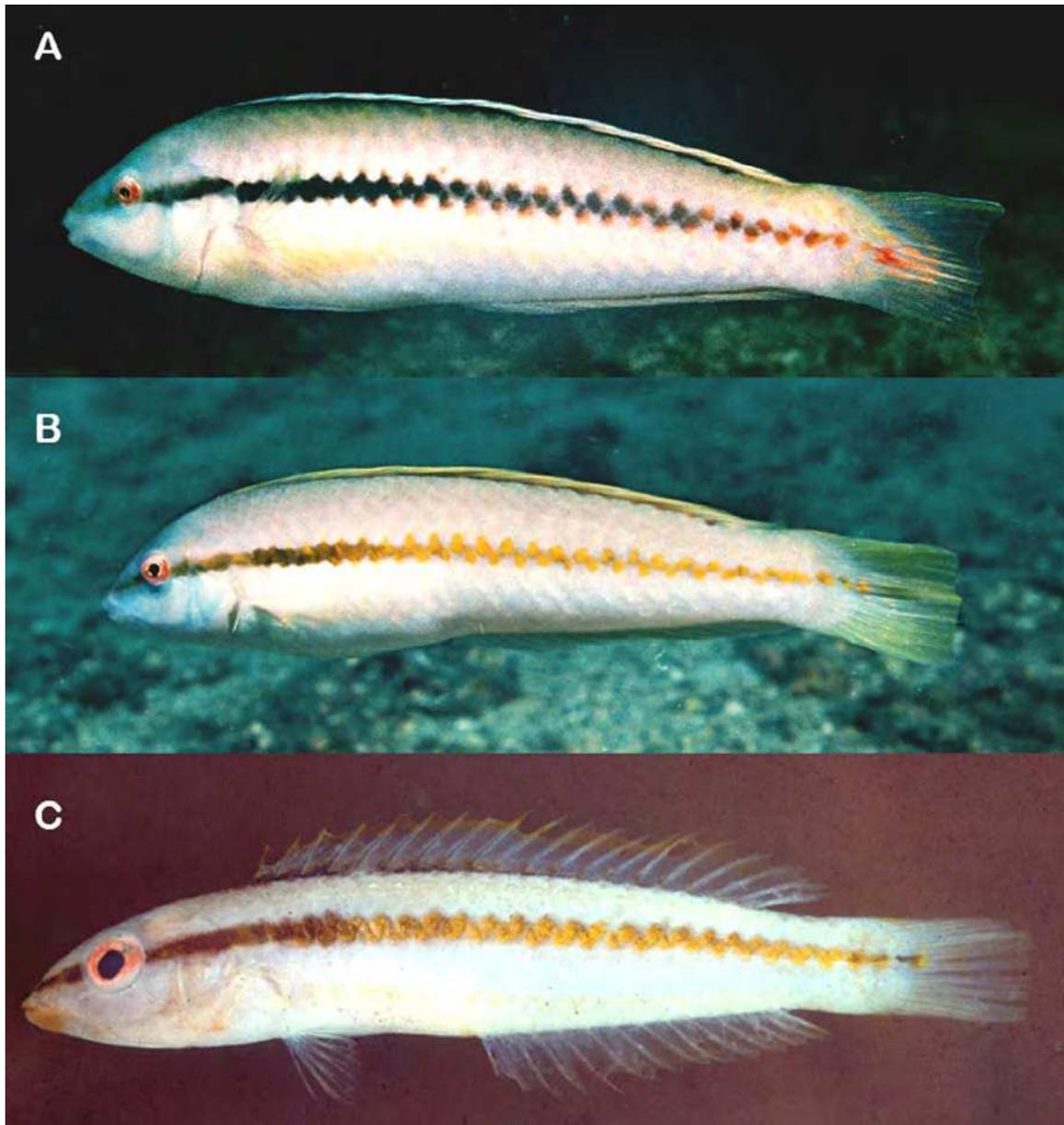


Figure 1. Underwater photographs of *Halichoeres sazimai*: (A) terminal phase male, (B) initial phase/female, and (C) newly collected recruit. Photographs by (A-B) O. J. Luiz Jr., and (C) A. Carvalho-Filho.

Table 1. Morphometrics of *Halichoeres sazimai* and its sister species *H. bathyphilus*. For *H. sazimai* the holotype is the first specimen listed, followed by the mean and range in the entire type series. For *H. bathyphilus*, mean and range of values are given, and number of specimens examined indicated in parentheses. Standard length is in mm, all other measurements are expressed as percentage of standard length. Characters that do not overlap are indicated with (*).

	<i>Halichoeres sazimai</i> (n=6)			<i>H. bathyphilus</i> (n= 8)	
	Holotype	Mean (range)			
Standard Length (mm)	214.0	176.3 (150.0–214.0)		128.0 (63.7–191.0)	
Head length	27.57	29.0 (27.6–29.9)		32.2 (30.6–33.7)*	
Eye diameter	3.93	4.2 (3.8–5.0)		5.6 (4.8–7.1)	
Interorbital width	5.56	5.4 (5.2–5.7)		5.7 (4.7–5.8)	
Body width	11.64	11.8 (10.4–13.0)		11.1 (9.9–12.8)	
Body depth	25.14	23.7 (21.7–25.6)		24.6 (20.7–27.0)	
Caudal ped. depth	12.06	12.0 (11.5–12.4)		11.8 (10.1–12.4)	
Caudal ped. length	8.36	10.5 (8.4–11.7)		10.9 (8.3–14.3)	
Snout length	8.93	9.24 (8.9–9.8)		10.2 (9.5–11.0)	
Predorsal length	25.05	25.2 (24.4–26.4)		29.8 (27.9–31.9)*	
Preanal length	53.18	51.7 (49.5–53.5)		54.0 (52.1–56.3)	
First dorsal spine	5.42	5.9 (5.4–6.3)		5.1 (4.1–5.3)*	
Longest dorsal ray	9.77	11.6 (9.8–12.8)		11.8 (10.0–13.3)	
Length third anal spine	6.59	7.6 (6.6–8.5)		7.5 (5.8–8.7)	
Longest anal ray	8.69	10.1 (8.7–11.1)		10.8 (10.0–11.9)	
Middle caudal ray	17.71	18.8 (17.7–19.8)		20.0 (18.8–22.3)	
Longest pectoral ray	15.37	16.0 (15.2–16.8)		18.0 (15.9–19.4)	
Pelvic fin length	15.61	15.0 (13.0–16.1)		16.8 (12.2–20.1)	

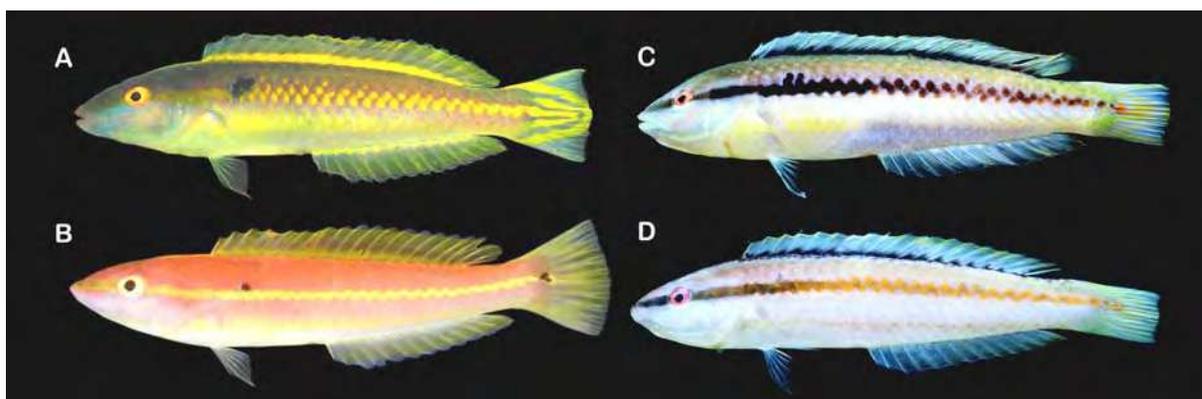


Fig. 2. Comparison of color photographs of *Halichoeres bathyphilus* (A) terminal phase male, (B) initial phase/female and *H. sazimai* (C) terminal phase male, (D) initial phase/female. Photographs by (A-B) W. Smith-Vaniz and (C-D) A. Carvalho-Filho.

Description. Dorsal rays IX, 11; anal rays III,12; all dorsal and anal soft rays branched, the last to base; pectoral rays 13 (one individual 12) upper ray unbranched; pelvic rays I, 5; principal caudal rays 14, first and last unbranched; Lateral line scales 27 (one individual 26), each with a single pore opening dorsally; four scale rows above lateral line to origin of dorsal fin, two above anterior portion of lateral line to base of middle dorsal spines; eight scale rows below lateral line to origin of anal fin. Circumpeduncular scales 15-16. Gill rakers 17-18, 6 on the upper limb; Vertebrae 10+14. Proportional measures are listed in Table 1.

Body slender, depth 4.0 (3.9–4.6) in SL, and moderately compressed, width 2.2 (1.97–2.08) in body depth; caudal peduncle depth greater than peduncle length, 2.3 (2.3–2.55) in head length; head length 3.6 (3.3–3.4) in SL; opercular flap extending slightly beyond the upper end of pectoral fin base but not beyond the lower end of pectoral fin base; dorsal profile of head uniformly convex; eye above the midlateral line of head, distance above eye to dorsal edge of head nearly half than distance below eye to ventral edge; eye relatively small, fleshy orbit diameter 7.0 (6.0–7.3) in head length.

Mouth terminal, protusible, oblique, upper jaw forming angle of about 30° to horizontal axis of head and body; snout moderately pointed, its length 3.1 (3.0–3.3) in head length; pair of forward-projecting, slightly outcurved, canine teeth at front of upper jaw, two pairs in lower jaw, outer pair also curving laterally; Posterior canine sharp and well developed (Fig. 4). Conical teeth in upper jaw 11 to 14.

Sub-orbital pores five (five to seven). Nostrils with anterior short tube and posterior flap. Caudal fin truncate to slightly rounded in young, double emarginated in adults. Free vertical and horizontal margins of preopercle smooth. Scales end just above preopercle on nape, head naked. Scales on chest smaller than body, extending anteriorly to rear margin of isthmus. Single large, elongate scale between pelvic-fin bases. Three rows of scales on caudal fin, gradually decreasing in size to rear of lateral line. Lateral line continuous with an abrupt downward curve below last three dorsal rays, extending along midline to caudal peduncle.

Coloration in life. The body is white with a distinctive stripe running on midline of the body from the snout, through the eye to tail. The stripe is straight, broadest and continuous from the snout to the shoulder, when it turns into a line of close-set spots in a zigzag pattern on alternate scales of two adjoining rows. In juveniles and initial phase females the stripe is brown on the first third of its length and yellow to golden on the last two thirds; two dark blotches, linked to the central stripe, are present below the fourth and fifth dorsal spines, sometimes golden in very large terminal males. Terminal phase males have the stripe entirely black or black at the first half becoming brownish, some with golden spots above and below scales; they also have a second stripe, lower and much less conspicuous, from the thorax through lower pectoral fin base to ventral part of caudal peduncle; this lower stripe is yellow, has a faded appearance and is not clearly visible in live individuals. The coloration of terminal males is darkened on the dorsum and the abdomen, becoming grayish or greenish in the area just above the mid-body stripe to the base of the dorsal fin; head blue dorsally and whitish ventrally; cheeks often with a pink to orange area bordered by a bluish line; a broad dark blue area present in the belly from the pelvic fin base to the caudal peduncle, immediately below the lower yellow stripe. Dorsal fin grayish to dusky, often with a greenish hue in terminal males and yellowish in females and a dark base in both phases, the terminal males often with red spots in the soft portion base; the anal fin has its base colored as the belly, and the rest of the fin is dusky green in males and dusky yellow in females; ventral fins white in females light green in terminal males; pectoral fins translucent. Caudal fin with a translucent background, greenish in terminal males and yellowish in females. Terminal males have the upper and lower margins with thin yellow or reddish borders and patterned with a series of bands with the same color of the borders, which run diagonally from the base of the fin to the tip of the middle rays; the two outer bands starting at the upper and lower bases of the fin and meeting at the central tip of the tail; two similar inner bands running parallel inside these and meeting at tips; a central straight band of same color running directly from the mid caudal base to the tip of tail. Eye red to orange, the upper and lower parts sometimes pale in the young and females.

Coloration in alcohol. Body pale brown, fin membranes yellowish brown, lighter than body. Brown stripe present and conspicuous along the midline of body from snout to tail, corresponding to black and yellow stripes in life, for males and females respectively. Dorsal fin with a dark base. Males with the dorsal part of body darker, from immediately above the stripe to the base of dorsal fin and nape. Ventral side, from the thorax to the belly darkened but not more so than the dorsal side from the anus to the lower lateral of the body, not reaching the mid-body stripe, allowing two to three rows of scales from the end of the darkened ventral band to the stripe retain the background coloration. Females have a more homogenous pale brown body, being slightly darker on the dorsum, with the conspicuous brown midline body stripe (Fig. 3).

Comparisons with congeners. *Halichoeres sazimai* was previously misidentified as *H. bathyphilus* due morphological similarities. However, they can be distinguished by coloration in live and preserved specimens (Fig. 2, 3). Despite similar patterns between *H. sazimai* and *H. bathyphilus* body textures as the mid-body zigzag patterned stripe, the diagonal bands on the caudal and colored base of dorsal fin separate those species. Terminal male *H. bathyphilus* have a green or bright yellow mid-body stripe vs. black and brownish in *H. sazimai*; the body color of the male *H. bathyphilus* is lilac on middle of sides, becoming dull at upper sides and yellow on lower sides, which contrast with the general white appearance with discrete green and blue tints respectively on the dorsal and ventral sides of the male *H. sazimai*. Males of *H. bathyphilus* also have a yellow base on dorsal and anal fin and a yellow dorsal fin outer margin while *H. sazimai* have black pigments on the base of the dorsal fin, and its outer margin is not yellow. Females of *H. bathyphilus* have a reddish-pink body color and a black spot at the base of caudal, whereas the females of *H. sazimai* have a body prominent white without the spot at the base of caudal (Fig. 2). Preserved specimens could also be distinguished by its coloration, since in *H. bathyphilus* the mid-body stripe is lost with only the two black blotches above the pectoral fin remaining on homogenous body color, whereas in *H. sazimai* the stripe is retained and is very conspicuous (Fig. 3).

Sequence divergence at the mitochondrial DNA cytochrome b gene between *H. sazimai* and *H. bathyphilus* (its sister species) is 1.02%. Even though this distance is smaller than that observed in other sister species pairs of *Halichoeres* in the Atlantic (2.2 to 6% in other pairs; Rocha 2004; Weaver & Rocha 2007), we think that the genetic difference in combination with the color pattern differences presented herein warrant the recognition of this species. Using the molecular clock proposed for *Halichoeres* (Barber & Bellwood 2005; Weaver & Rocha 2007) this distance corresponds to a separation of approximately 300,000 years, however, this time frame must be taken as a rough estimate because of the error associated with the molecular clock.

Among other species of *Halichoeres* occurring in Brazil that resemble *H. sazimai* in color, juveniles of *H. bivittatus* and *H. penrosei* either have a white body with a dark stripe running along the mid-body. *Halichoeres sazimai* could be distinguished from *H. bivittatus* by possessing a single pore in each lateral line scale while *H. bivittatus* have anterior lateral-line scales with more than one pore. Additionally, the posterior two thirds of the mid-body stripe of *H. sazimai* consisted in a line of close-set spots in a zigzag pattern on alternate scales of two adjoining rows while in *H. bivittatus* the mid-body stripe is a sequence of close-set spots in the same row. Moreover, *H. sazimai* and *H. bivittatus* are not sympatric. The known range of *H. bivittatus* in the South West Atlantic is restricted to the North Eastern coast of Brazil, from Parcel Manuel Luiz to the hump of Brazil, whereas *H. sazimai* occurs only in the South Eastern coast of Brazil, from Espírito Santo to Santa Catarina States. *Halichoeres sazimai* could be distinguished from *H. penrosei* by possessing 12 soft rays in the anal fin and two pairs of enlarged canines anteriorly in lower jaw vs. 11 soft rays in the anal fin and a single pair of enlarged canines anteriorly in lower jaw. The mid-body stripe in juveniles *H. penrosei* is broader than in *H. sazimai*, covering two or more rows continuously, and is black, whereas it is golden or dark yellow in juveniles *H. sazimai*. Moreover, the body of juveniles *H. penrosei* is not entirely white, being the upper body brownish-pink from the head to caudal peduncle.

Among *Halichoeres* species occurring in other biogeographical provinces, juveniles of *H. maculipinna* from the tropical North Western Atlantic and initial phase adults of *H. scapularis* from the tropical Indo-Pacific most resemble *H. sazimai* in color. *Halichoeres sazimai* can be distinguished from juveniles *H. maculipinna* by the same diagnostic characteristics showed above for juveniles *H. penrosei*, except for the upper body being yellowish-green. Finally, *H. sazimai* can be distinguished from *H. scapularis* by possessing 12 anal soft rays vs. 11. Additionally, the mid-body stripe of initial phase adults *H. scapularis* starts just behind the eye to the upper part of the caudal peduncle while in *H. sazimai* it start at snout and continues through the eye to the mid of tail. The mid-body stripe of *H. scapularis* is slight curved towards the dorsal fin at its anterior part while straight in *H. sazimai*.

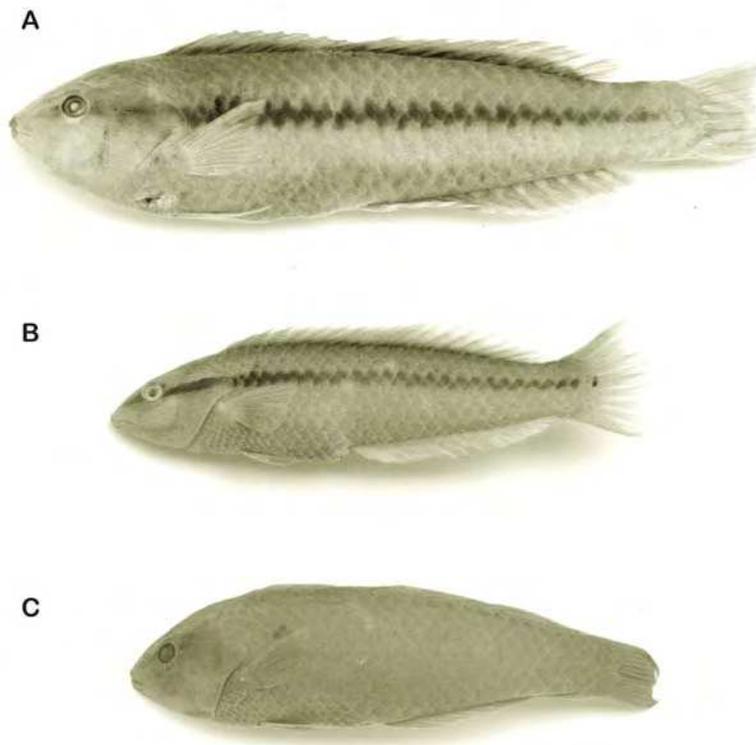


Figure 3. Lateral view of preserved specimens of *Halichoeres sazimai*, (A) holotype ZUEC 6323, (B) paratype MZUSP 98973, and *H. bathyphilus* UF 203925. Photographs by J.L. Gasparini and J.-C. Joyeux.

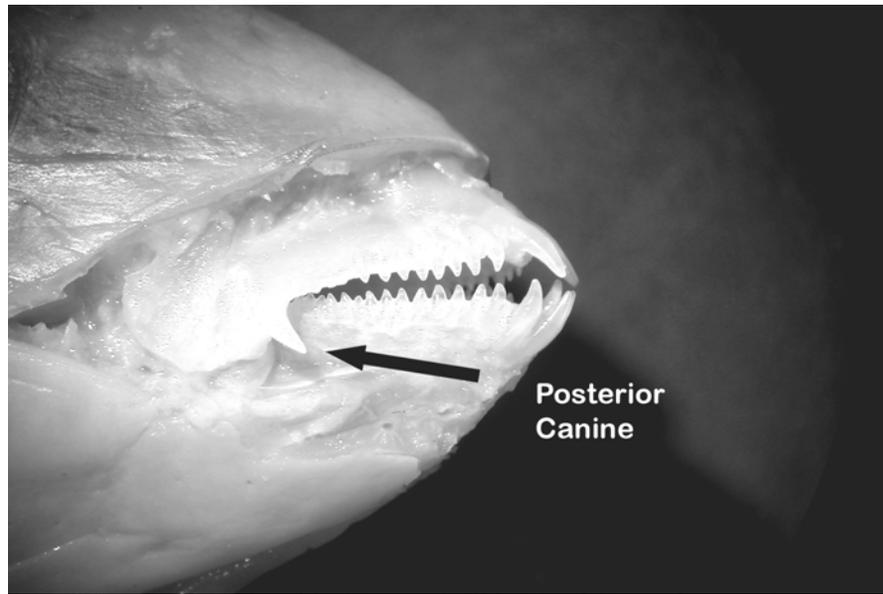


Figure 4. Mandibular apparatus of *Halichoeres sazimai*, showing the posterior canine (ZUEC 6324, female, 171 mm). Photograph by J.L. Gasparini and J.-C. Joyeux.

Habitat and behavior. This species was regularly observed solitary foraging on sand bottoms immediately adjacent to the lower end of rocky reefs. Harems composed of a few (five to ten) individuals are not common but occasionally seen. Sometimes the fishes venture over the reefs, but generally never shallower than 20 m depth depending on water temperature (they seem to be associated with temperatures lower than 18°C). As observed in other labrids, *Halichoeres sazimai* forages mostly on mobile invertebrates on soft and hard substratum, being more commonly observed foraging on sand bottoms. This behavior makes *H. sazimai* a potential nuclear species in following associations, as it has been observed in other species of *Halichoeres* (Strand 1988; Sazima *et al.* 2007) and underwater observations revealed that *H. sazimai* is followed by *Haemulon aurolineatum* (Fig. 5). It was also observed acting as a follower of other nuclear species (Luiz Jr. *et al.* 2008), namely *Dactylopterus volitans*, *Pseudocaranx dentex* and *Pseudupeneus maculatus*. Spawning occurs during the summer, probably from December to March, and the juveniles (20 mm TL) associate with the substrate, mainly reef sheltered areas and algae

patches. They may be observed mixed in small groups with juvenile *H. poeyi* and *H. brasiliensis* as well as with larger females of its own species (A. Carvalho-Filho, pers. com.).



Figure 5. A terminal phase *Halichoeres sazimai* foraging while being followed by a *Haemulon aurolineatum* school at Laje de Santos Marine State Park. Photograph by O.J. Luiz Jr.

Distribution and ecology. *Halichoeres sazimai* is apparently restricted to the South Eastern and Southern coast of Brazil, from Linhares, Espírito Santo State (J. L. Gasparini pers. com.) to the Arvoredo Marine Biological Reserve, Santa Catarina State (D. Barneche pers. com.). A single specimen was collected in North Eastern Brazil, at Arembepe, Bahia State (record based on one juvenile recruit collected by A. Carvalho-Filho; MZUSP 46386), but no established population was found there. It is most commonly observed at the deeper parts of rocky reefs on the islands of São Paulo State (Laje de Santos, Alcatrazes and Vitória islands), and Rio de Janeiro State (Cagarras Archipelago and Ilha de Cabo Frio, Arraial do Cabo). These fish were not abundant in visual census performed from 20 to 35 meters deep in the Brazilian South Eastern coast (mean density for Arraial do Cabo 23°S, 42°W = 0.1 / 40m²). As this

species is restricted to the deeper part of the reefs and shows apparently low abundance, one need to have caution in categorizing its conservation status.

Etymology. The specific name honors Dr. Ivan Sazima for his contributions to the advancement of the taxonomy and natural history of Brazilian reef fishes, as well for his exemplary guidance, which influenced a generation of Brazilian ichthyologists.



Figure 6. Southernmost record of *Halichoeres sazimai* at Arvoredo Marine Biological Reserve. Photograph by Banco de Imagens Rebiomar Arvoredo, Marcelo Kammers.

Acknowledgements

We are very grateful for the fundamental support and help in specimens' analyses we received from João Luiz Gasparini and Jean-Christophe Joyeux; Alfredo Carvalho-Filho for photographs, suggestions and unpublished information; Bill Smith-Vaniz for the photographs of *H. bathyphilus*; Diego Barneche and Marcelo Kammers for unpublished information and photographs. Sergio Floeter and two anonymous

reviewers for comments in the manuscript. We thank Dr. Damaris Rodriguez, from the American Museum of Natural History, and Dr. James S. Albert, from the Florida Museum of Natural History for the loan of collection specimens. Type specimens were collected under permit from IBAMA. Essential financial support was provided by CNPq (MSc. grant 135112/2007-9 to OJLJr).

LITERATURE CITED

- Barber, P. & Bellwood, D. R. (2005) Biodiversity hotspots: evolutionary origins of biodiversity in wrasses (*Halichoeres*: Labridae) in the Indo-Pacific and new world tropics. *Molecular Phylogenetics and Evolution*, 35, 235–253.
- Beebe, W. & Tee-Van, J. (1932) New Bermuda fish, including six new species and forty-three species hitherto unrecorded from Bermuda. *Zoologica*, 13, 109–119.
- Carvalho-Filho, A (1999) *Peixes: Costa Brasileira*. 3th ed. Ed. Melro, São Paulo. 320 pp.
- Cervigón, F. (1993) *Los peces marinos de Venezuela*. Vol. 2. Fundacion Científica Los Roques, Caracas. 425 pp.
- Joyeux, J.-C., Floeter, S. R., Ferreira, C. E. L. & Gasparini, J. L. (2001) Biogeography of tropical reef fishes: the south Atlantic puzzle. *Journal of Biogeography*, 28, 831–841.
- Leviton, A. E., & Gibbs, Jr., R. H. (1988) Standards in herpetology and ichthyology. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Supplement No. 1: additions and corrections. *Copeia*, 1988, 280–282.
- Leviton, A. E., Gibbs, Jr., R. H., Heal, E. & Dawson, C. E. (1985) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, 1985(3), 802–832.
- Luiz Jr., O. J., Carvalho-Filho, A., Ferreira, C. E. L., Floeter, S. R., Gasparini, J. L. & Sazima, I. (2008) The reef fish assemblage of the Laje de Santos Marine State Park, Southwestern Atlantic:

- annotated checklist with comments on abundance, distribution, trophic structure, symbiotic associations, and conservation. *Zootaxa*, 1807, 1–25.
- Menezes, N. A. & Figueiredo, J. L. (1985) *Manual de Peixes Marinhos do Sudeste do Brasil V. Teleostei (4)*. Museu de Zoologia da Universidade de São Paulo, São Paulo. 105 pp.
- Moura, R. L. & Castro, R. M. C., (2002) Revision of Atlantic sharpnose pufferfishes (Tetraodontiformes: Tetraodontidae: *Canthigaster*), with description of three new species. *Proceedings of the Biological Society of Washington*, 115(1), 32–50.
- Moura, R. L. & Sazima, I. (2003) Species richness and endemism levels of the Southwestern Atlantic reef fish fauna. *Proceedings 9th International Coral Reef Symposium*, 1, 481–486.
- Moura, R. L., Gasparini, J. L. & Sazima, I. (1999) New records and range extensions of reef fishes in the Western South Atlantic, with comments on reef fish distribution along the Brazilian coast. *Revista Brasileira de Zoologia*, 16(2), 513–530.
- Parenti, P. & Randall, J. E. (2000) An annotated checklist of the species of the Labroid fish families Labridae and Scaridae. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology*, 68:1–97.
- Posada, D. & Crandall, K. A. (1998) Model Test: testing the model of DNA substitution. *Bioinformatics*, 14, 817–818.
- Randall, J. E. & Böhlke, J. E. (1965) Review of the Atlantic labrid fishes of the genus *Halichoeres*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 117(7), 235–259.
- Randall, J. E. & Lobel, P. S. (2003) *Halichoeres socialis*: a new labrid fish from Belize. *Copeia*, 2003, 124–130.
- Rangel, C. A., Chaves, L. C. T. & Monteiro-Neto, C. (2007) Baseline assessment of the reef fish assemblage from Cagarras Archipelago, Rio de Janeiro, Southeastern Brazil. *Brazilian Journal of Oceanography*, 55(1), 7–17.

- Rocha, L. A. (2004) Mitochondrial DNA and color pattern variation in three western Atlantic *Halichoeres* (Labridae), with the revalidation of two species. *Copeia*, 2004, 770–782.
- Rocha L. A., & Rosa, R. S. (2001) *Halichoeres brasiliensis* (Bloch, 1791), a valid wrasse species (Teleostei: Labridae) from Brazil, with notes on the Caribbean species *Halichoeres radiatus* (Linnaeus, 1758). *Aqua, Journal of Ichthyology and Aquatic Biology* 4, 161–166.
- Rocha, L. A., Robertson, D. R., Roman, J. & Bowen, B. W. (2005) Ecological speciation in tropical reef fishes. *Proceedings of the Royal Society B* 272, 573–579.
- Rocha, L. A., Craig, M. T. & Bowen, B. W. (2007) Phylogeography and the conservation of coral reef fishes. *Coral Reefs*, 26, 501–512.
- Sazima, C., Krajewski, J. P., Bonaldo, R. M. & Sazima, I. (2007) Nuclear-follower foraging associations of reef fishes and other animals at an oceanic island. *Environmental Biology of Fishes*, 80, 351–361.
- Smith-Vaniz, W. F., Collette, B. B. & Luckhurst, B. E. (1999) *Fishes of Bermuda: History, zoogeography, annotated checklist, and identification keys*. Allen Press, Lawrence. 424 pp.
- Strand, S. (1988) Following behavior: interspecific foraging association among Gulf of California reef fishes. *Copeia*, 1988, 351–357.
- Tamura, K. & Nei, M. (1983) Estimating the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, 15, 512–526.
- Weaver, D. C. & Rocha, L. A. (2007) A new species of *Halichoeres* (Teleostei: Labridae) from the western Gulf of Mexico. *Copeia*, 2007, 798–807.

ANEXO 2

SEASONAL OCCURRENCES OF *MANTA BIROSTRIS* (CHONDRICHTHYES: MOBULIDAE) ON SOUTHEASTERN BRAZIL *

OSMAR J. LUIZ JR ^{1,2}, ANA PAULA BALBONI ², GUILHERME KODJA ²,
MAURÍCIO ANDRADE ³ & HELOISA MARUM ³

¹*Depto. de Zoologia, Universidade Estadual de Campinas, 13083-970, Campinas, SP, Brasil.*

²*Instituto Laje Viva, São Paulo, SP, Brasil. www.lajeviva.org.br*

³*Explorer Dive Center, São Paulo, SP, Brasil.*

* **Artigo publicado no periódico *Ichthyological Research***

Abstract: An analysis of 79 underwater photographs of *Manta birostris* gathered during nine years in a marine protected area at southeastern Brazil suggests a great predictability of manta rays occurrences in the region at the austral winter (June to September). The reasons for this are probably related to the seasonal oceanographic conditions, characterized by the presence of a coastal front on the study site in winter and a consequently plankton enrichment providing a feeding opportunity for manta rays. In addition, a melanistic individual similar in color to the Pacific Ocean's "black manta" is recorded for the first time in the Atlantic Ocean.

Key words *Manta birostris* · seasonality · coastal front · melanism · Laje de Santos Marine State Park.

INTRODUCTION

The manta ray, *Manta birostris* (Walbaum), is one of the largest fishes of the world, reaching a disc width of 6 m and weighing more than 1,300 kg (Bigelow and Schroeder, 1953). The ecology and behavior of *M. birostris* are scarcely known, most based on occasional observations (Bigelow and Schroeder, 1953; Homma et al., 1999; Yano et al., 1999). Notarbartolo-di-Sciara and Hillyer (1989) and Lobel (2003) reported patterns of seasonal occurrences at Venezuela (Southern Caribbean) and Johnston Atoll (Central Pacific). These authors infer that aggregations occur in temporal and spatial predictable foraging grounds where blooms of plankton arise. Seasonality in other large planktivores elasmobranches such as basking sharks, whale sharks, and *Mobula* rays is often related to temporal variability in abundance of their zooplankton prey (Notarbartolo-di-Sciara, 1988; Taylor, 1996; Sims et al., 1997; Wilson et al., 2001).

Manta rays are usually seen and photographed by recreational scuba divers in southeastern Brazil, especially at the Laje de Santos Marine State Park (*Parque Estadual Marinho da Laje de Santos*, Fig.1), a popular dive site from where most of reports on these rays from Brazil originate. These occurrences of *M. birostris* are supposed to be seasonal, such that the local dive agencies which drive recreational diving operations usually advertise a “Manta Ray Season” during the austral winter months, from June to August. In an attempt to detect temporal trends of occurrences of *M. birostris* in the Laje de Santos Marine State Park we analyzed a random, nine-year collection of manta ray photographs taken by scuba divers.

MATERIAL AND METHODS

The Laje de Santos Marine State Park (24°15'S; 46°10'W) is located 40 kilometers off the city of Santos in southeastern Brazil (Fig. 1). The proximity (less than 145 km) of São Paulo, the

largest city of the country, makes the Laje de Santos Marine State park one of the most frequented dive sites in Brazil.

The image bank analyzed started with a series of manta ray photographs made by the authors inside park boundaries. We also requested images made by local divers (*i.e.* dive instructors, staff guides and frequent users). Only photographs with a known date were used. The identification of *M. birostris* on photographs followed the diagnostic characters used by Duffy and Abbott (2003).

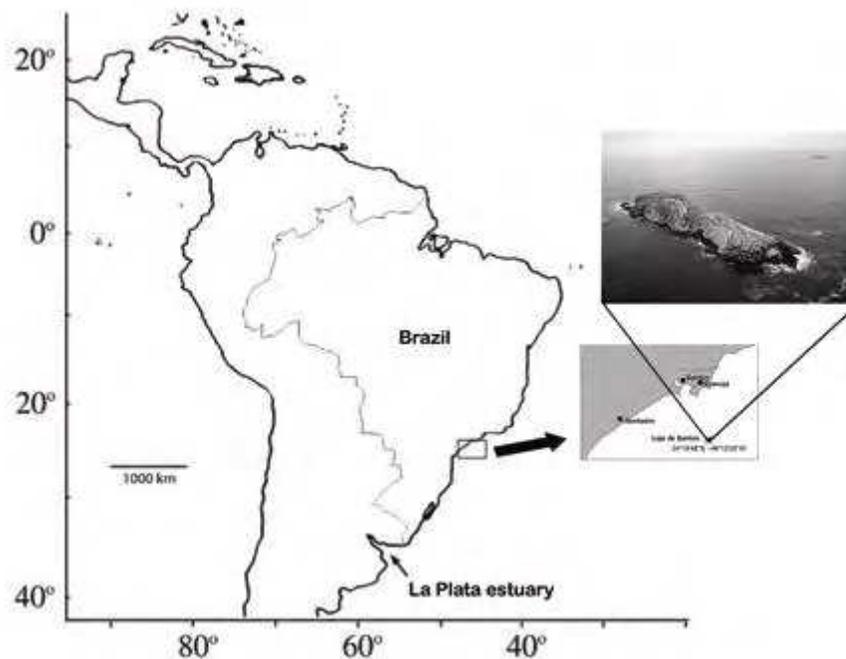


Figure 1. The Laje de Santos Marine State Park localization in western South Atlantic. The photograph shows the island where most of dives occurred (Photo by C.L.B. Francini).

RESULTS AND DISCUSSION

A total of 79 photographic records of *Manta birostris* were obtained from a nine year period (1999 to 2007) at the Laje de Santos Marine State Park (Fig. 2, Table 1). The authors and other collaborators usually visit the marine park all year round. All pictures of *M. birostris*, however, were taken only from March to September, with a peak in July (Fig. 3). Dive trips to the study area could be eventually canceled due rough weather episodes. Data obtained from diver operator's logbooks show that about 10% of the trips are cancelled during the austral summer (December – March) while in winter (June – September) this number rises up to 40%. Because the sampling effort was not constant and was higher in the summer, there is a bias to underestimating the winter sightings of *M. birostris*. This, in fact, strengthens our observations. Data thus provide strong evidence of a temporal trend in *M. birostris* occurrences suggesting much higher probabilities of manta ray encounters at the Laje de Santos Marine State Park during the austral winter.

The reasons for these seasonal occurrences of manta rays in southeastern Brazil are not known, but inferences can be made after reviewing the oceanographic patterns that affects the study site. Zooplanktivorous vertebrates usually follow their prey transported by oceanic currents, and congregate in areas where seasonal upwellings and fronts enhance plankton productivity (Sims and Quayle, 1998; Wilson, 2004; Etnoyer et al., 2006). Water masses along coastal southeastern South America were derived from different sources with varying influence along the year. The warm Brazil Current runs southward carrying tropical oligotrophic waters from the equator and in the summer is intensified by the trade winds (Campos et al. 1995). In the winter, however, the Brazil Current loses strength and the direction of coastal waters changes to northward (Pereira, 1989) allowing waters from the southern Falklands Current to reach areas of the study site (Campos et al., 1996; Pimenta et al., 2005). A characteristic seasonal pattern is the displacement of a low salinity front, derived from the discharge of La Plata River, which is carried by the Falklands Current toward lower latitudes (to 23° S) during the winter (Campos et al., 1996;

Pimenta et al., 2005) and the permanency of this front at the vicinity of the La Plata River mouth in summer.

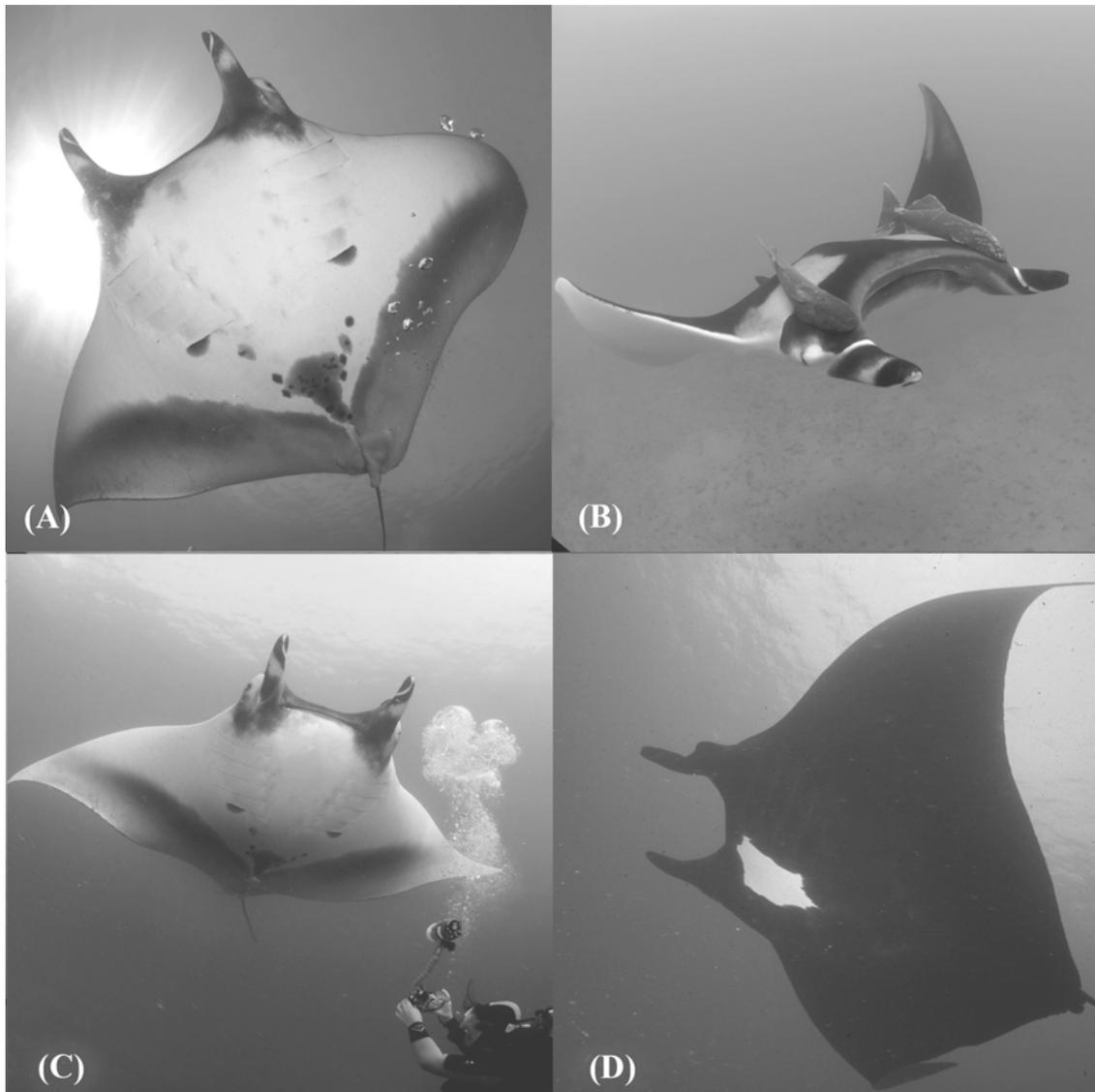


Figure 2. Selected examples of manta rays photographs analyzed: (A) Jul 3 2004, (B) Sep 4 2004, (C) Aug 2001, (D) Jul 2002 (Photos by M. Andrade).

The co-occurrence of *Manta birostris* and the coastal front in the winter at the study site could be coincidence, but the potential of this relationship cannot be dismissed. The coastal front is part of the subtropical shelf front (Piola et al., 2000) that has important ecological implications for marine organisms

(Acha et al., 2004; Molina Schiller et al., 2005). Marine fronts are well known for their bio-accumulative properties, concentrating plankton and generating patches of high productivity (Le Fèvre, 1986; Franks, 1992) to which filter-feeding predators are associated.

Table 1. Monthly occurrences of *Manta birostris* in the nine-year period from 1999 to 2007 on the Laje de Santos Marine State Park

	Months with <i>M. birostris</i> occurrences							Total
	<i>Mar</i>	<i>Apr</i>	<i>May</i>	<i>Jun</i>	<i>Jul</i>	<i>Aug</i>	<i>Sep</i>	
1999				1	2			3
2000			1					1
2001				1	12	4		17
2002				2	4	3		9
2003						1		1
2004					5	1	5	11
2005					1			1
2006		1		4	3			8
2007	1		1	3	23			28
Total	1	1	2	11	50	9	5	

Milessi and Oddone (2003) recorded a manta ray at the mouth of La Plata River in the austral summer, and the fisheries records of Itajaí Harbour, in the state of Santa Catarina (27°S, Brazil) report landings of *M. birostris* only for the months of March and April (Mazzoleni and Schwingel, 1999; R. Mazzoleni pers.comm.). Although few, these records would fit into space and time-frame expected under a hypothesis correlating manta ray occurrences with the front generated by the La Plata River's discharge. Further studies using satellite telemetry (Eckert and Stewart, 2001; Clark, 2005) should improve our understanding of the manta rays migration patterns in southeastern South America.

In a photograph made in July 2002 an odd colored individual of *M. birostris* was documented (Fig. 2d). The specimen was entirely black with the exception of a small white blotch at the thorax. Such a color pattern is typical of that displayed by the “black manta” form that had been previously only recorded in the Pacific Ocean (Barton, 1948; Homma et al., 1999). This represents the first record of a “black manta” for the Atlantic Ocean.

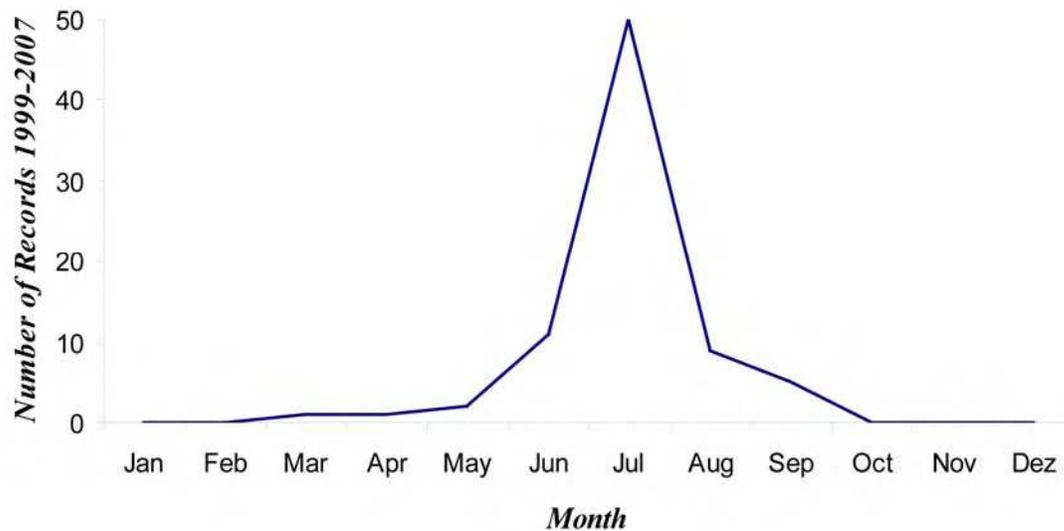


Figure 3. Monthly frequency of occurrences of *Manta birostris* in southeastern Brazil during nine year study period of 1999-2007 (n=79).

Acknowledgements. We are very grateful to all our colleagues and dive buddies that contributed with photographs: Adilson Policiclio, Armando de Luca Jr., Christian Souza, Christina Vieira, Christina Zeppini, Eduardo Guariglia, Jean Marcel, Lara Cheidde, Lucas Persona, Paula Romano, Paulão Amorim, Rafael Esteves, Regis Ezipato, Renata Linger, Ricardo Feres, Roberto “Turcão” Ajaj, Silvio Stefanelli, Tércio Leal, Ulisses Turati, Valter Marquart and Willian Spinetti. Clovis B. de Carvalho (Centralmar Dive

Center) and Instituto Laje Viva provided much valuable logistic support. We also thank Steven Wilson, Jean-C. Joyeux, João P. Barreiros and Michael Feeley for comments on the manuscript. Rodrigo Mazzoleni and Paulo Bertuol contributed unpublished information. This work was part of the project 'Foto-identificação e sazonalidade da raia manta (*Manta birostris*) no Parque Estadual Marinho da Laje de Santos' developed by the *Instituto Laje Viva* with the support of the *Instituto Florestal – SP* (COTEC - 42.637/2006). This paper is dedicated to the memory of Kazunari Yano.

LITERATURE CITED

- Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava RA (2004) Marine fronts at the continental shelves of austral South America: physical and ecological processes. *J Mar Syst* 44:83-105
- Barton O (1948) Color notes on Pacific manta, including a new form. *Copeia* 1948:146-147
- Bigelow HB, Schroeder WC (1953) Sawfishes, guitarfishes, skates and rays. In: Tee-Van J, Breder CM, Hildebrand SF, Parr AE, Schroeder WC (eds) *Fishes of the western North Atlantic, part 2*. Yale University, New Haven, pp 1–588
- Campos EJD, Miller JL, Müller TJ, Peterson RG (1995) Physical oceanography of the Southwest Atlantic Ocean. *Oceanography* 8:87-91.
- Campos EJD, Lorenzetti JA, Stevenson MR, Stech JL, Souza RB (1996) Penetration of waters from the Brazil-Malvinas confluence region along the South American Continental Shelf up to 23°S. *Anais Acad Brasileira Ciências* 68(S1):49-58
- Clark T (2005) Remote tracking of the Manta Ray (*Manta birostris*) in Hawai'i. *Pac Sci* 59:111
- Duffy CAJ, Abbot D (2003) Sightings of mobulid rays from northern New Zealand, with confirmation of the occurrence of *Manta birostris* in New Zealand waters. *N Z J Mar Freshw Res* 37:715-721

- Eckert SA, Stewart BS (2001) Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean. *Environ Biol Fish* 60:299-308
- Etnoyer P, Canny D, Mate BR, Morgan LE, Ortega-Ortiz JG, Nichols WJ (2006) Sea surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep-Sea Res Part II* 53:340-358
- Franks PJS (1992) Sink or swim: accumulation of biomass at fronts. *Mar Ecol Prog Ser* 82:1-12
- Homma K, Maruyama T, Itoh T, Yshihara H, Uchida S (1999) Biology of the manta ray, *Manta birostris* Walbaum, in the Indo-Pacific. In Séret B, Sire J-Y (eds) Proceedings of the 5th Indo Pacific Fish Conference Nouméa, 1997. Societé Française d'Ichthyologie. Paris.
- Le Fèvre J (1986) Aspects of the biology of frontal systems. *Adv Mar Biol* 23:163-299.
- Lobel PS (2003) Marine life of Johnston Atoll, Central Pacific Ocean. Natural World Press. Boston.
- Mazzoleni RC, Schwingel PR (1999) Elasmobranch species landed in Itajaí Harbor Southern Brazil. *Notas Técnicas FACIMAR* 3:111-118
- Milessi AC, Oddone MC (2003) Primer registro de *Manta birostris* (Donndorff 1798) (Batoidea: Mobulidae) en el Rio de La Plata, Uruguay. *Gayana* 67:126-129
- Molina-Schiller D, Rosales SA, Freitas TRO (2005) Oceanographic conditions off coastal South America in relation to the distribution of Burmeister's porpoise, *Phocoena spinipinnis*. *LAJAM* 4:141-156
- Notarbartolo-di-Sciara G (1988) Natural history of the rays of the genus *Mobula* in the Gulf of California. *Fish Bull* 86:45-66
- Notarbartolo-di-Sciara G, Hillyer EV (1989) Mobulid rays off eastern Venezuela (Chondrichthyes, Mobulidae). *Copeia* 1989:607-614
- Pereira CS (1989) Seasonal variability in the coastal circulation on the Brazilian continental shelf (29°S-35°S). *Continent Shelf Res* 9:285-299
- Pimenta FM, Campos EJD, Miller JL, Piola AR (2005) A numerical study of the Plata River plume along the southeastern South American continental shelf. *Brazil J Oceanogr* 53:129-146

- Piola AR, Campos EJD, Möller Jr OO, Charo M, Martinez C (2000) The subtropical shelf front off eastern South America. *J Geophys Res* 105:6565-6578
- Sims DW, Quayle VA (1998) Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature* 393:460-464
- Sims DW, Fox AM, Merrett DA (1997) Basking shark occurrence off south-west England in relation to zooplankton abundance. *J Fish Biol* 51:436-440
- Taylor JG (1996) Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at the Ningaloo Reef, Western Australia. *Mar Freshw Res* 47:637-642
- Wilson SG (2004) Basking sharks (*Cetorhinus maximus*) schooling in the southern Gulf of Maine. *Fish Oceanogr* 13:283-286
- Wilson SG, Taylor JG, Pearce AF (2001) The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Niño/ Southern Oscillation. *Environ Biol Fish* 61:1-11
- Yano K, Sato F, Takahashi T (1999) Observations of mating behavior of the manta ray, *Manta birostris*, at the Ogasawara Islands, Japan. *Ichthyol Res* 46:289-296