UNIVERSIDADE FEDERAL DO PARANÁ SETOR DE CIÊNCIAS BIOLÓGICAS PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO

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BIOGEOGRAFIA, ECOLOGIA E PRIORIDADES ESPACIAIS PARA A CONSERVAÇÃO DE VERTEBRADOS MARINHOS BRASILEIROS

> CURITIBA 2014

#### CIRO COLODETTI VILAR DE ARAUJO

#### BIOGEOGRAFIA, ECOLOGIA E PRIORIDADES ESPACIAIS PARA A CONSERVAÇÃO DE VERTEBRADOS MARINHOS BRASILEIROS

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Universidade Federal do Paraná, como requisito parcial para obtenção do título de Doutor em Ecologia e Conservação.

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#### PARECER

Os abaixo-assinados, membros da banca examinadora da defesa da tese, a que se submeteu Ciro Colodetti Villar de Araujo para fins de adquirir o título de Doutor em Ecologia e Conservação, são de parecer favorável à APROVAÇÃO do trabalho de conclusão do candidato.

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"He who loves practice without theory is like the sailor who boards ship without a rudder and compass and never knows where he may be cast."

Leonardo da Vinci (1452-1519)

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### SUMÁRIO

RESUMO GERAL	9
GENERAL ABSTRACT	11
INTRODUÇÃO GERAL	13
LITERATURA CITADA	
CAPÍTULO I – LOCAL AND REGIONAL ECOLOGICAL DRIVERS OI	F FISH
ASSEMBLAGES IN BRAZILIAN ESTUARIES	22
ABSTRACT	23
INTRODUCTION	24
MATERIALS AND METHODS	26
Study area	26
Data acquisition	27
Ichthyofauna	27
Local-scale predictors of assemblages	
Regional-scale predictors of assemblages	29
Data analysis	
RESULTS	
Assemblage composition along the coast	
Comparison of local and regional variability	40
Regional determinantes of assemblages	43
Local determinantes of assemblages	44
DISCUSSION	45
Biogeographic patterns	45
Local vs. regional variability	47
Relative importance of regional ecological processes	48
Relative importance of local ecological processes	50
CONCLUSIONS	51
LITERATURE CITED	

CAPÍTULO II – RIQUEZA DE ESPÉCIES, RARIDADE E ESC	COLHA DE ÁREAS
PARA A CONSERVAÇÃO: UM ESTUDO DE CASO COM PEI	XES ESTUARINOS
BRASILEIROS	57
RESUMO	58
ABSTRACT	59
INTRODUCÃO	60
MATERIAL E MÉTODOS	61
Base de dados	61
Análises	62
RESULTADOS	63
DISCUSSÃO	65
LITERATURA CITADA	69
CAPÍTULO III – SETTING PRIORITIES FOR THE CONSERVA	ATION OF MARINE
VERTEBRATES IN BRAZILIAN WATERS	72
ABSTRACT	73
INTRODUCTION	74

INTRODUCTION	74
METHODS	76
Species distribution data	76
Seascape prioritization	77
Comparison of alternative scenarios	78
RESULTS	79
DISCUSSION	
REFERENCES	
CONSIDERAÇÕES FINAIS	94
LITERATURA CITADA	97
APÊNDICES	

#### **RESUMO GERAL**

Nesse estudo, foram investigadas as mudanças na estrutura da ictiofauna estuarina em diferentes escalas geográficas, os processos ecológicos subjacentes a essas mudanças, bem como a localização de áreas prioritárias para a conservação na zona marinha brasileira. No Capítulo 1, um desenho de amostragem hierárquico foi usado para comparar a variação na estrutura das assembleias de peixes entre duas escalas espaciais e para estimar os efeitos individuais e sinergéticos de alguns parâmetros ambientais e da distância geográfica na estruturação da fauna. Para isso, foram amostradas oito áreas separadas por 0,7–25 km (escala local) dentro de cada um dos cinco estuários separados por 970-600 km (escala regional). As análises revelaram diferenças significativas na estrutura das assembleias (em termos de biomassa relativa e presença/ausência das espécies) para ambas as escalas e que a variação regional foi comparativamente maior do que a variação local. Porém, os cinco estuários amostrados segregaram-se em dois grupos amplamente congruentes com as províncias biogeográficas Brasileira e Argentina. Três variáveis ambientais (temperatura média da água no mês mais frio, área de manguezal e precipitação média anual) e a distância entre os estuários explicaram, respectivamente, 44,8 e 16,3% da variabilidade regional na biomassa relativa das espécies. Em escala local, os resultados sugerem que as assembleias de diferentes estuários são estruturadas por fatores distintos. No Capítulo 2, os padrões geográficos de riqueza de espécies e raridade da ictiofauna estuarina foram mapeados e integrados para identificar regiões importantes para a conservação na costa brasileira. Além disso, também foi analisada a efetividade do sistema nacional de áreas protegidas para representar essas regiões. Quarenta e oito bandas, com 0,25° de latitude cada, foram consideradas prioritárias para a conservação, por possuírem simultaneamente uma alta riqueza de espécies e assembleias relativamente raras. Também foi verificado que o sistema atual de áreas protegidas é ineficiente para proteger essas bandas. Por fim, no Capítulo 3, foram elaboradas alternativas para a expansão das áreas marinhas protegidas (AMPs) em águas brasileiras, que maximizam a representação das espécies e evitam conflitos com atividades econômicas relevantes. Para isso, foram utilizados dados de distribuição de 750 espécies de vertebrados marinhos (incluindo mamíferos, aves, tartarugas e peixes), das AMPs existentes e das concessões para exploração/produção de

petróleo e gás natural na Zona Econômica Exclusiva do País. As soluções elaboradas mostraram que uma rede de AMPs, abrangendo 10% da área de estudo com alta prioridade para a conservação, poderia proteger, em média, entre 85,8 e 86,5% da distribuição das espécies. Foi constatado que a inclusão das AMPs existentes e das concessões para exploração de petróleo e gás no processo de priorização causou somente uma pequena perda na representação de espécies em perigo e ameaçadas de extinção. Os resultados sugerem, no entanto, que é possível compatibilizar a produção atual de petróleo e gás com a expansão da rede nacional de AMPs. As informações apresentadas nesse estudo podem contribuir para a tomada de decisões vinculadas ao objetivo do Brasil, de proteger 10% da sua zona marinha e costeira até 2020.

**Palavras-chave**: comunidade de peixes, biodiversidade, estuários, planejamento para conservação, áreas marinhas protegidas, raridade.

#### GENERAL ABSTRACT

The present study aims to investigate changes in estuarine ichthyofauna across different spatial scales, the ecological process underlining these changes, as well as the localization of priority areas for conservation at Brazilian marine zone. In Chapter 1, a hierarchical sampling design was used to quantify variations in assemblage structures of Brazilian estuarine fish across two spatial scales and to estimate the individual and synergetic effects of selected environmental variables and of geographical distance on the ichthyofauna structure. For this analysis, eight areas separated by 0.7 to 25 km (local scale) were sampled in five estuaries separated by 970 to 6000 km (regional scale). Multivariate analysis revealed that assemblage structure varied significantly in terms of relative biomass and presence/absence of species on both scales, and that the regional variation was greater than the local variation for either dataset. However, the five estuaries sampled segregated into two major groups largely congruent with the Brazilian and Argentinian biogeographic provinces. Three environmental variables (mean temperature of the coldest month, mangrove area and mean annual precipitation) and distance between estuaries explained 44.8 and 16.3%, respectively, of the regional-scale variability in the species relative biomass. At the local scale, the importance of environmental predictors for the spatial structure of the assemblages differed between estuarine systems. In Chapter 2, geographic patterns of species richness and rarity of the estuarine ichthyofauna were mapped and integrated to identify important regions for biodiversity conservation across the Brazilian coast. Furthermore, also was analyzed the effectiveness of the national system of protected areas to represent these regions. Forty-eight bands of 0.25° latitude each were recognized as conservation priorities by harbor simultaneously high species richness and assemblages that are relatively rare. Also was found that the existing system of protected areas is inefficient to represent priority bands identified in this study. Lastly, in Chapter 3 were developed alternatives for the expansion of current marine protected areas (MPAs) in Brazilian waters that maximize species representation and reduce potential conflicts with relevant economic activities. For this were utilized distribution data of 750 marine vertebrate species (including mammals, birds, turtles and fishes), of established MPAs and of the areas concessioned for oil and gas exploitation. The results showed that a MPA network encompassing 10% of the study area with high conservation priority would protect, on average, between 85.8 and 86.5% of species distribution. It was found that incorporating existing MPAs and areas concessioned for oil and gas exploitation in the prioritization process caused only a small loss in representation of near-threatened and threatened species. The results highlight, therefore, that it is possible to reconcile current offshore oil and gas production with the expansion of the national MPA network, without significant losses in species' representation. The solutions presented here may be useful as scientific support in political negotiations about Brazil's commitment to protect 10% of its coastal and marine areas by 2020.

**Key-words**: fish communities, biodiversity, estuaries, conservation planning, marine protected areas, rarity.

#### INTRODUÇÃO GERAL

O interesse em desvendar os padrões espaciais da biodiversidade e os processos que os determinam remonta à época de pesquisadores como Jean-Baptiste de Lamarck (1744–1829), Charles Darwin (1809–1882), Alfred Russel Wallace (1823–1913), entre outros pioneiros, e ainda está presente na biogeografia e na ecologia moderna (Beisner et al. 2006, Svenning et al. 2011, McClain et al. 2012). A busca por padrões, especialmente por aqueles que se repetem, é atraente porque eles representam a base para definição de novas regularidades ("leis") nos sistemas ecológicos (MacArthur 1968). A partir deles, diferentes hipóteses sobre os fatores reguladores das comunidades também têm sido formuladas e testadas (Diamond 1975, Hubbell 2001, Gotelli & McCabe 2002, Field et al. 2009). Todavia, apesar do número crescente de publicações propondo novas teorias (e.g. Clark 2009), criticando as que já existem (e.g. Mc Gill 2003) ou recomendando unificações das mesmas (e.g. Gravel et al. 2006), ainda não há um consenso sobre os processos responsáveis pela estruturação das comunidades locais (Mc Gill 2010).

O conhecimento acumulado, entretanto, sugere que as assembleias locais de espécies resultam de sucessivas "filtragens" da biota global por múltiplos fatores (bióticos e abióticos) que operam em escalas espaciais distintas. Juntos, eles são responsáveis por gerar e manter a heterogeneidade estrutural das comunidades biológicas, em escalas que variam desde poucos milímetros a milhares de quilômetros (Levin 1992). Conhecer esses fatores e os padrões geográficos da biota é um passo importante para entender, predizer e mitigar potenciais impactos derivados das ações humanas, incluindo aqueles relacionados às mudanças climáticas previstas para esse século (Lourie & Vincent 2004, Mouillot 2007).

Duas teorias comumente usadas para explicar as variações espaciais na estrutura das comunidades são fundamentadas no nicho ecológico e na capacidade de dispersão das espécies. A teoria do nicho, por um lado, postula que todas as espécies possuem limites dentro dos quais elas podem persistir, sendo esses definidos pelo conjunto de condições bióticas e abióticas do ambiente (Hutchinson 1957). Com base nessa teoria, tem sido então hipotetizado que os padrões espaciais na estrutura das comunidades são determinados pelas distintas relações das espécies, com filtros ambientais que limitam a distribuição delas. Por outro lado, a teoria neutra unificada da biodiversidade e biogeografia prediz que todos os indivíduos são ecologicamente equivalentes e que a similaridade entre comunidades decai com a distância, mesmo em ambientes homogêneos, devido à dispersão limitada dos organismos (Hubbell 2001). Porém, o conjunto de evidências disponíveis sugere que essas duas visões não são mutuamente exclusivas, e que o efeito relativo das características ambientais – defendido pela teoria do nicho – e da capacidade de dispersão das espécies – defendido pela teoria neutra – pode variar em função da escala de investigação e do objeto de estudo (Beisner et al. 2006, Svenning et al. 2011, Landeiro et al. 2012, McClain et al. 2012).

Um dos objetivos centrais desta tese, no entanto, é testar se as predições dessas duas teorias (i.e. nicho e neutra) podem ser usadas para explicar as variações espaciais na composição taxonômica das assembleias de peixes estuarinos da costa brasileira. Além dessas hipóteses, também foram investigados no Capítulo 1: (1) os padrões geográficos na composição taxonômica da ictiofauna estuarina ao longo de um extenso gradiente ambiental; (2) a magnitude de variação na composição das assembleias, em duas escalas espaciais (i.e. dentro dos estuários e entre estuários); e (3) os efeitos individuais e sinergéticos de algumas variáveis ambientais e da distância geográfica na estruturação dessas assembleias. Para essas análises, foram utilizados dados coletados através do projeto Uso e Apropriação de Recursos Costeiros (RECOS), em cinco estuários brasileiros, distribuídos por aproximadamente 6.000 km.

Embora o conhecimento sobre a ictiofauna estuarina brasileira tenha aumentado substancialmente nos últimos 10 anos, muitas lacunas ainda permanecem. Os estudos existentes focam tipicamente nas variações das comunidades de peixes em escala local, então grande parte do conhecimento disponível refere-se aos mecanismos de estruturação das comunidades dentro dos estuários (e.g. Garcia et al. 2001, Araújo et al. 2002, Barletta et al. 2005, Chagas et al. 2006, Vilar et al. 2011, Mouchet et al. 2013). Relativamente pouca atenção, no entanto, tem sido dada a abordagens mais amplas, que possam evidenciar padrões e processos que ocorrem em larga escala. Estudos dessa natureza podem ser aplicados para a solução de problemas que estão além do âmbito do estudo da ecologia teórica. Eles podem ser úteis, por exemplo, no desenvolvimento de estratégias de conservação em nível nacional e global (Lourie & Vincent 2004). Com a disponibilidade crescente de dados sobre a composição das assembleias de peixes nos estuários ao londo da costa, agora é possível examinar com maior

precisão a distribuição das espécies, determinar semelhanças e diferenças geográficas, nas características da fauna, e identificar áreas particularmente importantes para a conservação da biodiversidade desses ambientes.

Estuários possuem uma biota única e estão entre os ecossistemas aquáticos mais produtivos do planeta (McLusky & Elliott 2004). Eles providenciam múltiplos benefícios (ou "serviços ecossistêmicos") para a população humana, incluindo a proteção da linha de costa contra erosões, filtragem de poluentes, fornecimento de alimentos e de áreas para recreação (Barbier et al. 2011). Ao mesmo tempo, os estuários estão entre os ecossistemas marinhos mais profundamente usados e impactados pelas ações antrópicas em todo o mundo (Lotze et al. 2006, Halpern et al. 2008).

Pelo menos desde o século XV, quando se iniciou a expansão colonial da Terra pelos europeus, os estuários já eram visados para ocupação humana. Eles eram selecionados como áreas de estabelecimento, devido o fornecimento de abrigo para as embarcações, a disponibilidade de alimentos (peixes, crustáceos, moluscos, etc.) e de água doce, a prevalência de terras férteis ao redor e a acessibilidade para o interior providenciada pelos rios (Edgar et al. 2000). Com a expansão do comércio mundial e o desenvolvimento industrial, intensificaram-se também a construção de portos, o fluxo de embarcações, bem como a dragagem dos canais de navegação e o desenvolvimento urbano e industrial ao redor dos estuários. A localização desses ambientes na interface oceano-continente faz com que eles sejam os primeiros ecossistemas marinhos a receber os dejetos humanos e industriais carregados pelos rios. Atividades desenvolvidas nas bacias de drenagem, tais como construções de barragens, agricultura e desmatamento, também têm causado alterações profundas nas características desses ambientes (McLusky & Elliott 2004). Coletivamente, essas atividades têm resultado na deterioração da qualidade da água, na queda da produtividade pesqueira, na redução de habitats importantes como manguezais e marismas, e no declínio das populações de peixes (Joyeux & Ward 1998, Edgar et al. 2000, Lotze et al. 2006).

A necessidade urgente de ações para conter a destruição da biodiversidade global, tanto marinha como terrestre, tem sido repetidamente destacada nas conferências internacionais (e.g. Convenção Sobre a Diversidade Biológica – CDB, Congresso Mundial de Parques, Conferencia Mundial do Clima, etc.). Entre essas ações, a ampliação da área global protegida por unidades de conservação é uma

das principais sugestões. Em particular, a CDB recomenda que todos os países signatários protejam pelo menos 10% das áreas marinhas e costeiras até 2020 (CDB 2010). Atualmente, somente cerca de 1,5% da área marinha sob jurisdição brasileira está legalmente protegida por algum tipo de unidade de conservação (CNUC/MMA 2012). Iniciativas como a criação do "Plano nacional de áreas protegidas" (MMA 2006a) e das "Metas nacionais de biodiversidade para 2010" (MMA 2006b) foram desenvolvidas pelo governo brasileiro para auxiliar no alcance dos compromissos assumidos no âmbito da CDB, mas na prática, infelizmente, tiveram pouco efeito.

Como em outros lugares do mundo, os obstáculos para alcançar as metas de conservação instituídas pelo Ministério do Meio Ambiente (MMA 2006a, b) incluem: (1) escassez de recursos para a criação de novas unidades de conservação; (2) instabilidade política; (3) falta de engajamento político para solucionar os problemas ambientais; (4) conflitos de interesses entre setores do governo e da sociedade; e (5) carência de informações biológicas que posam servir de apoio à tomada de decisões, especialmente no ambiente marinho. Com a proposta de remediar o último problema, no Capítulo 2 da presente tese, foram analisados os padrões espaciais de riqueza de espécies e raridade da ictiofauna estuarina ao longo de toda costa brasileira. Adicionalmente, essas informações foram integradas para responder a seguinte questão: quais áreas que, se conservadas, representariam simultaneamente uma alta riqueza de espécies e táxons relativamente raros, que são inerentemente propensos à extinção?

Planejamentos para a conservação focam frequentemente em espécies raras (e.g. Villalobos et al. 2013), ameaçadas (e.g. Cunha & Loyola 2011), endêmicas (e.g. Myers et al. 2000) e eventualmente em uma combinação das mesmas (e.g. Tognelli et al. 2005). No entanto, existe um debate intenso sobre se áreas selecionadas com base em um grupo restrito de espécies podem representar a biodiversidade como todo (Andelman & Fagan 2000, Rodrigues & Brooks 2007). Testes indicam que a capacidade de um táxon, ou de um grupo de táxons, para representar outros componentes da biodiversidade é altamente variável entre escalas espaciais (Mellin et al. 2011), entre regiões biogeográficas (Lawler & White 2008) e entre os próprios elementos da biodiversidade (Tognelli et al. 2005). Consequentemente, a fim de maximizar a representação da biodiversidade de uma região, múltiplos grupos de espécies com diferentes preferências ambientais devem (idealmente) ser integrados

para definir prioridades espaciais para a conservação (Margules & Sarkar 2007). Por essa razão, no Capítulo 3, foram compilados dados de distribuição de peixes, tartarugas, aves e mamíferos marinhos para identificar áreas prioritárias para a conservação na Zona Econômica Exclusiva brasileira. Além disso, como a implementação de ações de conservação pode ser dificultada ou até mesmo impedida por outras formas de uso do espaço, também foram levadas em conta as áreas concessionadas para o desenvolvimento de uma das principais atividades econômicas do País: a produção de petróleo e gás natural. Por fim, foram incorporadas nas análises as áreas marinhas protegidas, já estabelecidas na área de estudo.

Uma síntese dos principais resultados alcançados em cada capítulo e áreas férteis para pesquisas futuras são apresentadas na última seção desta tese – Considerações Finais.

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## Capítulo I

# Local and regional ecological drivers of fish assemblages in Brazilian estuaries

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#### ABSTRACT

Spatial patterns in assemblage structures are generated by ecological processes that occur on multiple scales. Identifying these processes is important for the prediction of impact, for restoration and for conservation of biodiversity. This study used a hierarchical sampling design to quantify variations in assemblage structures of Brazilian estuarine fish across 2 spatial scales and to reveal the ecological processes underlying the patterns observed. Eight areas separated by 0.7 to 25 km (local scale) were sampled in 5 estuaries separated by 970 to 6000 km (regional scale) along the coast, encompassing both tropical and subtropical regions. The assemblage structure varied significantly in terms of relative biomass and presence/absence of species on both scales, but the regional variation was greater than the local variation for either dataset. However, the 5 estuaries sampled segregated into 2 major groups largely congruent with the Brazilian and Argentinian biogeographic provinces. Three environmental variables (mean temperature of the coldest month, mangrove area and mean annual precipitation) and distance between estuaries explained 44.8 and 16.3%, respectively, of the regional-scale variability in the species relative biomass. At the local scale, the importance of environmental predictors for the spatial structure of the assemblages differed between estuarine systems. Overall, these results support the idea that on a regional scale, the composition of fish assemblages is simultaneously determined by environmental filters and species dispersal capacity, while on a local scale, the effect of environmental factors should vary depending on estuary-specific physical and hydrological characteristics.

KEY WORDS: Fish communities · Estuarine fish · Spatial patterns · Multi-scale · Atlantic Ocean · Brazil

#### INTRODUCTION

Identifying patterns of species distribution and revealing their causes are among the central goals of ecology. Typically, the ecological processes underlying the distribution of organisms operate at specific scales, and together can generate variability between sites separated by only a few millimetres to thousands of kilometres (Levin 1992). For these reasons, ecologists have recognised that multiscale approaches are necessary for a comprehensive understanding of the spatial patterns of community organisation and the factors controlling them (Wiens 1989, Levin 1992, Azovsky 2000). Once the scale(s) is identified at which variation is highest, hypotheses about the factors possibly causing the observed patterns can be generated and tested (Levin 1992).

In estuaries, spatial variability in the composition of fish assemblages has been attributed to a number of variables that act in a hierarchy of scales. In a regional context, there is evidence that assemblage composition can be influenced by factors such as the latitudinal temperature gradient, the width of the estuary mouth, tidal amplitude, mangrove area and rainfall (Vieira & Musick 1994, Blaber 2000, Ley 2005, Harrison & Whitfield 2006, Sheaves & Johnston 2009). Another factor possibly working on a large scale is the distance between estuaries, which may reflect differences in the recruitment and dispersal of certain species (Sheaves & Johnston 2009). On a local scale, in contrast, spatial patterns in the ichthyofauna structure have often been related to changes in salinity, depth, dissolved oxygen, transparency and the distance from the point of connection to the sea (Araújo et al. 2002, Barletta et al. 2005, Chagas et al. 2006, Vilar et al. 2011).

Although Brazil's coastline extends for approximately 8000 km, ranging from macrotidal equatorial estuaries in the north to subtropical microtidal estuaries in the south, studies investigating the composition of its estuarine fish assemblages have traditionally been conducted on a local scale (e.g. Garcia et al. 2001, Araújo et al. 2002, Barletta et al. 2005, Vilar et al. 2011). Consequently, there is still a severe lack of information regarding the geographical distribution and particularly the abundance of fish species along this latitudinal gradient, which has hindered the understanding of the biogeographic patterns and ecological processes driving the assemblages.

The few biogeographical studies undertaken previously, however, have identified some regional distinctions in the estuarine ichthyofauna along the coast of the country. Based on a dendrogram of species presence/absence data obtained from the literature, Vieira & Musick (1994) separated the fauna of the western Atlantic into 3 groups. From this analysis, 2 faunal components were defined on the coast of Brazil: (1) 'tropical', represented by fauna captured in estuaries located between Colombia and northeastern Brazil (10°N–11°S), and (2) 'warm-temperate', which includes estuaries distributed between the States of São Paulo and Rio Grande do Sul (24°–32°S). The groups found in this analysis corresponded in part to the Brazilian and Argentinian biogeographical provinces proposed by Briggs (1995), whose transition area is located in Cabo Frio (22°S). However, Araújo & Costa de Azevedo (2001) observed that the fish of Lagoa dos Patos and other estuaries in the south of the country (near 32°S) were substantially different from those found in systems in the adjacent southeastern region (22–28°S). All these results, therefore, indicate the existence of factors that limit the geographical distribution of species, although the identity of these factors remains to be empirically investigated.

To address this issue, the present study used data collected by the authors as part of the project 'Use and Appropriation of Coastal Resources' ('Uso e Apropriação de Recursos Costeiros' – RECOS, in Portuguese) from coordinated sampling in 5 estuaries distributed along the Brazilian coast between latitudes 0° and 32°S (for details, see Lana et al. 2006). The ichthyofauna of these estuaries was collected using standardized fishing gear and a similar sampling protocol, which yielded comparable databases. Using standardized procedures allowed us to appropriately analyse the presence of spatially distinct faunal components along this extensive latitudinal gradient; something that had been suggested in previous studies using presence/absence data collected with disparate sampling methods (see Vieira & Musick 1994, Araújo & Costa de Azevedo 2001).

Based on a comprehensive dataset, this study aimed to (1) identify biogeographic patterns in the composition of estuarine ichthyofauna along the Brazilian coast, (2) quantify and compare the magnitude of variation in the compositions of assemblages between the local (i.e. within the estuaries) and regional (i.e. between estuaries) scales and (3) analyse the relative importance of a set of environmental and spatial variables in structuring local and regional fish assemblages. More precisely, the geographic patterns were investigated based on the contributions of the main families to the total species richness and the biomass captured in each estuary, as well as through the identification of the major species responsible for similarities and differences in ichthyofaunal composition among the systems.

#### MATERIALS AND METHODS

#### Study area

Five permanently open estuaries distributed between the Amazon delta and the extreme southern Brazilian coast were studied (from north to south): Curuçá, Santa Cruz, Piraquê-Açú, Paranaguá and Lagoa dos Patos (Fig. 1). These systems represent the main coastal morphoclimatic domains of the country, encompassing an equatorial macrotidal zone with one of the largest mangrove areas in the world in the north (Curuçá; Kjerfve & Lacerda 1993) to a subtropical microtidal area dominated by salt marshes in the south (Lagoa dos Patos; Costa et al. 1997). Along this area, 3 oceanographic currents are present (Fig. 1). The North Brazil Current influences the north and northeast regions and flows towards the Caribbean. The Brazil Current flows southward, carrying relatively warm water to most of the coast. The Malvinas Current brings cold water from the temperate region to southern/southeastern Brazil (Peterson & Stramma 1991, Campos et al. 1996).

Geomorphologically, the estuaries sampled can be divided into 4 types: (1) drowned river valleys, formed by 2 channels that come together before flowing into the sea, with the mouth width relatively greater than the headwaters (e.g. Curuçá and Piraquê-Açú); (2) tectonic, originating from the flooding of a fault in the earth's surface, where the contribution of continental water is relatively small (e.g. Santa Cruz); (3) embayment, which is composed of several sub-estuaries, surrounded by a coastal plain that extends 50 km inland to the base of the Serra do Mar mountain range (e.g. Paranaguá); and (4) coastal lagoon, dominated by shallow areas, oriented parallel to the coast and connected to the ocean by a single channel (e.g. Lagoa dos Patos). The substrate in these estuaries is composed primarily of sand and mud, with the presence of some scattered rock formations. Additionally, extensive seagrass meadows occur within the Santa Cruz estuary (Medeiros et al. 2001). Impacts resulting from fishing and other anthropogenic activities such as recreational use, partial urbanisation of margins and release of untreated sewage, occur in all systems. For each estuary, other environmental information is shown in

Table 1.



**Fig. 1.** Location of the 5 sampled estuaries, sea surface temperature (average from 2003 to 2007 with 0.05 degree resolution; MODIS Aqua Level-3) and the major superficial currents (modified from Peterson & Stramma 1991) influencing the Brazilian coast. CU: Curuçá; SC: Santa Cruz; PA: Piraquê-Açú; PG: Paranaguá; LP: Lagoa dos Patos.

#### **Data acquisition**

#### Ichthyofauna

Between April 2003 and July 2004, 40 areas, separated by 0.7 to 25 km (local scale) were sampled in the subtidal of 5 estuaries (8 areas in each estuary). These estuaries were separated by 970 to 6000 km (regional scale) along the Brazilian coast, covering tropical (Curuçá, Santa Cruz and Piraquê-Açú) and subtropical

(Paranaguá and Lagoa dos Patos) regions. The sampling areas were chosen to represent a large gradient of environmental conditions within these systems. The straight-line distance among them ranged between 1.5 and 8 km at Curuçá, 0.7 and 10 km at Santa Cruz, 1 and 6 km at Piraquê-Açú, 2 and 25 km at Paranaguá and 1.3 and 14 km at Lagoa dos Patos. In each area, 1 (at Santa Cruz) or 2 (in the other estuaries) samples were collected during each sampling occasion. An otter trawl (10.43 m footrope and 8.62 m headrope, with 13 and 5 mm mesh-size in the body and in the cod-end, respectively) was towed by a boat for 4 to 15 min to collect fish. Captured individuals were kept on ice and subsequently identified and weighed (wet weight in g) in the laboratory. All estuaries were sampled during the day (06:30 h to 18:00 h) in neap tides using the same fishing equipment. Sampling occurred monthly in Piraquê-Açú (for 13 months, n = 204), bimonthly in Curuçá (7 sampling periods, n = 111), in Lagoa dos Patos (7 sampling periods, n = 112) and in Paranaguá (6 sampling periods, n = 91), and seasonally in Santa Cruz (4 sampling periods, n = 31), resulting in a database with 549 samples.

Only the taxa identified to the species level and whose natural ranges included the Brazilian coast were considered in subsequent analyses. The taxa included in this study as *Stellifer* sp. and *Mugil* sp. refers to species that are distinct from their congeners but yet undescribed (Menezes et al. 2003). The taxonomic classification and species nomenclature follows Eschmeyer (2011).

#### Local-scale predictors of assemblages

Five environmental parameters were tested as local-scale predictors of fish assemblages (Table 1). The over-water distance from each sampling area to the mouth of the estuary was determined using a Geographic Information System (GIS; Google Earth). The other variables were measured before each trawl (at Piraquê-Açú and Paranaguá) or immediately after the first trawl within each area (at Curuçá, Santa Cruz and Lagoa dos Patos) on each sampling trip; exceptions were depth at Curuçá (measured at the beginning and end of each trawl) and Paranaguá (measured at each minute of trawling). Where multiple readings were taken, the mean of each variable per area was used in the analysis.

	Curuçá	Santa Cruz	Piraquê-Açú	Paranaguá	Lagoa dos Patos
	0°33'S, 47°50'W	7°41'S, 34°50'W	19°57'S, 40°09'W	25°32'S, 48°20'W	32°09'S, 52°05'W
Local-scale variables					
Salinity	17.4 (6.1–40.8)	29.4 (24.7–35)	28.4 (0.4–37.9)	25.5 (20.5–29.5)	5.7 (0–19.4)
Water temperature (°C)	26.3 (20.6–31)	28.7 (27.2–30)	25.7 (22.5–29.7)	23.6 (17.8–29.2)	19.5 (11–25)
Dissolved oxygen (mg l <sup>-1</sup> )	5.4 (3.3–8.4)	-	-	-	-
Secchi transparency (m)	-	1.7 (1.2–2.8)	-	1.9 (1.1–3.6)	0.6 (0.15–1.5)
Depth (m)	3.7 (2–7.5)	4.4 (1.5–6.6)	5.1 (1.3–11)	4.8 (2.5–7.7)	-
Distance from estuary mouth (km)	14.7 (11.5–18.8)	5.6 (1.5–8.7)	5.4 (2.6–8.8)	17.4 (9.8–23)	22.3 (12.9–30.9)
Regional-scale variables					
Mean annual water temperature (°C)	26.3	28.2 <sup>a</sup>	25.7	23.6	19.5
Mean water temperature in the coldest month (°C)	21	26.8 <sup>a</sup>	23.2	18.3	11.2
Tidal range (m) <sup>b</sup>	4.7	2.2	1.5	1.8	0.4
Mouth width (m)	4465	2759	291	5616	588
Estuary area (km <sup>2</sup> )	200 <sup>c</sup>	824 <sup>a</sup>	5.1 <sup>d</sup>	551.8 <sup>e</sup>	10360 <sup>f</sup>
Mangrove area (km <sup>2</sup> )	116 <sup>c</sup>	28.1 <sup>a</sup>	12.3 <sup>d</sup>	295 <sup>e</sup>	0 <sup>g</sup>
Mean annual precipitation (mm) <sup>h</sup>	2526	2394	1250	2500	1300

**Table 1.** Local- and regional-scale environmental variables measured or obtained from the literature for each estuary. Values of local variables correspond to the means (min.–max.); '–' indicates variables were not measured

Sources: <sup>a</sup>Medeiros et al. (2001), <sup>b</sup>Brazilian Navy Hydrographic and Navigation Directorate (www.mar.mil.br/dhn/chm/tabuas/index.htm), <sup>c</sup>Giarrizzo & Krumme (2007), <sup>d</sup>Barroso (2004), <sup>e</sup>Noernberg et al. (2004), <sup>f</sup>Garcia et al. (2001), <sup>g</sup>Kjerfve & Lacerda (1993), <sup>h</sup>National Agency of Waters (hidroweb.ana.gov.br/). For the other variables/regions, see 'Materials and methods'

#### Regional-scale predictors of assemblages

Eight variables describing the spatial relationships between estuaries (i.e. distance) as well as the physiographic and hydrological characteristics were obtained for each estuary (Table 1). Four of these variables (mangrove area, mean annual precipitation, tidal amplitude and estuary area) were taken from the literature (presented in Table 1), while 2 variables (width of estuary mouth and distance between estuaries) were measured using satellite images and GIS. An additional 2 variables (mean and minimum water temperature) were obtained from the literature (for Santa Cruz) or obtained during field collections (other estuaries). The distance between estuaries was measured from Curuçá by following the coastline without considering the indentations, to represent the shortest possible distance between any 2 locations. The width of the estuary mouth was obtained from the shortest distance between the margin edges at the point where one or both of them turn and follow the

direction of the coast. In estuaries with more than one connection to the sea (i.e. Curuçá, Santa Cruz and Paranaguá), the sum of the widths of all connections was used. The mean annual precipitation data obtained from the literature for the drainage basin of each estuary covered a time series  $\geq 10$  years.

#### Data analysis

Initially, data were standardized to avoid potential problems associated with differences in trawl duration (4 to 15 min). Standardized values were calculated by dividing the biomass of each fish species in a given sample by the total biomass captured in that sample (×100; hereafter relative biomass). Relative biomass data were square-root transformed, re-coded as presence/absence and analysed using PRIMER v6 (Clarke & Warwick 2001) and the PERMANOVA+ add-on package (Anderson et al. 2008). Square-root transformed biomass data reveal patterns of both the most and intermediately abundant species, as they tend to have larger quantitative differences between samples. On the other hand, presence/absence data tend to emphasize the rare species, as the abundant species tend to occur in a large number of samples and contribute little to the differentiation of the assemblages (Clarke & Warwick 2001).

Geographic patterns of similarity were analysed from the means of transformed relative biomass and the presence/absence data of each species per site using the Bray-Curtis and Sørensen indices, respectively. The resulting similarity matrices were subjected to hierarchical cluster analysis using the unweighted pairgroup average (UPGMA). Similarity profile tests (SIMPROF) were performed to investigate the significance of groupings in each cluster analysis (Clarke et al. 2008). This test compares a true similarity profile calculated by ranking the similarity matrix with a mean profile created by permuting the values of each species among the samples (here estuaries) and recalculating the profile repeatedly. A statistic ( $\pi$ ) is then calculated as the deviation of the real profile from the mean permuted profile. The observed value of  $\pi$  is compared with its null distribution generated by permutations to determine significance (Clarke et al. 2008).

Spatial differences in the relative biomass and the presence/absence of species were tested using a permutational multivariate ANOVA (PERMANOVA; Anderson et al. 2008), considering the estuaries (5 levels, fixed) and areas (8 levels,

random, nested within estuaries) as factors. The components of variation for each term included in the analyses were also calculated to quantify the variation in assemblage composition within- and between-estuaries. A posteriori paired comparisons were performed with distance-based permutational t-tests (Anderson et al. 2008) using similarity matrices built from all samples (n = 542 after exclusion of 7 samples with zero individuals from Lagoa dos Patos). Significance levels were determined from 4999 permutations of residuals under a reduced model for each term analysed (Anderson 2001). PERMANOVA and permutational t-test were applied in the present study because they can handle unbalanced sampling designs (Anderson et al. 2008).

When paired t-test detected significant differences in assemblage composition between estuaries, a similarity percentages analysis (SIMPER) was performed on the relative biomass data to identify the species contributing most to within-estuaries similarity (i.e. characteristic species) and between-estuaries dissimilarity (i.e. discriminating species; Clarke and Warwick 2001). Non-metric multidimensional scaling (nMDS) was used to visualise the variability of assemblages, considering both the transformed relative biomass (using Bray-Curtis) and the presence/absence data (using Sørensen).

To test whether changes in assemblage structure between the estuaries were correlated with the regional-scale predictors, distance-based linear models (DistLM; Anderson et al. 2008) were applied using 2 sets of analyses: conditional test with forward selection, in which the predictor variable with the greatest coefficient of determination is selected first, followed by the variable with the greatest coefficient after inclusion of the first (i.e. partial  $r^2$ ), and so on, until it is no longer possible to increase the total variance explained by the model (i.e.  $R^2$ ); and the marginal test, in which the variance explained by each variable is calculated independently of the others, as in a simple regression (i.e.  $r^2$ ). When 2 predictors were redundant (i.e. Spearman correlation > 0.8), only the most explicative was considered in the conditional tests.

The relationship between the site-averaged relative biomass data and the local-scale predictors was analysed independently for each estuary on each sampling occasion using DistLM. As the tests were repeated separately for each sampling occasion, the spatial 'effect' (if any) of environmental variables on the local

distribution of the species was isolated, and any effect related to the assemblage differences between sampling occasions for a given sampling area (i.e. temporal effect) was discarded. To determine the relative importance of each predictor, an approach based on 2 complementary metrics was adopted: (1) the coefficients of determination (r<sup>2</sup>) of the predictors when modelled separately in DistLM marginal tests (described above) and (2) the prevalence, defined as the proportion of times a given predictor was significantly correlated (i.e.  $p \le 0.05$ ) with the spatial structure of the assemblages relative to the total number of times it had been tested. The first measure provides information regarding the magnitude of the relationship between environmental variables and the spatial structure of the fish assemblages, while the second indicates whether the frequency of that relationship was stronger than expected by chance. These analyses were conducted for 4 of the 5 estuaries sampled; Santa Cruz was not included due to the lack of local abiotic data for some of the sampling events. The conditional test was also used to model the total variance explained by the local-scale environmental variables, when they were analysed together. DistLM tests were based on log-transformed predictor variables, Bray-Curtis similarity and 999 permutations (Anderson et al. 2008).

Finally, a one-way nonparametric ANOVA (npANOVA) was applied to compare the  $r^2$  values between the local-scale predictors, considering each estuary separately. These analyses were performed with matrices of the Euclidean distances between the coefficients of determination of each variable, using the same procedures as described above for PERMANOVA. As all DistLM analyses to test the effect of the local-scale predictors were performed on an equal number of observations (n = 8 areas per estuary), no correction of the coefficient of determination was necessary.

#### RESULTS

#### Assemblage composition along the coast

Samples collected in the 5 estuaries along the Brazilian coast yielded 646 kg of fish, which represented 184 species belonging to 118 genera and 56 families (listed in Table S1 in the Supplement at www.int-res.com/articles/suppl/m485p181\_supp.pdf). At all sites except Santa Cruz, the species accumulation curve tends to stabilize, suggesting that the sampling effort

was adequate for the characterisation of most assemblages (Fig. S1 in the Supplement). Overall, Sciaenidae had the greatest richness (22 species), followed by Engraulidae (13), Ariidae (10), Carangidae (10), Achiridae, Gobiidae and Paralichthyidae (8 each). Ariidae provided most of the total biomass (32.5%), followed by Sciaenidae (12.8%), Tetraodontidae (11.7%), Achiridae (7.4%), Diodontidae (6.9%), Gerreidae (3.6%) and Lutjanidae (3.6%). The total number of species recorded ranged from 82 in Piraquê-Açú to 37 in Lagoa dos Patos. More than half of the species (53.8%; 99) occurred only in a single estuary, and a small proportion (8.7%; 16) occurred in 4 estuaries (none occurred in all 5 estuaries). The only locally endemic species was *Parapimelodus nigribarbis*, which occurs only in the basin of Lagoa dos Patos.

The most representative species in terms of biomass differed between estuaries, and several of these were exclusive to one estuary (Fig. 2). In Curuçá, for example, Cathorops agassizii (17.6%), Stellifer naso (15.2%) and Sciades herzbergii (7.3%) were among the 5 dominant species in terms of biomass, but were not captured anywhere else. Similarly, Bagre marinus (18%) had the highest contribution in Santa Cruz and was absent in the other estuaries, as well as 3 of the 4 species with the greatest biomass percentages in Lagoa dos Patos (i.e. Geophagus brasiliensis, Hoplias malabaricus and Paralichthys orbignyanus). In contrast, *Cathorops spixii* had the third highest contribution in Curuçá (9.1% of total biomass) and ranked first in Paranaguá (42.6%). Chilomycterus spinosus (26.1%), Sphoeroides testudineus (18.2%), Lutjanus synagris (6.8%) and Achirus declivis (5.5%) were dominant in Piraquê-Açú, while Genidens genidens (20.0%), Pomadasys corvinaeformis (5.8%) and Chaetodipterus faber (5.1%) dominated in Paranaguá. Species that exhibited a geographic consistence in abundance include Colomesus psittacus in northern estuaries (7.7% in Curuçá and 11.4% in Santa Cruz) and G. genidens in southern estuaries (20.0% in Paranaguá and 5.3% in Lagoa dos Patos) (Fig. 2). The proportion of total biomass represented by the dominant species increased southward from about 18% in Curuçá and Santa Cruz to 44.2% in Lagoa do Patos (Fig. 2).



**Fig. 2.** Regional variation in the relative biomass of the most abundant fish species caught in 5 estuaries on the Brazilian coast: Curuçá (CU), Santa Cruz (SC), Piraquê-Açú (PA), Paranaguá (PG) and Lagoa dos Patos (LP). The diameter of the circles is proportional to the species' percentage contribution to total biomass captured in each estuary. The percentage value of the most abundant species in each estuary is presented for comparative purpose. •: contributes  $\leq 1\%$  of the total biomass captured in each in each estuary; (+) present but not captured; (–) absent

In all locations, Sciaenidae (together with Gerreidae in Lagoa dos Patos) was the most species-rich family (Fig. 3). For Achiridae and Engraulidae, the number of species decreased progressively from north to south, while Lutjanidae occurred only in the estuaries north of Paranaguá and was particularly rich in Santa Cruz (5 species). Paralichthyidae had the highest number of species in Piraquê-Açú (7), located in the centre of the Brazilian coast, with species richness gradually decreasing towards the estuaries present at either end of the coast (Fig. 3).

In terms of relative biomass, Sciaenidae was again important in all estuaries, being among the 7 families with the largest contributions. The capture of Sciaenidae varied from 44.4% of the total biomass in Lagoa dos Patos to 3.6% in Santa Cruz (Fig. 4). Additionally, Ariidae contributed greatly to the fauna captured to the north (Curuçá and Santa Cruz) and south (Paranaguá and Lagoa dos Patos) of Piraquê-Açú, where they contributed only 2.2% of the total biomass. The highest percent biomass for Achiridae occurred in tropical estuaries, where their contributions reached 7.7% in Curuçá, 21.0% in Santa Cruz and 10.2% in Piraquê-Açú. In contrast, other relatively important families at Lagoa dos Patos, such as Cichlidae (23.6%), Erythrinidae (7.6%) and Pimelodidae (3.2%), were missing or not representative in other locations (Fig. 4).


**Fig. 3.** Regional distribution of the number of fish species for the richest (≥2 species) families in each estuary, with the total number of species belonging to each family shown in parentheses. The species are divided into unique species (occurring in only one estuary) and non-unique species (occurring in more than one estuary)



**Fig. 4.** Regional variations in the relative biomass of fish families in each estuary. Black bars: those families collectively responsible for ca. 90% of the total biomass caught in each system; white bars: less important families



**Fig. 5.** Hierarchical cluster analysis derived from the Bray-Curtis similarity of squareroot transformed relative biomass data (above) and the Sørensen similarity of presence/absence data (below) of fish species collected at 5 estuaries along the Brazilian coast. Significant groups (p < 0.05) determined by similarity profile test (SIMPROF) are indicated by black lines. Estuaries labelled according to Fig. 1

The cluster analyses based on relative biomass and presence/absence of species aggregated 4 estuaries (Curuçá, Santa Cruz, Piraquê-Açú and Paranaguá) into a group well differentiated from the estuary located further south (Lagoa dos Patos), with the division occurring at a level of similarity of 5.1% and 14.9%, respectively (Fig. 5). The Santa Cruz, Piraquê-Açú and Paranaguá estuaries formed a subgroup separated at the 36.6% similarity level from Curuçá, but only in the analysis considering presence/absence. All these clusters were significant (SIMPROF; Fig. 5). The true similarity profile calculated from the 5 estuaries differed markedly from the mean permuted profile for both relative biomass ( $\pi = 8.4$ , p =

0.001) and presence/absence ( $\pi$  = 5.9, p = 0.001). In the presence/absence analysis, however, the subgroup was separated from Curuçá by only  $\pi$  = 2.5 (p = 0.042).

**Table 2.** Species contributing most to within-estuaries similarity according to the similarity percentages analysis (SIMPER) based on relative biomass data. The percentage of the contribution for the within-estuaries similarity and the rank (superscript number) of each species are also shown

Species	Curuçá	Santa Cruz	Piraquê-Açú	Paranaguá	Lagoa dos Patos
Stellifer naso	22.42 <sup>1</sup>				
Cathorops agassizii	16.92 <sup>2</sup>				
Achirus lineatus	7.65 <sup>3</sup>	18.89 <sup>1</sup>	7.73 <sup>4</sup>	5.41 <sup>8</sup>	
Cathorops spixii	$7.53^{4}$			10.72 <sup>3</sup>	
Stellifer rastrifer	6.54 <sup>5</sup>				
Genyatremus luteus	6.14 <sup>6</sup>				
Colomesus psittacus	5.46 <sup>7</sup>	4.13 <sup>8</sup>			
Sphoeroides testudineus	4.98 <sup>8</sup>	2.07 <sup>12</sup>	16.16 <sup>3</sup>	7.72 <sup>6</sup>	
Sciades herzbergii	4.67 <sup>9</sup>				
Symphurus plagusia	3.43 <sup>10</sup>	8.28 <sup>5</sup>			
Lycengraulis grossidens	1.9 <sup>11</sup>				12.72 <sup>2</sup>
Batrachoides surinamensis	<b>1.47</b> <sup>12</sup>				
Citharichthys spilopterus	<b>1.41</b> <sup>13</sup>				
Diapterus auratus		15.47 <sup>2</sup>	1.71 <sup>7</sup>		
Bagre marinus		$9.58^{3}$			
Chaetodipterus faber		9.13 <sup>4</sup>		8.39 <sup>5</sup>	
Bairdiella ronchus		7.67 <sup>6</sup>			
Achirus achirus		6.72 <sup>7</sup>			
Diapterus rhombeus		2.97 <sup>9</sup>	1.3 <sup>10</sup>		
Sphoeroides greeleyi		2.68 <sup>10</sup>	2.92 <sup>6</sup>		
Achirus declivis		2.44 <sup>11</sup>	5.31 <sup>5</sup>		
Chilomycterus spinosus			36.56 <sup>1</sup>		
Lutjanus synagris			16.39 <sup>2</sup>		
Symphurus tesselatus			1.61 <sup>8</sup>		
Eucinostomus gula			1.44 <sup>9</sup>		
Genidens genidens				25.37 <sup>1</sup>	
Eucinostomus argenteus				11.2 <sup>2</sup>	
Etropus crossotus				$9.93^{4}$	
Menticirrhus americanus				5.47 <sup>7</sup>	
Diplectrum radiale				4.53 <sup>9</sup>	
Pomadasys corvinaeformis				1.93 <sup>10</sup>	
Micropogonias furnieri					73.43 <sup>1</sup>
Geophagus brasiliensis					5.03 <sup>3</sup>

In the SIMPER analysis, *Achirus lineatus* ranked in the top 8 most important species for fauna characterisation at all sites with the exception of Lagoa dos Patos (where it was absent), with a particularly high contribution in the 3 northern estuaries (Curuçá, Santa Cruz and Piraquê-Açú; Table 2). Of the remaining species, *Stellifer* 

naso, Cathorops agassizii and Cathorops spixii contributed the most to the characterisation of the fauna of Curuçá, while Diapterus auratus, Bagre marinus, Chaetodipterus faber and Symphurus plagusia were typical of Santa Cruz. Other species, such as Chilomycterus spinosus, Lutjanus synagris and Sphoeroides testudineus, had relatively high biomass at Piraquê-Açú and were the most important in the characterisation of the fauna at this estuary. The species characterizing Paranaguá were Genidens genidens, Eucinostomus argenteus, C. spixii and Etropus crossotus, and those typical of Lagoa dos Patos were Micropogonias furnieri, Lycengraulis grossidens and Geophagus brasiliensis (Table 2).

## Comparison of local and regional variability

Relative biomass and presence/absence data were significantly different among estuaries (PERMANOVA for relative biomass: pseudo-F4,503 = 22.8, p < 0.001; presence/absence: pseudo-F4,503 = 28.8, p < 0.001) and between areas within them (relative biomass: pseudo-F35,503 = 2.5, p < 0.001; presence/absence: pseudo-F35,503 = 2.6, p < 0.001). However, the components of variation showed that for both data sets, these differences were much greater at the regional scale (mean relative biomass dissimilarity: 38.5%; mean presence/absence dissimilarity: 41.0%) than at the local scale (17.8%; 17.0%). Paired t-tests indicated that all estuaries differed significantly for both the quantitative and qualitative data (p < 0.001in all tests).

These results were supported by the nMDS ordinations made with the relative biomass and presence/absence. In both analyses, the points representing the assemblages of the 8 sampled areas for each location were primarily distributed in accordance with the estuaries and, secondarily, according to the location inside each of them (Fig. 6). The only exceptions were 2 Santa Cruz points which formed a separate group in the presence/absence analysis. However, this group was strongly influenced by relatively low species richness in these areas (12 species), which resulted in a high Sørensen similarity (40%) even with only 3 shared species. There was no overlap among the assemblages of the 5 estuaries in ordination plots (Fig. 6). The Lagoa dos Patos assemblage was the most distinct compared to all of the other estuaries, remaining relatively isolated.



**Fig. 6.** Non-metric multidimensional scaling (nMDS) ordinations derived from (a) the mean relative biomass and (b) the presence/absence data of each species captured in 8 areas sampled in each estuary. The groups were defined using similarity cut-off levels of 21% (for relative biomass) and 38% (for presence/absence) in the cluster analysis (not shown)

The most important species to discriminate the assemblage of Curuçá from those of other estuaries were *Stellifer naso* and *Cathorops agassizii* (Table 3). *Achirus lineatus* and *Bagre marinus* ranked among the top 3 discriminator species of Santa Cruz in all paired SIMPER comparisons, whereas the major contributions to differentiate the fauna of Piraquê-Açú came from *Chilomycterus spinosus* and *Sphoeroides testudineus*. *Genidens genidens* and *Cathorops spixii* had the greatest contribution to distinguish the assemblage of Paranaguá from that of other estuaries, and *Micropogonias furnieri* and *Lycengraulis grossidens* to distinguish the fauna of Lagoa dos Patos. **Table 3.** Species contributing most to between-estuaries dissimilarity according to the similarity percentages analysis (SIMPER) based on relative biomass data. Species are listed in decreasing order of their contribution to distinguish the estuary at the top of column from the others

	Curuçá (CU)	Santa Cruz (SC)	Piraquê-Açú (PA)	Paranaguá (PG)	Lagoa dos Patos (LP)
CU		Achirus lineatus	Chilomycterus spinosus	Genidens genidens	Micropogonias furnieri
		Bagre marinus	Sphoeroides testudineus	Cathorops spixii	Lycengraulis grossidens
		Diapterus auratus	Lutjanus synagris	Sphoeroides testudineus	Citharichthys spilopterus
		Chaetodipterus faber	Achirus declivis	Chaetodipterus faber	Geophagus brasiliensis
		Achirus achirus	Lutjanus jocu	Eucinostomus argenteus	Parapimelodus nigribarbis
SC	Stellifer naso		Chilomycterus spinosus	Genidens genidens	Micropogonias furnieri
	Cathorops agassizii		Sphoeroides testudineus	Sphoeroides testudineus	Lycengraulis grossidens
	Colomesus psittacus		Lutjanus synagris	Cathorops spixii	Geophagus brasiliensis
	Cathorops spixii		Achirus declivis	Eucinostomus argenteus	Citharichthys spilopterus
	Sphoeroides testudineus		Sphoeroides greeleyi	Etropus crossotus	Parapimelodus nigribarbis
PA	Stellifer naso	Achirus lineatus		Genidens genidens	Micropogonias furnieri
	Cathorops agassizii	Bagre marinus		Cathorops spixii	Lycengraulis grossidens
	Achirus lineatus	Diapterus auratus		Eucinostomus argenteus	Geophagus brasiliensis
	Cathorops spixii	Chaetodipterus faber		Chaetodipterus faber	Citharichthys spilopterus
	Stellifer rastrifer	Bairdiella ronchus		Etropus crossotus	Parapimelodus nigribarbis
PG	Stellifer naso	Achirus lineatus	Chilomycterus spinosus		Micropogonias furnieri
	Cathorops agassizii	Chaetodipterus faber	Sphoeroides testudineus		Lycengraulis grossidens
	Achirus lineatus	Bagre marinus	Lutjanus synagris		Geophagus brasiliensis
	Stellifer rastrifer	Diapterus auratus	Achirus lineatus		Citharichthys spilopterus
	Colomesus psittacus	Bairdiella ronchus	Achirus declivis		Parapimelodus nigribarbis
LP	Stellifer naso	Achirus lineatus	Chilomycterus spinosus	Genidens genidens	
	Cathorops agassizii	Bagre marinus	Sphoeroides testudineus	Cathorops spixii	
	Cathorops spixii	Diapterus auratus	Lutjanus synagris	Eucinostomus argenteus	
	Achirus lineatus	Chaetodipterus faber	Achirus lineatus	Chaetodipterus faber	
	Colomesus psittacus	Bairdiella ronchus	Achirus declivis	Sphoeroides testudineus	

# **Regional determinants of assemblages**

When tested separately, all 8 predictor variables were significantly related to the regional variation in relative species biomass (e.g. p = 0.001 in the marginal tests). Among them, the mean temperature of water in the coldest month explained most of the variability in assemblage structure (22.8%), and the width of the estuary mouth had the lowest explanation (17%; Fig. 7). The model constructed using the forward procedure identified 4 factors that were significantly related to variability in the biotic data (i.e. mean temperature of the coldest month, distance between estuaries, mangrove area and mean annual precipitation), explaining together 61.2% of the total variance. The variables with the largest contributions in the model were the mean temperature of water in the coldest month and distance between estuaries, which explained 22.8% and 16.3% of the variance in relative species biomass, respectively (Fig. 7).



**Fig. 7.** Percent variation in the assemblage composition explained by the regionalscale variables according to the conditional test (partial) and marginal tests based on the mean relative biomass of each species in the 8 sampling areas within 5 estuaries (n = 40). The total variations explained by the conditional test including CT+DAE+MA+AR are also shown. The relationships were significant for all variables in the marginal tests and the 4 variables included in the conditional test by the forward selection method (p = 0.001 in all cases). CT: mean water temperature in the coldest month; DAE: distance among estuaries; MA: mangrove area; AR: mean annual rainfall; AT: mean annual water temperature; TR: tidal range; EA: estuary area; MW: mouth width

**Table 4.** Mean coefficients of determination (Mean  $r^2 \pm SE$ ) derived from marginal distance-based linear models (DistLM) and the prevalence of local predictors of fish assemblages in each estuary (n = 8 in each test). The results of npANOVAs comparing the coefficients of determination of the predictors and the forward conditional tests (R<sup>2</sup>) with the greatest explanatory power (including all predictors) are also shown. N: number of marginal DistLM tests made for each predictor. Note that some variables were not measured in the 4 estuaries (see 'Materials and methods' for details) and that the marginal tests were made for 12 of the 13 months sampled in Piraquê-Açú due to the unavailability of predictor variables on one occasion (July 2004)

Estuaries	Predictors	Ν	Mean $r^2(R^2)$	Prevalence		
Curuçá (pseudo- <i>F</i> <sub>4,30</sub> = 1.39, p = 0.256, n = 34)						
	Salinity	7	18.6 ± 2.4	28.5		
	Dist. mouth	7	18.5 ± 1.8	28.5		
	Temperature	7	17.9 ± 2.3	28.5		
	Oxygen	7	16.8 ± 1.9	14.2		
	Depth	7	13.0 ± 1.3	0		
	Total explained		(95.2)			
Piraquê-Açú (pseudo- <i>F</i> <sub>3,44</sub> = 1.21, p = 0.317, n = 47)						
	Depth	12	18.7 ± 1.9	25.0		
	Temperature	12	17.4 ± 2.2	25.0		
	Salinity	12	15.9 ± 1.7	16.6		
	Dist. mouth	12	14.2 ± 1.1	0		
	Total explained		(65.1)			
Paranaguá (pseudo- <i>F</i> <sub>4,25</sub> = 1.37, p = 0.261, n = 29)						
	Salinity	6	20.1 ± 4.0	33.3		
	Depth	6	18.9 ± 4.4	16.6		
	Dist. mouth	6	19.4 ± 3.0	16.6		
	Transparency	6	17.5 ± 1.7	0		
	Temperature	6	11.0 ± 1.5	0		
	Total explained		(78.3)			
L. dos Patos (pseudo- $F_{3,21} = 0.52$ , p = 0.663, n = 24)						
	Dist. mouth	7	24.4 ± 4.7	42.8		
	Transparency	4	14.0 ± 7.3	25.0		
	Salinity	7	19.8 ± 5.6	14.2		
	Temperature	7	17.1 ± 5.8	14.2		
	Total explained		(80.0)			

### Local determinants of assemblages

No significant differences were detected between the coefficients of determination of the explanatory variables in any estuary (Table 4). However, based on the percentage of DistLM tests with significant results (i.e. prevalence), the most important variables were salinity, distance from estuary mouth (DEM) and

temperature (each with 28% of tests significant) in Curuçá; depth and temperature (both with 25%) in Piraquê-Açú; salinity (33%), DEM and depth (both with 16.6%) in Paranaguá; and DEM (42.8%) and transparency (25%) in Lagoa dos Patos (Table 4). The best models obtained by the forward conditional tests explained between 95.2% (in Curuçá) and 65.1% (in Piraquê-Açú) of the total variability in the relative biomass of the species (Table 4). These results support the hypothesis that all variables analysed are potential drivers of the spatial structures of fish assemblages and also highlight clear changes in their relative importance between estuaries.

# DISCUSSION

# **Biogeographic patterns**

Some biogeographic patterns emerged from the comparisons of fauna captured in the estuaries spread over ~6000 km along the Brazilian coast. These patterns are clearly observed when the occurrences, relative biomasses and/or species richness of some families are compared. For example, Batrachoididae, Achiridae, Centropomidae and Lutjanidae were richer and more abundant in tropical estuaries (Curuçá, Santa Cruz and Piraquê-Açú) than in the subtropics (Paranaguá and Lagoa dos Patos; Figs. 3 & 4). In contrast, the relative biomass of Paralichthyidae contributed more to the assemblage at Lagoa dos Patos (32°S) (Fig. 4), mainly owing to the capture of a temperate-affinity species (Paralichthys orbignyanus). Diodontidae, represented solely by Chilomycterus spinosus in this study, was abundant only in Piraquê-Açú (Fig. 4), where 92% of its total biomass was captured. Although this species was not among the most abundant in the innerportion of a nearby estuary (Chagas et al. 2006), it ranked among the dominant species in terms of biomass at this estuary's inlet (Araujo et al. 2008) and on soft bottom of the shallow shelf (Pinheiro et al. 2009), suggesting a general pattern for the region (~19–21°S).

In contrast, a recurrent feature in most estuaries was the high biomass contribution from the families Ariidae and Sciaenidae (Fig. 4), which is similar to that observed in the catches from other tropical and subtropical estuaries in the Western Atlantic (e.g. Vieira & Musick 1994, Araújo et al. 2002, Jaureguizar et al. 2004, Barletta et al. 2005), tropical Eastern Atlantic, Indo-West Pacific and (for Ariidae)

northeastern Australia (Blaber 2000, Ley 2005). These families are widely distributed worldwide and occur in freshwater, estuarine and marine environments (Nelson 2006), which indicates a great evolutionary plasticity. Interestingly, both are capable of emitting sounds through structures that have undergone convergent evolution and that can be used to intimidate predators, for sexual attraction and in agonistic interactions with competitors (Helfman et al. 2009). Members of Ariidae, in particular, have a set of adaptations that are important for explaining the success of this family, such as (1) the presence of stingers (usually poisonous) in the dorsal and pectoral fins, (2) chemical anti-predator alarms (Schreckstoff), (3) a wide variability in thermal tolerance (eurythermia) and (4) the Weberian apparatus (Halstead et al. 1990, Nelson 2006, Marceniuk & Menezes 2007, Helfman et al. 2009). The relatively high number of Sciaenidae species (Fig. 3) with different trophic characteristics (e.g. from omnivorous to piscivorous; Chaves & Vendel 1998, Chaves & Umbria 2003) appears to further contribute to the abundance of this family in this and other studies. However, even though many families were shared among the estuaries, most species were not widely distributed.

The substantial distinction between the ichthyofauna of Lagoa dos Patos and those of other estuaries (see Fig. 5) is highlighted by the fact that about 62% (23) of species captured at Lagoa dos Patos were not recorded elsewhere. This is principally due to the capture of species that occur only in the temperate region of the southwestern Atlantic—e.g. Trachinotus marginatus, Platanichthys platana, Brevoortia pectinata, Symphurus jenynsi, Anchoa marinii, Paralichthys orbignyanus and Percophis brasiliensis (Menezes et al. 2003)—and to the presence of continental Odontesthes argentinensis, Hoplias malabaricus, species—e.g. Geophagus brasiliensis, Parapimelodus nigribarbis, Pimelodus maculatus, Charax stenopterus and Cyphocharax voga (Buckup et al. 2007). Three of the latter species ranked among the 4 dominant in biomass and/or are among the most important in distinguishing the local fauna (Fig. 2, Table 3), reflecting the high continental influence in the Lagoa dos Patos. The presence of a relatively narrow inlet (588 m for a water body of 10 360 km<sup>2</sup>) and the low tidal range (47 cm) contribute to the relatively low average salinity (5.7 vs. ≥17.4 in other estuaries), which favours the occurrence of freshwater taxa and the biomass dominance of so-called 'estuarinedependent' species, such as Micropogonias furnieri.

The separation of the ichthyofauna at Curuçá from those at other tropical locations (Fig. 5, below) was due to the capture of species that occurs only (or predominantly) in warm and turbid waters influenced by the discharge of Amazonian rivers in north Brazil (about 4°N–3°S). This group of species is composed of *Aspredinichthys tibicen*, *Amphiarius rugispinis*, *Ogcocephalus nasutus*, *Stellifer naso*, *Anchoviella guianensis*, *A. cayennensis*, *Pterengraulis atherinoides* and *Apionichthys dumerili*. One, *S. naso*, had a relatively high biomass and is the most important species in distinguishing Curuçá ichthyofauna (Fig. 2, Table 3). With the exception of *O. nasutus*, these are typically estuarine or freshwater species that occur primarily within estuaries and that may have limited capacity to disperse over long distances.

Overall, the geographical structure of the fauna illustrated by cluster analyses is consistent with the new arrangement of the Brazilian and Argentinian biogeographic provinces proposed by Briggs & Bowen (2012). The realignments proposed by these authors are based on the validation, or refutation, of the provinces (as originally defined by Briggs 1995) using a comprehensive data set of Atlantic reef fishes that suggested an extension of the Brazilian province toward the south (28°S; see Floeter et al. 2001, 2008). In fact, the sharp drop observed in similarity between Lagoa dos Patos and the other estuaries suggests a transition from one to another biogeographical entity in southern Brazil (Fig. 5) that coincides with a reduction in water temperature (Fig. 1, Table 1).

#### Local vs. regional variability

The composition of fish assemblages differed at the regional and local scales, but the variability was much higher at the regional scale (Fig. 6). As the distances between estuaries (970–6000 km) were relatively large compared with those of the points sampled within them (0.7–25 km), these results are consistent with the scale of variation of many physical properties of nature which tend to increase continuously with distance (Bell et al. 1993). A pattern of variability similar to that identified here was obtained for the fish fauna on unconsolidated and consolidated substrates of the northwest coast of Australia (Travers et al. 2010), for Caribbean coral reefs (Pandolfi 2002) and for trees in the Amazon (Tuomisto et al. 2003). Paradoxically, on the northeast coast of Australia, the variability in the compositions of ichthyofauna was

higher among estuaries within the same bay (separated by <20 km) than between bays (separated by >100 km; Sheaves 2006).

The few studies that analysed the spatial variability of estuarine fish assemblages using a nested design provided seemingly conflicting results (e.g. this study vs. Sheaves 2006). However, this disparity likely reflects differences in the geographical range covered by these investigations, which can strongly influence the pattern of variability identified (Wiens 1989, Levin 1992). Samples in this study extended over ~6000 km of coastline covering 2 zoogeographical regions, whereas the study conducted by Sheaves covered a smaller extent (~180 km). Theoretically, as the sampled area increases, a greater proportion of spatial heterogeneity is represented as a greater variety of landscape elements is included in the study area (Wiens 1989). Thus, in nested analyses where the larger scale investigated covers climatically and biologically distinct areas, as in this study, it is likely that the variability in the taxonomic composition of the assemblages will be greater on the broadest scale.

### Relative importance of regional ecological processes

Among the 8 regional predictors of the assemblages, the mean temperature of the coldest month and the distance between estuaries independently explained most of the variation in relative species biomass (Fig. 7). These results indicate that thermal preference or physiological constraints associated with temperature, and the dispersal capacity of each species are the major large-scale processes driving the structure of the assemblages. In fact, the idea that temperature is the primary driver of the geographical distribution of species has received strong empirical support in the literature, both for aquatic and terrestrial environments (Roy et al. 1998, Field et al. 2009). In relation to ichthyofauna, for example, temperature explained approximately 60% of the variability in the assemblages of South African estuaries (Harrison & Whitfield 2006), 41% of the variability in the assemblages on the shallow shelf and 53% in reef areas of Australia (Travers et al. 2010), and played an important role in distinguishing reef ichthyofauna along the Brazilian coast (Floeter et al. 2001). As expected, the mean water temperature in the coldest month of the 5 estuaries sampled decreased from north to south, ranging from 26.8°C in Santa Cruz (7°41'S) to 11.2°C in Lagoa dos Patos (32°09'S) (Table 1). This result broadly fits

with the distribution of estuary samples along the nMDS ordinations based on relative biomass and the presence/absence of species (Fig. 6).

In a similar way, the significant effect of distance between the estuaries on the structuring of fish assemblages is compatible with the contemporary view that marine populations remain more isolated than previously considered (Cowen et al. 2006, Levin 2006). This has been corroborated by molecular analyses that revealed a reduced connectivity among marine fish populations. For example, on the Atlantic coast of South America, genetic studies identified not only geographically isolated populations for an estuarine species that inhabits semi-enclosed environments such as bays and lagoons (e.g. *Atherinella brasiliensis*; Stoiev 2009), but also for a marine species that lives on the shelf and occasionally enters estuaries (e.g. *Macrodon ancylodon*; Santos et al. 2003). In both cases, the genetic heterogeneity of populations was positively correlated with geographic distance. These results parallel the prediction of neutral theory of biogeography, in which the dispersal limitation of species is one of the major factors responsible for the differences in species composition among sites (Hubbell 2001).

Mangrove area and mean annual rainfall were also important factors for the regional structuring of fish assemblages (Fig. 7). Mangroves are known to attract several species of fish owing to the provision of protection from predators, increased food availability and foraging efficiency within this habitat (Blaber 2000, Laegdsgaard & Johnson 2001). Correspondingly, some species identified by SIMPER analysis as being characteristic of 2 or more mangrove-fringed estuaries, such as *Cathorops spixii, Colomesus psittacus* and *Sphoeroides testudineus*, were also predominant in catches in mangrove channels reported by other authors (Giarrizzo & Krumme 2007, Oliveira-Neto et al. 2008). However, dependency on this ecosystem is possibly restricted to *C. psittacus*, which is known to feed primarily within mangroves (Krumme et al. 2007).

It is important to note, finally, that changes in rainfall can be ecologically important because they usually alter other factors that are directly related to the distribution and abundance of fish species in estuaries, including salinity, transparency, productivity and the depths of these environments (Garcia et al. 2001, Whitfield 1999, this study). Therefore, the significant and singular (although relatively weak) correlation of mean annual rainfall with the biotic data (Fig. 7) should actually represent the effect of these and correlated variables, but not rainfall itself. These results are supported by previous studies that also reported indirect effects of rainfall on the dynamics of the ichthyofauna in Lagoa dos Patos (Garcia et al. 2001) and in several other estuaries in South Africa (see Whitfield 1999 for a review).

# Relative importance of local ecological processes

At the local scale, the relative importance of environmental variables as predictors of fish assemblages varied in relation to estuaries, although the average r<sup>2</sup> for salinity was slightly higher in 2 of the 4 locations (Curuçá and Paranaguá, see Table 4). As salinity has been considered by several studies to be important for the spatial structure of estuarine fish assemblages (e.g. Barletta et al. 2005, Vilar et al. 2011), this result was partially expected. In contrast, the prevalence values for temperature (especially in Curuçá and Piraquê-Açú) were unexpected, since this variable has been previously associated with temporal variation, but not with the local-scale spatial variation in ichthyofauna (e.g. Bacheler et al. 2009, Vilar et al. 2011). However, this inconsistency seems to be related to the fact that, commonly, the spatial and temporal effects of explanatory variables in species distribution have been analysed together, making it impossible to determine the operational scale (i.e. spatial or temporal). Thus, these results highlight the need for spatial structure of the fauna and possible ecological drivers.

The distance from the mouth of the estuary also had an important role as a predictor of fish assemblage composition, especially in the Lagoa dos Patos and Curuçá (Table 4). As the measurement of this variable can be performed using GIS, it is relatively easy, inexpensive and fast to obtain compared with other predictors. Thus, these attributes make it particularly attractive as a predictor of the relative biomass of species, especially where data are scarce or nonexistent. Depth had a considerable role as predictor of the fish assemblages at Piraquê-Açú and Paranaguá (Table 4), similar to that observed in Vitória Bay (southeastern Brazil), where depth had the most influence on species abundance (Chagas et al. 2006). However, none of the 7 DistLM analyses performed for Curuçá revealed a significant correlation between depth and the biotic data, showing an inconsistency between estuaries. For transparency, of the 10 DistLM tests performed (6 in Paranaguá and 4

in Lagoa dos Patos), only one was significant for Lagoa dos Patos, which resulted in a relatively high prevalence in this estuary, although it had a relatively low  $r^2$  (Table 4). Overall, the heterogeneity in the relative importance of environmental variables between estuaries emphasises the role of idiosyncratic physical and hydrological features in determining the spatial structure of the fauna, and that the effects of these variables must be examined individually.

### CONCLUSIONS

Our results showed that, although the composition of fish assemblages is significantly different at both local and regional scales, the variability in composition of the fauna is much higher between estuaries than between sampling sites within them. The analysis correlating the relative biomass of species with a set of environmental and spatial variables provided some evidences of the main processes generating and maintaining this pattern of variability. At the regional scale (between estuaries), the variability in relative biomass of the species was explained by 3 independent environmental variables (in decreasing order: mean water temperature of the coldest month, mangrove area and mean annual precipitation) and by the distance between estuaries. At the local scale (between sampling sites within a given estuary), all predictors examined can act as modulators of the spatial structure of the assemblages, but their relative importance differs among estuaries. Overall, these results provide support for the idea that the geographic patterns in the compositions of the assemblages are simultaneously determined by environmental filters (especially water temperature) and the dispersal capacity of species, while localscale spatial patterns are additionally influenced by other variables that vary in importance depending on estuary-specific physical and hydrological characteristics.

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# Capítulo II

# Riqueza de espécies, raridade e escolha de áreas para a conservação: um estudo de caso com peixes estuarinos brasileiros

Ciro C. Vilar, Jean-Christophe Joyeux, Henry L. Spach

# RESUMO

Prioridades espaciais para a conservação têm sido frequentemente instituídas com base no número de espécies. Porém, áreas priorizadas a partir da riqueza de espécies não necessariamente são eficientes para representar outras características biológicas relevantes. Neste estudo, os padrões geográficos de rigueza de espécies e raridade da ictiofauna estuarina foram mapeados e integrados para identificar regiões importantes para a conservação da biodiversidade na costa brasileira. Além disso, também foi analisada a efetividade do sistema nacional de áreas protegidas para representar essas regiões. Das 154 bandas latitudinais consideradas (com 0,25° de latitude cada), 48 foram identificadas como prioritárias para a conservação por possuírem simultaneamente uma alta riqueza de espécies e assembleias relativamente raras. Dessas, 20 foram exclusivamente identificadas quando todas as espécies foram incluídas, 23 quando somente as espécies endêmicas foram consideradas e apenas 5 foram selecionadas usando ambos os conjuntos de dados. Portanto, os resultados indicam que as áreas prioritárias para a conservação de espécies endêmicas devem ser distintas daquelas para todas as espécies, e viceversa. Também foi verificado que o sistema atual de áreas protegidas é ineficiente para proteger as bandas prioritárias para a conservação, identificadas nesse estudo. Essa constatação realça que uma ampliação estratégica da rede nacional de unidades de conservação estuarinas é urgentemente necessária para resguardar áreas com alto valor para a conservação da ictiofauna.

PALAVRAS-CHAVE: Endemismo · Ictiofauna · Estuário · Planejamento para conservação · Áreas protegidas · Priorização · Brasil

# ABSTRACT

Spatial conservation priorities have usually been established based on species number. However, areas prioritized from species richness data are not necessarily efficient to protect others important biological proprieties. In this study, geographic patterns of species richness and rarity of the estuarine ichthyofauna were mapped and integrated to identify important regions for biodiversity conservation across the Brazilian coast. Furthermore, we also analyzed the effectiveness of the national system of protected areas to represent these regions. Of the 154 latitudinal bands considered (with 0.25° of latitude each), 48 were recognized as conservation priorities by harbor simultaneously high species richness and assemblages that are relatively rare. Of these, 20 were exclusively identified when all species were taking into account, 23 when only endemic species were considered and just five were selected using both datasets. Therefore, these results indicate that priority areas for conservation of endemic species should be different from those for conservation of all species, and vice-versa. Also was found that the existing system of protected areas is inefficient to represent priority bands identified in this study. This finding indicates that a strategic expansion of the national network of estuarine conservation units is urgently necessary to protect areas with high conservation value. Our results could help to inform where are located some of these places.

KEY WORDS: Endemism · Ichthyofauna · Estuary · Conservation planning · Protected areas · Prioritization · Brazil

# INTRODUÇÃO

Estratégias espaciais para a conservação são geralmente baseadas nos padrões geográficos da biodiversidade (Roberts et al. 2002, Brooks et al. 2006). Para serem eficientes, tais estratégias requerem informações espacialmente acuradas e representativas sobre a distribuição da biota. No entanto, a falta de dados sobre a distribuição das espécies tem dificultado a aplicação de métodos para priorização de áreas para a conservação e o manejo, particularmente no ambiente marinho. A obtenção de uma medida abrangente dos padrões geográficos da biodiversidade é ainda dificultada pela própria natureza multidimensional do conceito (Price 2002). Talvez por essas razões, as estratégias de conservação focam frequentemente em medidas particulares, tal como o número de espécies, para identificar locais prioritários para atuação (Brooks et al. 2006, Allen 2008, Trebilco et al. 2011).

O número total de espécies (doravante riqueza de espécies) ou de espécies endêmicas é uma medida relativamente simples e direta do valor de uma área para a conservação. Para o ambiente marinho, evidências apontam que locais ricos em espécies possuem também maior capacidade de manter serviços ecossistêmicos fundamentais (e.g., produção de alimentos, manutenção da qualidade da água, etc.) e de se recuperar de distúrbios (Worm et al. 2006). A riqueza local de espécies, porém, representa apenas uma das múltiplas facetas da biodiversidade. Isso significa que escolher áreas para proteção com base apenas na riqueza de espécies pode ser inadequado para representar outras características biológicas relevantes (Orme et al. 2005). Então, o valor de uma estratégia espacial de conservação pode ser potencializado se medidas de riqueza forem associadas a outras variáveis ecológicas (Fleishman et al. 2006).

Recentemente, uma abordagem que integra riqueza de espécies e raridade foi proposta para definir prioridades espaciais para a conservação em escalas geográficas amplas (veja Villalobos et al. 2013a, b). Espécies consideradas raras devido à distribuição geográfica restrita, usualmente, possuem populações relativamente pequenas, dois atributos que as tornam mais vulneráveis à extinção (Roberts & Hawkins 1999). Por causa disso, raridade *per se* tem sido considerada uma ameaça dupla (Gaston 1998). Espécies raras possuem também traços distintos daquelas comuns e funções que não podem ser suportadas por outras espécies, fundamentais para a estruturação das assembleias e o funcionamento dos ecossistemas (i.e., baixa redundância funcional, Mouillot et al. 2013). Tais características ressaltam a importância de conservar espécies raras mesmo em ecossistemas relativamente ricos, onde é esperada uma elevada redundância ecológica (Gaston 1998, Mouillot et al. 2013).

Neste estudo, os padrões geográficos de riqueza de espécies e de raridade da ictiofauna estuarina foram mapeados e integrados para identificar regiões importantes para a conservação na costa brasileira, utilizando-se como base a abordagem proposta por Villalobos et al. (2013a). Também foi analisada a efetividade do sistema existente de áreas protegidas para representar essas regiões. O objetivo central foi responder as seguintes questões: (1) quais são as áreas mais ricas em espécies? (2) onde a distribuição geográfica das espécies é em média menor? (3) quais áreas possuem simultaneamente alta riqueza de espécies e assembleias com distribuição relativamente restrita? (4) qual é o percentual atual de proteção dessas áreas?

# MATERIAL E MÉTODOS

# Base de dados

Uma lista de espécies de peixes estuarinos brasileiros foi compilada usando informações disponíveis na literatura e em coleções ictiológicas (ver lista de referências no Apêndice 1). A coleta de informações restringiu-se a ambientes explicitamente descritos como um estuário ou que puderam ser identificados como tal (e.g., a partir de imagens de satélites, descrição da área de estudo, etc.). Em uma segunda etapa, as espécies primariamente dulcícolas, oceânicas, introduzidas, vagantes e/ou de ocorrência duvidosa na costa brasileira (i.e., representadas por um único registro e não confirmadas pela literatura) foram excluídas da base de dados. Essa triagem resultou em uma lista com 412 espécies de peixes estuarinos *lato sensu* (Apêndice 2).

Em uma terceira etapa, a distribuição de cada espécie ao longo da costa brasileira foi mapeada usando-se 154 bandas latitudinais com 0,25° de latitude cada (adaptado de Tognelli et al. 2009). Essas bandas foram dimensionadas de forma a providenciar as soluções mais detalhadas possíveis dentro das limitações espaciais

de resolução dos dados biológicos disponíveis. A presença/ausência de cada espécie em cada banda foi inicialmente determinada com base no "Catálogo das Espécies de Peixes Marinhos do Brasil" (Menezes et al. 2003). Os limites de distribuição das espécies foram posteriormente ajustados utilizando-se informações mais precisas, como listas locais de espécies obtidas em artigos científicos, revisões taxonômicas e de distribuição, extensões de ocorrência documentadas, e as localidades de captura de espécimes depositados em coleções ictiológicas.

# Análises

A riqueza de espécies em cada banda latitudinal foi calculada como a soma de todas as espécies presentes. A raridade das assembleias habitando cada banda foi determinada como a distribuição geográfica (em termos do número de bandas ocupadas) média das espécies que ocorrem em cada banda (Villalobos et al. 2013a). A partir dessas informações foram identificadas bandas que possuem simultaneamente alta riqueza de espécies e assembleias com distribuição relativamente restrita. Para isso, foi utilizada uma abordagem baseada na divisão dos valores em quantis, empregada comumente para definição de "hotspots" de biodiversidade (e.g., Tittensor et al. 2010) e de espécies raras (e.g., Kreft et al. 2006). As bandas pertencentes ao quarto quartil de riqueza de espécies (i.e., relativamente ricas) e ao primeiro quartil de distribuição geográfica (i.e., com os menores valores de distribuição média das espécies) foram definidas como "ricasraras" (Villalobos et al. 2013b). Essas análises foram repetidas, incluindo apenas 28 espécies endêmicas da costa brasileira (c.f., Menezes et al. 2003, Floeter et al. 2008). O número de espécies, a distribuição média das assembleias em cada banda, bem como a localização geográfica das bandas ricas-raras foram mapeadas usando o programa ArcGIS 9.3 (ESRI 2009).

Arquivos vetoriais ("shapefile") das Unidades de Conservação (UCs) estabelecidas em território brasileiro foram obtidos do Ministério do Meio Ambiente (http://mapas.mma.gov.br/i3geo/datadownload.htm) e utilizados para identificar UCs marinhas e terrestres que abrangem áreas estuarinas dentro dos seus limites. Essas UCs foram usadas para definir quais bandas ao longo da costa do Brasil estão atualmente protegidas. Neste estudo, todas as bandas que possuem pelo menos uma UC de Proteção Integral (i.e., categorias I–IV da IUCN) que abrange qualquer

área estuarina foram consideradas protegidas. Usando-se essa definição, foi determinada a representatividade das bandas ricas-raras pelo sistema brasileiro de UCs.

### RESULTADOS

Das 412 espécies de peixes estuarinos consideradas, 371 são Actinopterygii e 41 Elasmobranchii. O número total de espécies nas bandas latitudinais com pelo menos um estuário variou de 160 a 328 (média  $\pm$  DP = 281  $\pm$  51,6 espécies). As bandas mais ricas em espécies localizam-se na costa sudeste (estado do Rio de Janeiro), onde é prevista a ocorrência de 79,6% das espécies analisadas em uma única banda. A partir desse ponto houve um decréscimo progressivo na riqueza até o sul do Brasil, que representa a área menos rica em espécies no País (Fig. 1A). O número de espécies endêmicas por banda latitudinal variou entre 4 e 18 (média  $\pm$ DP = 11  $\pm$  4,6 espécies). O padrão espacial de riqueza de espécies endêmicas diferiu daquele observado para todas as espécies: houve uma baixa concentração de espécies endêmicas no norte da costa, um pico na região nordeste (costa da Bahia) e uma redução gradativa em direção ao sul (Fig. 1B).

Considerando todas as espécies, a distribuição média das assembleias em cada banda variou entre 119 e 130 bandas latitudinais (média  $\pm$  DP = 104,9  $\pm$  46,2 bandas latitudinais). As áreas habitadas por espécies que, em média, possuem distribuições mais amplas concentraram-se nas regiões nordeste e sudeste do País, enquanto as bandas ocupadas por espécies que possuem distribuições mais restritas localizaram-se no norte e no sul da costa (Fig. 1C). Para as espécies endêmicas, a distribuição média das assembleias de cada banda variou entre 78 e 123 bandas latitudinais (média  $\pm$  DP = 94,4  $\pm$  10,2 bandas latitudinais). As bandas ocupadas por espécies com distribuição relativamente ampla situaram-se no norte, no nordeste e no sul da costa, enquanto as bandas habitadas por espécies endêmicas com distribuição relativamente restrita localizaram-se principalmente na região central, mas também no extremo sul e no norte da costa (Fig. 1D).



**Fig. 1.** Padrões geográficos de riqueza de espécies (A), endemismo (B) e de distribuição para todas as espécies (C) e para as espécies de peixes estuarinos endêmicas da costa brasileira (D). Os valores denotam o número de espécies (A e B) e a distribuição média em número de bandas (C e D). Bandas hachuradas não contêm estuários. Note que as bandas latitudinais foram estendidas longitudinalmente para melhor visualização.

A vasta maioria dos peixes (296 ou 71,8% das espécies) ocorre em mais do que 50% das bandas latitudinais, enquanto poucas espécies (54 ou 13,1%) ocorrem em menos do que um quarto da costa brasileira. Dessas, apenas *Achirus mucuri* ocorre em somente uma banda latitudinal. Esse padrão resultou em uma distribuição de frequência assimétrica à esquerda (assimetria = -0.67), com muito mais espécies com distribuição ampla do que o contrário (Fig. 2A). Um padrão de distribuição

oposto foi encontrado para as espécies endêmicas, uma vez que a maioria delas (20 ou 71,4%) ocorre em menos do que 50% das bandas. Das 28 espécies endêmicas consideradas. apenas 3 ocorrem mais do que 75% da em costa. Consequentemente, a distribuição de frequência das amplitudes geográficas é assimétrica à direita (assimetria = 0.37), já que a maioria das espécies tem distribuição restrita (Fig. 2B).



**Fig. 2.** Frequência de ocorrência por classe de distribuição geográfica para todas as espécies (A) e para as espécies endêmicas da costa brasileira (B).

Dezesseis das 119 bandas que possuem pelo menos um estuário contam com Unidades de Conservação (UCs) de Proteção Integral, 53 com UCs de Uso Sustentável e 7 possuem UCs de ambas as categorias. Apenas 36% (9) das bandas mais ricas em espécies e que também possuem assembleias com distribuições mais restritas (i.e., "ricas-raras") têm atualmente pelo menos uma UC de Proteção Integral (Fig. 3A). Em relação às espécies endêmicas, a situação é ainda pior: somente 7,1% (2) das bandas ricas-raras estão atualmente protegidas por UCs de Proteção Integral (Fig. 3B).

# DISCUSSÃO

Os dados compilados neste trabalho permitiram que, pela primeira vez, fossem mapeados os padrões geográficos de riqueza de espécies, endemismo e raridade da fauna de peixes estuarinos ao longo da costa brasileira. Os resultados revelaram: (1) que os centros de riqueza de espécies e de endemismo da ictiofauna estuarina são geograficamente incongruentes, (2) que o padrão espacial de raridade

encontrado para o conjunto total de espécies possui diferenças notáveis daquele observado para as espécies endêmicas, e (3) que áreas importantes, tanto para a conservação do conjunto regional de espécies quanto para a conservação de espécies endêmicas, estão atualmente desprotegidas na costa brasileira.



**Fig. 3.** Localização das bandas ricas-raras identificadas a partir de todas as espécies (A) e a partir das espécies endêmicas (B). Bandas que contêm unidades de conservação de proteção integral também são indicadas. Note que as bandas latitudinais foram estendidas longitudinalmente para melhor visualização.

Com base na distribuição de todas as espécies, um pico de riqueza emergiu na costa sudeste (21°23'–23°09'S) do Brasil em vez de na costa norte, próxima ao Equador. Esse resultado é consistente com os de estudos prévios sobre peixes recifais (Floeter et al. 2001), peixes ósseos costeiros (Tittensor et al. 2010) e tubarões (Lucifora et al. 2011), o que reforça as constatações deste estudo. Para peixes recifais, a coocorrência de espécies tropicais e temperadas na costa sudeste brasileira tem sido frequentemente considerada a causa desse padrão (Moura e Sazima 2000, Floeter et al. 2001, Luiz Jr. et al. 2008), o que potencialmente pode aplicar-se para a ictiofauna estuarina, bem como para os demais grupos de organismos. Essa região coincide com o limite sul da Província Brasileira e o limite norte da Província Argentina, originalmente estabelecidos em Cabo Frio (22°S; Briggs 1995). Ela se encontra em uma zona de transição biogeográfica, onde espécies de peixes de águas frias e quentes alcançam seus limites norte e sul de distribuição, respectivamente (Moura & Sazima 2000, Floeter et al. 2001). Porém, é importante notar que, essa e outras hipóteses (tal como "the mid-domain effect", Colwell & Lees 2000) sobre a causa do padrão de riqueza repetidamente observado na costa do Brasil ainda devem ser testadas.

A partir de uma perspectiva aplicada, as incongruências espaciais entre riqueza total e o número de espécies endêmicas (Fig. 1A, B) indicam que "hotspots" de riqueza têm utilidade limitada para representar centros de endemismo. Por exemplo, regiões com alta riqueza de espécies endêmicas como o sul da costa nordeste, assim como regiões com baixa riqueza como a costa norte do Brasil, têm valores intermediários de riqueza total. Em termos ecológicos, esses resultados sugerem que os padrões geográficos de diferentes componentes da biodiversidade são determinados por mecanismos distintos. No entanto, em termos de conservação, esses resultados indicam que reservas estabelecidas com base na riqueza total tendem a não contemplar áreas onde ações de manejo são obviamente necessárias para evitar a perda global de espécies (Myers et al. 2000). Isso é reforçado por outros estudos que encontraram resultados similares para peixes recifais (Roberts et al. 2002) e aves terrestres (Orme et al. 2005).

De forma similar, as diferenças encontradas entre os padrões geográficos de riqueza e raridade sugerem que estratégias de conservação baseadas apenas em "hotspots" de diversidade podem negligenciar muitas espécies raras, já que elas ocorrem tanto em regiões ricas como em regiões pobres em espécies. Para o conjunto total de espécies, por exemplo, bandas com alta riqueza de espécies localizadas na costa sudeste do País e com riqueza intermediária, localizadas na costa nordeste, abrigam assembleias com distribuição média relativamente grande. Em contraste, bandas pobres em espécies, situadas particularmente na região sul do Brasil, abrigam assembleias com distribuição relativamente restrita (Fig. 1A, B). De fato, essa região possui uma fauna de peixes significativamente diferente do restante do País, em termos de composição taxonômica (Vilar et al. 2013). Isso significa que a conservação desses "coldspots" de biodiversidade também deve ser considerada para uma representação mais eficiente da biota regional.

Por considerar riqueza total e endemismo separadamente para definir prioridades, as alternativas para investimento apresentadas aqui foram ampliadas e incluem múltiplos objetivos de conservação. Isso providencia aos tomadores de decisões a oportunidade de avaliar e escolher áreas para atuação em consonância com objetivos particulares e com potenciais impedimentos para implementação das ações de manejo em campo. Mais precisamente, os resultados reforçam que as áreas prioritárias para a conservação de espécies endêmicas devem ser distintas daquelas para todas as espécies, já que apenas 10,4% (5) das bandas ricas-raras foram comuns aos conjuntos selecionados, considerando cada uma dessas variáveis. Mas, ao mesmo tempo, eles também indicam que existem bandas eficientes tanto para a proteção de espécies endêmicas como para a proteção da ictiofauna como todo, que, no entanto, devem ter alta prioridade de conservação.

Estuários são ecossistemas particularmente afetados pelas ações humanas e apresentam evidências de que se tornarão centros de extinção de espécies marinhas (Roberts et al. 1999). Apesar de fornecerem bens e serviços relevantes para a população humana (Barbier et al. 2011), eles têm um baixo percentual global de proteção se comparados a outros ecossistemas marinhos (Wood et al. 2008). Os resultados desse estudo mostram que a rede brasileira de UCs é altamente ineficiente para a proteção de áreas identificadas como prioritárias para a conservação da ictiofauna estuarina, particularmente para espécies endêmicas com distribuição restrita. Mesmo usando um critério "liberal" para definir uma banda como protegida (i.e., qualquer porção de um estuário dentro de uma banda abrangida por uma UC), grandes lacunas no sistema existente de UCs foram identificadas ao longo da costa brasileira (Fig. 3). Um exemplo proeminente é a região entre os estados do Piauí e o sul da Bahia, onde está localizada a maior parte das bandas ricas-raras identificadas a partir de espécies endêmicas. Essas observações são consistentes com o fato de que estuário é o ecossistema costeiro menos protegido pelas UCs brasileiras de proteção integral (~ 0,2% da área total), que muitas vezes abrangem apenas áreas adjacentes (e.g., manguezais, recifes de coral, costões rochosos) (Prates et al. 2012). Frente a esse panorama, é urgentemente necessária a concepção, a implantação e o monitoramento de uma estratégia nacional de conservação das áreas estuarinas.

Experiências anteriores têm ilustrado que é inviável um único esquema de priorização incorporar todas as facetas da biodiversidade que podem ser consideradas para informar o processo de tomada de decisão. Por isso, desenvolver estratégias espaciais de conservação usando medidas alternativas e, posteriormente, analisar congruências e diferenças pode ajudar a identificar locais

mais eficientes para representação da biodiversidade (e.g., Price 2002, Brooks et al. 2006, Devictor et al. 2011). Utilizar riqueza de espécies, endemismo e raridade, como foi feito aqui, é uma alternativa pragmática para guiar a alocação de recursos e o desenvolvimento de estratégias de conservação mais detalhadas em escala local. Por fim, espera-se que os resultados deste estudo contribuam para o avanço dos esforços de conservação dos ecossistemas estuarinos brasileiros e da ictiofauna que habita essas áreas, em particular.

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# Capítulo III

# Setting priorities for the conservation of marine vertebrates in Brazilian waters

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Biological Conservation (in review)

#### Abstract

The global panorama of biodiversity loss has motivated international agreement to enhance the protection of the world's oceans. Given the conflicting interests arising from multiple uses of seascapes and finite funds for conservation, developing costeffective strategies for marine biodiversity conservation is crucial to support decision making. Here, we present alternatives for the expansion of current marine protected areas (MPAs) in Brazilian waters that maximize species representation and reduce potential conflicts with relevant economic activities. We compared conservation benefits provided by three conservation-planning scenarios that incorporate the distribution of 750 marine vertebrate species while considering established MPAs and areas concessioned for oil and gas exploitation. The results showed that a MPA network encompassing 10% of the study area with high conservation priority would protect between 85.8 and 86.5% of species distribution on average. We found that incorporating existing MPAs and areas concessioned for oil and gas exploitation in the prioritization process caused only a small loss in representation of nearthreatened and threatened species. Our results highlight, therefore, that it is possible to reconcile current offshore oil and gas production with the expansion of the national MPA network, without significant losses in species' representation. The solutions presented here, may be useful as scientific support in political negotiations about Brazil's commitment to protect 10% of its coastal and marine areas by 2020. In addition, our approach provides an example on how to integrate freely available information to reconcile biodiversity conservation with the development of important economic activities in data-poor regions of the world.

Keywords: Marine protected areas, Conservation planning, Convention on Biological Diversity, Zonation, Brazil, Priority setting

#### 1. Introduction

Over time, marine protected areas (MPAs) have become a key component of ocean conservation strategies around the world. The growing use of this tool is supported by the accumulated evidence that MPAs can restore species' biomass and density, increase diversity of assemblages, improve fishery productivity, and maintain ecosystem services essential to human well-being (see Sobel and Dalgren, 2004; Floeter et al., 2006; Sala et al., 2013). In recent decades, these benefits were explicitly recognized by multilateral international organizations that integrated MPA establishment into their plans for the conservation of the world's oceans (Laffoley, 2006). A notable example is the recommendation from the Convention on Biological Diversity (CBD) for all signatory countries to conserve at least 10% of their coastal and marine areas by 2020, "...through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures..." (CBD, 2010).

Nevertheless, the failure of the previous agreement to protect 10% of the marine area on the planet (Mittermeier et al., 2010) shows that implementing this goal is an enormous challenge for most countries involved. Current levels of funding are not only insufficient to meet global conservation targets, as they are also inadequate for managing already established MPAs, both in developed and developing nations (Balmford et al., 2004; Gerhardinger et al., 2011). In addition, conflicting interests arising from multiple uses of seascapes by different sectors of the society clearly hinder the expansion of MPAs (Douvere, 2008) and consequently contribute for current low levels of marine protection worldwide (Wood et al., 2008). These constraints, therefore, make essential the use of conservation triage for allocation of limited conservation funds (Margules and Pressey, 2000; Bottrill et al., 2008). Which areas are more important for marine biodiversity conservation? Which areas should receive immediate management intervention, and which could wait? Where funds should be invested to maximize the number of protected species using a specific pre-established budget? Which areas, if conserved, would best represent biodiversity and minimize the potential for conflict with socioeconomic activities? Certainly, answering these questions is a critical step towards building efficient MPA networks.

Despite methodological advances for prioritizing areas for MPA establishment, literature reviews have described relatively few national-level marine plans based on multiple taxa (Leslie, 2005; Pinto and Grelle, 2009) that could efficiently guide MPAs spatial allocation and aid countries to fulfill international agreements (but see Tognelli et al., 2009 and Allnutt et al., 2012). Various obstacles have contributed to this deficiency, including lack of extensive georeferenced data related to species distribution (and other biodiversity features) as well as to relevant social and economic factors (Leathwick et al., 2009; Moilanen, 2012). These obstacles are especially problematic for underdeveloped countries with an extensive coastline. In general, such regions are insufficiently sampled and support numerous human activities (e.g., oil and natural gas production, fishing, tourism, maritime transport) that can preclude marine conservation initiatives (Miloslavich et al., 2011; Allnutt et al., 2012).

The exploration for and production of oil and natural gas are particularly important activities in Brazilian waters that demand special attention during the initial stages of MPAs planning. Between 2000 and 2012, for example, an average of 88.2% and 64.9% of the total oil and gas produced in the country, respectively, were extracted from wells at sea (ANP, 2012). Currently, a large portion (≈332,961 km<sup>2</sup> or 9.5%) of the marine area under the Brazilian jurisdiction is controlled by oil and gas companies (Fig. 1; ANP, 2012). The political and economic status of the large organizations exploring these resources, aligned with the likely negative environmental impacts of the oil sector, poses additional and urgent challenges for marine spatial conservation planning in Brazil and elsewhere.

Here, we assembled an extensive database with the geographic distribution of marine vertebrates, established MPAs and areas concessioned for oil and gas exploitation to identify priority sites for biodiversity conservation in Brazilian waters. Using these data, we developed three alternative spatial conservation scenarios aiming at (1) identifying sites with the best conservation return on investment if the entire seascape were available for protection; (2) establishing the most important sites to complement the current MPA system; and (3) producing an effective solution to expand the already established network of MPAs while considering the spatial limitations imposed by economic activities linked to the oil and gas industry. Finally,

we examine the trade-offs among networks of MPAs proposed under the three analyzed scenarios.



**Fig. 1.** Areas concessioned for offshore oil and natural gas exploration and production in Brazilian waters. EEZ stands for Economic Exclusive Zone.

### 2. Methods

2.1. Species distribution data

We obtained range maps for 61 seabird species (Ridgely et al., 2012), 35 marine mammal species (IUCN version 2012.1; http://www.iucnredlist.org/technicaldocuments/spatial-data#mammals) and five marine turtle species (Halpin et al., 2009; Wallace et al., 2010) reported to inhabit Brazil, as well as occurrence records for 649 marine and estuarine fishes (listed in Table A1). Data on fish distribution were derived from a comprehensive database with >31 600 occurrence records compiled from major ichthyologic collections in Brazil (via speciesLink; http://www.splink.org.br/), the Ocean and Biogeographic Information System (http://www.iobis.org/), books, peer-reviewed articles and gray literature (PhD and MSc theses, and unpublished reports). The occurrence of each fish species in Brazilian waters was confirmed based on the work of Menezes et al. (2003), Floeter et al. (2008), and original species descriptions. We excluded from the database (1) non-native species introduced in Brazil; (2) vagrants species (recorded as a few individuals in only one or two places); (3) freshwater species; and (4) doubtful occurrences (e.g., records of estuarine or coastal species in areas far away from the coast, where they are not expected occur) likely associated to erroneous locality records. Species nomenclature followed Eschmeyer (2012) for fishes and Appeltans et al. (2012) for all other taxonomic groups.

Range maps and occurrence records for each species were overlayed onto a grid of  $0.25^{\circ} \times 0.25^{\circ}$  cells (ca. 27.7 km of latitude and longitude near the equator). This grid included 5,275 cells covering the coastline up to the 200 nm offshore limit of Brazil's Exclusive Economic Zone (EEZ) (Fig. 1). We then built binary maps for each species assuming it is present in cells that overlap with any portion of its range maps (for non-fish species) or with occurrence records (for fishes) and it is absent elsewhere. These maps were used as inputs for spatial conservation prioritization analyses described below.

#### 2.2. Seascape prioritization

We used the Zonation conservation planning software (Moilanen et al., 2005) to solve the "utility maximization problem", i.e., to identify sites that maximize biodiversity representation while taking into account a specific proportion of the study area. The Zonation algorithm produce a hierarchical ranking of conservation priorities for all cells within a determined area using in the selection process the occurrence

level for biodiversity features (in this study, species) in grid cells, the connectivity, and the complementarity of cells (Moilanen et al., 2005). The software applies a reverse heuristic algorithm which begins with the full set of cells and iteratively removes single cells based on the criterion of minimization of marginal loss (i.e., the relative importance of a cell compared to all others). Therefore, cells with the smallest marginal loss are removed first, and cells with high marginal loss (i.e., greatest conservation value) are removed last. Here, we used the core-area cell removal rule to calculate the marginal loss of each cell. This variant prioritizes high-quality locations for all species (the "core-areas" of species' distribution) in the final outcome and also takes into account the weight (or priority) given to them (see Moilanen et al., 2005, 2009 for further details).

We applied a weighting scheme that varies according to species conservation status (adapted from Lemes and Loyola, 2013), where: 1 = least concern, data deficient and not assessed species; 97 = near threatened species; 98 = vulnerable species; 99 = endangered species; and 100 = critically endangered species. The level of threat assigned to each species was determined primarily based on the National Red List of Threatened Species (MMA, 2004, 2005), but additional information were obtained from the IUCN Red List (IUCN, 2011) for species yet not evaluated regarding their conservation status at the national level. To investigate the effects of our weighting scheme on the proportion of species' range captured, we ran a sensitivity analysis that compared results obtained using the above-mentioned weighting scheme with results obtained using equal weight (i.e., 1) for all species (Fig. A1; see also Faleiro and Loyola, 2013, for more details).

#### 2.3. Comparison of alternative scenarios

We used replacement cost analyses (Cabeza and Moilanen, 2006) to compare the conservation value of the areas prioritized under three different scenarios. In the first scenario (henceforth referred to as "unconstrained" scenario), the Zonation algorithm was free to determine which cells had the best conservation return based solely on species' distributions and weights, without any spatial constraint. In the second scenario ("MPAs fixed" scenario), we constrained the algorithm selection space by treating cells that overlap with the contemporary network of strictly protected areas (categories I–IV of IUCN) as top-ranked sites, using a mask layer based on data from IUCN and UNEP-WCMC (2012). This scenario identifies the best sites for expanding and complementing the current network of MPAs, assuming that all non-protected areas are available for conservation. In the third scenario ("oil and gas" scenario), we constrained the algorithm by simultaneously including already established MPAs as top-ranked sites and cells containing areas concessioned for oil and gas exploration or production (according to data from National Agency of Petroleum, available at http://maps.bdep.gov.br/website/maps/viewer.htm) as being least important, regardless of their real conservation value. This scenario, in turn, identifies the best areas to expand and complement the current network of MPAs while avoiding areas being used by the oil and gas industry and, therefore, circumvent potential conflicts between alternative seascape uses and the protection of areas at risk of losing conservation value. We integrated the areas used for oil exploration and production into our analyses for two main reasons. First, these areas were temporarily conceded to companies with a right to exclusive use and are currently unavailable for conservation. Second, because the oil industry is one of the primary pillars of the national economy, a reserve network planned such that it does not interfere with these sector's activities would have a greater chance of implementation.

Finally, we used a one-way ANOVA to determine if the proportion of species distribution captured (dependent variable) differed among the three conservation scenarios (factor). Data were arcsine-transformed before tests to approach the assumptions of normality and homocedasticity. For these analyses, we grouped species into the following three groups: non-threatened (least concern, data deficient and not assessed species), near threatened and threatened (vulnerable, threatened and critically threatened), and compared scenarios for each group separately. The percent distribution of each species included in each scenario was computed using the top-ranked 10% of seascape, which is in accordance with target defined for the coastal and marine areas by the Aichi Biodiversity Target 11 (CBD, 2010).

#### 3. Results

Results for the unconstrained scenario showed that a MPA network encompassing 10% of the study area with high conservation priority would assure an average coverage of 85.8% of species distribution (Fig. 2). All 750 studied species would receive some measure of protection. The laughing gull (*Leucophaeus atricilla*) was the species with the lowest proportion of distribution represented (4.2%), while three mammals, six seabirds and 445 fishes had the highest representations (100%). Under this scenario, high priority areas were identified from the extreme north to the extreme south of the Brazilian coast and encompassed both coastal and oceanic regions near the outer edge of the EEZ (Fig. 3A). However, some locations were notably important, such as the coastal region between the states of Ceará and Alagoas, the southern coast of the state of Bahia (Abrolhos Bank), the coastal region between the states of Paraná and Santa Catarina, a vast southern area in Rio Grande do Sul and the oceanic region surrounding Trindade and Martin Vaz archipelago (Fig. 3A).



**Fig. 2.** Minimum and mean proportions of species' distribution represented in the three conservation scenarios according to the percentage of seascape protected. Blue line: unconstrained scenario; dotted line: MPAs fixed scenario; red line: oil and gas scenario. The vertical line indicates the 10% target used in our analyses.

Top conservation areas selected in the MPAs fixed scenario reached a mean percentage of species distribution of 86.5%, a value slightly greater (0.7%) than the unconstrained scenario (Fig. 2). This small gain was accompanied by an approximate loss of 0.1% in the area of distribution for near-threatened and threatened species compared to the unconstrained scenario. To reach the goal of protecting 10% of the Brazil's EEZ, 460 cells would need to be protected beyond the

68 presently representing established MPAs. The most important cells (0–10% in Fig. 3B) were 84.2% similar to those in the unconstrained scenario (Fig. 3B). This means that 15.8% of the best cells in this scenario represent already established MPAs that have a conservation value lower than alternative cells selected in the unconstrained scenario.



**Fig. 3.** Conservation priority ranking determined for the unconstrained scenario (A), for the MPAs fixed scenario (B), and for the oil and gas scenario (C). States mentioned in the text are indicated by their acronyms: MA, Maranhão; CE, Ceará; AL, Alagoas; BA, Bahia; SP, São Paulo; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul.

Priority sites for MPAs establishment indicated by our oil and gas scenario would protect a mean proportion of species distribution of 86.2%, an intermediate level between the unconstrained and MPAs fixed scenarios (Fig. 2). The spatial configuration of priority cells identified after forcing the exclusion of sites concessioned for oil and gas exploitation (Fig. 3C) were 87.3% and 86.9% congruent with the unconstrained and the MPAs fixed scenarios, respectively. As in both previous analyses, all 750 studied species were represented inside the best 10% of seascape for this scenario. It is important to note, however, that this high representativeness can be reached without any loss in current oil and natural gas production in Brazilian waters.

Finally, comparisons among scenarios of species representation for each taxonomic group showed that, in general, there was a lower representation of non-threatened species and a higher representation of near-threatened and threatened species in the unconstrained scenario, compared with the two others (Fig. 4). The difference among scenarios varied from 0.2–1.1% for mammals, 0.5–5.5% for seabirds, 0.02% for turtles, and 0.6–0.8% for fishes (Fig. 4A–D). However, proportion of the distribution area captured by each scenario was similar for threatened (ANOVA,  $F_{2, 213} = 0.018$ , p = 0.982), near-threatened ( $F_{2, 72} = 0.075$ , p = 0.928) and non-threatened species ( $F_{2, 1959} = 0.279$ , p = 0.757), when we analyzed all taxonomic groups together (Fig. 4E).

#### 4. Discussion

Despite the ambitious conservation agenda assumed by Brazil under the aegis of the CBD, plans that aid in achieving conservation targets are rare for the country, especially for the marine environment (Pinto and Grelle, 2009). Our study contributes to fill this gap through a spatially explicit and taxonomically comprehensive approach to select priority areas for conservation in the Brazilian marine zone. Our approach was developed under the light of representativeness, cost-efficiency, vulnerability and flexibility principles of spatial conservation prioritization (Wilson et al., 2009). The results indicate key areas for conservation of the Brazilian marine vertebrate fauna, where management actions will yield the greatest return on investment for biodiversity protection.



**Fig. 4.** Mean proportions of species' distribution represented in the three conservation scenarios for non-threatened/assessed, near-threatened and threatened species of marine mammals (A), seabirds (B), turtles (C), fishes (D), and for all of the taxonomic groups pulled together (E). White bars: unconstrained scenario; grey bars: MPAs fixed scenario; black bars: oil and gas scenario. Note that all turtle species in this study are currently classified as threatened and no mammal species are classified as near-threatened.

Currently, only 1.5% of the country's marine area is legally protected by sustainable-use protected areas (1.4% of total area) and no-take zones (only 0.1%), according to the Brazilian Ministry of Environment (CNUC/MMA, 2012). It has been argued that a strategic expansion of Brazil's MPAs is urgently needed to achieve an ecologically representative and effective MPA system (Magris et al., 2013). Therefore, our analyses may be useful as a technical support in political negotiations with stakeholders during the implementation of political objective of the Brazilian government to protect 10% of the coastal and marine zone (see MMA, 2006a, 2006b). In this sense, however, it is worth emphasizing that the choice of the most appropriate scenario is a hard task which should balance biological and political factors, including species representation, likelihood of adoption, compliance of stakeholders and persistence of MPAs that will be implemented (Allnutt et al., 2012; Faleiro and Loyola, 2013).

The absence of spatial design limitations in our unconstrained scenario allowed for the algorithm to determine among all cells those with the highest conservation value, and hence this scenario could represent a higher proportion of near-threatened and threatened species' distributions compared to the other two scenarios. From a purely conservationist point of view, concentrated conservation efforts based on such scenario would be the best alternative as it provides a greater representation of species facing a higher risk of extinction that therefore require conservation interventions more urgently. Indeed, this idea of attributing high priority to areas with elevated threatened-species richness has been applied in some conservation priority setting schemes (Hoffmann et al., 2008). However, the establishment of a MPA network based on our unconstrained scenario could be hampered or even prevented by the presence of alternative seascape uses of high socioeconomic and political relevance (e.g., oil and gas exploitation) and by the presence of already protected areas.

Considering existing MPAs during the selection process of new conservation areas is one of the major stages of the systematic conservation planning framework (Pressey and Cowling, 2001). Although often established without an adequate scientific background (e.g., Leathwick et al., 2009), existing MPAs can contribute to reach conservation targets, incorporate additional biological features not considered into priority setting analysis, besides representing already legally protected areas that contributes for conservation of marine ecosystems (Sobel and Dalgren, 2004). Nevertheless, it should be noted that a MPA network based on the top-ranked areas in our MPA fixed scenario would represent a lower proportion of threatened species' distribution than if based on our unconstrained scenario. This is because, according to the data and criteria used in our analyses, part of the MPAs currently established in the Brazil's EEZ is in suboptimal locations. Similar loss in biodiversity representation due to the establishment of ad hoc protected areas has already been reported in Australia (Stewart et al., 2003) and New Zealand (Leathwick et al., 2009). These findings reinforce the importance of conservation planning analyses to improve the performance of on-the-ground management actions (Margules and Pressey 2000; Stewart et al., 2003), especially for countries with limited conservation investments such as Brazil (Gerhardinger et al., 2011).

Despite the increasing concession of offshore areas for oil and gas exploitation in the Brazilian EEZ (Jablonski, 2008), the impact of such concessions on the performance of a national-scale MPA system was hitherto unknown. Our results indicate that it is possible to reconcile current offshore oil and gas production with the expansion of the national MPA network without significant losses in species' representation. This result reflects the capacity of species protection at different sites due to the broad distributions of several them (particularly of mammals, seabirds and turtles), as well as spatial mismatches between the areas from where our data (for fishes) were collected and the areas currently concessioned for oil and gas companies. The differences between the oil and gas scenario and the two other scenarios, in terms of conservation value, could be greater if the distribution of some restricted-range species were completely overlapping with concessioned areas. In this case, the options for conservation would be restricted and avoiding the areas used by the oil and gas industry would cause the loss of such species. Therefore, all species included in this study can be represented inside a MPA network based on the oil and gas scenario. Perhaps more important, these findings pave an avenue in which economic development and biodiversity conservation can go together. We believe that a MPA system based on our oil and gas scenario (Fig. 3C) has a prominent potential for implementation as it avoid conflicts with economic activities of paramount importance (i.e., ca. 12% of the national gross domestic product; CNI, 2012), protects areas at risk of loss conservation value, incorporates existing MPAs, and provides conservation benefits similar to the other scenarios.

Overall, sites with high priority for protection in Brazil's EEZ identified in our scenarios coincide with areas previously recognized by experts as important for conservation of several threatened species. Among these are the manatee *Trichechus manatus* (de Andrade et al., 2011), the humpback whale *Megaptera novaeangliae* (Martins et al., 2013), the franciscana dolphin *Pontoporia blainvillei* (Campos et al., 2010), and the sea turtles *Caretta caretta, Chelonia mydas* and *Eretmochelys imbricata* (Wallace et al., 2010; Marcovaldi et al., 2011). Additionally, there were also spatial congruences with priority areas proposed for wider taxonomic groups such as coral reefs (Moura, 2002), as well as with areas harboring a relatively high richness of seabirds species under high extinction risk (Machado et al., 2013) and with centers of endemism for reef fishes in the southwestern Atlantic (Moura, 2002; Floeter et al., 2008).

Although we have used wide-ranging data collection to identify conservation priorities, certain considerations are necessary. The range maps we used (for mammals, seabirds and turtles) tend to overestimate the area occupied by a species and increase the false positive frequency (Rondinini et al., 2006). As such, a given species may be mistakenly considered protected in a network of MPAs based on these data, while in reality it is unprotected. To minimize this concern we used only the species native range (and exclude the areas where it occurs only as a vagrant), which substantially reduces the species range and consequently the false-positive rate. On the other hand, data from occurrence records (used for fishes) are spatially biased, underestimate the species range and increase the false negative frequency (Rondinini et al., 2006). Thus, the areas available for protecting a given species can be underestimated in the analyses based on such data. However, occurrence records are relatively more conservative than the distribution maps because they minimize commission errors and avoid erroneous priority area selection for management actions. Furthermore, we have not considered other important socioeconomic (e.g., fishing, tourism, maritime transport) and ecological variables (e.g., population viability, connectivity among habitats, species' home ranges). Together, such limitations illustrate why conservation plans require periodic critical revisions, following the refinement of available data and the arising of new information (Grantham et al., 2010).

In conclusion, given the current panorama of increasing marine biodiversity loss in Brazil (Floeter et al., 2006; Luiz and Edwards, 2011), conservation actions for

the country's seascapes are urgent and cannot wait, indefinitely, for the Wallacean shortfall solution (Whittaker et al., 2005). The delay to 2020 to implement the CDB protocol is an opportunity to strategically achieve the government's conservation targets and reconcile biological representation with the sustainable economic development for Brazil. Our study provides a scientific foundation to support the negotiation process with representatives from the multiple sectors involved either with marine conservation or with marine exploitation and can, hopefully, contribute to an effective outcome to maintain the Brazilian biodiversity. Finally, we emphasize that our MPAs scenarios should to be viewed as part of a more comprehensive framework for management, integrating fishing quotas, size restriction for some species, temporal closures of certain fisheries, bycatch reduction devices, watershed-based management, and a more effective political engagement.

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#### Considerações Finais

Entender como as assembleias de espécies se estruturam no espaço é crucial para fundamentar o desenvolvimento teórico e de iniciativas de conservação eficientes para uma biodiversidade em declínio. No entanto, estudos empíricos fornecendo informações sobre os padrões de variação da ictiofauna estuarina em diferentes escalas espaciais são surpreendentemente raros. Os mecanismos ecológicos que promovem tais padrões são, indubitavelmente, ainda menos estudados e entendidos. Os resultados da presente tese contribuem para o preechimento de tais lacunas, através de uma comparação detalhada dos padrões de variação na estrutura taxonômica da ictiofauna estuarina entre as escalas local (dentro dos estuários) e regional (entre estuários), usando como alicerce uma ampla base de dados (ver Capítulo 1).

Para as assembleias de peixes em estuários brasileiros, os resultados apontam que há maior variabilidade na estrutura taxonômica (i.e. diversidade beta) entre estuários separados por milhares de quilômetros do que entre áreas separadas por centenas ou milhares de metros dentro desses estuários. Dada essa observação, espera-se que a proteção de locais amplamente espaçados ao longo da costa possa providenciar uma representação mais eficiente da ictiofauna regional do que a proteção de áreas com diferentes condições ambientais, mas localizadas dentro de um ou de poucos estuários próximos. Em termos ecológicos, esses resultados indicam que a variabilidade geográfica na estrutura da ictiofauna relaciona-se especialmente com mecanismos que operam em larga escala.

A costa brasileira fornece condições ideais para investigar tais mecanismos, devido à alta heterogeneidade ambiental ao longo de sua extensão. O uso de uma metodologia similar para amostragem dos peixes e dos parâmetros ambientais permitiu que as diferenças na fauna e possíveis mecanismos estruturadores fossem explorados simultâneamente em um contexto local e biogeográfico. As análises mostraram que existem dois componentes faunísticos distintos nos estuários brasileiros em termos de composição e abundância relativa das espécies e das famílias dominantes em riqueza e biomassa. Essas diferenças parecem estar associadas principalmente ao gradiente térmico presente na área de estudo, assim como à dificuldade de algumas espécies para se dispersarem por longas distâncias. Dentro de cada sistema, as análises correlativas indicaram que as principais forças governando a distribuição das espécies variam frequentemente. No entanto, isso sugere que generalizações sobre o papel dos fatores que controlam a estruturação local da ictiofauna parecem ser inadequadas. Cada estuário possui características ambientais particulares, que podem atuar não só diretamente sobre a estruturação das assembleias de peixes, mas também indiretamente através de mudanças na abundância e composição de suas presas, competidores e predadores (Blaber 2000). Em todos os estuários, porém, a distribuição espacial das espécies foi especialmente governada por filtros ambientais, visto que o percentual das variações locais na composição da ictiofauna explicado pelas análises DistLM foi geralmente elevado (Capítulo 1, Tabela 4).

O padrão de riqueza encontrado indica que a maior concentração de espécies de peixes estuarinos não se localiza na região tropical próxima ao Equador. Ao invés disso, a riqueza de espécies é relativamente maior na região sudeste brasileira (≈21°18'-23°22'S), especificamente na costa do estado do Rio de Janeiro (Capítulo 2, Fig. 1A). Estudos prévios encontraram um padrão similar para peixes recifais (Floeter et al. 2001), peixes ósseos costeiros (Tittensor et al. 2010) e tubarões (Lucifora et al. 2011), reforçando as constatações deste estudo. Supõe-se que a concentração de espécies de peixes nessa região seja um reflexo da coocorrência de táxons com afinidades tropicais e temperadas, tendo em vista que a área está sob influência tanto da corrente do Brasil (de águas quentes) quanto da corrente das Malvinas (de águas frias) (Moura & Sazima 2000).

No entanto, espécies com opções de conservação limitadas, tal como aquelas endêmicas e/ou raras, podem apresentar padrões geográficos de riqueza distintos daqueles encontrados quando a fauna é analisada como um todo, conforme demonstrado pelas incongruências espacias evidenciadas no Capítulo 2 (Fig. 1A–D). A heterogeneidade espacial observada neste estudo entre riqueza total, endemismo e raridade das espécies de peixes estuarinos sugere que tais parâmetros são controlados por diferentes processos ecológicos, históricos ou biogeográficos. Portanto, uma abordagem agregando variáveis relacionadas à diferentes facetas das assembleias pode ser mais adequada para determinar prioridades espaciais para a conservação da ictiofauna.

Planos de conservação baseados em um único táxon correm o risco de identificar áreas apropriadas para a proteção de organismos particulares, mas não para a biodiversidade em geral. A inclusão de quatro grupos de organismos (peixes, répteis, aves e mamíferos) no Capítulo 3 da presente tese expandiu o potencial de aplicação dos resultados obtidos para solução de problemas de conservação contemporâneos (e.g. alcançar as Metas de Aichi). As análises revelaram que a proteção de apenas 10% da área de estudo com alta prioridade de conservação incluiria, em média, entre 85,8 e 86,5% da área de distribuição das espécies, dependendo do cenário. A região localizada no extremo sul da Zona Econômica Exclusiva brasileira e as ilhas oceânicas Trindade e Martin Vaz foram, consistentemente, priorizadas em todas as soluções analisadas. As constatações mais importantes deste capítulo são: (1) é possível ampliar a rede existente de áreas marinhas protegidas, sem afetar a produção atual de petróleo e gás natural e (2) sem reduções significativas na área de distribuição das espécies protegidas, quando se compara à solução sem restrições. Essas observações realçam a possibilidade de compatibilizar o desenvolvimento econômico e a preservação do patrimônio natural marinho. Para isso, no entanto, o uso das ferramentas de priorização espacial disponíveis é fundamental.

O valor de um plano de conservação é maximizado se os resultados de sua implementação forem monitorados e eventuais adaptações forem realizadas ao longo do tempo (Grantham et al. 2010). As soluções de conservação apresentadas neste estudo foram obtidas a partir dos melhores dados disponíveis no momento das análises. Contudo, a ausência de variáveis socioeconômicas relevantes, tais como a pesca, recreação, portos, marinas, etc., pode criar uma polarização desnecessária entre os interessados na conservação da biodiversidade e os que vivem do mar. Um dos desafios subsequentes está relacionado, então, à inclusão de outras formas de uso do espaço para minimizar o potencial de conflitos. Acredita-se que assim será reduzido o abismo existente entre os campos teórico e prático do planejamento espacial para a conservação.

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#### Apêndices

#### Capítulo II

Apêndice 1. Referências usadas para compilação da lista de espécies de peixes estuarinos brasileiros.

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Famílias	Espécies	Famílias	Espécies
Acanthuridae	Acanthurus bahianus		Atherinella brasiliensis
	Acanthurus chirurgus		Membras dissimilis*
	Acanthurus coeruleus		Odontesthes argentinensis
Achiridae	Achirus achirus		Odontesthes bonariensis
	Achirus declivis		Odontesthes incisa
	Achirus lineatus	Balistidae	Balistes capriscus
	Achirus mucuri*		Balistes vetula
	Apionichthys dumerili	Batrachoididae	Amphichthys cryptocentrus
	Catathyridium garmani		Batrachoides surinamensis
	Trinectes microphthalmus		Porichthys plectrodon
	Trinectes paulistanus		Porichthys porosissimus
Albulidae	Albula vulpes		Thalassophryne montevidensis
Anablepidae	Anableps anableps		Thalassophryne nattereri
	Anableps microlepis		Thalassophryne punctata*
	Jenynsia multidentata	Belonidae	Strongylura marina
Antennariidae	Antennarius striatus		Strongylura timucu
	Histrio histrio		Tylosurus acus
Arhynchobatidae	Sympterygia acuta		Tylosurus crocodilus
	Sympterygia bonapartii	Blenniidae	Hypleurochilus fissicornis
Ariidae	Amphiarius phrygiatus		Lupinoblennius paivai*
	Amphiarius rugispinis		Parablennius pilicornis
	Aspistor luniscutis		Scartella cristata
	Bagre bagre	Bothidae	Bothus ocellatus
	Bagre marinus		Bothus robinsi
	Cathorops agassizii	Carangidae	Alectis ciliaris
	Cathorops arenatus		Carangoides bartholomaei
	Cathorops spixii		Carangoides ruber
	Genidens barbus		Caranx crysos
	Genidens genidens		Caranx hippos
	Genidens machadoi		Caranx latus
	Genidens planifrons*		Chloroscombrus chrysurus
	Notarius grandicassis		Hemicaranx amblyrhynchus
	Notarius quadriscutis		Oligoplites palometa
	Potamarius grandoculis*		Oligoplites saliens
	Sciades couma		Oligoplites saurus
	Sciades herzbergii		Parona signata
	Sciades parkeri		Selar crumenophthalmus
	Sciades passany		Selene setapinnis
	Sciades proops		Selene vomer
Aspredinidae	Aspredo aspredo		Seriola lalandi
Atherinopsidae	Atherinella blackburni*		Trachinotus carolinus
	Trachinotus cayennensis		Himantura schmardae

Apêndice 2. Espécies de peixes capturadas em estuários brasileiros. Espécies endêmicas são indicadas por um asterisco (\*).

		Diadautidaa	
	Trachinotus faicatus	Diodontidae	
	Trachinotus goodei		
	Trachinotus marginatus		Diodon noiocanthus
	I rachurus lathami		Diodon hystrix
	Uraspis secunda	Echeneidae	Echeneis naucrates
Carcharhinidae	Carcharhinus acronotus		Remora remora
	Carcharhinus leucas	Eleotridae	Dormitator maculatus
	Carcharhinus limbatus		Eleotris pisonis
	Carcharhinus obscurus		Erotelis smaragdus
	Carcharhinus porosus		Guavina guavina
	Carcharinus plumbeus	Elopidae	Elops saurus
	lsogomphodon oxyrhynchus	Engraulidae	Anchoa filifera
	Rhizoprionodon lalandii		Anchoa hepsetus
	Rhizoprionodon porosus		Anchoa januaria*
Centropomidae	Centropomus ensiferus		Anchoa lyolepis
	Centropomus parallelus		Anchoa marinii
	Centropomus pectinatus		Anchoa parva
	Centropomus undecimalis		Anchoa pectoralis*
Chaetodontidae	Chaetodon ocellatus		Anchoa spinifer
	Chaetodon striatus		Anchoa tricolor*
Clinidae	Ribeiroclinus eigenmanni		Anchovia clupeoides
Clupeidae	Brevoortia pectinata		Anchovia surinamensis
	Harengula clupeola		Anchoviella brevirostris
	Harengula jaguana		Anchoviella cayennensis
	Lile piquitinga		Anchoviella guianensis
	Opisthonema oglinum		Anchoviella lepidentostole
	Platanichthys platana		Cetengraulis edentulus
	Ramnogaster arcuata		Engraulis anchoita
	Rhinosardinia amazonica		Engraulis eurystole
	Rhinosardinia bahiensis		Lycengraulis grossidens
	Sardinella brasiliensis		Pterengraulis atherinoides
Congridae	Conger orbignianus	Ephippidae	Chaetodipterus faber
Coryphaenidae	Coryphaena hippurus	Epinephelidae	Epinephelus itajara
Cynoglossidae	Symphurus diomedeanus		Epinephelus morio
	Symphurus jenynsi		Hyporthodus nigritus
	Symphurus oculellus		Hyporthodus niveatus
	Symphurus plagusia		Mycteroperca acutirostris
	Symphurus tessellatus		Mycteroperca bonaci
Dactylopteridae	Dactylopterus volitans		Mycteroperca interstitialis
Dasyatidae	Dasyatis americana		Mycteroperca marginata
	Dasyatis centroura		Mycteroperca microlepis
	Dasyatis geijskesi		Mycteroperca tigris
	Dasyatis guttata	Exocoetidae	Cheilopogon melanurus
	Dasyatis marianae*		Parexocoetus brachypterus
	Dasyatis hypostigma	Fistulariidae	Fistularia petimba

Famílias	Espécies	Famílias	Espécies
	Fistularia tabacaria		Pomadasys crocro
Gerreidae	Diapterus auratus		Pomadasys ramosus
	Diapterus rhombeus	Hemiramphidae	Hemiramphus balao
	Eucinostomus argenteus		Hemiramphus brasiliensis
	Eucinostomus gula		Hyporhamphus roberti roberti
	Eucinostomus havana		Hyporhamphus unifasciatus
	Eucinostomus melanopterus	Holocentridae	Holocentrus adscensionis
	Eugerres brasilianus		Myripristis jacobus
	Gerres cinereus	Labrisomidae	Malacoctenus delalandii
	Ulaema lefroyi		Paraclinus arcanus*
Ginglymostomatidae	Ginglymostoma cirratum	Lobotidae	Lobotes surinamensis
Gobiesocidae	Gobiesox strumosus	Lutjanidae	Lutjanus alexandrei*
Gobiidae	Akko dionaea*		Lutjanus analis
	Awaous tajasica		Lutjanus jocu
	Bathygobius soporator		Lutjanus purpureus
	Chriolepis vespa		Lutjanus synagris
	Ctenogobius boleosoma		Lutjanus vivanus
	Ctenogobius shufeldti		Ocyurus chrysurus
	Ctenogobius smaragdus		Rhomboplites aurorubens
	Ctenogobius stigmaticus	Megalopidae	Megalops atlanticus
	Ctenogobius thoropsis	Merlucciidae	Merluccius hubbsi
	Evorthodus lyricus	Microdesmidae	Microdesmus longipinnis
	Gnatholepis cauerensis	Monacanthidae	Aluterus heudelotii
	Gobioides broussonnetii		Aluterus monoceros
	Gobioides grahamae		Monacanthus ciliatus
	Gobionellus oceanicus		Stephanolepis hispidus
	Gobionellus stomatus*		Stephanolepis setifer
	Gobiosoma hemigymnum	Mugilidae	Mugil curema
	Gobius boekeri*		Mugil curvidens
	Microgobius meeki		Mugil hospes
Gymnuridae	Gymnura altavela		Mugil incilis
	Gymnura micrura		Mugil liza
Haemulidae	Anisotremus surinamensis		<i>Mugil</i> sp.
	Anisotremus virginicus		Mugil trichodon
	Boridia grossidens	Mullidae	Mullus argentinae
	Conodon nobilis		Pseudupeneus maculatus
	Genyatremus luteus		Upeneus parvus
	Haemulon aurolineatum	Muraenesocidae	Cynoponticus savanna
	Haemulon parra	Muraenidae	Gymnothorax funebris
	Haemulon squamipinna*		Gymnothorax ocellatus
	Haemulon steindachneri	Myliobatidae	Aetobatus narinari
	Orthopristis ruber		Mobula hypostoma
	Pomadasvs corvinaeformis		Mvliobatis goodei

## Apêndice 2. (Continuação)

	Rhinoptera bonasus		Pellona harroweri
Narcinidae	Diplobatis pictus	Rachycentridae	Rachycentron canadum
	Narcine brasiliensis	Rhinobatidae	Rhinobatos horkelii
Nettastomatidae	Hoplunnis tenuis		Rhinobatos percellens
Ogcocephalidae	Ogcocephalus nasutus		Zaptervx brevirostris
ogooophallado	Ogcocephalus notatus	Scaridae	Sparisoma axillare*
	Ogcocenhalus vesnertilio	Coundad	Sparisoma frondosum*
Onhichthidae	Ahlia eqmontis		Sparisoma radians
opmontinduo	Echiophis intertinctus	Sciaenidae	Bairdiella ronchus
	Murichthys ocellatus	Oclacillac	Ctenosciaena aracilicirrhus
	Myrichinys ocenatus		
	Ophichthus cylindroidous		
Opictognothidoo			
Opisiognalinuae			Cynoscion relatchus
Ostraciidae	Acanthostracion polygonius		
	Lactophrys trigonus		
Paralichthyidae	Citharichthys arenaceus		Isopistnus parvipinnis
	Citharichthys cornutus		Larimus breviceps
	Citharichthys macrops		Lonchurus elegans
	Citharichthys spilopterus		Lonchurus lanceolatus
	Etropus crossotus		Macrodon ancylodon
	Etropus longimanus		Macrodon atricauda
	Paralichthys brasiliensis*		Menticirrhus americanus
	Paralichthys orbignyanus		Menticirrhus littoralis
	Paralichthys patagonicus		Micropogonias furnieri
	Paralichthys triocellatus		Nebris microps
	Syacium micrurum		Ophioscion punctatissimus
	Syacium papillosum		Paralonchurus brasiliensis
Percophidae	Percophis brasiliensis		Plagioscion auratus
Phycidae	Urophycis brasiliensis		Plagioscion squamosissimus
Pinguipedidae	Pinguipes brasilianus		Plagioscion surinamensis
Pleuronectidae	Oncopterus darwinii		Pogonias cromis
Poeciliidae	Poecilia vivipara		Stellifer brasiliensis*
	Tomeurus gracilis		Stellifer microps
Polynemidae	Polydactylus oligodon		Stellifer naso
	Polydactylus virginicus		Stellifer rastrifer
Pomacanthidae	Pomacanthus arcuatus		Stellifer sp.n.*
	Pomacanthus paru		Stellifer stellifer
Pomacentridae	Abudefduf saxatilis		Umbrina canosai
Pomatomidae	Pomatomus saltatrix		Umbrina coroides
Priacanthidae	Priacanthus arenatus	Scombridae	Scomberomorus brasiliensis
Pristidae	Pristis pectinata		Scomberomorus cavalla
	Pristis pristis		Scomberomorus regalis
Pristigasteridae	Chirocentrodon bleekerianus	Scorpaenidae	Pontinus corallinus*
	Odontognathus mucronatus		Scorpaena brasiliensis

Famílias	Espécies	Famílias	Espécies
	Scorpaena isthmensis		Cosmocampus elucens
	Scorpaena petricola*		Halicampus crinitus
	Scorpaena plumieri		Hippocampus erectus
Serranidae	Acanthistius brasilianus*		Hippocampus reidi
	Alphestes afer		Microphis lineatus
	Diplectrum formosum		Pseudophallus mindii
	Diplectrum radiale		Syngnathus folletti
	Dules auriga		Syngnathus pelagicus
	Rypticus randalli		Syngnathus scovelli
	Serranus atrobranchus	Synodontidae	Synodus foetens
	Serranus baldwini		Synodus intermedius
	Serranus flaviventris		Synodus poeyi
	Serranus phoebe	Tetraodontidae	Colomesus psittacus
Sparidae	Archosargus probatocephalus		Lagocephalus laevigatus
	Archosargus rhomboidalis		Lagocephalus lagocephalus
	Calamus calamus		Sphoeroides greeleyi
	Calamus penna		Sphoeroides spengleri
	Calamus pennatula		Sphoeroides testudineus
	Diplodus argenteus argenteus		Sphoeroides tyleri
Sphyraenidae	Sphyraena barracuda	Triakidae	Galeorhinus galeus
	Sphyraena guachancho		Mustelus canis
	Sphyraena sphyraena		Mustelus fasciatus
	Sphyraena tome*	Trichiuridae	Trichiurus lepturus
Sphyrnidae	Sphyrna lewini	Triglidae	Prionotus nudigula
	Sphyrna tiburo		Prionotus punctatus
	Sphyrna tudes	Uranoscopidae	Astroscopus sexspinosus
Squatinidae	Squatina argentina		Astroscopus y-graecum
Stromateidae	Peprilus paru	Urolophidae	Urobatis jamaicensis
	Stromateus brasiliensis	Urotrygonidae	Urotrygon microphthalmum
Syngnathidae	Bryx dunckeri	Zeidae	Zenopsis conchifer

# Apêndice 2. (Continuação)
# Capítulo III

Table A1. List of species included in prioritization analyses with their respective conservation status (sensu MMA, 2004, 2005; IUCN, 2011) and weight. '-' indicates species not assessed under the IUCN Red List Categories and Criteria until the time of analyses.

_		Conser	<b>Conservation status</b>	
Taxon	Species	MMA	IUCN	– weigth
Fishes	Ablennes hians	_	_	1
	Abudefduf saxatilis	_	-	1
	Acanthistius brasilianus	_	Data deficient	1
	Acanthistius patachonicus	_	-	1
	Acanthocybium solandri	_	Least concern	1
	Acanthostracion polygonius	_	-	1
	Acanthostracion quadricornis	_	-	1
	Acanthurus bahianus	_	-	1
	Acanthurus chirurgus	_	-	1
	Acanthurus coeruleus	_	_	1
	Achirus achirus	_	_	1
	Achirus declivis	_	_	1
	Achirus lineatus	_	_	1
	Achirus mucuri	_	-	1
	Acyrtus pauciradiatus	_	_	1
	Aetobatus narinari	_	Near threatened	97
	Ahlia egmontis	_	-	1
	Albula vulpes	_	-	1
	Alectis ciliaris	-	Least concern	1
	Alepisaurus ferox	-	Least concern	1
	Alopias superciliosus	-	Vulnerable	98
	Alopias vulpinus	-	Vulnerable	98
	Alphestes afer	-	Least concern	1
	Aluterus heudelotii	-	-	1
	Aluterus monoceros	_	-	1
	Aluterus scriptus	_	-	1
	Amblycirrhitus pinos	-	-	1
	Amphiarius phrygiatus	_	-	1
	Amphiarius rugispinis	-	-	1
	Amphichthys cryptocentrus	-	Least concern	1
	Anableps anableps	_	-	1
	Anableps microlepis	-	-	1
	Anchoa filifera	_	-	1
	Anchoa hepsetus	_	-	1
	Anchoa januaria	_	_	1
	Anchoa lyolepis	_	-	1
	Anchoa marinii	_	_	1

Anchoa parva	_	_	1
Anchoa pectoralis	_	-	1
Anchoa spinifer	_	-	1
Anchoa tricolor	_	-	1
Anchovia clupeoides	_	_	1
Anchovia surinamensis	_	_	1
Anchoviella brevirostris	_	Least concern	1
Anchoviella cayennensis	_	_	1
Anchoviella guianensis	_	_	1
Anchoviella lepidentostole	_	_	1
Anisotremus moricandi	_	Endangered	99
Anisotremus surinamensis	_	_	1
Anisotremus virginicus	_	_	1
Antennarius multiocellatus	_	_	1
Antennarius striatus	_	-	1
Anthias salmopunctatus	Vulnerable	Vulnerable	98
Apionichthys dumerili	_	_	1
Apogon americanus	_	_	1
Apogon planifrons	_	_	1
Apogon pseudomaculatus	_	_	1
Apogon quadrisquamatus	_	_	1
Archosargus probatocephalus	_	_	1
Archosargus rhomboidalis	_	_	1
Aspistor luniscutis	_	-	1
Aspredinichthys filamentosus	_	-	1
Aspredinichthys tibicen	_	_	1
Aspredo aspredo	_	-	1
Astrapogon puncticulatus	_	-	1
Astrapogon stellatus	_	-	1
Astroscopus sexspinosus	_	_	1
Astroscopus y-graecum	_	_	1
Atherinella blackburni	_	_	1
Atherinella brasiliensis	_	-	1
Aulostomus maculatus	_	_	1
Aulostomus strigosus	_	-	1
Awaous tajasica	_	-	1
Bagre bagre	_	-	1
Bagre marinus	_	-	1
Bairdiella ronchus	_	_	1
Balistes capriscus	_	_	1
Balistes vetula	_	Vulnerable	98
Barbulifer ceuthoecus	_	_	1
Barbulifer enigmaticus	_	_	1
Bathygobius geminatus	_	_	1
Bathygobius soporator	_	_	1
Batrachoides surinamensis	_	Least concern	1

Taxon	Species	Conservation status		– Weiath
	opecies	MMA	IUCN	meigun
	Bodianus insularis	Vulnerable	Least concern	98
	Bodianus pulchellus	_	Least concern	1
	Bodianus rufus	_	Least concern	1
	Boridia grossidens	_	_	1
	Bothus lunatus	_	_	1
	Bothus maculiferus	_	_	1
	Bothus ocellatus	_	_	1
	Bothus robinsi	-	-	1
	Brama brama	-	-	1
	Brama caribbea	-	-	1
	Brevoortia pectinata	_	_	1
	Bryx dunckeri	_	_	1
	Calamus bajonado	_	_	1
	Calamus calamus	_	_	1
	Calamus mu	_	_	1
	Calamus penna	_	_	1
	Calamus pennatula	_	_	1
	Callionymus bairdi	_	_	1
	Cantherhines macrocerus	_	_	1
	Cantherhines pullus	_	_	1
	Canthidermis sufflamen	_	_	1
	Canthigaster figueiredoi	_	_	1
	Carangoides bartholomaei	_	_	1
	Carangoides ruber	_	_	1
	Caranx crysos	_	Least concern	1
	Caranx hippos	_	_	1
	Caranx latus	_	_	1
	Caranx lugubris	_	_	1
	Carcharhinus acronotus	_	Near threatened	97
	Carcharhinus brevipinna	_	Near threatened	97
	Carcharhinus falciformis	-	Near threatened	97
	Carcharhinus galapagensis	-	Near threatened	97
	Carcharhinus leucas	-	Near threatened	97
	Carcharhinus limbatus	-	Near threatened	97
	Carcharhinus longimanus	-	Vulnerable	98
	Carcharhinus obscurus	-	Vulnerable	98
	Carcharhinus perezii	-	_	1
	Carcharhinus plumbeus	-	Vulnerable	98
	Carcharhinus porosus	-	Data deficient	1
	Carcharias taurus	-	Vulnerable	98
	Catathyridium garmani	-	-	1
	Cathorops agassizii	-	-	1
	Cathorops spixii	_	_	1

Caulolatilus chrysops	-	-	1
Centropomus ensiferus	-	-	1
Centropomus parallelus	-	-	1
Centropomus pectinatus	-	-	1
Centropomus undecimalis	-	-	1
Centropyge aurantonotus	-	Least concern	1
Cephalopholis fulva	-	Least concern	1
Cetengraulis edentulus	-	-	1
Chaetodipterus faber	-	-	1
Chaetodon ocellatus	-	Least concern	1
Chaetodon sedentarius	-	-	1
Chaetodon striatus	-	Least concern	1
Channomuraena vittata	-	-	1
Cheilopogon cyanopterus	-	-	1
Cheilopogon melanurus	-	-	1
Chilomycterus antillarum	-	-	1
Chilomycterus reticulatus	_	_	1
Chilomycterus spinosus	_	_	1
Chirocentrodon bleekerianus	_	Least concern	1
Chloroscombrus chrysurus	_	_	1
Chromis enchrysura	_	_	1
Chromis flavicauda	_	Data deficient	1
Chromis jubauna	_	_	1
Chromis limbata	_	_	1
Chromis multilineata	_	_	1
Chromis scotti	_	_	1
Citharichthys arenaceus	_	_	1
Citharichthys cornutus	_	_	1
Citharichthys macrops	_	_	1
Citharichthys spilopterus	-	_	1
Clepticus brasiliensis	_	Least concern	1
Cnesterodon decemmaculatus	_	_	1
Colomesus psittacus	_	_	1
Conger orbignianus	-	_	1
Conodon nobilis	-	_	1
Cookeolus japonicus	_	_	1
Coryphaena equiselis	_	Least concern	1
Coryphaena hippurus	_	Least concern	1
Coryphopterus dicrus	_	_	1
Coryphopterus glaucofraenum	_	_	1
Coryphopterus thrix	_	_	1
Cosmocampus albirostris	_	_	1
Cosmocampus elucens	_	Least concern	1
Cryptotomus roseus	_	Least concern	1
Ctenogobius boleosoma	_	_	1
Ctenogobius saepepallens	_	_	1
<b>S</b> 11			

Tayon	Snecies —	Conservation status		— Weigth
Тахон	Species	MMA	IUCN	morgan
	Ctenogobius shufeldti	_	_	1
	Ctenogobius smaragdus	_	_	1
	Ctenogobius stigmaticus	_	_	1
	Ctenosciaena gracilicirrhus	_	_	1
	Cynoponticus savanna	_	_	1
	Cynoscion acoupa	_	Least concern	1
	Cynoscion guatucupa	_	_	1
	Cynoscion jamaicensis	_	_	1
	Cynoscion leiarchus	_	_	1
	Cynoscion microlepidotus	_	_	1
	Cynoscion steindachneri	_	_	1
	Cynoscion virescens	_	_	1
	Dactylopterus volitans	_	_	1
	Dactyloscopus crossotus	_	_	1
	Dactyloscopus foraminosus	_	_	1
	Dactyloscopus tridigitatus	_	_	1
	Dasyatis americana	_	Data deficient	1
	Dasyatis centroura	_	Least concern	1
	Dasyatis geijskesi	_	Near threatened	97
	Dasyatis guttata	_	Data deficient	1
	Dasyatis hypostigma	_	Data deficient	1
	Dasyatis marianae	_	Data deficient	1
	Dasyatis say	_	Least concern	1
	Decapterus macarellus	_	_	1
	Decapterus punctatus	_	_	1
	Decapterus tabl	_	_	1
	Dermatolepis inermis	_	Near threatened	97
	Diapterus auratus	_	_	1
	Diapterus rhombeus	_	_	1
	Diodon holocanthus	_	_	1
	Diodon hystrix	_	_	1
	Diplectrum formosum	_	_	1
	Diplectrum radiale	_	_	1
	Diplodus argenteus argenteus	_	_	1
	Doratonotus megalepis	_	Least concern	1
	Dormitator maculatus	_	_	1
	Dules auriga	_	_	1
	Echeneis naucrates	_	_	1
	Echidna catenata	-	-	1
	Echiophis intertinctus	-	_	1
	Elacatinus figaro	Vulnerable	_	98
	Elacatinus phthirophagus	-	_	1
	Elacatinus pridisi	_	_	1

Elagatis bipinnulata	-	_	1
Eleotris pisonis	-	_	1
Elops saurus	-	_	1
Emblemariopsis occidentalis	_	_	1
Emblemariopsis signifer	_	Least concern	1
Enchelycore anatina	_	_	1
Enchelycore carychroa	_	_	1
Enchelycore nigricans	_	_	1
Engraulis anchoita	_	_	1
Enneanectes altivelis	_	_	1
Enneanectes smithi	-	_	1
Entomacrodus nigricans	-	_	1
Entomacrodus vomerinus	-	_	1
Epinephelus adscensionis	-	Least concern	1
Epinephelus itajara	-	Critically endangered	100
Epinephelus morio	-	Near threatened	97
Equetus lanceolatus	_	_	1
Equetus punctatus	_	_	1
Erotelis smaragdus	-	_	1
Etropus crossotus	_	_	1
Etropus longimanus	_	_	1
Eucinostomus argenteus	_	_	1
Eucinostomus gula	_	_	1
Eucinostomus havana	-	_	1
Eucinostomus melanopterus	-	_	1
Eugerres brasilianus	-	_	1
Euthynnus alletteratus	-	Least concern	1
Evorthodus lyricus	-	_	1
Exocoetus volitans	-	_	1
Fistularia petimba	-	_	1
Fistularia tabacaria	-	_	1
Galeocerdo cuvier	-	Near threatened	97
Galeorhinus galeus	Critically endangered	Vulnerable	100
Gempylus serpens	_	_	1
Genidens barbus	_	_	1
Genidens genidens	_	Least concern	1
Genidens machadoi	_	_	1
Genidens planifrons	_	_	1
Genyatremus luteus	_	_	1
Gephyroberyx darwinii	-	_	1
Gerres cinereus	_	_	1
Gillellus greyae	-	_	1
Ginglymostoma cirratum	Vulnerable	Data deficient	98
Gnatholepis thompsoni	-	_	1
Gobiesox barbatulus	-	_	1
Gobiesox punctulatus	-	_	1

Taxon	Species -	Conservation status		— Woigth
Тахоп	Species	ММА	IUCN	
	Gobiesox strumosus	_	-	1
	Gobioides broussonnetii	_	-	1
	Gobionellus oceanicus	_	_	1
	Gobionellus stomatus	_	_	1
	Gobiosoma hemigymnum	_	_	1
	Gobulus myersi	_	_	1
	Gonioplectrus hispanus	_	Least concern	1
	Gramma brasiliensis	Vulnerable	_	98
	Guavina guavina	-	-	1
	Gymnothorax funebris	_	_	1
	Gymnothorax miliaris	_	_	1
	Gymnothorax moringa	_	_	1
	Gymnothorax ocellatus	_	_	1
	Gymnothorax polygonius	_	_	1
	Gymnothorax vicinus	_	-	1
	Gymnura altavela	_	Vulnerable	98
	Gymnura micrura	_	Data deficient	1
	Haemulon aurolineatum	_	-	1
	Haemulon melanurum	_	-	1
	Haemulon parra	_	-	1
	Haemulon plumierii	_	-	1
	Haemulon squamipinna	_	-	1
	Haemulon steindachneri	_	Least concern	1
	Halichoeres bivittatus	_	Least concern	1
	Halichoeres brasiliensis	_	Data deficient	1
	Halichoeres dimidiatus	_	Least concern	1
	Halichoeres penrosei	_	Least concern	1
	Halichoeres poeyi	_	Least concern	1
	Halichoeres radiatus	_	Least concern	1
	Halichoeres rubrovirens	_	-	1
	Halichoeres sazimai	_	-	1
	Harengula clupeola	_	_	1
	Harengula jaguana	_	_	1
	Hemicaranx amblyrhynchus	_	_	1
	Hemiramphus balao	_	_	1
	Hemiramphus brasiliensis	_	_	1
	Heteroconger camelopardalis	_	_	1
	Heteropriacanthus cruentatus	_	_	1
	Hippocampus erectus	_	Vulnerable	98
	Hippocampus reidi	_	Data deficient	1
	Hirundichthys affinis	_	_	1
	Histrio histrio	_	_	1
	Holacanthus ciliaris	_	Least concern	1

		I	
Holacanthus tricolor	-	Least concern	1
	-	-	1
Hopiunnis tenuis	-	-	1
Hypieurocniius fissicornis	-	-	1
Hypleurochilus pseudoaequipinnis	-	-	1
Hypleurochilus brasil	-	-	1
Hyporhamphus roberti roberti	-	-	1
Hyporhamphus unitasciatus	-	-	1
Hyporthodus flavolimbatus	-	Vulnerable	98
Hyporthodus mystacinus	-	Least concern	1
Hyporthodus nigritus	-	Critically endangered	100
Hyporthodus niveatus	_	Vulnerable	98
Hypsoblennius invemar	-	-	1
Ichthyapus ophioneus	-	-	1
lsogomphodon oxyrhynchus	Endangered	Critically endangered	99
Isopisthus parvipinnis	-	-	1
Istiophorus albicans	-	-	1
Isurus oxyrinchus	-	Vulnerable	98
Jenynsia multidentata	-	-	1
Katsuwonus pelamis	-	Least concern	1
kyphosus incisor	-	-	1
Kyphosus sectatrix	-	-	1
Labrisomus conditus	-	-	1
Labrisomus cricota	-	-	1
Labrisomus kalisherae	-	-	1
Labrisomus nuchipinnis	-	-	1
Lactophrys trigonus	-	-	1
Lagocephalus laevigatus	-	-	1
Lagocephalus lagocephalus	-	-	1
Larimus breviceps	_	_	1
Lile piquitinga	_	Least concern	1
Liopropoma carmabi	_	-	1
Lobotes surinamensis	_	_	1
Lonchurus lanceolatus	_	-	1
Lupinoblennius paivai	_	-	1
Lutjanus alexandrei	-	-	1
Lutjanus analis	-	Vulnerable	98
Lutjanus buccanella	-	-	1
Lutjanus cyanopterus	-	Vulnerable	98
Lutjanus jocu	_	-	1
Lutjanus purpureus	_	-	1
Lutjanus synagris	_	_	1
Lutjanus vivanus	_	_	1
Lycengraulis grossidens	_	_	1
Lythrypnus brasiliensis	_	-	1
Macrodon ancylodon	_	-	1
-			

Taxon	Species —	Conse	Conservation status	
Taxon	Species	ММА	IUCN	margui
	Macrodon atricauda	_	_	1
	Makaira nigricans	-	Vulnerable	98
	Malacanthus plumieri	_	_	1
	Malacoctenus aff. triangulatus	_	_	1
	Malacoctenus brunoi	_	_	1
	Malacoctenus delalandii	_	_	1
	Manta birostris	_	Vulnerable	98
	Megalops atlanticus	_	_	1
	Melichthys niger	_	_	1
	Membras dissimilis	_	_	1
	Menticirrhus americanus	_	_	1
	Menticirrhus littoralis	_	_	1
	Merluccius hubbsi	_	_	1
	Micrognathus crinitus	_	_	1
	Microgobius carri	_	_	1
	Microgobius meeki	_	_	1
	Microphis lineatus	_	_	1
	Micropogonias furnieri	_	_	1
	Microspathodon chrysurus	_	_	1
	Mobula hypostoma	_	Data deficient	1
	Mobula japanica	_	Near threatened	97
	Mobula tarapacana	_	Data deficient	1
	Mobula thurstoni	_	Near threatened	97
	Mola mola	_	_	1
	Monacanthus ciliatus	_	_	1
	Moringua edwardsi	_	Least concern	1
	Mugil curema	-	-	1
	Mugil curvidens	_	_	1
	Mugil gaimardianus	-	-	1
	Mugil hospes	_	Least concern	1
	Mugil incilis	-	Least concern	1
	Mugil liza	_	-	1
	Mugil trichodon	-	-	1
	Mulloidichthys martinicus	_	-	1
	Mullus argentinae	-	-	1
	Muraena melanotis	_	-	1
	Muraena pavonina	-	-	1
	Muraena retifera	-	-	1
	Mustelus canis	-	Near threatened	97
	Mustelus fasciatus	-	Critically endangered	100
	Mycteroperca acutirostris	-	Least concern	1
	Mycteroperca bonaci	-	Near threatened	97
	Mycteroperca interstitialis	-	Vulnerable	98

Mycteroperca marginata	_	Endangered	99
Mycteroperca microlepis	_	Least concern	1
Mycteroperca tigris	_	Least concern	1
Mycteroperca venenosa	_	Near threatened	97
Myliobatis goodei	_	Data deficient	1
Myrichthys breviceps	_	_	1
Myrichthys ocellatus	_	_	1
Myripristis jacobus	_	_	1
Myrophis punctatus	_	_	1
Narcine brasiliensis	_	Data deficient	1
Nebris microps	_	_	1
Negaprion brevirostris	Vulnerable	Near threatened	98
Nicholsina usta usta	_	-	1
Nomeus gronovii	_	-	1
Notarius grandicassis	_	_	1
Notarius quadriscutis	_	_	1
Ocyurus chrysurus	_	_	1
Odontesthes argentinensis	_	_	1
Odontesthes bonariensis	_	_	1
Odontesthes incisa	_	Least concern	1
Odontognathus mucronatus	_	_	1
Odontoscion dentex	_	_	1
Ogcocephalus nasutus	_	_	1
Ogcocephalus notatus	_	_	1
Ogcocephalus vespertilio	_	_	1
Oligoplites palometa	_	_	1
Oligoplites saliens	_	_	1
Oligoplites saurus	-	-	1
Oncopterus darwinii	_	_	1
Ophichthus cylindroideus	_	_	1
Ophichthus gomesii	_	_	1
Ophichthus ophis	_	_	1
Ophioblennius trinitatis	_	_	1
Ophioscion punctatissimus	-	_	1
Opisthonema oglinum	-	_	1
Opistognathus aff. aurifrons	-	_	1
Opistognathus cuvierii	-	_	1
Opistognathus whitehursti	-	_	1
Orthopristis ruber	-	_	1
Oxyporhamphus micropterus	_	_	1
Pagrus pagrus	_	Endangered	99
Parablennius marmoreus	_	_	1
Parablennius pilicornis	_	_	1
Paraclinus arcanus	_	_	1
Paraclinus rubicundus	_	Least concern	1
Paraclinus spectator	_	_	1
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Taxon	Species -	Conservation status		— Weigth
Тахон	Opecies	ММА	IUCN	Weight
	Paralichthys brasiliensis	_	_	1
	Paralichthys orbignyanus	_	_	1
	Paralichthys patagonicus	_	_	1
	Paralichthys triocellatus	_	_	1
	Paralonchurus brasiliensis	_	_	1
	Paranthias furcifer	_	_	1
	Pareques acuminatus	_	_	1
	Parexocoetus brachypterus	_	_	1
	Parona signata	-	-	1
	Pellona castelnaeana	_	_	1
	Pellona harroweri	_	_	1
	Pempheris poeyi	_	_	1
	Pempheris schomburgkii	_	_	1
	Peprilus paru	_	Least concern	1
	Percophis brasiliensis	_	_	1
	Phaeoptyx pigmentaria	_	_	1
	Pinguipes brasilianus	_	_	1
	Plagioscion auratus	_	_	1
	Plagioscion squamosissimus	_	_	1
	Platanichthys platana	_	_	1
	Platybelone argalus	_	Least concern	1
	Plectrypops retrospinis	_	-	1
	Poecilia vivipara	_	_	1
	Pogonias cromis	_	-	1
	Polydactylus oligodon	_	_	1
	Polydactylus virginicus	_	-	1
	Polyprion americanus	_	Data deficient	1
	Pomacanthus arcuatus	_	Least concern	1
	Pomacanthus paru	_	Least concern	1
	Pomadasys corvinaeformis	_	-	1
	Pomadasys crocro	_	_	1
	Pomadasys ramosus	_	_	1
	Pomatomus saltatrix	_	_	1
	Pontinus corallinus	_	_	1
	Porichthys kymosemeum	_	_	1
	Porichthys plectrodon	_	_	1
	Porichthys porosissimus	_	_	1
	Potamarius grandoculis	_	_	1
	Priacanthus arenatus	_	_	1
	Priolepis dawsoni	_	_	1
	Prionace glauca	_	Near threatened	97
	Prionotus nudigula	_	_	1
	Prionotus punctatus	_	_	1

Pristipomoides aquilonaris	_	_	1
Pristis pectinata	Endangered	Critically endangered	99
Prognathodes brasiliensis	_	Least concern	1
Prognathodes guyanensis	_	Least concern	1
Prognathodes obliguus	Vulnerable	Data deficient	98
Pronotogrammus martinicensis	_	_	1
Pseudocaranx dentex	_	_	1
Pseudocarcharias kamoharai	_	Near threatened	97
Pseudophallus mindii	_	_	1
Pseudupeneus maculatus	_	_	1
Psilotris celsus	_	_	1
Ptereleotris randalli	_	_	1
Pterengraulis atherinoides	_	_	1
Pteroplatytrygon violacea	_	Least concern	1
Rachycentron canadum	_	_	1
Ramnogaster arcuata	_	_	1
Remora albescens	_	Least concern	1
Remora brachyptera	_	Least concern	1
Remora osteochir	_	_	1
Remora remora	_	_	1
Rhincodon typus	Vulnerable	Vulnerable	98
Rhinobatos horkelii	Endangered	Critically endangered	99
Rhinobatos percellens	_	Near threatened	97
Rhinoptera bonasus	_	Near threatened	97
Rhinosardinia amazonica	_	_	1
Rhinosardinia bahiensis	_	_	1
Rhizoprionodon lalandii	_	Data deficient	1
Rhizoprionodon porosus	_	Least concern	1
Rhomboplites aurorubens	_	_	1
Ribeiroclinus eigenmanni	_	_	1
Ruvettus pretiosus	_	_	1
, Rypticus bistrispinus	_	_	1
Rypticus randalli	_	_	1
Rypticus saponaceus	_	_	1
Rypticus subbifrenatus	_	_	1
Sardinella brasiliensis	_	_	1
Sargocentron bullisi	_	_	1
Scartella cristata	_	_	1
Scartella itajobi	_	_	1
Scartella poiti	_	_	1
, Scarus quacamaia	Vulnerable	Near threatened	98
Scarus trispinosus	_	Endangered	99
Scarus zelindae	_	Data deficient	1
Sciades couma	_	Least concern	1
Sciades herzbergii	_	_	1
Sciades parkeri	_	Near threatened	97
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Taxon	Species —	Conservation status		Woigth
		MMA	IUCN	weight
	Sciades passany	-	-	1
	Sciades proops	_	_	1
	Scomberomorus brasiliensis	_	Least concern	1
	Scomberomorus cavalla	_	Least concern	1
	Scomberomorus regalis	_	Least concern	1
	Scorpaena brasiliensis	_	-	1
	Scorpaena dispar	_	-	1
	Scorpaena grandicornis	_	_	1
	Scorpaena isthmensis	_	_	1
	Scorpaena plumieri	_	_	1
	Scorpaenodes caribbaeus	_	_	1
	Scorpaenodes insularis	_	_	1
	Scorpaenodes tredecimspinosus	_	_	1
	Selar crumenophthalmus	_	_	1
	Selene brownii	_	_	1
	Selene setapinnis	_	_	1
	Selene vomer	_	_	1
	Seriola dumerili	_	_	1
	Seriola fasciata	_	_	1
	Seriola lalandi	_	_	1
	Seriola rivoliana	_	_	1
	Serranus annularis	_	_	1
	Serranus atrobranchus	_	-	1
	Serranus baldwini	_	_	1
	Serranus flaviventris	_	_	1
	Serranus phoebe	_	-	1
	Sparisoma amplum	_	Least concern	1
	Sparisoma axillare	_	Data deficient	1
	Sparisoma frondosum	_	Data deficient	1
	Sparisoma radians	_	Least concern	1
	Sparisoma rocha	_	-	1
	Sparisoma tuiupiranga	-	Least concern	1
	Sphoeroides greeleyi	-	-	1
	Sphoeroides pachygaster	_	-	1
	Sphoeroides spengleri	-	-	1
	Sphoeroides testudineus	_	-	1
	Sphoeroides tyleri	-	-	1
	Sphyraena barracuda	_	-	1
	Sphyraena borealis	_	-	1
	Sphyraena guachancho	-	-	1
	Sphyraena sphyraena	-	-	1
	Sphyraena tome	_	_	1
	Sphyrna lewini	_	Endangered	99

Sohvroa tihuro	_	Least concern	1
Sphyrna tudes	_	Vulnerable	י مع
Squatina argentina	_	Endangered	90
Starksia brasiliensis	_		1
Starksia multilenis	_	_	1
Stenastes fuscus	_	l east concern	1
Stegastes nictus	_	_	1
Stegastes rocasensis	_	_	1
Stegastes sanctinauli	Vulnerable	Vulnerable	98
Stegastes variabilis			1
Stellifer brasiliensis	_	_	1
Stellifer microns			1
Stellifer pase	_	_	1
Stellifer restrifer	_	-	1
Stellifer stellifer	-	-	1
Stenhenslenie bienidue	-	-	1
Stephanolepis hispidus	-	-	1
Stephanolepis setifer	_	-	1
Storrsia olsoni	_	-	1
Stromateus brasiliensis	-	-	1
Strongylura marina	-	Least concern	1
Strongylura timucu	-	-	1
Stygnobrotula latebricola	-	Least concern	1
Syacium micrurum	_	_	1
Syacium papillosum	-	-	1
Symphurus diomedeanus	_	-	1
Symphurus jenynsi	-	-	1
Symphurus plagusia	-	-	1
Symphurus tessellatus	-	-	1
Sympterygia acuta	-	Vulnerable	98
Sympterygia bonapartii	-	Data deficient	1
Syngnathus folletti	-	-	1
Syngnathus pelagicus	-	-	1
Syngnathus scovelli	-	-	1
Synodus foetens	-	-	1
Synodus intermedius	-	-	1
Synodus poeyi	-	-	1
Synodus synodus	-	-	1
Tetrapturus albidus	_	Vulnerable	98
Tetrapturus pfluegeri	_	Least concern	1
Thalassoma noronhanum	_	Least concern	1
Thalassophryne maculosa	_	_	1
Thalassophryne montevidensis	_	_	1
Thalassophryne nattereri	_	_	1
Thalassophryne punctata	_	_	1
Thunnus alalunga	_	Near threatened	97
Thunnus albacares	_	Near threatened	97

Taxon	Species	Conservation status		Woigth
		MMA	IUCN	weigin
	Thunnus atlanticus	-	Least concern	1
	Thunnus obesus	-	Vulnerable	98
	Tomeurus gracilis	-	_	1
	Tomicodon australis	-	Least concern	1
	Trachinocephalus myops	-	_	1
	Trachinotus carolinus	_	_	1
	Trachinotus cayennensis	_	_	1
	Trachinotus falcatus	_	_	1
	Trachinotus goodei	_	Least concern	1
	Trachinotus marginatus	_	_	1
	Trachurus lathami	_	_	1
	Trichiurus lepturus	_	_	1
	Trinectes maculatus	_	_	1
	Trinectes microphthalmus	_	_	1
	Trinectes paulistanus	_	_	1
	Tylosurus acus	_	_	1
	Tylosurus crocodilus	_	_	1
	Ulaema lefroyi	_	_	1
	Umbrina canosai	_	_	1
	Umbrina coroides	_	_	1
	Upeneus parvus	_	_	1
	Uraspis secunda	_	_	1
	Urophycis brasiliensis	_	_	1
	Uropterygius macularius	_	_	1
	Urotrygon microphthalmum	-	Least concern	1
	Xiphias gladius	-	Least concern	1
	Xyrichtys incandescens	-	Least concern	1
	Xyrichtys martinicensis	-	Least concern	1
	Xyrichtys novacula	-	Least concern	1
	Xyrichtys splendens	-	Least concern	1
	Zapteryx brevirostris	-	Vulnerable	98
	Zenopsis conchifer	-	-	1
Marine turtles	Caretta caretta	Vulnerable	Endangered	98
	Chelonia mydas	Vulnerable	Endangered	98
	Dermochelys coriacea	Critically endangered	Critically endangered	100
	Eretmochelys imbricata	Endangered	Critically endangered	99
	Lepidochelys olivacea	Endangered	Vulnerable	99
Seabirds	Anous minutus	-	Least concern	1
	Anous stolidus	-	Least concern	1
	Calonectris diomedea	-	Least concern	1
	Chlidonias niger	-	Least concern	1
	Daption capense	-	Least concern	1
	Diomedea dabbenena	Endangered	Critically endangered	99

Diomedea epomophora	Vulnerable	Vulnerable	98
Diomedea exulans	Vulnerable	Vulnerable	98
Diomedea sanfordi	Endangered	Endangered	99
Fregata ariel	Critically endangered	Least concern	100
Fregata magnificens	_	Least concern	1
Fregata minor	Critically endangered	Least concern	100
Fregetta grallaria	_	Least concern	1
Fregetta tropica	_	Least concern	1
Fulmarus glacialoides	_	Least concern	1
Gygis alba	_	Least concern	1
Larus atlanticus	Vulnerable	Vulnerable	98
Larus atricilla	_	Least concern	1
Larus cirrocephalus	_	Least concern	1
Larus dominicanus	_	Least concern	1
Larus maculipennis	_	Least concern	1
Macronectes giganteus	_	Least concern	1
Oceanites oceanicus	_	Least concern	1
Oceanodroma leucorhoa	_	Least concern	1
Pachyptila belcheri	_	Least concern	1
Pachyptila desolata	_	Least concern	1
Pelecanus occidentalis	_	Least concern	1
Phaethon aethereus	Vulnerable	Least concern	98
Phaethon lepturus	Vulnerable	Least concern	98
Phalacrocorax brasilianus	_	Least concern	1
Phoebetria fusca	_	Endangered	99
Procellaria aequinoctialis	Vulnerable	Vulnerable	98
Procellaria conspicillata	Endangered	Vulnerable	99
Pterodroma arminjoniana	Vulnerable	Vulnerable	98
Pterodroma incerta	Vulnerable	Endangered	98
Puffinus gravis	_	Least concern	1
Puffinus griseus	_	Near threatened	97
Puffinus puffinus	_	Least concern	1
Spheniscus magellanicus	_	Near threatened	97
Stercorarius longicaudus	_	Least concern	1
Stercorarius maccormicki	_	Least concern	1
Stercorarius parasiticus	_	Least concern	1
Stercorarius pomarinus	_	Least concern	1
Stercorarius skua	_	Least concern	1
Sterna antillarum	_	Least concern	1
Sterna dougallii	_	Least concern	1
Sterna fuscata	_	Least concern	1
Sterna hirundinacea	_	Least concern	1
Sterna hirundo	_	Least concern	1
Sterna maxima	_	Least concern	1
Sterna nilotica	_	Least concern	1
Sterna paradisaea	-	Least concern	1

Taxon	Species	Conservation status		— Weigth
		ММА	IUCN	Hoigui
	Sterna sandvicensis	_	Least concern	1
	Sterna trudeaui	_	Least concern	1
	Sterna vittata	_	Least concern	1
	Sula dactylatra	_	Least concern	1
	Sula leucogaster	_	Least concern	1
	Sula sula	_	Least concern	1
	Thalassarche chlororhynchos	Vulnerable	Endangered	98
	Thalassarche chrysostoma	_	Vulnerable	98
	Thalassarche melanophrys	Vulnerable	Endangered	98
Marine mammals	Arctocephalus australis	_	Least concern	1
	Balaenoptera musculus	Critically endangered	Endangered	100
	Delphinus delphis	_	Least concern	1
	Eubalaena australis	Endangered	Least concern	99
	Feresa attenuata	_	Data deficient	1
	Globicephala macrorhynchus	_	Data deficient	1
	Globicephala melas	_	Data deficient	1
	Grampus griseus	_	Least concern	1
	Hyperoodon planifrons	_	Least concern	1
	Kogia breviceps	_	Data deficient	1
	Kogia simus	_	Data deficient	1
	Lagenodelphis hosei	_	Least concern	1
	Lissodelphis peronii	_	Data deficient	1
	Mesoplodon densirostris	_	Data deficient	1
	Mesoplodon gravi	_	Data deficient	1
	Mesoplodon lavardii	_	Data deficient	1
	Mirounga leonina	_	Least concern	1
	Orcinus orca	_	Data deficient	1
	Otaria flavescens	_	Least concern	1
	Peponocephala electra	_	Least concern	1
	Phocoena dioptrica	_	Data deficient	1
	Phocoena spinipinnis	_	Data deficient	1
	Physeter macrocephalus	Vulnerable	Vulnerable	98
	Pontoporia blainvillei	Endangered	Vulnerable	99
	Pseudorca crassidens		Data deficient	1
	Sotalia quianensis	_	Data deficient	1
	Stenella attenuata	_	Least concern	1
	Stenella clymene	_	Data deficient	1
	Stenella coeruleoalba	_	Least concern	1
	Stenella frontalis	_	Data deficient	1
	Stenella Innairostris	_	Data deficient	1
	Steno bredanensis	_	Least concern	1
	Trichechus manatus	- Critically endengered		י 100
	Tursions truncatus		l east concern	1
	Zinhius cavirostris	_	Least concern	1



Fig. A1. Results of the sensitivity analysis comparing the proportion of the species' distribution represented in conservation scenarios using our weighting scheme (solid lines) and equal weights (i.e., 1; dashed lines) for all species. Note that our weighting scheme tend to increase more the protection of higher weight species (e.g., *Fregata minor*) than of lower weight species (e.g., *Spheniscus magellanicus*) when compared to the protection levels provided to them in an unweighted analysis.