Renato Morais Araujo

FATORES PREDITORES DA VARIAÇÃO ESPACIAL NA BIOMASSA DE PEIXES RECIFAIS AO LONGO DA PROVÍNCIA BRASILEIRA

Dissertação submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Mestreem Ecologia.

Orientador: Prof. Dr. Sergio Ricardo Floeter

Florianópolis
2014

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Araujo, Renato Morais
FATORES PREDITORES DA VARIAÇÃO ESPACIAL NA BIOMASSA DE PEIXES RECIFAIS AO LONGO DA PROVÍNCIA BRASILEIRA / Renato Morais Araujo ; orientador, Sergio Ricardo Floeter - Florianópolis, SC, 2014.
100 p.

Dissertação (mestrado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas. Programa de Pós-Graduação em Ecologia.

Inclui referências

1. Ecologia. 2. Biomassa de peixes recifais. 3. Estrutura de assembleias. 4. Grupos funcionais. 5. Múltiplas escalas espaciais. I. Floeter, Sergio Ricardo. II. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. III. Título.

“Fatores preditores da variação espacial na biomassa de peixes recifais ao longo da província brasileira”

por

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Florianópolis, 30 de abril de 2014.

À vovó Zulma,
O anjo que seguiu o seu caminho durante este trabalho.

AGRADECIMENTOS

Agradeço a quem me concebeu, gerou, criou, sustentou, amou e apoiou nos últimos 26 anos. Agradeço por viver, por poder aproveitar esse mundo extraordinário e pelas infinitas possibilidades que se abrem para o futuro. Obrigado a todos os que se encaixaram e àqueles que ainda hoje se encaixam em uma ou muitas dessas fases. Aos meus colegas, amigos, família e à minha pequena pela paciência, parceria, amizade e amor que pude receber. E retribuir.

Agradeço pelas oportunidades que tive ao longo deste trabalho. Por ter conhecido lugares fantásticos, por ter tido experiências indescritíveis e por ter sorte. Agradeço às pessoas e instituições que me deram a oportunidade de participar desse trabalho desde o início. Especificamente ao meu orientador Sergião e ao Cadu porque sei que ainda vou sambar muito para honrar essas oportunidades. Muito obrigado Gustavo por ter brotado nesse laboratório no momento mais crítico do meu mestrado e ter me ensinado boa parte das ferramentas que viabilizaram chegar às conclusões que chegamos. Agradeço também às pessoas geniais que trabalharam para inventar duas ferramentas essenciais para a realização desse trabalho, o mergulho autônomo de SCUBA e o R.

Agradeço aos brasileiros que trabalharam e por vias indiretas financiaram a Rede SISBIOTA, através do CNPq e FAPESC e também a minha bolsa pela Capes.

RESUMO

Atividades humanas vem alterando a topologia dos ecossistemas recifais, sendo que a atividade pesqueira é responsável pela retirada de vastas quantidades de biomassa de peixes a nível global. Avaliações dos padrões da biomassa de peixes recifais em escala regional tem ajudado a identificar lugares que ainda mantem características pristinas e a dimensionar a influência da pesca em largas escalas espaciais. A Província Brasileira se estende por mais de 4000 km de linha de costa e inclui quatro ilhas oceânicas, contudo ainda é menos ecologicamente conhecida do que outras regiões tropicais. Este trabalho apresenta dados da biomassa de peixes recifais ao longo de toda a Província Brasileira e testa a capacidade de três modelos, os modelos ambiental, de influência humana e o modelo completo em explicá-los. A biomassa disponível (standing biomass) variou em uma escala de 100 vezes entre os sítios de todas as localidades, a maior amplitude de variação já reportada até hoje por um único estudo. Sítios tenderam a se agrupar independentemente da região geográfica em grupos com alta e baixa biomassa tanto por uma perspectiva funcional quanto por uma perspectiva taxonômica. Localidades isoladas ou protegidas, como Alcatrazes, Trindade, Parcel de Manuel Luís e Recifes a Norte de Natal tiveram a maior parte dos sítios com alta biomassa, ao passo que localidades costeiras e acessíveis como Arraial do Cabo, Baía de Todos os Santos, Ilha Grande e a Costa dos Corais tiveram a maior parte dos sítios com baixa biomassa. Abrolhos e Fernando de Noronha, apesar de relativamente isolados e de terem sítios teoricamente protegidos, tiveram baixa biomassa total de de predadores, mostrando limitada efetividade com relação à proteção de espécies alvo da pesca. Em termos funcionais, sítios com alta biomassa tenderam a possuir também alta biomassa de macrocarnívoros, grandes herbívoros e detritívoros e carnívoros de pequeno porte. Esses grupos incluem a maioria dos peixes recifais de grande porte, alto nível trófico e/ou formadores de grandes cardumes e são os alvos preferencias das atividades pesqueiras. Onívoros apresentaram maior biomassa em ilhas oceânicas e em recifes do sul-sudeste e zooplanctívoros nas ilhas oceânicas e em alguns recifes submersos do norte-nordeste. Taxonomicamente, sítios com alta biomassa tenderam também a possuir alta biomassa de Kyphosidae, Labridae e Epinephelidae. Haemulidae esteve associado com a maioria dos sítios costeiros, Pomacanthidae com sítios costeiros do sul-sudeste, Balistidae com ilhas oceânicas e Pomacentridae esteve largamente distribuída. Esses padrões de variação na biomassa disponível foram melhor aproximados pelos modelos completo e de influência humana, ao passo que o modelo ambiental não obteve suporte. Distância da costa enquanto medida de isolamento foi a variável mais influente na biomassa de uma forma geral, estando inversamente correlacionada com a intensidade pesqueira. A pesca é provavelmente a influência humana mais destrutiva em assembleias de peixes e os resultados deste trabalho indicam que em comparação a seus efeitos intensos e de larga-escala, variáveis ambientais tiveram limitada influência no contexto deste trabalho sobre peixes de grande porte responsáveis pela maior parte da biomassa disponível. Enquanto membro signatário da COP-10, o Brasil concordou em conservar de maneira efetiva 10% de sua área marinha até 2020. Considerando o ano de 2014, ainda nos encontramos muito longe da meta proposta uma vez que menos de 0.2% de nossa área marinha possui proteção teórica e parte desta é inefetiva na conservação de aspectos do funcionamento ecossistêmico como a biomassa disponível de peixes. De maneira adicional, o presente trabalho discrimina áreas que ainda carregam assembleias de peixes com características conservadas e funcionais, que são ameaçadas pela atividade pesqueira de larga escala e não regulada e não possuem nenhum tipo de proteção oficial.

Palavras-chave: Biomassa de peixes recifais, estrutura de assembleias, grupos funcionais, pequena a grande escala.

ABSTRACT

Human activities have altered the topology of reef ecosystems with fishing largely withdrawing fish biomass globally. Assessing patterns of reef fish biomass over regional scales has helped to identify places that still maintain pristine characteristics and to dimension large spatial scale influence of fishing. The Brazilian Province stretches for more than 4000 km of coastline and includes four oceanic islands, but is still less ecologically known than other tropical regions. This work presents data of reef fish standing biomass from all over Brazilian Province and tests the capacity of three models, an environmental, a human-influence and the full model in explaining it. Standing biomass varied 100-fold between sites from all localities, the largest range reported to date by a single study. Sites tended to group irrespective of geographic region in low-biomass or high-biomass groups both from a functional and taxonomic point of view. Isolated or protected localities such as Alcatrazes, Trindade, Manuel Luís Reefs and Northern Natal reefs had most of high biomass sites, while accessible and coastal places such as Arraial do Cabo, Todos os Santos Bay, Ilha Grande and Coral Coast had most of the low biomass ones. Abrolhos and Fernando de Noronha, despite being relatively isolated and having sites theoretically protected, had low total and predator biomass, showing limited effectivity for the protection of target species. Functionally, high-biomass sites tended to have also high biomass of macrocarnivores, large herbivores and detritivores and lower-level carnivores. These include most large-bodied, high trophic level and/or large shoaling reef fishes, the ones preferentially targeted by fisheries. Omnivores presented more biomass in oceanic islands and south-southeastern reefs and zooplanktivores in oceanic islands and some submerged north-northeastern reefs. Taxonomicaly, high-biomass sites tended also to have high biomass of Kyphosidae, Labridae and Epinephelidae. Haemulidae was associated with most coastal sites, Pomacanthidae with coastal southeastern sites, Balistidae with oceanic islands and Pomacentridae was widely distributed. These variation patterns in standing biomass were better approached by both the full and the human-influence models with no support for environmental model at all. Distance from the coast as a measure of isolation was the most influential variable on overall biomass, and correlates inversely with fishing intensity. Fishing is probably the most destructive human influence on fish assemblages and results indicate that, comparing to its intense and large-scale effects, environmental variables have limited influence on large-bodied fishes responsible for most of standing biomass in the context of this study. As a signatory member of the COP-10, Brazil agreed to effectively conserve 10% of its marine environment by 2020. As of 2014 we are still very far from the proposed target, since we have less than 0.2% of area with theoretical protection and some of it is clearly ineffective in conserving ecosystem functioning aspects such as fish standing biomass. Moreover, this work points out other areas that still carry functional fish assemblages with conserved characteristics that are threatenned by large-scale unregulated fishing and have no official protection.

Keywords: Reef fish biomass, assemblage structure, functional groups, small to large scale.

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LISTA DE ABREVIATURAS E SIGLAS

ABR	Abrolhos
ALC	Alcatrazes
ARR	Arraial do Cabo
ASP	Saint Pauls Rocks
BTS	Todos os Santos Bay
CCO	Coral Coast
CEA	Ceará Coast
ESA	Espírito Santo
ILB	Ilhabela
ILG	Ilha Grande
LHD	Large herbivores and detritivores
LLC	Lower-level carnivores
LSA	Laje de Santos
MCA	Macrocarnivores
MLU	Manuel Luís Reefs
NOR	Fernando de Noronha
OMN	Omnivores
RNN	Northern Natal Reefs
RNP	Parrachos do RN
RNS	Southern Natal Reefs
ROC	Rocas Atoll
SCN	Northern Santa Catarina
SCS	Southern Santa Catarina
SHD	Small herbivores and detritivores
TRI	Trindade and Martin Vaz
ZPK	Zooplanktivores

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INTRODUÇÃO GERAL

A ABORDAGEM EM LARGA ESCALA E A MACROECOLOGIA

Entender os padrões de distribuição e abundância dos organismos é um dos principais objetivos dos ecólogos. Embora estudos em pequena escala sejam fundamentais para identificar os fatores locais que influenciam nesses padrões, é inegável que as perguntas mais gerais só podem ser respondidas com a consideração de escalas maiores em ambos tempo e espaço. Nesse contexto a Teoria de Equilíbrio da Biogeografia de Ilhas (MACARTHUR e WILSON 1963) e a Ecologia Geográfica (MACARTHUR 1972) foram iniciativas importantes que forneceram as bases teóricas para os estudos em larga escala. Contudo, um arcabouço completo envolvendo também procedimentos metodológicos e empíricos foi desenvolvido somente a partir do fim da década de 1980, com o surgimento da Macroecologia (BROWN e MAURER 1989, BROWN 1995). Esta é uma disciplina que visa estudar as relações entre organismos e seu ambiente e que envolve caracterizar e explicar padrões estatísticos em abundância, distribuição e diversidade (BROWN 1995). Em última análise, pretende-se responder o que influencia a distribuição dos organismos em grandes escalas temporais e espaciais, utilizando-se de dados observacionais e abordagens estatísticas multivariadas (BROWN e MAURER 1989).

Nos ecossistemas marinhos, peixes recifais são utilizados como importantes modelos para estudos em macroecologia. Suas assembleias são conspícuas, apresentam grande diversidade de espécies (KULBICKI et al. 2013, PARRAVICINI et al. 2013), são bem conhecidas taxonomicamente (ESCHMEYER et al. 2010) e são troficamente ligadas com inúmeras sociedades humanas, formando a base da alimentação de diversos povos (HOLMLUND e HAMMER 1999). Estudos utilizando esse grupo como modelo investigaram a influência de fatores como produtividade primária, temperatura, área recifal e intensidade da pesca sobre abundância, riqueza e/ou biomassa de peixes recifais (e.g. MORA et al. 2011, PARRAVICINI et al. 2013). Entender a influência desses fatores em assembleias de peixes em larga escala pode ser uma estratégia para dimensionar nosso próprio impacto sobre esses organismos, de modo a propor atividades de manejo e/ou conservação.

PESCA E A CRISE DOS AMBIENTES RECIFAIS

Durante a última década espalhou-se a noção de uma crise global dos ambientes recifais gerada por fatores como pesca, poluição, tempestades, doenças e aumento da temperatura atuando em sinergia (BELLWOOD et al. 2004). Desses fatores a pesca talvez seja o mais crítico dado o seu caráter previsível e seus impactos diretos e multiescala. Essa atividade tem resultado não só na perda local de biodiversidade, mas também em alterações estruturais e de funcionamento a nível ecossistêmico (JACKSON et al. 2001, BELLWOOD et al. 2004, BELLWOOD et al. 2012). Além disso, essa perda de biodiversidade ocorre de maneira desbalanceada ao longo das cadeias tróficas, afetando desigualmente predadores de topo (PAULY et al. 1998) com vastas consequências para níveis tróficos inferiores (DUFFY 2002). Por exemplo, a ausência de predadores em recifes de coral do Pacífico, revelou estar relacionada a maior longevidade e maior crescimento de peixes-presa (RUTTENBERG et al. 2011), aumento na quantidade de microrganismos potencialmente patogênicos (DINSDALE et al. 2012), redução no recrutamento de corais (SANDIN et al. 2008), dentre outras alterações com consequências ecossistêmicas.

Além de predadores de topo, espécies de tamanho corporal grande responsáveis por processos críticos no funcionamento ecossistêmico também tendem a ser afetadas pela pesca, fazendo com que impactos nesses organismos sejam sentidos nos processos dos quais participam (BRUGGEMAN et al. 1996, BIRKELAND e DAYTON 2005, MCCAULEY et al. 2010, BELLWOOD et al. 2012). Por exemplo, Bellwood e colaboradores (2012) estimaram que a pesca diferencial de peixes-papagaio de grande porte, poderosos raspadores e escavadores do substrato, pode resultar em reduções drásticas dos níveis de bioerosão e predação em corais de recifes do Indo-Pacífico. McCauley e colaboradores (2010) realizaram um experimento de exclusão somente de peixes grandes (>25 cm) em um atol quase pristino no Pacífico Central. Esses autores observaram nas áreas experimentais alterações em diversos processos, como redução de herbivoria em algumas espécies de algas com consequente aumento de competição com recrutas de corais, e redução na abundância de pequenos invertebrados móveis. Essas e outras evidências apontam para a necessidade de abordagens de conservação a nível ecossistêmico, como por exemplo o uso áreas marinhas protegidas e reservas marinhas (HALPERN 2003, MORA et al. 2006, ROBERTS 2012, EDGAR et al. 2014).

ÁREAS MARINHAS PROTEGIDAS E RESERVAS MARINHAS

A ideia de criar áreas reservadas à reprodução e crescimento de animais marinhos como estratégia de manejo pesqueiro, as reservas marinhas, data do início do século XX (ROBERTS 2012). Contudo, somente a partir das décadas de 1970 e 1980 foram implementadas as primeiras áreas marinhas protegidas (BALLANTINE 2014). O próprio conceito de áreas marinhas protegidas (AMP) é mais amplo do que o de reservas marinhas (RUSS 2002), sendo estas as AMPs em que a pesca (*no-take*) ou mesmo a entrada de pessoas é proibida (*no-entry*). Além dessas condições, AMPs incluem áreas em que alguns tipos de pesca são permitidos, porém sob restrições (*limited-fishing*); bem como áreas abertas à pesca e com restrições a outras atividades (*open-fishing*, ROBBINS et al. 2006).

Em 2010, durante a 10ª reunião da Conferência das Partes (COP-10) da Convenção da Diversidade Biológica, vários países do mundo assinaram um documento se comprometendo até 2020 a "conservar através de sistemas bem conectados de áreas marinhas protegidas que sejam ecologicamente representativos e efetivamente manejados, pelo menos 10% de suas áreas costeiras e marinhas" (CDB 2010). Apesar de discrepâncias políticas com relação aos números reais, é fato que a maioria dos países signatários encontra-se atualmente muito longe dessa meta. De maneira a aumentar essa proporção protegida, nos últimos anos teve início uma corrida política entre países para criar as maiores áreas marinhas protegidas do mundo (JONES 2011, PALA 2013). Essas "megareservas" da ordem de centenas de milhares de quilômetros quadrados, apesar de constituírem um inequívoco avanço no contexto da conservação marinha mundial, não devem ser alardeadas como a panaceia da sobrepesca global. Isso porque em geral tem sido estabelecidas em locais isolados e muitas vezes desabitados e compreendem vastas áreas de mar aberto onde pouco ou nenhum conflito fundiário e econômico existe (JONES 2011, PALA 2013). Além disso, algumas dessas "megareservas" trazem pouca ou nenhuma restrição oficial às atividades de pesca (PALA 2013). Nesse contexto deve ser salientada a importância concomitante de pequenas AMPs costeiras, totalmente protegidas da pesca e que sejam efetivamente manejadas e incluam espécies que habitam outros ambientes que não o oceânico (PALA 2013).

Vários estudos demonstram os benefícios ecológicos e econômicos da existência de reservas marinhas. Estas, quando bem manejadas e fiscalizadas atuam aumentando a densidade, tamanho e idade médios de espécies-alvo da pesca em seu interior (RUSS 2002, HALPERN et al. 2003, ROBBINS et al. 2006, GARCÍA-CHARTON et al. 2008, ABURTO-OROPEZA et al. 2011) e exportando larvas, adultos e comportamentos susceptíveis à pesca para áreas adjacentes não protegidas (efeito de transbordamento, RUSS 2002, RUSS et al. 2003, AMARGÓS et al. 2007, HARRISON et al. 2012, JANUCHOWSKI-HARTLEY et al. 2013). Por exemplo, já é conhecido que peixes alvo de pesca são menos ariscos no interior de reservas (FEARY et al. 2011). Além disso, Januchowski-Hartley e colaboradores (2013) recentemente demostraram que o FID (do inglês *Flight Initiation Distance*, Distância Inicial de Fuga), uma medida de quão arisco é um peixe na presença de um mergulhador, aumenta linearmente à medida em que se vai do interior para o exterior de uma reserva. Esses pesquisadores observaram que o FID de espécies alvo da pesca é menor em áreas exteriores que sejam próximas à reserva do que em áreas exteriores distantes, evidenciando um efeito de reserva em exportar também comportamentos susceptíveis à pesca (JANUCHOWSKI-HARTLEY et al. 2013).

À parte de seus potenciais efeitos positivos, diversos fatores políticos e econômicos podem fazer com que AMPs existam somente na teoria, de maneira semelhante aos chamados "*paper parks*" da conservação terrestre (KAREIVA 2006). De fato, é essencial entender a efetividade das AMPs já existentes com relação à conservação da biodiversidade marinha. Mora e colaboradores (2006) avaliaram a adequação de AMPs para a proteção de ecossistemas de recife de coral em escala global. Considerando aspectos como grau de regulamentação de coleta, existência de coleta ilegal, tamanho e isolamento, esses autores chegaram à conclusão de que somente 2% da área desse ecossistema está localizada em AMPs consideradas adequadas, sendo 0.01% em áreas *no-take*. Em estudo mais recente, Edgar e colaboradores (2014) avaliaram características que tornam AMPs efetivas em conservar assembleias de peixes recifais com relação a descritores de riqueza e biomassa. As característcias avaliadas foram proibição à pesca (*no-take*), existência de fiscalização, idade (>10 anos desde a criação), área (>100 km²) e isolamento. Esses autores chegaram à conclusão de que somente AMPs com quatro ou cinco dessas características eram efetivas em aumentar os descritores medidos. Essas AMPs possuíram o dobro de espécies de grande porte (>25 cm TL) por amostra, cinco vezes mais biomassa total e até 14 vezes mais biomassa de tubarões quando comparadas a áreas em que a atividade pesqueira era permitida (EDGAR et al. 2014). Infelizmente, como ressaltam os autores, somente nove AMPs contaram com quatro ou cinco características, possuindo a grande maioria das AMPs analizadas (59%) somente uma ou duas dessas características e sendo indistinguíveis de locais não protegidos.

PESQUISA ECOLÓGICA E CONSERVAÇÃO DE PEIXES RECIFAIS NO BRASIL

Uma retrospectiva ampla dos estudos taxonômicos e faunísticos de peixes recifais brasileiros está além dos objetivos desta introdução e pode ser obtida em Moura (2003). Um dos períodos de maior avanço na compreensão de nossa ictiofauna se deu a partir das décadas de 1970 e 1980 quando pesquisadores, principalmente ingleses, passaram a utilizar-se do mergulho autônomo (SCUBA) como ferramenta para a realização de pesquisas (MOURA 2003). Os primeiros estudos naturalísticos e ecológicos com relação à ictiofauna recifal se deram pelos trabalhos gerados pela Expedição Cambridge de 1979 (EDWARDS 1979) e capitaneados por Roger Lubbock e Alastair Edwards (EDWARDS e LUBBOCK 1983A, EDWARDS e LUBBOCK 1983B), e paralelamente pelos trabalhos do professor Ivan Sazima (SAZIMA 1983, SAZIMA 1986). Nas décadas de 1990 e 2000 seguiram-se os primeiros estudos quantitativos (FERREIRA et al. 1995, ROSA e MOURA 1997, FERREIRA et al. 1998A, FERREIRA et al. 1998B, FERREIRA et al. 2001, ROCHA E ROSA 2001). Com relação à estrutura de assembleias, além dos diversos estudos locais (e.g. FERREIRA et al. 2001, FERREIRA et al. 2006, FLOETER et al. 2007, HONÓRIO et al. 2010, PINHEIRO et al. 2011), grande conhecimento foi gerado por estudos de larga escala investigando como essas assembleias variam ao longo da costa (FLOETER et al. 2001, MOURA 2003, FERREIRA et al. 2004, FLOETER et al. 2004, FLOETER et al. 2005). Todavia, poucos desses estudos locais e nenhum dos estudos regionais incluiu biomassa como um descritor das assembleias de peixes recifais. Vários estudos vem reconhecendo a importância de se considerar, além da abundância dos organismos, também considerações acerca de seu tamanho e sua participação nos fluxos de energia dos ecossistemas (BROWN 1995, FRIEDLANDER e PARRISH 1998, ROBERTSON 1998, MORA et al. 2011). Isso é particularmente importante quando se quer avaliar a influência da atividade pesqueira sobre essas assembleias, visto que a pesca, em última instância trata-se da retirada de biomassa para consumo humano. Dessa maneira, estudos que se valham desse indicador tem a possibilidade de auxiliar na compreensão da efetividade das estratégias de conservação da ictiofauna recifal como, por exemplo, a efetividade de áreas marinhas protegidas já estabelecidas (e.g. ABURTO-OROPEZA et al. 2011, SALA et al. 2011, EDGAR et al. 2014)

O panorama da conservação da ictiofauna recifal no Brasil encontra-se atrelado à situação do sistema de áreas marinhas protegidas do país. Nesse contexto, o Brasil é um dos países que encontra-se muito longe da meta da COP-10 de proteger pelo menos 10% de sua área marinha até 2020. Atualmente, somente 1.57% de nossa Zona Econômica Exclusiva está inserida em alguma Área Marinha Protegida de qualquer status (MMA 2010), com 0.14% em Unidades de Proteção Integral (áreas *no-take*). Esse panorama torna-se ainda mais impressionante quando se leva em conta que o país foi um dos primeiros no mundo a declarar uma reserva marinha, a Reserva Biológica do Atol das Rocas, em 1978. Na década de 1980 surgiram outras importantes reservas marinhas (no sentido de áreas *no-take*), como o Parque Nacional Marinho dos Abrolhos (1983) e o Parque Nacional Marinho de Fernando de Noronha (1988). Esse processo de criação de AMPs no país, entretanto, foi desacelerado durante a década de 1990, tendo praticamente cessado a partir dos anos 2000, na contramão de muitos países no mundo. Além da pequena área que ocupam, as AMPs brasileiras não compreendem adequadamente os padrões de riqueza de organismos marinhos na costa, e alguns hotspots como o litoral norte da Bahia, Pernambuco, Paraíba e sul do Espírito Santo são pouco representados por AMPs (VILA-NOVA 2014). Com relação à efetividade dessas AMPs, apesar de vasto conhecimento prático de muitos pesquisadores na área, poucos esforços padronizados em larga escala foram realizados até hoje (uma importante exceção é o trabalho de Ferreira e Maida 2006). O presente estudo apresenta dados inéditos de biomassa de peixes recifais na escala nacional, incluindo sítios desprotegidos, as principais AMPs e todas as reservas marinhas do país. Dessa forma, embora não tenha sido especificamente desenhado para tal, os dados aqui apresentados podem contribuir para uma melhor compreensão da efetividade das AMPs e reservas marinhas no Brasil.

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Capítulo Único

SPATIAL VARIATION IN REEF FISH STANDING BIOMASS THROUGH THE BRAZILIAN PROVINCE: PATTERNS AND PROCESSES

ABSTRACT

Assessing patterns of reef fish biomass over regional scales has to identify places that still maintain pristine characteristics and to dimension large spatial scale influence of fishing. The Brazilian Province, despite large and oceanographically diverse, remains less ecologically known than other tropical regions. This work presents data of reef fish standing biomass from all over Brazilian Province and tests the capacity of three models, an environmental, a human-influence and the full model in explaining it. Standing biomass varied 100-fold between sites from all localities, the largest range reported to date by a single study. Isolated or protected localities had most of high biomass sites, while accessible and coastal places had most of low biomass ones. We identify isolated and theoretically protected localities which had low total and predator biomass, showing limited effectivity for the protection of target species. Large-bodied functional groups and families were normally associated with high biomass sites. Full and human-influence models better predicted biomass, with environmental variables adding little information to it. Distance from the coast as a measure of isolation was the most influential variable on overall biomass, and correlates inversely with fishing intensity. Results indicate that, comparing to the intense and large-scale effects of fishing, environmental variables have limited influence on large-bodied fishes responsible for most of standing biomass in the present context. This work helps to evaluate effectiveness of shallow water marine protected areas from Brazil. If we are to reach the target of 10% of marine environment protection to 2020, we should better aim to both enlarge protected areas and enforce existing ones.

Keywords: Reef fish biomass, assemblage structure, functional groups, small to large scale.

INTRODUCTION

Spatial patterns in reef fish assemblage have been extensively studied at the local scale, and include variation in species richness, composition, abundance and/or biomass. These community descriptors are known to be influenced separately or synergistically by different drivers such as habitat complexity (LUCKHURST and LUCKHURST 1978, ROBERTS and ORMOND 1987, FERREIRA et al. 2001), exposure and hydrodynamics (MCGHEE 1994, WAINWRIGHT and BELLWOOD 2001, FLOETER et al. 2007, KRAJEWSKI et al. 2011), benthic composition (BOUCHON-NAVARRO and BOUCHON 1989, MUNDAY 2002, KRAJEWSKI and FLOETER 2011) and depth (WILLIAMS 1991, FRIEDLANDER and PARRISH 1998, FRIEDLANDER et al. 2010) to name a few. Despite the historical focus on small spatial scales, recent studies have expanded this framework by investigating how these factors shape reef fish assemblages in wider spatial scales such as archipelago (FRIEDLANDER and DEMARTINI 2002, RICHARDS et al. 2012), ocean basin (NEWMAN et al. 2006, FLOETER et al. 2008, SALA et al. 2011) or even globally (MORA et al. 2011, PARRAVICINI et al. 2013, EDGAR et al. 2014). Biogeographic context, water temperature, net productivity and human-related activities are known to transcend localized effects and exert their influence also in larger scales.

The standing biomass of a group of organisms can be recognized as a surrogate for the energy fluxes and matter cycles they participate in an ecosystem (BROWN 1995, FRIEDLANDER and PARRISH 1998, ROBERTSON 1998, MORA et al. 2011). In the context of marine communities, fishing activities provide the link between fish biomass withdrawal and human societies (HOLMLUND and HAMMER 1999). The impacts of fishing on the oceans are global and have been acting for centuries past (JACKSON 1997, JACKSON et al. 2001, ROBERTS 2007). Although places lightly or no affected by fishing nowadays are rare, they provide insights into how energy and biomass are allocated on food chains in the absence of this pervasive human activity (FRIEDLANDER and DEMARTINI 2002, STEVENSON et al. 2007, FRIEDLANDER et al. 2010, WILLIAMS et al. 2011). This is crucial, as energy concentrates in different proportions along trophic levels and these are differentially affected by fishing (MORA et al. 2011). Large-bodied top predators, for example, are the first species to be impacted, and are known to diminish even in lightly-fished places (e.g. PAULY et al. 1998, GRAHAM et al. 2010).

The tropical Southwestern Atlantic Ocean reefs are still poorly known when compared to other regions of the world (CASTRO and PIRES 2001). They stretch for well over 4000 km, comprehending high variability of oceanographic conditions, including oceanic islands, and having been recognized as a separate biogeographic province by Briggs (1974), the Brazilian Province. Despite that, knowledge of this region has lagged behind other places. As an example, most endemic fish species have been described or revalidated only in the last two decades (e.g. MOURA 1995, SAZIMA et al. 1997, SAZIMA et al. 1998, MOURA et al. 2001). This resulted in a know endemism rate of more than 25% for this group (FLOETER et al. 2008). Reef fish assemblages are still being ecologically studied both at the local (e.g. FLOETER et al. 2007A, KRAJEWSKI and FLOETER 2011, PINHEIRO et al. 2011, GIBRAN and MOURA 2012) and regional scales (FERREIRA et al. 2004, FLOETER et al. 2004, FLOETER et al. 2005). Most of these studies, however, did not evaluate biomass as a community descriptor (but see KRAJEWSKI and FLOETER 2011, PINHEIRO et al. 2011) and we still lack comprehension on how reef fish standing biomass vary from small to large scales. The present work takes advantage of a large dataset including reef fish assemblages from all over Brazilian Province to address this variation and potential processes related to it. This is, as far as we are concerned, the first attempt to investigate these issues based on a representative sampling of Brazilian Province.

Considering this framework, we aim to understand: 1) how reef fish standing biomass varies along southwestern Atlantic reefs of Brazilian Province in small to large spatial scales; and 2) which factors could better explain these variations and help to predict standing biomass. To do that we model standing biomass among sites in localities and among functional groups, deliberately testing the capacity of three models in explaining it: an "environmental model" (EM) with only environmental variables, a "human influence model" (HIM) containing only variables that denote human impact, and a full model containing both set of variables. Our two hypotheses are that: 1) given the extent of human activities affecting shallow marine ecosystems, variables that denote human influence will be more informative than environmental variables for the predictive model; and 2) target functional groups (such as large predators and herbivores) will be influenced sharply by these human variables while non-target groups will not. We base these hypotheses on the profound influence of fishing on assemblage structure that includes disproportionate impact on different functional groups

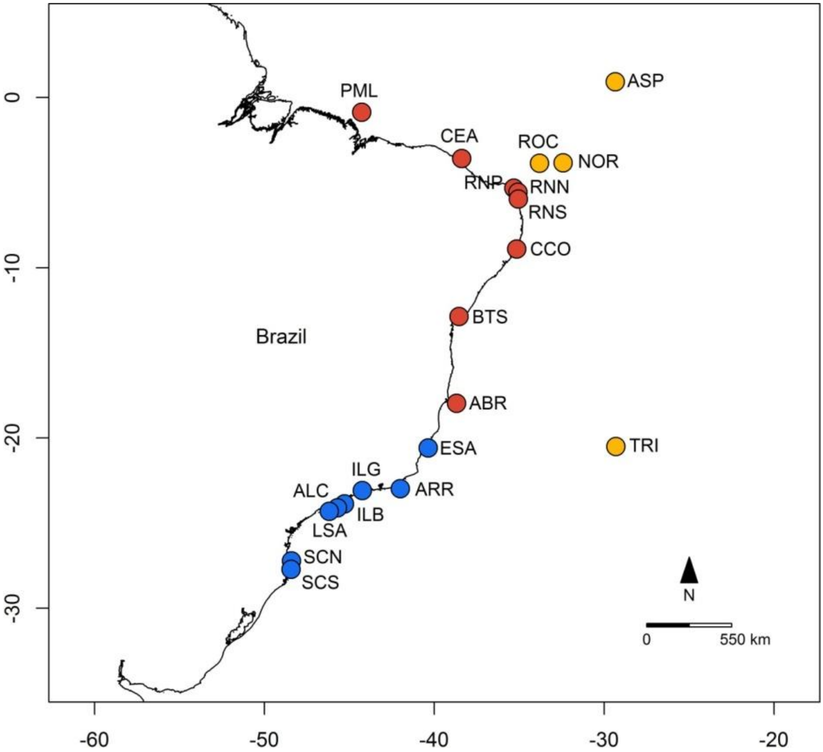
(FRIEDLANDER AND DEMARTINI 2002, SANDIN ET AL. 2008, WILLIAMS ET AL. 2011).

METHODS

Biological database, study area and sampling

Biological database was composed of 3,700 samples collected in surveys from 128 sites and 20 localities, ranging from the northernmost coastal biogenic reef (Manuel Luís reefs, 0°52'S; 44°15'W) to the southernmost coastal rocky reefs in Brazilian Province (Santa Catarina coastal islands, 27°50'S; 48°26'W, Figure 1, Supplementary Table 1), as well as the four Brazilian oceanic island groups (Saint Paul´s Rocks, 0°54'N;29°20'W; Rocas Atoll, 3°52'S; 33°48'W; Fernando de Noronha Archipelago, 3°51'S; 32°25'W; and Trindade and Martin Vaz Island Group, 20°29'S; 29°19'W). These sites included a diverse set of environmental conditions such as tropical and subtropical, biogenic, sandstone, granitic and volcanic reefs, in coastal or oceanic habitats.

Figure 1 -Sampled localities in the Southwestern Atlantic Ocean. Yellow, red and blue dots stand for, respectively, oceanic islands, north and northeastern reefs, and south and southeastern rocky reefs. Acronyms may be seen in Supplementary Table 1.



Each sample was composed of a 20x2m strip transect in which a diver first identified, counted and estimated size (Total Length in cm) of large, fast swimming, colorful and water column fishes, and then returned doing the same procedure for benthic, small and cryptic species (FLOETER et al. 2007A; KRAJEWSKI and FLOETER 2011). All transects were positioned in order to characterize fish assemblages in the depth range of each study site. Nonetheless, 98.5% of these transects were in depths shallower than 30m.

Functional groups and standing biomass

Each fish species was assigned to a functional group based on species diet and individual total length. Information on diet was obtained in a global reef fish species database (GASPAR database). Functional groups were: small herbivores and detritivores (SHD), herbivores or detritivores smaller than 30cm TL; large herbivores and detritivores (LHD), herbivores or detritivores larger than 30cm TL; zooplanktivores (ZPK) regardless of their size; omnivores (OMN) regardless of their size; lower-level Carnivores (LLC), zoobentivores or piscivores smaller than 50cm TL; and macrocarnivores (MAC), zoobentivores or piscivores larger than 50cm TL. Supplementary Table 2 contains species recorded and their respective functional groups.

Body mass was estimated for each fish through the power function $W = a.TL^b$, in which W is estimated weight, TL is total length estimated on a fish count, and the parameters *a* and *b* are allometric growth species-specific constants obtained directly from references contained in Froese and Pauly 2013. Functional group and total standing biomass were calculated respectively by summing all individuals´ body mass from a functional group and all functional groups´ standing biomass.

Oceanographic, geographical and human related variables

Explanatory variables were chosen based on *a priori* known direct or indirect relationships with reef fish assemblages. Environmental variables were based in two different hypotheses: 1) energetics and 2) topographic complexity. Energetic variables included mean and minimum sea surface temperature (sstmean and sstmin) and diffuse attenuation of light (damean). All these were obtained from online Bio-ORACLE database (Supplementary Table 3, TYBERGHEIN et al. 2012) with 'raster' package in R software (R CORE TEAM 2013) using the bilinear method.

For topographic complexity, an index combining the geographical distance (in km) to the 50m isobath (disdeep) and the depth range (in m) of each site (deprange) was calculated. These variables capture a topographic inclination and complexity measure in two nested scales. Deprange was calculated from depth data collected *in situ* for each sample. Disdeep was calculated as the smallest distance of the site to the 50m bathimetry using packages 'rgeos', 'rgdal', 'maptools' and 'geosphere' in software R. This variable scaled negatively with the perceived topographic complexity aspect it should capture and so, its opposite was calculated by subtracting each value of disdeep from the sum of the maximum and minimum values (oppdisdeep). The topographic complexity index (topind) was calculated as the natural logarithm of the product of deprange and oppdisdeep.

Human related variables can be separated in direct and indirect measures of human influence in each site. Direct measures were human population density (popdens) and number of professional artisanal fishers (fishdens). Data were obtained for each coastal municipality from Instituto Brasileiro de Geografia e Estatística - IBGE (popdens) and Ministério da Pesca e Aquicultura (fishdens). These data were spatialized in the territorial sea of each municipality (12 nautical miles from the coast) using a geographic information system and then transformed to raster. A buffer zone of 25km was created around each site and the mean of cell values intercepted by this buffer was used to represent each variable in a site. Twenty-five km was an arbitrary cut-point that the authors assumed to be an average of distance covered by artisanal fishers and recreational fishers and tourists. For the purpose of shortening the scale, popdens was transformed by natural logarithm.

Indirect measures of human influence included an index of protection (protind) and the distance to the coast (discoast) for each site. Protind was calculated as the weighed mean of three other variables assigned to each site: fishing and tourism (0 = permitted, 1 = regulated, 2 = prohibited), and enforcement (0 = absent, 1 = low, 2 = high), with tourism weighing 1, fishing weighing 2 and enforcement weighing 3. Discoast calculation followed the same procedures of disdeep, but calculated the smallest distance of the site to the continental coastline or to large coastal islands such as Ilhabela, Ilha Grande and Ilha de Santa Catarina (>150 km^2). As popdens, discoast was also transformed by natural logarithm.

Data analysis and modelling

The mean standing biomass of all transects from a given site was used as the sampling unit, with the mean value from a locality being represented by the mean of sites. This approach deals with the unbalanced design across sites that varied from five to 242 transects (mean ± ep = 29.8 ± 2.7). We used non-metric Multidimensional Scalings (nMDS) for viewing patterns in site segregation according to locality and geographic region (oceanic islands, north-northeastern reefs and south-southeastern reefs). They were calculated with raw Bray-

Curtis similarity index of sites based on family and functional group data. Pearson´s r was used to assess the influence of different functional groups and families in total biomass. Permutational Multivariate Analysis of Variance (PERMANOVA) was performed to investigate how much of the variance in both functional and family data geographic region could explain. The function *adonis* of the package 'vegan' from the software R was used for this analysis.

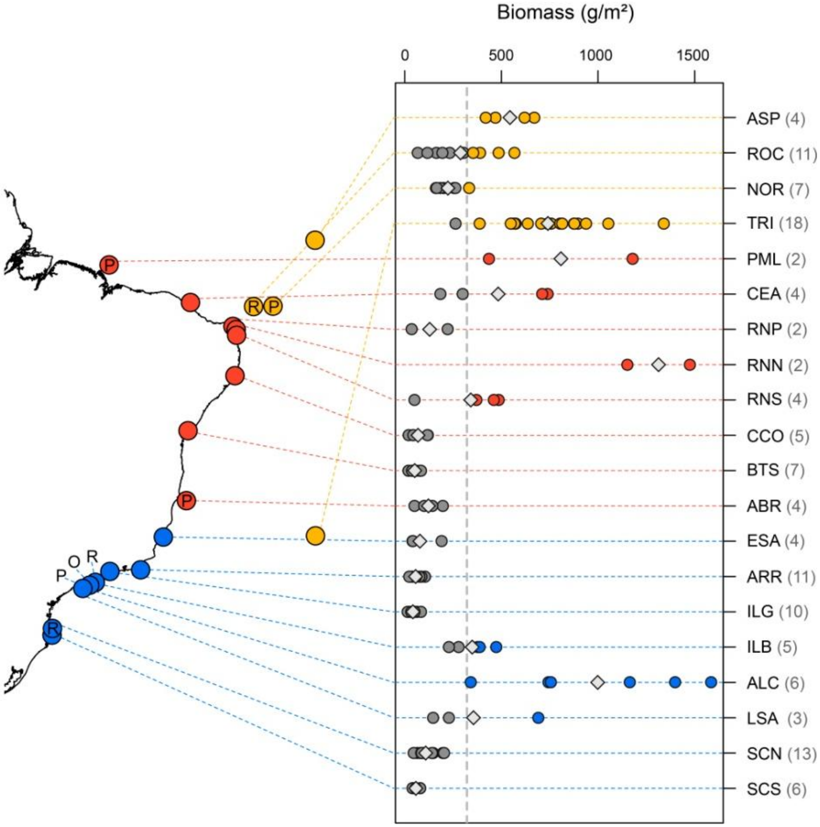
To fit the model, the response variable (standing biomass) values were log+1 transformed so that residuals approximated normal distribution. Correlation of variables was also inspected. Sstmin and sstmean, damean, lnpopdens, fishdens and discoast were all correlated (all $r > 0.6$). This led to the exclusion of most of the explanatory variables, and the full model retained only sstmean, topind, protind and lndiscoast.

A linear mixed-effects model was fitted to the data, with fixed effects comprising the four continuous variables plus functional group (categorical with six levels) and its interaction with protind and lndiscoast. Locality was included as a random effect. In order to compare the relative influence of each variable in the model through its coefficients, all explanatory variables were standardized. Model was fitted using the fast *lmer* function on the 'lme4' package in the software R. The full model was contrasted with two nested competing models: 1) the "environmental model", which included functional group and only the environmental variables (sstmean and topind); and 2) the "human influence model", which included functional group and only the indirect measures of human influence (protind and lndiscoast). These were compared concerning their fit and parsimony through AIC and AIC weight. Ajusted R^2 was calculated as an argument by the function "dredge" and utilizes the formulae proposed by Nagelkerke (1991). For predictions of the final model, coefficients were calculated by model averaging. All these analyses were conducted with the 'MuMIn' package in the R software. Graphical representation of the model was made using two datasets: 1) predicted y-variable values based on measured x-variables´ values (points); and 2) predicted y-variable values based on one x-variable varying and all others being equal to their mean value. This permited evaluation of the influence each variable had at the predicted values of the model. To generate this graphic, model averaged coefficients used to calculate predicted values came from models fitted with untransformed (by standardization) data.

RESULTS

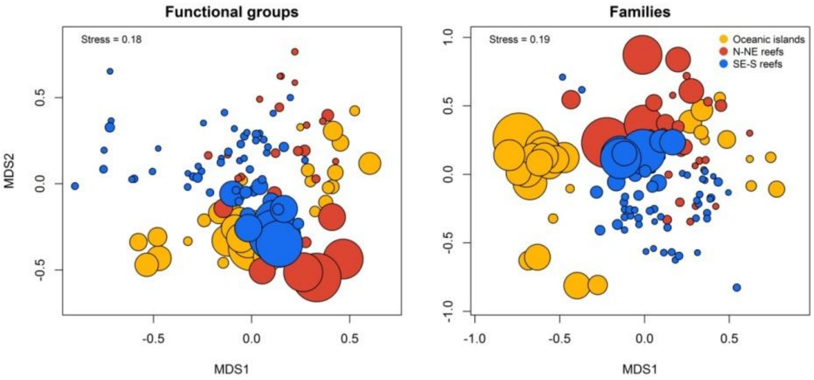
Total standing biomass ranged from 15 to 1585 g/m² in the studied sites, a 100-fold variation. Sites with biomass greater than the overall mean occurred in all three geographic regions (Figure 2, dashed vertical grey line), but were more common in oceanic islands (65% of sites) than in north-northeastern (30% of sites) or south-southeastern reefs (17% of sites). Besides that, there was no consistent pattern in variation of total biomass among geographical region or localities, with variation at the site scale as large as these higher scales. Isolated or protected localities such as Trindade Island (TRI), Manuel Luís Reefs (PML), Northern Natal Reefs (RNN) and Alcatrazes (ALC) had most high biomass sites while low biomass sites were more common in accessible and coastal places such as Arraial do Cabo (ARR), Todos os Santos Bay (BTS), Ilha Grande (ILG) and Coral Coast (CCO).

Figure 2 - Fish biomass of sites in each of the 20 localities sampled at the Southwestern Atlantic. White diamonds indicate the mean biomass of each locality. Grey dashed vertical bar represent the mean biomass for all localities. Grey dots represent sites whose fish biomass is lower than the overall biomass and colored dots sites whose biomass is greater. Of these, yellow, red and blue dots stand for, respectively, oceanic islands, north and northeastern reefs, and south and southeastern reefs. Letters associated with localities in the map indicate if localities contain sites where fishing activities are prohibited, with R = Reserve, P = Park, O = other kind of protection. Numbers in parentheses associated with localities acronyms stand for the number of sites in each locality. Acronyms may be seen in Supplementary Table 1.



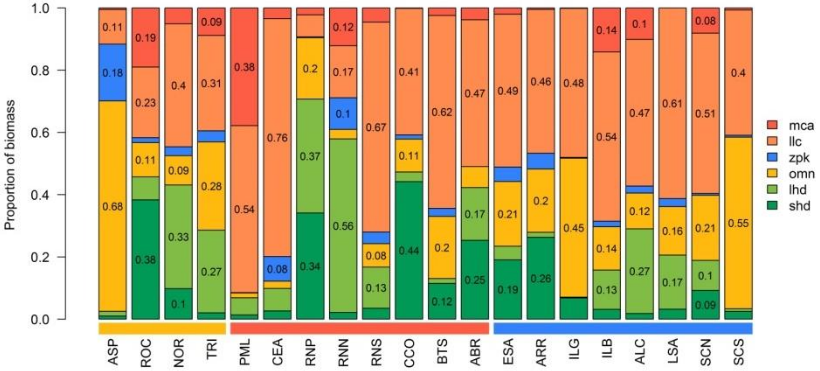
Geographic region explained a small part of the variance in both functional (PERMANOVA $r^2 = 0.18$, $F_{2,127} = 13.48$, $p < 0.001$) and taxonomic (PERMANOVA $r^2 = 0.19$, $F_{2,127} = 15.03$, $p < 0.001$) assemblage structure. Low biomass sites segregated from high biomass sites in both nMDS along the secondary axis (Figure 3) irrespective of the geographic region. Despite that, there is a formation of small subgroups of sites from the same region, probably similar sites from the same locality.

Figure 3 - Non-metric Multidimensional Scaling of functional and taxonomic (family-level) structure in standing biomass of reef fishes from different geographic regions at the Southwestern Atlantic. Circles are proportional to total standing biomass of each site.



A divergent pattern in functional structure is distinguishable between localities (Figure 4). Lower-level carnivores (LLC) were the only functional group that comprised an important fraction of standing biomass in almost all localities, with mean relative contribution of 44%. Omnivores (OMN), large herbivores and detritivores (LHD), and small herbivores and detritivores (SHD) were important in some localities each. OMN were almost absent from north-northeastern reefs such as PML, CEA and RNN, with growing importance towards south-southeastern localities. SHD were mostly important in localities with very shallow reefs surveyed (< 5 m depth) like those in ROC, RNP and CCO. LHD were scarce in some highly fished (like CCO, BTS, ESA, ARR and ILG) localities, but also in isolated (like ASP and PML) and cold waters (SCS), where these fishes seem to be naturally rare. Zooplanktivores (ZPK) and macrocarnivores (MCA) comprised a small part of standing biomass in almost all localities. ZPK were important only at the oceanic island of ASP and the mid-deep (> 16 m depth) reefs of north-eastern coast, CEA and RNN. MCA, similarly to LHD, were rare on localities highly fished, and more important on isolated localities (like PML) or localities with protected sites (like ROC, ILB and ALC).

Figure 4 - Proportional contribution of functional groups to total standing biomass in each sampled locality in the Southwestern Atlantic. Numbers indicate these proportions with only values greater than 0.07 shown. Colored lines above locality names indicate the geographic regions studied. Acronyms may be viewed in Supplementary Tables 1 and 2.



The separate influence of each functional group on the biomass in the scale of sites can be viewed in Figure 5, which is the same nMDS of Figure 3 (left) but plotted proportionally to the biomass of each functional group. Standing biomass of MCA, LHD and LLC are correlated with total standing biomass (all Pearson´s r > 0.68) and moderately correlated with each other (all Pearson´s r > 0.46). These three groups had their biggest standing biomass in specific sites from the three geographical regions, mainly in sites from isolated localities (TRI, PML, RNN) or localities with protected sites (ALC, ILB). SHD, ZPK and OMN were mainly associated with sites in oceanic islands, respectively in sites from ROC, ASP, and ASP and TRI, with some coastal sites also important for these (Figure 4).

The influence of eight of the 10 most important families in terms of standing biomass (except Holocentridae and Lutjanidae) at the site-level is represented in Figure 6, which is the same nMDS of Figure 3 (right) but plotted proportionally to the biomass of each of these families. Standing biomass of Kyphosidae, Labridae and Epinephelidae were correlated with total biomass (all Pearson´s r > 0.67) and moderately correlated with each other (all Person´s r > 0.50). These three families were important in high biomass sites from the oceanic island of TRI, as well as in coastal sites especially from ALC and RNN. Haemulidae and Balistidae were negatively correlated (Pearson´ r = -0.19), the first being important especially in coastal sites and the second only at the oceanic islands of TRI and ASP. Pomacentridae had a spatially wide importance to site-standing biomass, except for some sites at northeastern reefs. Acanthuridae and Pomacanthidae, on the contrary, were important mainly in spatially localized sites, both from ALC and the first also from ROC. Supplementary Figure 1 shows variation patterns of other six important families for the study.

Figure 5 - Non-metric Multidimensional Scaling of functional structure in standing biomass of reef fishes from different geographic regions at the Southwestern Atlantic. In each plot, circles are proportional to the biomass of the referred functional group. Acronyms may be viewed in Supplementary Tables 1 and 2.

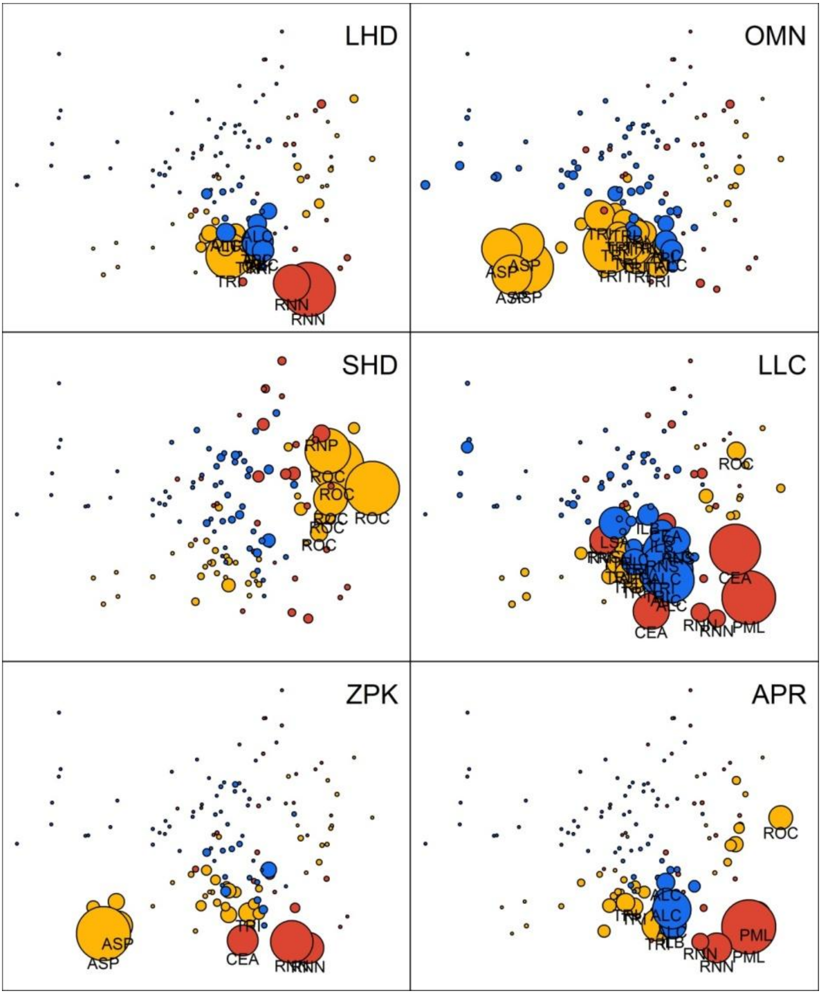
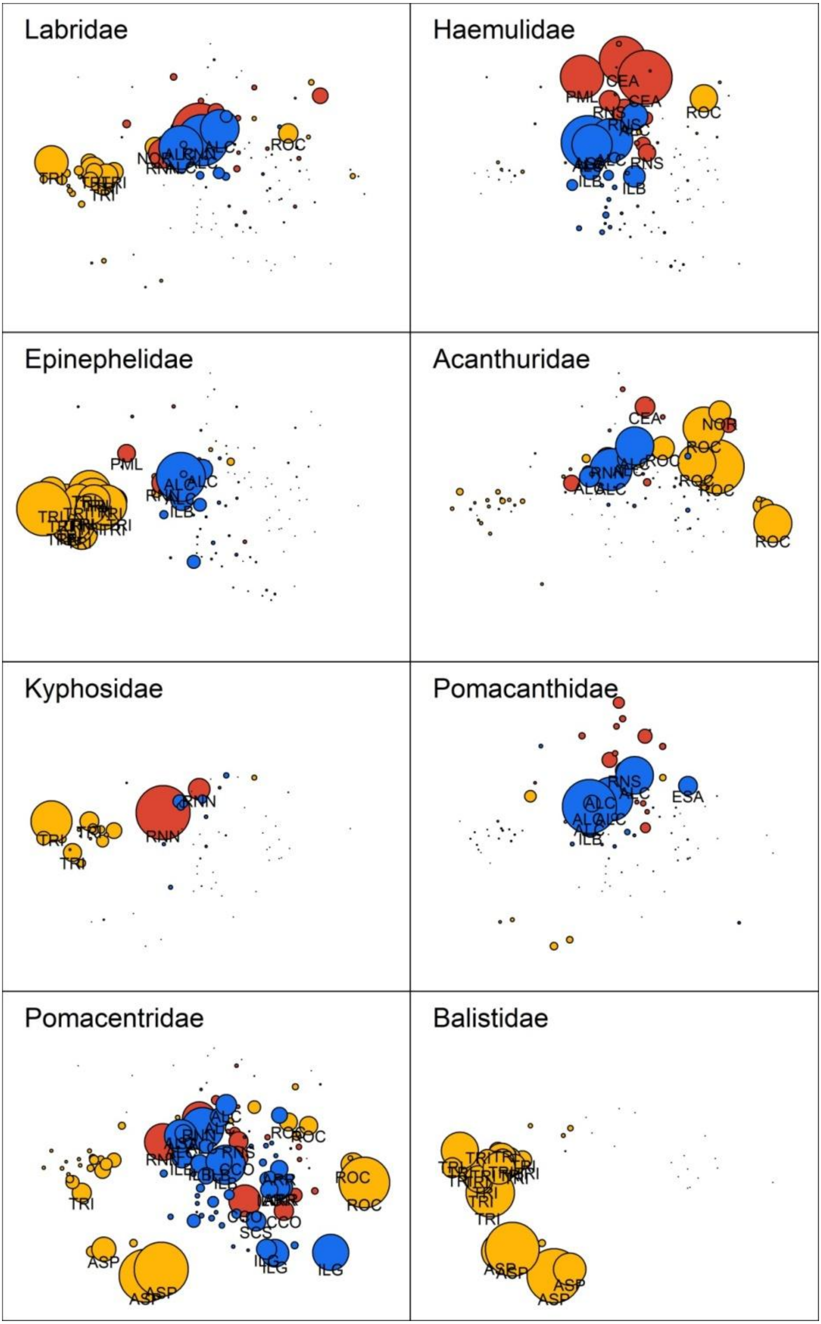


Figure 6- Non-metric Multidimensional Scaling of structure in standing biomass of eight families of reef fishes from different geographic regions at the Southwestern Atlantic. In each plot, circles are proportional to the biomass of the referred family. Acronyms may be viewed in Supplementary Tables 1 and 2.


Labridae
TRI
TRI
NOR
ALC
RNN
ROC
Haemulidae
CEA
PML
CEA
RNS
ROC
ALC
RNS
ILB
ILB
Epinephelidae
PML
ALC
ALC
RNN
ILB
TRI
Acanthuridae
CEA
NOR
ROC
ROC
RNN
ALC
ROC
ROC
ROC
Kyphosidae
RNN
RNN
TRI
TRI
Pomacanthidae
RNS
ALC
ESA
ALC
ILB
Pomacentridae
ALC
ROC
RNN
RNS
ILB
CCO
ROC
ROC
TRI
CCO
SCS
ASP
ILG
ILG
ASP
Balistidae
TRI
TRI
TRI
TRI
ASP
ASP
ASP

The Full model (FM) had the lowest AICc among the three tested models (Table 1), with an Akaike weight of 72%. Despite that, we could not confidently assign it as the best model, since the "human influence" model (HIM) had a ΔAICc of only 1.88 and a weight of 28%. This indicates that indirect variables of human impact (lndiscoast and protind) exerts an important influence in standing biomass of reef fishes along Brazilian coast and oceanic islands. Both models had an adjusted R^2 of more than 0.6 (Table 1), showing that they were capable of explaining most of the observed variance. Environmental variables (topind and sstmean), although present in the full model, added little information to it, revealing a secondary importance in this case. Model averaged coefficients for each parameter can be seen in Supplementary Table 4. Locality explained 31.2% and 29.4% of total random variance, respectively in HIM and FM.

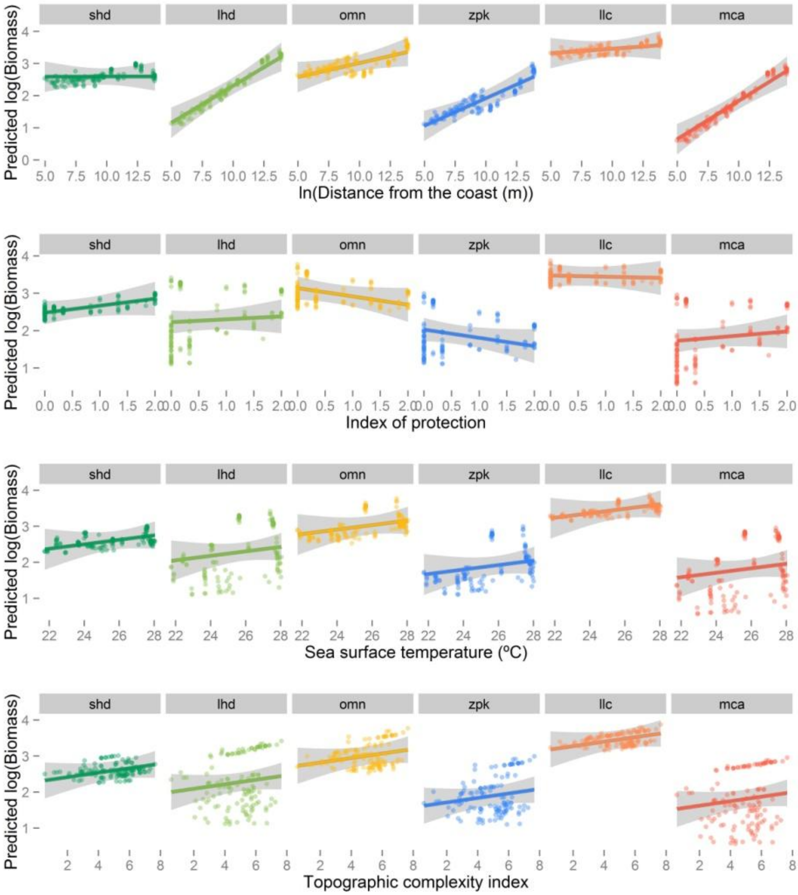
.

Table 1 - Fixed effects´ **c**oefficients of the three models tested regarding the influence of environmental and human-related variables in the standing biomass of reef fishes in the Southwestern Atlantic. Degrees of freedom (df) are proportional to the number of parameters on each model.

Model	**Intercept**	**topind**	**lndiscoast**	**protind**	**sstmean**	**func**	**func : lndiscoast**	**func : protind**	**df**	**Adj R^2**	**AICc**	**ΔAICc**	**weight**
FM	1.8024	0.1243	0.6286	0.1000	0.1696	+	+	+	22	0.609	1845.3	0.00	0.72
HIM	1.8107		0.6935	0.0781		+	+	+	20	0.606	1847.2	1.88	0.28
EM	1.7690	0.1676			0.2679	+			10	0.542	1931.2	85.90	0.00

Slope coefficients of variables protind, sstmean and topind were small (Figure 7, Supplementary Table 4). For both sstmean and topind, a small increase in standing biomass is predicted to occur with increase in these variables. Protind showed interaction with functional group, having a very small positive effect on MCA and SHD, and a small negative effect on OMN and ZPK, with no effect at all in LLC. Lndiscoast was the most influential variable in standing biomass. A high increase in standing biomass of MCA, LHD and ZPK was observed with an increase in this variable, as well as a moderate increase in OMN and almost no increase in LLC and SHD.

Figure 7 - LMM predictions of standing biomass of reef fishes from the Southwestern Atlantic in relation the four explanatory variables composing the full model. Predictions are based on the model averaged coefficients of the three models tested (see text).



DISCUSSION

Spatial variation in reef fish standing biomass

A variety of studies have described the baseline state of tropical reef fish assemblages through samplings in remote locations where the human hand have historically been light (FRIEDLANDER and DEMARTINI 2002, STEVENSON et al. 2007, SANDIN et al. 2008, FRIEDLANDER et al. 2010, 2012, 2014). These studies report high biomass assemblages composed mainly of large predators and/or large herbivores (SANDIN et al. 2008, FRIEDLANDER et al. 2010). Isolation is regarded as a crucial factor for these places to be held pristine or "near-pristine" in a context of generalized human influence all over the globe. The Brazilian Province (BRIGGS 1974, FLOETER and GASPARINI 2001, FLOETER et al. 2008) comprises tropical and subtropical waters of the Southwestern Atlantic Ocean and encompasses a wide range of oceanographic features and human exploitation histories along almost 4500 km of reef habitats, spanning a 28 degrees latitudinal gradient. This variability of conditions is reflected by the hundred-fold fish standing biomass range observed between sites in the present study. Although absolute numbers should not be directly compared between different studies since sampling methods differ, it stands as the greatest biomass gradient reported to date by one study (FRIEDLANDER and DEMARTINI 2002, GARCÍA-CHARTON et al. 2004, NEWMAN et al. 2006, SANDIN et al. 2008, WILLIAMS et al. 2010, SALA et al. 2011), similar to the range of variation found at the Mediterranean (GARCÍA-CHARTON et al. 2004, SALA et al. 2011).

Compared to other places around the world, Brazilian reef fish fauna remained largely unknown until SCUBA became popular among scientists by the early and mid 1990´s (FERREIRA et al. 1995, ROSA and MOURA 1997, FERREIRA et al. 1998, ROCHA et al. 1998). As recently as the beginning of the 21st century some regions were still completely unexplored (CASTRO and PIRES 2001) and patterns in reef fish assemblages are still being described (FERREIRA et al. 2004, FLOETER et al. 2007A, KRAJEWSKI and FLOETER 2010, PINHEIRO et al. 2011, GIBRAN and MOURA 2012). The present study shows that isolation, as an indirect measure of human impact, is a strong factor shaping these assemblages also through Brazilian Province. Isolated localities such as Trindade Island, Saint Paul´s Rocks, Rocas Atoll and Manuel Luís Reefs all comprised sites with high total biomass.

Despite of this strong influence of isolation on standing biomass, some of the sites with the highest biomass in this study were located near the coast (Figure 2). Sites from Alcatrazes and Northern Natal Reefs presented biomass values ranging between 700 and 1500 g/m² albeit being relatively accessible. These sites have been partially protected from human influences due to factors others than isolation that act at regional and local scales. Alcatrazes is a rocky archipelago located 32 km from southeastern Brazilian coast in the state of São Paulo. Despite being next to the most populous city in Latin America (São Paulo) and the greatest density of boats from Brazil, it has been protected for military purposes. Since 1982 the Brazilian Navy has declared it a delta area where boat traffic and fishing is prohibited (KODJA et al. 2012). This side-effect protection for more than 30 years has resulted in high fish standing biomass, 400% greater than other rocky island at a similar distance from the coast at the same region (e.g. Búzios Island) not subjected to such prohibitions. Northern Natal Reefs comprised two sites located 15 and 17 km from the coast, in depths ranging from 14 to 22 m. These reefs, despite their small size and relatively shallow depths, are located next to oceanic waters in a region that hosts a mosaic of unmapped submerged reefs known only to fishermen (TESTA 1997, CASTRO and PIRES 2001). Presently there is no estimate of these reefs´ spatial extent, but evidences from local fishermen reveal they might occupy a considerable reef area. A better knowledge of oceanographic and biological features of Northern Natal reefs is needed in order to better comprehend the reasons of this high fish biomass. One hypothesis we raise is that the abundance of reef area associated with the fact that fishing on the region have historically depended on small sailing vessels (named "jangadas") might have deterred depletion of fishing stocks from some of these sites.

Functional and taxonomic patterns of standing biomass

Recent studies have claimed pristine fish assemblages to hold inverted biomass pyramids, in the way that top predators compose more standing biomass than lower trophic levels (SANDIN et al. 2008, FRIEDLANDER et al. 2010). As energy flows through ecosystems, losses in each trophic level result in energetic content decreasing with trophic level increase. For steady state systems this energetic content is proportional to standing biomass (ODUM and ODUM 1955), which we might expect to diminish from herbivores to macrocarnivores. Inverted pyramids may occur in "subsided communities", where larger consumers have access to external sources of production that smaller ones have not (TREBILCO et al. 2013). In the present study, no fish assemblage was characterized by such inverted biomass pyramid, with only one site presenting more than 40% of standing biomass by macrocarnivores and nine out of 128 with more than 25%.

Overall macrocarnivores´ (MCA), large herbivores and detritivores´ (LHD) and lower-level carnivores´ (LLC) standing biomass were correlated with total standing biomass (Figures 3 and 5). In special, MCA and LHD biomass was high almost only on high biomass sites. These groups include target fishes like sharks, groupers, jacks and parrotfishes and are the first ones to disappear in heavily fished reef areas (FRIEDLANDER and DEMARTINI 2002). High biomass of these predators was again only found at isolated and/or protected sites. Among these fishes, sharks are probably the most sensible to fishing (FERRETTI et al. 2008, FERRETTI et al. 2010) as even small scale fisheries in isolated areas may seriously deplete their stocks (FERRETTI et al. 2010, GRAHAM et al. 2010, LUIZ and EDWARDS 2011). In most surveyed sites, sharks were simply not found. Nurse sharks (*Ginglymostoma cirratum*) occurred in some coastal north-northeastern sites from Ceará and Southern Natal Reefs, as well as on the oceanic islands. Other sharks were common at Rocas Atoll, could occasionally be observed at the oceanic islands of Trindade and Fernando de Noronha and completely absent from Saint Paul´s Rocks. The islands of Trindade and Saint Paul´s Rocks are the most isolated Brazilian islands and were historically known for the unusual abundance of sharks in the past centuries (NICHOLS and MURPHY 1914, LOBO 1919, EDWARDS and LUBBOCK 1982, LUIZ and EDWARDS 2011). Longline fishing has decimated shark populations of Trindade (PINHEIRO et al. 2010, PINHEIRO et al. 2011), mainly composed of the Caribbean reef shark, *Carcharhinus perezii*, to the extent that they are only occasionally seen today. At Saint Paul´s Rocks the situation is even worse. A resident population of the Galapagos shark, *Carcharhinus galapagensis*, is considered to have become extinct due to fishing undertaken in the last 50 years (LUIZ and EDWARDS 2011). This is in stark contrast to the situation of the Rocas Atoll. In 1978, this reef and surrounding waters up to 1000 m deep were declared a Marine Reserve. Although illegal fishing has occurred for some time, it has declined sharply in recent years as a result of enforcement improvement. Isolated from other fishing grounds, it comprises a nursery and development area for three shark species: the nurse shark (CASTRO et al. 2005), the Caribbean reef shark (GARLA et al. 2006), and the Lemon shark, *Negaprion brevirostris* (FREITAS et al. 2006, WETHERBEE et al. 2007). Sighting these sharks is very common especially at the northeastern channel where they concentrate possibly to feed.

Groupers (Epinephelidae), snappers (Lutjanidae) and jacks (Carangidae) are important top predators in tropical reefs, and may be abundant even in communities where sharks are rare or have been decimated (ABURTO-OROPEZA et al. 2011, FRIEDLANDER et al. 2014). In the present study, most sites had depleted assemblages of these fishes (Figure 6, Supplementary Figure 1). Exceptions were, again, isolated localities such as Manuel Luís Reefs and Trindade, and the protected Alcatrazes archipelago (Figure 6). At these places, epinephelids were still abundant and sometimes large in size. Manuel Luís Reefs were the only sampled sites where the gigantic goliath grouper (*Epinephelus itajara*) was frequently observed. This species was common in coastal reefs from places such as Arraial do Cabo and Santa Catarina by the 1950´s (SOUZA 2000), but have been extensively fished and is now rarely seen. At Trindade island, historical reports account for the abundance, size and facility of capturing large groupers of "more than 40 kg" (LOBO 1919, MIRANDA-RIBEIRO 1919). These large specimens were probably the Warsaw grouper, *Hyporthodus nigritus*, and the yellowfin grouper, *Mycteroperca venenosa*, both species extremely rare today in shallow reefs around the island, but still captured by fishing vessels in deeper waters (PINHEIRO et al. 2010). The rock hind (*Epinephelus adscensionis*) is the most common apex predator today, still abundant in shallow depths but threatened by the constant capture by fishing vessels and recreational fishers on the island (PINHEIRO and GASPARINI 2009, PINHEIRO et al. 2010). At Alcatrazes archipelago, dusky groupers (*Epinephelus marginatus*) of >70 cm TL can be commonly observed hiding at the rocks. These fishes are characteristic of south-southeastern Brazilian rocky reefs but have been heavily targeted by line and hook and spearfishing almost everywhere (SOUZA 2000, BEGOSSI and SILVANO 2008). Large snappers were mainly represented by the dog snapper (*Lutjanus jocu*), which attained high biomass in sites from Rocas Atoll and Manuel Luís Reefs (Supplementary Figure 1). In both places, aggregations of tens of these fishes can be found, some attaining up to 90 cm TL. There was no evidence of sexual activity during these aggregations and we believe it might be a common behavior of the species in isolated and protected places. Schools were impressive near shipwrecks of Manuel Luís Reefs, easily surpassing the biomass of smaller carnivores. Large shoals of jacks from the genus *Caranx* as observed in Pacific reefs (FRIEDLANDER and DEMARTINI 2002, ABURTO-OROPEZA et al. 2011) were rare even on high biomass sites. Smaller groups of large *Seriola* spp. however, were common at some sites from Alcatrazes, Ilhabela, Northern Santa Catarina and Trindade (Supplementary Figure

1), probably related to the schools of prey (sardines and anchovies) that regularly approach reefs at these localities.

Despite the low proportion of top predators in most of the study sites, some protected places such as Abrolhos islands and Fernando de Noronha stood out as negative surprises. Both are located far from the coast and include National Parks in ts boundaries with fishing prohibition since the decade of 1980. This way, it would be expected that, if protection was effective, sites from these localities contained high total and apex predator biomass, but we observed the opposite (Figure 1, Figure 5). In fact, enforcement seems not to be adequate in these parks and illegal fishing is known to occur, especially at Abrolhos´s submerged reefs and islands (DUTRA et al. 2005). Other study have reported comparable levels of total fish biomass in other "protected" and "unprotected" reefs from the bank of Abrolhos (BRUCE et al. 2012) meaning that such low values are not exclusive of the sites investigated here. Biomass of apex predators was not provided for comparison. At Fernando de Noronha, park area include 70% of the island area and marine habitats to the isobath of 50m. Outside of these limits fishing is allowed and has historically occurred, aiming especially for predators (KRAJEWSKI and FLOETER 2011), INCLUDING FOR SHARKS (GARLA et al. 2006). Krajewski and Floeter (2011) report also low predator biomass and comment on anedoctal acounts of old spearfishers of abundant sharks and large groupers from 40 years ago that are nowadays rarely seen.

The absence of apex predators in reefs is predicted to result in trophic cascades with ecosystem-wide effects (ESTES et al. 2011), such as changes in behavior and abundance of prey (HEITHAUS et al. 2008, RUTTENBERG et al. 2011). Patterns consistent with changes in prey abundance following trophic cascades have been shown for Tropical Eastern Pacific (EDGAR et al. 2011), but causal relationships are still controversial (HEITHAUS et al. 2008). In this study lower-level carnivores, as expected, contributed mostly to standing biomass in almost all sites and localities (Figures 4 and 5), although this could not be assigned to derive from trophic cascades. These generalist or specialist small-sized carnivores include fishes from a diverse set of families (e.g. Haemulidae, Labridae, Holocentridae, Lutjanidae and Mullidae), and are known to dominate temperate and tropical reefs all over the world (JONES et al. 1991, WAINWRIGHT and BELLWOOD 2002, FERREIRA et al. 2004), linking the productive algal turfs to higher trophic levels (JONES et al. 1991, KRAMER et al. 2013). Despite generalized importance of the group, there was considerable geographical variation at the family level, being worth noting: 1) the small importance of the genus *Haemulon* at oceanic islands compared to coastal sites; and 2) of lutjanids in south-southeastern sites compared to north-northeastern sites. Species from the genus *Haemulon* comprise a great part of the biomass of LLC in coastal sites, especially the Tomtate grunt (*Haemulon aurolineatum*) and the yellowstripped grunt (*H. squamipinna*), which formed schools of thousands of individuals in some sites. The smallmouth grunt (*Haemulon chrysargyreum*) is the sole species of the genus in Brazilian oceanic islands, occurring only in Fernando de Noronha and Rocas Atoll (FERREIRA et al. 2004, PINHEIRO et al. 2011). Even at these localities, however, it is restricted to specific sites (Figure 6). Small and medium-sized snappers are very abundant and compose most of the catches from north-northeastern Brazil (FRÉDOU et al. 2006), but are of small importance to south-southeastern fisheries (VASCONCELLOS and GASALLA 2001). Moreover, these fishes are rare on rocky reefs from this region (FERREIRA et al. 2001, FLOETER et al 2007, GIBRAN and MOURA 2012) probably because of their affinity for tropical waters, a pattern already noted by Ferreira et al. (2004).

Similar to benthic carnivores, zooplanktivorous fishes link reefs to an important source of production: the pelagic environment. This external production may be abundant, resulting in a considerable input in nutrient and energy to reef ecosystems both by planktivores´ faeces and predation by piscivores (HOBSON 1991). This linking, however, may vary not only with planktonic production, but also with water flux and transparency (HOBSON 1991, JOHANSEN and JONES 2013). This occurs because these organisms are visually oriented and turbidity is known to exert a major influence on their capacity to successfully capture prey (JOHANSEN and JONES 2013). Therefore, it is expected them to increase in importance from coastal to oceanic habitats following a reduction on water suspended particles (FERREIRA et al. 2004). In Brazilian reefs, overall, zooplanktivores composed a small part of standing biomass, even at the oceanic islands (Figure 4). In only a few sites from Saint Paul´s Rocks, Ceará, Northern Natal Reefs and Arraial do Cabo these fishes attained more than 10% of total standing biomass. Overall richness of zooplanktivores in Brazilian reefs is small and standing biomass seem to be similar to or even smaller than for Caribbean reefs (NEWMAN et al. 2006). This contrasts to some Indo-Pacific reefs where zooplanktivores attain higher importance (BELLWOOD et al. 2004, WILLIAMS et al. 2011).

Forming the basis of reef energetic pathways, primary consumers have to deal with low-caloric, frequently hard-to-digest and toxic food sources (CHOAT 1991, HARMELIN-VIVIEN 2002). Although historically regarded simply as "herbivores", it is clear today that most of these reef fishes rely on detritus, sediment, microorganisms, and animal matter at varying degrees for their nutrition (CHOAT 1991, CHOAT et al. 2002, CROSSMAN et al. 2005). They are expected to constitute most of reef fish standing biomass, with some lineages large in size largely affected by fishing (CHOAT 1991, BELLWOOD et al. 2012).

Omnivores were most important in oceanic islands and high latitude coastal sites (Figures 4 and 5) predominated, respectively by Balistidae, and Pomacanthidae and Sparidae (Figure 6 and Supplementary Figure 1). The black triggerfish (*Melichthys niger*) is a circumtropical feeding generalist species that reaches remarkable densities in some remote islands around the world (Kavanagh and Olney 2006). It has long been known to dominate fish assemblages of mid-Atlantic oceanic islands, including Trindade and Saint Paul´s Rocks (LOBO 1919, LUBBOCK 1980, FEITOZA et al. 2003, PINHEIRO et al. 2011). At these islands swarms of these fishes sustain high standing biomass and feed from almost everything, from benthic algae to other injured fishes (LOBO 1919, GASPARINI and FLOETER 2001). In coastal sites, omnivore importance was greater in south-southeastern sites (Figures 4 and 5), similar to the observed by Ferreira et al. (2004). The silver porgy *Diplodus argenteus* (Sparidae) and the french angelfish *Pomacanthus paru* (Pomacanthidae) were the most important contributors to this pattern. The silver porgy changes its diet according to season, consuming algae during summer and preferentially animal matter during the winter (DUBIASKI-SILVA and MASUNARI 2006). The last species attained unusually high densities and size at the protected Alcatrazes archipelago.

Large herbivores and detritivores were found in high biomass in sites from Trindade island, Alcatrazes and Northern Natal Reefs (Figure 4). These include principally large parrotfishes (Scarinae labrids) and chubs (Kyphosidae) known to perform crucial ecosystem functions on Indo-Pacific and Caribbean reefs (GREEN and BELLWOOD 2009, MUMBY 2009, BURKEPILE and HAY 2011, BELLWOOD et al. 2012). Parrotfishes, for example, prevent the growth of algae that smother corals and participate actively on these reefs´ calcium carbonate cycle (BELLWOOD et al. 2006, BELLWOOD et al. 2012, VERGÉS et al. 2012). These fishes are important target species including for

Brazilian coastal sites (FLOETER et al. 2007b, EDWARDS et al. 2014). On the protected rocky reefs of Alcatrazes islands, *Sparisoma* species, especially *S. frondosum* and *S. axillare,* attained impressive sizes of up to 55 and 65 cm TL respectively, the probable upper limit for these species. The reef parrotfish, *Sparisoma amplum* is the largest species of its genus and attained high biomass on Fernando de Noronha and Trindade islands. Especially in Trindade groupings of up to 12 terminal males could be observed and individuals sometimes attained 70 cm TL. The greenback parrotfish, *Scarus trispinosus* is the largest Brazilian parrotfish and was known to form huge schools of tens of adults in the past, but has been heavily fished on recent decades (FLOETER et al. 2007b). In the present study huge schools were observed nowhere and small groups occurred at some sites from Abrolhos, Maracajaú reef (RNP) and Manuel Luís Reefs, but only in the last seemed to be relatively unafraid of the human presence. Contrary to parrotfishes, kyphosids are avoided by Brazilian fishermen as one of its common names ("Maria-cagona") suggests. Although huge schools of large individuals were found at Trindade island and Northern Natal Reefs, their presence should not be attributable directly to low fishing levels. Species from the genus *Kyphosus* are known to aggregate to feed on exposed places subject to high hydrodynamics (FLOETER et al. 2007a) where they browse pieces of macroalgae (GREEN and BELLWOOD 2009). Therefore, its huge biomass at the referred sites might be an indicative of exposure and hydrodinamics rather than fishing. Contrary to Ferreira et al. (2004) we found no latitudinal trend for this group.

Small herbivores and detritivores were especially important in some sites from Rocas Atoll (Figure 5), where small surgeonfishes *Acanthurus chirurgus* formed large flocks of hundreds of individuals. Pomacentrids from the genus *Stegastes* were the most common SHD, but had small importance to standing biomass given their small sizes. This group was consistent throughout most of Brazilian Province, and seemed to be constrained only at the edge of tropical fish fauna distribution in Southern Santa Catarina. At this locality they were functionally absent, a probable response to physiological constraints (FERREIRA et al. 2004).

Variables affecting total and functional standing biomass at the larger scale

Model selection confirmed our hypothesis that human-related variables would better predict geographic variation in reef fish standing biomass at the investigated spatial scales. Environmental variables (topographic complexity and sea surface temperature) added little information to geographic variation in reef fish assemblages at this scale, while human-influence variables were central to the predictive model. Both variables (distance from the coast and level of protection) stand as proxies for and capture different facets of fishing activities. Numerous studies have arguably shown that reef fishes are dependent upon their environment (e.g. ROBERTS and ORMOND 1987, CHABANET et al. 1997, FRIEDLANDER and PARRISH 1998). But fishing has been so pervasive at marine ecosystems that it has at the same time homogeneized fish assemblages´ biomass where it has acted, and made them completely distinct from least disturbed ones (FRIEDLANDER and DEMARTINI 2002, SANDIN et al. 2008, WILLIAMS et al. 2011). Large scale historical changes similar to those recorded for Caribbean and Pacific marine communities (JACKSON 1997, JACKSON et al. 2001, ROBERTS 2007, ESTES et al. 2011) have also happened to some degree in Brazilian reefs (e.g. SOUZA 2000, LUIZ and EDWARDS 2011). These changes, as reported by a lot of studies, affect disproportionally predators and large-bodied species (e.g. PAULY et al. 1998, ESTES et al. 2011). In our model, the distance from the coast was a particularly informative variable, and scaled positively with biomass for large bodied functional groups (large herbivores and detritivores and macrocarnivores, Figure 7), but not for smaller-sized ones. All this leads us to conclude that for Brazilian Province, fishing is the most important factor shaping large-bodied and shoaling species that compose most of the biomass of reef fishes.

Concluding remarks and recommendations

The standing biomass of Brazilian fish assemblages have diminished due to intense fishing, especially in coastal sites, including more than 50 years of spearfishing and even dynamite fishing. As a result, apex predators are extremely reduced and total biomass is low all over coastal sites. Exceptions on Brazilian Province are a few isolated and/or protected localities. Alcatrazes, Manuel Luís Reefs and Northern Natal Reefs were localities that contained sites with both high total and apex predator biomass. Atol das Rocas, despite having relatively low total biomass hosted sites with the biggest proportion of top predators, and low biomass might be caused by other factors. Some isolated reefs historically known for the abundance of fishes, mainly Trindade and

Saint Paul´s Rocks, despite sustaining high biomass assemblages, presently comprise few apex predators and especially the generalist omnivore black triggerfish *Melychthis niger*. In the particular case of Trindade predators are still occasionaly seen and the potential of recovery could still exist, albeit the situation seems to be worse for Saint Paul´s Rocks. Finally, Abrolhos and Fernando de Noronha are places theoretically protected by no-take MPAs that, however, lack enforcement and/or have suffered with historical fisheries. They held low total and apex predator biomass, especially Abrolhos, and is clear that in the absence of enforcement improvement they have limited capacity of protecting large-bodied fish assemblages.

As a signatory of the Convention on Biological Diversity (CDB 2010) Brazil assumed the compromise to effectively protect 10% of its marine ecosystems until 2020. As of the year 2014, however, our situation is very far from it. Only 0.14% of our Economic Exclusive Zone is located inside marine reserves (MMA 2010), and only a small part of this reduced percentage is effectively protected through enforcement. Our study might contribute to improvement of marine resources management both by pointing out marine reserves that lack efectivity for improvement, and places that still carry functional fish assemblages with conserved characteristics that are threatened by large-scale unregulated fishing.

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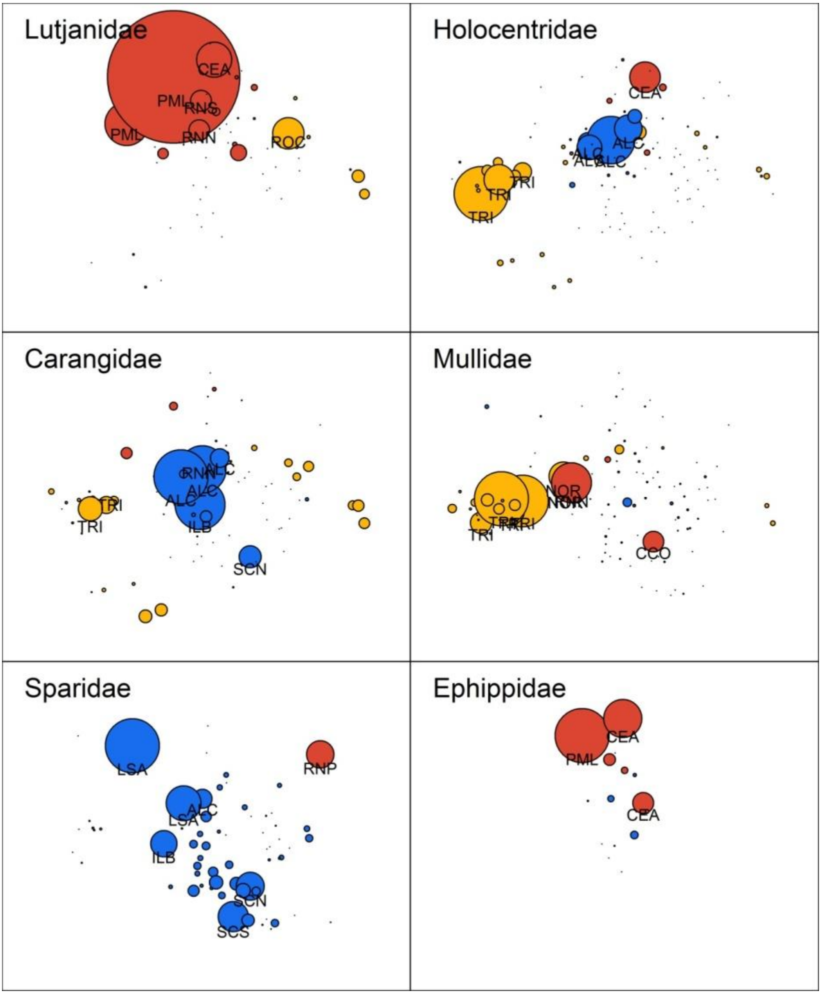
SUPPLEMENTARY MATERIAL

Supplementary Figure 1 - Non-metric Multidimensional Scaling of structure in standing biomass of six families of reef fishes from different geographic regions at the Southwestern Atlantic. In each plot, circles are proportional to biomass of the referred family. Acronyms may be viewed in Supplementary Tables 1 and 2.



Supplementary Table 1 -Geographic coordinates and number of samples (n) in each site from each locality sampled in Southwestern Atlantic Ocean.

Acronym	Locality	Site	Longitude	Latitude	n
ASP	Saint Pauls Rocks	Bóia	-29.3466	0.9175	11
ASP	Saint Pauls Rocks	Cabeço da tartaruga	-29.3455	0.9160	15
ASP	Saint Pauls Rocks	Enseada	-29.3455	0.9171	149
ASP	Saint Pauls Rocks	Ilha de São Pedro outside	-29.3450	0.9179	24
ROC	Rocas Atoll	Piscina das âncoras	-33.8036	-3.8752	17
ROC	Rocas Atoll	Barretinha	-33.8181	-3.8597	5
ROC	Rocas Atoll	Piscina do cemitério	-33.8178	-3.8666	25
ROC	Rocas Atoll	Falsa Barreta	-33.8188	-3.8604	5
ROC	Rocas Atoll	Laguna	-33.7938	-3.8622	23
ROC	Rocas Atoll	Piscina das rocas	-33.7919	-3.8690	20
ROC	Rocas Atoll	Podes Crer	-33.8123	-3.8730	8
ROC	Rocas Atoll	Poita do Zeca	-33.8206	-3.8579	21
ROC	Rocas Atoll	Salão	-33.8094	-3.8747	6
ROC	Rocas Atoll	Piscina das tartarugas	-33.8094	-3.8730	20

Acronym	Locality	Site	Longitude	Latitude	n
ROC	Rocas Atoll	Piscina da Zulú	-33.7985	-3.8729	6
NOR	Fernando de Noronha	Cagarras	-32.3902	-3.8146	12
NOR	Fernando de Noronha	Canal	-32.3906	-3.8172	12
NOR	Fernando de Noronha	Praia da Conceição	-32.4150	-3.8390	23
NOR	Fernando de Noronha	Laje dos dois irmãos	-32.4406	-3.8465	10
NOR	Fernando de Noronha	Buraco da Raquel	-32.3948	-3.8344	10
NOR	Fernando de Noronha	Praia do Sancho	-32.4460	-3.8544	18
NOR	Fernando de Noronha	Baía do Sueste	-32.4228	-3.8668	7
TRI	Trindade and Martin Vaz	Praia das Cabritas	-29.3296	-20.4920	37
TRI	Trindade and Martin Vaz	Calheta	-29.3103	-20.5075	68
TRI	Trindade and Martin Vaz	Crista do galo	-29.3330	-20.4882	16
TRI	Trindade and Martin Vaz	Eme	-29.3406	-20.5146	33
TRI	Trindade and Martin Vaz	Farilhões	-29.4979	-20.5226	16
TRI	Trindade and Martin Vaz	Farol	-29.3210	-20.4990	28
TRI	Trindade and Martin Vaz	Lixo	-29.3206	-20.5248	45
TRI	Trindade and Martin Vaz	Martin Vaz west	-28.8568	-20.4741	5
TRI	Trindade and Martin Vaz	Monumento	-29.3443	-20.5028	23
TRI	Trindade and Martin Vaz	Orelhas	-29.3431	-20.4925	37

Acronym	Locality	Site	Longitude	Latitude	n
TRI	Trindade and Martin Vaz	Parcel das tartarugas	-29.2982	-20.5177	7
TRI	Trindade and Martin Vaz	Paredão do Túnel	-29.3046	-20.5276	11
TRI	Trindade and Martin Vaz	Pedra da Naja Monumento	-29.3449	-20.5001	46
TRI	Trindade and Martin Vaz	Ponta Norte	-29.3386	-20.4886	26
TRI	Trindade and Martin Vaz	Ilha da Racha	-29.3483	-20.5072	5
TRI	Trindade and Martin Vaz	Naufrágio Shing	-29.3174	-20.5049	54
TRI	Trindade and Martin Vaz	Praia das tartarugas	-29.3010	-20.5171	28
TRI	Trindade and Martin Vaz	Túnel	-29.3011	-20.5278	17
MLU	Manuel Luís Reefs	Naufrágio Ana Cristina	-44.2643	-0.8699	62
MLU	Manuel Luís Reefs	Naufrágio Basil	-44.2790	-0.8703	22
CEA	Ceará Coast	Cabeço do arrastado	-38.3917	-3.5981	11
CEA	Ceará Coast	Pedra da Risca do Meio	-38.4084	-3.5683	11
CEA	Ceará Coast	Pedra do Mar	-38.3808	-3.5736	11
CEA	Ceará Coast	Pedra do Paraíso	-38.3718	-3.5990	10
RNP	Parrachos do RN	Parrachos de Maracajaú	-35.2590	-5.3941	30
RNP	Parrachos do RN	Parrachos de Rio do Fogo	-35.3634	-5.2621	17
RNN	Northern Natal Reefs	Batente das Agulhas	-35.0725	-5.5644	17
RNN	Northern Natal Reefs	Pedra do Silva	-35.0901	-5.5645	24

Acronym	Locality	Site	Longitude	Latitude	n
RNS	Southern Natal Reefs	Barreirinha	-35.0393	-5.9562	25
RNS	Southern Natal Reefs	Cabeço do Leandro	-35.0372	-5.9500	17
RNS	Southern Natal Reefs	Mestre Vicente	-35.0344	-6.0007	14
RNS	Southern Natal Reefs	Parrachos de Pirangi	-35.1095	-5.9808	30
CCO	Coral Coast	Barra da Galé	-35.1927	-9.0327	10
CCO	Coral Coast	Galés	-35.1915	-9.0243	6
CCO	Coral Coast	Ilha do Meio	-35.0877	-8.7618	11
CCO	Coral Coast	Perua Preta	-35.0887	-8.7252	10
CCO	Coral Coast	Taocas	-35.1806	-8.9985	10
BTS	Todos os Santos Bay	Dentão	-38.5253	-12.8335	20
BTS	Todos os Santos Bay	Farol da Barra	-38.5308	-13.0083	11
BTS	Todos os Santos Bay	Ilha dos Frades	-38.6264	-12.8092	76
BTS	Todos os Santos Bay	Naufrágio Blackader	-38.5111	-12.9386	34
BTS	Todos os Santos Bay	Pedra Alva	-38.5290	-12.8700	31
BTS	Todos os Santos Bay	Pedra Cardinal	-38.5491	-12.8371	45
BTS	Todos os Santos Bay	Poste Quatro	-38.5717	-12.8147	12
ABR	Abrolhos	Chapeirão	-38.6625	-17.9628	44
ABR	Abrolhos	Mato Verde	-38.6953	-17.9647	25

Acronym	Locality	Site	Longitude	Latitude	n
ABR	Abrolhos	Portinho Norte	-38.6978	-17.9614	50
ABR	Abrolhos	Ilha da Siriba	-38.7158	-17.9706	45
ESA	Espírito Santo	Escalvada	-40.4076	-20.6996	242
ESA	Espírito Santo	Ilhas Rasas	-40.3662	-20.6766	11
ESA	Espírito Santo	Itatiaia	-40.2784	-20.3632	39
ESA	Espírito Santo	Três Ilhas	-40.3788	-20.6124	71
ARR	Arraial do Cabo	Saco do Anequim	-41.9845	-22.9805	90
ARR	Arraial do Cabo	Boqueirão	-42.0131	-22.9979	64
ARR	Arraial do Cabo	Cardeiros	-42.0017	-22.9651	20
ARR	Arraial do Cabo	Maramutá	-41.9988	-22.9911	63
ARR	Arraial do Cabo	Paredão	-42.0069	-23.0101	29
ARR	Arraial do Cabo	Pedra Vermelha	-41.9926	-22.9863	61
ARR	Arraial do Cabo	Ilha dos Porcos west	-41.9937	-22.9657	87
ARR	Arraial do Cabo	Ilha dos Porcos south	-41.9942	-22.9684	67
ARR	Arraial do Cabo	Ponta da Água	-42.0041	-22.9699	64
ARR	Arraial do Cabo	Ponta Leste	-41.9798	-22.9782	63
ARR	Arraial do Cabo	Saco dos Ingleses	-42.0080	-23.0064	46
ILG	Ilha Grande	Enseada do Itapinhoacanga	-44.2138	-23.0469	5

Acronym	Locality	Site	Longitude	Latitude	n
ILG	Ilha Grande	Ilha de Macacos	-44.2247	-23.0786	5
ILG	Ilha Grande	Ilha dos Arrependidos	-44.1400	-23.0434	6
ILG	Ilha Grande	Ilha Itacuatiba	-44.2533	-23.0700	9
ILG	Ilha Grande	Ponta Acaia	-44.3727	-23.1673	18
ILG	Ilha Grande	Ponta da Enseada	-44.1907	-23.1020	6
ILG	Ilha Grande	Gipoia Ponta Escalvada	-44.3789	-23.0319	5
ILG	Ilha Grande	Ponta Grossa de Sitio Forte	-44.2970	-23.1133	5
ILG	Ilha Grande	Abraão Praia dos Morcegos	-44.1477	-23.1246	5
ILG	Ilha Grande	Saco dos Castelhanos	-44.0990	-23.1638	6
ILB	Ilhabela	Ilha das Cabras	-45.3939	-23.8303	20
ILB	Ilhabela	Ilha dos Búzios Saco do Urubú	-45.1581	-23.8058	21
ILB	Ilhabela	Ponta da Enchova	-45.3363	-23.9201	24
ILB	Ilhabela	Saco do Diogo	-45.2836	-23.9354	20
ILB	Ilhabela	Saco do Sombrio	-45.2440	-23.8933	21
ALC	Alcatrazes	Ilha do Farol	-45.7027	-24.0959	10
ALC	Alcatrazes	Portinho center	-45.6981	-24.1002	15
ALC	Alcatrazes	Portinho northwest	-45.6933	-24.0958	10
ALC	Alcatrazes	Portinho southwest	-45.7025	-24.1052	10

Acronym	Locality	Site	Longitude	Latitude	n
ALC	Alcatrazes	Saco do Funil	-45.6885	-24.0978	10
ALC	Alcatrazes	Saco do Oratório	-45.7059	-24.1101	12
LSA	Laje de Santos	Âncoras	-46.1762	-24.3168	10
LSA	Laje de Santos	Ponta Leste	-46.1762	-24.3168	19
LSA	Laje de Santos	Portinho	-46.1762	-24.3168	75
SCN	Northern Santa Catarina	Arvoredo Baía da Tartaruga	-48.3638	-27.2906	47
SCN	Northern Santa Catarina	Arvoredo Saco do Capim	-48.3638	-27.2844	20
SCN	Northern Santa Catarina	Arvoredo Saco do Engenho	-48.3670	-27.2906	32
SCN	Northern Santa Catarina	Arvoredo Rancho Norte	-48.3725	-27.2783	20
SCN	Northern Santa Catarina	Arvoredo Saco d´Água	-48.3685	-27.2770	54
SCN	Northern Santa Catarina	Arvoredo Saco do Vidal	-48.3610	-27.2982	18
SCN	Northern Santa Catarina	Ilha Deserta north	-48.3317	-27.2645	64
SCN	Northern Santa Catarina	Ilha Deserta west	-48.3317	-27.2645	62
SCN	Northern Santa Catarina	Ilha da Galé Naufrágio Lili	-48.3991	-27.1746	23
SCN	Northern Santa Catarina	Ilha da Galé Ponta do Brás	-48.3991	-27.1746	41
SCN	Northern Santa Catarina	Ponta do Araçá right	-48.5136	-27.1181	15
SCN	Northern Santa Catarina	Ponta do Araçá left	-48.5211	-27.1178	16
SCN	Northern Santa Catarina	Ponta do Araçá Caixa d´Aço	-48.5242	-27.1222	15

Acronym	Locality	Site	Longitude	Latitude	n
SCS	Southern Santa Catarina	Ilha do Campeche north	-48.4674	-27.6905	53
SCS	Southern Santa Catarina	Ilha do Campeche south	-48.4684	-27.6980	21
SCS	Southern Santa Catarina	Ilhas Moleques do Sul north	-48.4320	-27.8455	28
SCS	Southern Santa Catarina	Ilhas Moleques do Sul south	-48.4320	-27.8455	12
SCS	Southern Santa Catarina	Ilha do Xavier west	-48.3876	-27.6035	91
SCS	Southern Santa Catarina	Ilha do Xavier Ponta Sul	-48.3876	-27.6035	14

Supplementary Table 2 -Species observed in visual census from 20 Southwestern Atlantic localities, and functional group attributed to each size estimated (TL in cm).

Family	Species	Func. Group	Range size (cm)
Acanthuridae	*Acanthurus bahianus*	SHD	0-30cm
Acanthuridae	*Acanthurus bahianus*	LHD	>30cm
Acanthuridae	*Acanthurus chirurgus*	SHD	0-30cm
Acanthuridae	*Acanthurus chirurgus*	LHD	>30cm
Acanthuridae	*Acanthurus coeruleus*	LHD	>30cm
Acanthuridae	*Acanthurus coeruleus*	SHD	0-30cm
Acanthuridae	*Acanthurus monroviae*	LHD	>30cm
Albulidae	*Albula vulpes*	LLC	0-50cm
Antennaridae	*Antennarius multiocellatus*	LLC	0-50cm
Apogonidae	*Apogon americanus*	ZPK	Any
Apogonidae	*Apogon pseudomaculatus*	ZPK	Any
Apogonidae	*Apogon* sp.	ZPK	Any
Aulostomidae	*Aulostomus strigosus*	MCA	>50cm
Aulostomidae	*Aulostomus strigosus*	LLC	0-50cm
Balistidae	*Balistes vetula*	LLC	0-50cm
Balistidae	*Balistes vetula*	MCA	>50cm

Family	Species	Func. Group	Range size (cm)
Balistidae	*Canthidermis sufflamen*	ZPK	Any
Balistidae	*Melichthys niger*	OMN	Any
Batrachoididae	*Amphichthys cryptocentrus*	LLC	0-50cm
Batrachoididae	*Porichthys porosissimus*	LLC	0-50cm
Belonidae	*Ablennes hians*	LLC	0-50cm
Belonidae	*Platybelone argalus*	LLC	0-50cm
Belonidae	*Strongylura timucu*	LLC	0-50cm
Blenniidae	*Entomacrodus spn*	SHD	0-30cm
Blenniidae	*Hypleurochilus fissicornis*	OMN	Any
Blenniidae	*Hypsoblennius invemar*	OMN	Any
Blenniidae	*Hypleurochilus pseudoaequipinnis*	SHD	0-30cm
Blenniidae	*Hypleurochilus brasil*	OMN	Any
Blenniidae	*Ophioblennius trinitatis*	SHD	0-30cm
Blenniidae	*Parablennius marmoreus*	OMN	Any
Blenniidae	*Parablennius pilicornis*	LLC	0-50cm
Blenniidae	*Parablennius* sp.	OMN	Any
Blenniidae	*Scartella cristata*	OMN	Any
Bothidae	*Bothus lunatus*	LLC	0-50cm

Family	Species	Func. Group	Range size (cm)
Bothidae	*Bothus ocellatus*	LLC	0-50cm
Callionymidae	*Callionymus bairdi*	LLC	0-50cm
Carangidae	*Alectis ciliaris*	MCA	>50cm
Carangidae	*Carangoides bartholomaei*	MCA	>50cm
Carangidae	*Carangoides bartholomaei*	LLC	0-50cm
Carangidae	*Caranx crysos*	MCA	>50cm
Carangidae	*Caranx crysos*	LLC	0-50cm
Carangidae	*Caranx hippos*	MCA	>50cm
Carangidae	*Caranx latus*	MCA	>50cm
Carangidae	*Caranx latus*	LLC	0-50cm
Carangidae	*Caranx lugubris*	MCA	>50cm
Carangidae	*Caranx lugubris*	LLC	0-50cm
Carangidae	*Carangoides ruber*	MCA	>50cm
Carangidae	*Carangoides ruber*	LLC	0-50cm
Carangidae	*Chloroscombrus chrysurus*	ZPK	Any
Carangidae	*Decapterus macarellus*	ZPK	Any
Carangidae	*Pseudocaranx dentex*	LLC	0-50cm
Carangidae	*Selene vomer*	LLC	0-50cm

Family	Species	Func. Group	Range size (cm)
Carangidae	*Seriola dumerili*	MCA	>50cm
Carangidae	*Seriola lalandi*	MCA	>50cm
Carangidae	*Seriola lalandi*	LLC	0-50cm
Carangidae	*Seriola rivoliana*	LLC	0-50cm
Carangidae	*Seriola rivoliana*	MCA	>50cm
Carangidae	*Trachinotus falcatus*	MCA	>50cm
Carangidae	*Trachinotus falcatus*	LLC	0-50cm
Carangidae	*Trachinotus goodei*	LLC	0-50cm
Carcharhinidae	*Carcharhinus perezii*	LLC	0-50cm
Carcharhinidae	*Carcharhinus perezii*	MCA	>50cm
Carcharhinidae	*Negaprion brevirostris*	MCA	>50cm
Centropomidae	*Centropomus undecimalis*	LLC	0-50cm
Centropomidae	*Centropomus undecimalis*	MCA	>50cm
Chaenopsidae	*Emblemariopsis signifer*	LLC	0-50cm
Chaenopsidae	*Emblemariopsis* sp3	LLC	0-50cm
Chaetodontidae	*Chaetodon ocellatus*	LLC	0-50cm
Chaetodontidae	*Chaetodon sedentarius*	LLC	0-50cm
Chaetodontidae	*Chaetodon striatus*	LLC	0-50cm

Family	Species	Func. Group	Range size (cm)
Chaetodontidae	*Prognathodes brasiliensis*	LLC	0-50cm
Chaetodontidae	*Prognathodes guyanensis*	LLC	0-50cm
Chaetodontidae	*Prognathodes marcellae*	LLC	0-50cm
Chaetodontidae	*Prognathodes obliquus*	LLC	0-50cm
Cirrhitidae	*Amblycirrhitus pinos*	LLC	0-50cm
Clupeidae	*Harengula clupeola*	ZPK	Any
Clupeidae	*Sardinella brasiliensis*	ZPK	Any
Dactylopteridae	*Dactylopterus volitans*	LLC	0-50cm
Dasyatidae	*Dasyatis americana*	MCA	>50cm
Diodontidae	*Chilomycterus reticulatus*	LLC	0-50cm
Diodontidae	*Chilomycterus spinosus*	LLC	0-50cm
Diodontidae	*Diodon holocanthus*	LLC	0-50cm
Diodontidae	*Diodon hystrix*	LLC	0-50cm
Diodontidae	*Diodon hystrix*	MCA	>50cm
Engraulidae	*Engraulis anchoita*	ZPK	Any
Ephippidae	*Chaetodipterus faber*	LLC	0-50cm
Ephippidae	*Chaetodipterus faber*	MCA	>50cm
Epinephelidae	*Alphestes afer*	LLC	0-50cm

Family	Species	Func. Group	Range size (cm)
Epinephelidae	*Cephalopholis fulva*	LLC	0-50cm
Epinephelidae	*Cephalopholis fulva*	MCA	>50cm
Epinephelidae	*Dermatolepis inermis*	MCA	>50cm
Epinephelidae	*Dermatolepis inermis*	LLC	0-50cm
Epinephelidae	*Epinephelus adscensionis*	MCA	>50cm
Epinephelidae	*Epinephelus adscensionis*	LLC	0-50cm
Epinephelidae	*Epinephelus itajara*	MCA	>50cm
Epinephelidae	*Epinephelus marginatus*	MCA	>50cm
Epinephelidae	*Epinephelus marginatus*	LLC	0-50cm
Epinephelidae	*Epinephelus morio*	MCA	>50cm
Epinephelidae	*Epinephelus morio*	LLC	0-50cm
Epinephelidae	*Hyporthodus niveatus*	LLC	0-50cm
Epinephelidae	*Menephorus punctiferus*	LLC	0-50cm
Epinephelidae	*Mycteroperca acutirostris*	LLC	0-50cm
Epinephelidae	*Mycteroperca acutirostris*	MCA	>50cm
Epinephelidae	*Mycteroperca bonaci*	LLC	0-50cm
Epinephelidae	*Mycteroperca bonaci*	MCA	>50cm
Epinephelidae	*Mycteroperca interstitialis*	LLC	0-50cm

Family	Species	Func. Group	Range size (cm)
Epinephelidae	*Mycteroperca interstitialis*	MCA	>50cm
Epinephelidae	*Mycteroperca microlepis*	LLC	0-50cm
Epinephelidae	*Mycteroperca* sp.	LLC	0-50cm
Epinephelidae	*Mycteroperca venenosa*	MCA	>50cm
Epinephelidae	*Paranthias furcifer*	ZPK	Any
Fistulariidae	*Fistularia petimba*	LLC	0-50cm
Fistulariidae	*Fistularia tabacaria*	MCA	>50cm
Fistulariidae	*Fistularia tabacaria*	LLC	0-50cm
Gerreidae	*Diapterus auratus*	LLC	0-50cm
Gerreidae	*Eucinostomus argenteus*	LLC	0-50cm
Gerreidae	*Eucinostomus melanopterus*	LLC	0-50cm
Gerreidae	*Eucinostomus* sp.	LLC	0-50cm
Gerreidae	*Eugerres* sp.	LLC	0-50cm
Gerreidae	*Gerres cinereus*	LLC	0-50cm
Ginglymostomatidae	*Ginglymostoma cirratum*	MCA	>50cm
Gobiidae	*Bathygobius soporator*	LLC	0-50cm
Gobiidae	*Coryphopterus dicrus*	LLC	0-50cm
Gobiidae	*Coryphopterus glaucofraenum*	LLC	0-50cm

Family	Species	Func. Group	Range size (cm)
Gobiidae	*Coryphopterus spbrasil*	OMN	Any
Gobiidae	*Coryphopterus thrix*	LLC	0-50cm
Gobiidae	*Ctenogobius saepepallens*	OMN	Any
Gobiidae	*Elacatinus figaro*	LLC	0-50cm
Gobiidae	*Elacatinus phthirophagus*	LLC	0-50cm
Gobiidae	*Elacatinus pridisi*	LLC	0-50cm
Gobiidae	*Gnatholepis thompsoni*	OMN	Any
Gobiidae	*Microgobius carri*	LLC	0-50cm
Grammatidae	*Gramma brasiliensis*	LLC	0-50cm
Haemulidae	*Anisotremus moricandi*	LLC	0-50cm
Haemulidae	*Anisotremus surinamensis*	LLC	0-50cm
Haemulidae	*Anisotremus surinamensis*	MCA	>50cm
Haemulidae	*Anisotremus virginicus*	LLC	0-50cm
Haemulidae	*Haemulon aurolineatum*	LLC	0-50cm
Haemulidae	*Haemulon chrysargyreum*	LLC	0-50cm
Haemulidae	*Haemulon melanurum*	LLC	0-50cm
Haemulidae	*Haemulon parra*	LLC	0-50cm
Haemulidae	*Haemulon plumierii*	LLC	0-50cm

Family	**Species**	**Func. Group**	**Range size (cm)**
Haemulidae	*Haemulon squamipinna*	LLC	0-50cm
Haemulidae	*Haemulon steindachneri*	LLC	0-50cm
Haemulidae	*Orthopristis ruber*	LLC	0-50cm
Hemiramphidae	*Hemiramphus brasiliensis*	OMN	Any
Holocentridae	*Holocentrus adscensionis*	MCA	>50cm
Holocentridae	*Holocentrus adscensionis*	LLC	0-50cm
Holocentridae	*Myripristis jacobus*	ZPK	Any
Holocentridae	*Sargocentron bullisi*	LLC	0-50cm
Kyphosidae	*Kyphosus cinerascens*	LHD	>30cm
Kyphosidae	*Kyphosus sectatrix*	SHD	0-30cm
Kyphosidae	*Kyphosus sectatrix*	LHD	>30cm
Kyphosidae	*Kyphosus spp_aotep*	SHD	0-30cm
Kyphosidae	*Kyphosus spp_aotep*	LHD	>30cm
Kyphosidae	*Kyphosus vaigiensis*	LHD	>30cm
Kyphosidae	*Kyphosus vaigiensis*	SHD	0-30cm
Labridae	*Bodianus insularis*	LLC	0-50cm
Labridae	*Bodianus pulchellus*	LLC	0-50cm
Labridae	*Bodianus rufus*	MCA	>50cm

Family	Species	Func. Group	Range size (cm)
Labridae	*Bodianus rufus*	LLC	0-50cm
Labridae	*Clepticus brasiliensis*	ZPK	Any
Labridae	*Cryptotomus roseus*	SHD	0-30cm
Labridae	*Doratonotus megalepis*	LLC	0-50cm
Labridae	*Halichoeres bivittatus*	LLC	0-50cm
Labridae	*Halichoeres brasiliensis*	LLC	0-50cm
Labridae	*Halichoeres brasiliensis*	MCA	>50cm
Labridae	*Halichoeres dimidiatus*	LLC	0-50cm
Labridae	*Halichoeres penrosei*	LLC	0-50cm
Labridae	*Halichoeres poeyi*	LLC	0-50cm
Labridae	*Halichoeres radiatus*	LLC	0-50cm
Labridae	*Halichoeres rubrovirens*	LLC	0-50cm
Labridae	*Halichoeres sazimai*	LLC	0-50cm
Labridae	*Nicholsina usta*	SHD	0-30cm
Labridae	*Scarus trispinosus*	LHD	>30cm
Labridae	*Scarus trispinosus*	SHD	0-30cm
Labridae	*Scarus zelindae*	SHD	0-30cm
Labridae	*Scarus zelindae*	LHD	>30cm

Family	**Species**	**Func. Group**	**Range size (cm)**
Labridae	*Sparisoma amplum*	SHD	0-30cm
Labridae	*Sparisoma amplum*	LHD	>30cm
Labridae	*Sparisoma axillare*	LHD	>30cm
Labridae	*Sparisoma axillare*	SHD	0-30cm
Labridae	*Sparisoma frondosum*	SHD	0-30cm
Labridae	*Sparisoma frondosum*	LHD	>30cm
Labridae	*Sparisoma radians*	SHD	0-30cm
Labridae	*Sparisoma rocha*	LHD	>30cm
Labridae	*Sparisoma rocha*	SHD	0-30cm
Labridae	*Sparisoma spbrasil*	SHD	0-30cm
Labridae	*Sparisoma tuiupiranga*	SHD	0-30cm
Labridae	*Thalassoma noronhanum*	ZPK	Any
Labrisomidae	*Labrisomus cricota*	LLC	0-50cm
Labrisomidae	*Labrisomus kalisherae*	LLC	0-50cm
Labrisomidae	*Labrisomus nuchipinnis*	LLC	0-50cm
Labrisomidae	*Malacoctenus brunoi*	LLC	0-50cm
Labrisomidae	*Malacoctenus delalandii*	LLC	0-50cm
Labrisomidae	*Malacoctenus* sp1	LLC	0-50cm

Family	Species	Func. Group	Range size (cm)
Labrisomidae	*Malacoctenus* sp2	LLC	0-50cm
Labrisomidae	*Malacoctenus* sp3	LLC	0-50cm
Labrisomidae	*Paraclinus spectator*	LLC	0-50cm
Labrisomidae	*Starksia* sp.	LLC	0-50cm
Lutjanidae	*Lutjanus alexandrei*	LLC	0-50cm
Lutjanidae	*Lutjanus analis*	LLC	0-50cm
Lutjanidae	*Lutjanus cyanopterus*	MCA	>50cm
Lutjanidae	*Lutjanus cyanopterus*	LLC	0-50cm
Lutjanidae	*Lutjanus griseus*	LLC	0-50cm
Lutjanidae	*Lutjanus jocu*	MCA	>50cm
Lutjanidae	*Lutjanus jocu*	LLC	0-50cm
Lutjanidae	*Lutjanus synagris*	LLC	0-50cm
Lutjanidae	*Ocyurus chrysurus*	LLC	0-50cm
Lutjanidae	*Rhomboplites aurorubens*	LLC	0-50cm
Malacanthidae	*Malacanthus plumieri*	MCA	>50cm
Malacanthidae	*Malacanthus plumieri*	LLC	0-50cm
Microdesmidae	*Ptereleotris randalli*	ZPK	Any
Monacanthidae	*Aluterus monoceros*	ZPK	Any

Family	Species	Func. Group	Range size (cm)
Monacanthidae	*Aluterus scriptus*	ZPK	Any
Monacanthidae	*Cantherhines macrocerus*	LLC	0-50cm
Monacanthidae	*Cantherhines pullus*	OMN	Any
Monacanthidae	*Stephanolepis hispidus*	LLC	0-50cm
Mugilidae	*Mugil curema*	LHD	>30cm
Mugilidae	*Mugil curema*	SHD	0-30cm
Mugilidae	*Mugil* sp.	SHD	0-30cm
Mullidae	*Mulloidichthys martinicus*	LLC	0-50cm
Mullidae	*Pseudupeneus maculatus*	LLC	0-50cm
Muraenidae	*Echidna catenata*	LLC	0-50cm
Muraenidae	*Echidna catenata*	MCA	>50cm
Muraenidae	*Enchelycore anatina*	LLC	0-50cm
Muraenidae	*Enchelycore nigricans*	LLC	0-50cm
Muraenidae	*Enchelycore nigricans*	MCA	>50cm
Muraenidae	*Gymnothorax funebris*	LLC	0-50cm
Muraenidae	*Gymnothorax funebris*	MCA	>50cm
Muraenidae	*Gymnothorax miliaris*	LLC	0-50cm
Muraenidae	*Gymnothorax miliaris*	MCA	>50cm

Family	Species	Func. Group	Range size (cm)
Muraenidae	*Gymnothorax moringa*	MCA	>50cm
Muraenidae	*Gymnothorax moringa*	LLC	0-50cm
Muraenidae	*Gymnothorax vicinus*	MCA	>50cm
Muraenidae	*Gymnothorax vicinus*	LLC	0-50cm
Muraenidae	*Muraena melanotis*	MCA	>50cm
Muraenidae	*Muraena melanotis*	LLC	0-50cm
Muraenidae	*Muraena pavonina*	MCA	>50cm
Muraenidae	*Muraena pavonina*	LLC	0-50cm
Muraenidae	*Muraena* sp.	LLC	0-50cm
Myliobatidae	*Aetobatus narinari*	MCA	>50cm
Myliobatidae	*Rhinoptera* sp	MCA	>50cm
Narcinidae	*Narcine brasiliensis*	LLC	0-50cm
Ogcocephalidae	*Ogcocephalus vespertilio*	LLC	0-50cm
Ophichthidae	*Myrichthys breviceps*	LLC	0-50cm
Ophichthidae	*Myrichthys breviceps*	MCA	>50cm
Ophichthidae	*Myrichthys ocellatus*	LLC	0-50cm
Ophichthidae	*Myrichthys ocellatus*	MCA	>50cm
Opistognathidae	*Opistognathus aurifrons*	ZPK	Any

Family	Species	Func. Group	Range size (cm)
Ostraciidae	*Acanthostracion polygonius*	LLC	0-50cm
Ostraciidae	*Acanthostracion quadricornis*	LLC	0-50cm
Ostraciidae	*Acanthostracion quadricornis*	MCA	>50cm
Ostraciidae	*Acanthostracion* sp.	LLC	0-50cm
Ostraciidae	*Lactophrys trigonus*	LLC	0-50cm
Ostraciidae	*Lactophrys triqueter*	MCA	>50cm
Ostraciidae	*Lactophrys triqueter*	LLC	0-50cm
Pempheridae	*Pempheris schomburgkii*	ZPK	Any
Pinguipedidae	*Pinguipes brasilianus*	LLC	0-50cm
Pomacanthidae	*Centropyge aurantonotus*	SHD	0-30cm
Pomacanthidae	*Holacanthus ciliaris*	LLC	0-50cm
Pomacanthidae	*Holacanthus tricolor*	LLC	0-50cm
Pomacanthidae	*Pomacanthus arcuatus*	OMN	Any
Pomacanthidae	*Pomacanthus paru*	OMN	Any
Pomacentridae	*Abudefduf saxatilis*	OMN	Any
Pomacentridae	*Chromis flavicauda*	ZPK	Any
Pomacentridae	*Chromis jubauna*	ZPK	Any
Pomacentridae	*Chromis limbata*	ZPK	Any

Family	Species	Func. Group	Range size (cm)
Pomacentridae	*Chromis multilineata*	ZPK	Any
Pomacentridae	*Chromis scotti*	ZPK	Any
Pomacentridae	*Microspathodon chrysurus*	SHD	0-30cm
Pomacentridae	*Stegastes fuscus*	SHD	0-30cm
Pomacentridae	*Stegastes pictus*	OMN	Any
Pomacentridae	*Stegastes rocasensis*	SHD	0-30cm
Pomacentridae	*Stegastes sanctipauli*	SHD	0-30cm
Pomacentridae	*Stegastes variabilis*	SHD	0-30cm
Priacanthidae	*Heteropriacanthus cruentatus*	LLC	0-50cm
Priacanthidae	*Priacanthus arenatus*	LLC	0-50cm
Priacanthidae	*Priacanthus arenatus*	MCA	>50cm
Rachycentridae	*Rachycentron canadum*	MCA	>50cm
Sciaenidae	*Equetus lanceolatus*	LLC	0-50cm
Sciaenidae	*Odontoscion dentex*	LLC	0-50cm
Sciaenidae	*Pareques acuminatus*	LLC	0-50cm
Scombridae	*Euthynnus alletteratus*	LLC	0-50cm
Scombridae	*Scomberomorus maculatus*	LLC	0-50cm
Scombridae	*Scomberomorus maculatus*	MCA	>50cm

Family	**Species**	**Func. Group**	**Range size (cm)**
Scorpaenidae	*Scorpaena brasiliensis*	LLC	0-50cm
Scorpaenidae	*Scorpaenodes caribbaeus*	LLC	0-50cm
Scorpaenidae	*Scorpaena isthmensis*	LLC	0-50cm
Scorpaenidae	*Scorpaena plumieri*	LLC	0-50cm
Scorpaenidae	*Scorpaena* sp.	LLC	0-50cm
Serranidae	*Acanthistius brasilianus*	LLC	0-50cm
Serranidae	*Anthias salmopunctatus*	ZPK	Any
Serranidae	*Diplectrum formosum*	LLC	0-50cm
Serranidae	*Diplectrum radiale*	LLC	0-50cm
Serranidae	*Dules auriga*	LLC	0-50cm
Serranidae	*Rypticus bistrispinus*	LLC	0-50cm
Serranidae	*Rypticus saponaceus*	LLC	0-50cm
Serranidae	*Serranus atrobranchus*	LLC	0-50cm
Serranidae	*Serranus baldwini*	LLC	0-50cm
Serranidae	*Serranus flaviventris*	LLC	0-50cm
Serranidae	*Serranus phoebe*	LLC	0-50cm
Serranidae	*Serranus alicei*	LLC	0-50cm
Sparidae	*Archosargus rhomboidalis*	OMN	Any

Family	**Species**	**Func. Group**	**Range size (cm)**
Sparidae	*Calamus calamus*	LLC	0-50cm
Sparidae	*Calamus penna*	LLC	0-50cm
Sparidae	*Diplodus argenteus*	OMN	Any
Sparidae	*Pagrus pagrus*	LLC	0-50cm
Sphyraenidae	*Sphyraena barracuda*	MCA	>50cm
Sphyraenidae	*Sphyraena barracuda*	LLC	0-50cm
Sphyraenidae	*Sphyraena guachancho*	LLC	0-50cm
Sphyraenidae	*Sphyraena picudilla*	MCA	>50cm
Sphyraenidae	*Sphyraena* sp.	LLC	0-50cm
Syngnathidae	*Cosmocampus albirostris*	LLC	0-50cm
Syngnathidae	*Hippocampus reidi*	LLC	0-50cm
Synodontidae	*Synodus intermedius*	LLC	0-50cm
Synodontidae	*Synodus synodus*	LLC	0-50cm
Tetraodontidae	*Canthigaster figueiredoi*	LLC	0-50cm
Tetraodontidae	*Sphoeroides greeleyi*	LLC	0-50cm
Tetraodontidae	*Sphoeroides spengleri*	LLC	0-50cm
Tetraodontidae	*Sphoeroides testudineus*	LLC	0-50cm

Supplementary Table 3 -Explanatory variables utilized in the initial model to predict reef fish biomass patterns in Southwestern Atlantic reefs.

Variable	Code	Scale	Unity	Source	Original source
Mean sea surface temperature	sstmean	Site	°C	Bio-Oracle	Aqua-MODIS
Minimum sea surface temperature	sstmin	Site	°C	Bio-Oracle	Aqua-MODIS
Mean light diffuse attenuation	damean	Site	1/m	Bio-Oracle	Aqua-MODIS
Distance to deep waters (50 m)	disdeep	Site-locality	m	Present work	Brazilian Navy nautical charts
Distance to the coast	discoast	Site-locality	km	Present work	NOAA GEODAS Coastline Extractor
Range of depths	deprange	Site	m	Present work	Sampling
Human population density	popdens	Site-locality	ind./km^2	Present work	IBGE
Number of fishers	fishdens	Site-locality	ind	Present work	Ministério de Pesca e Aquicultura (MPA)
Protection index	protind	Site	-	Present work	ICMBio, Brazilian Navy, Information from experts

Supplementary Table 4 - Model averaged estimated coefficients of explanatory variables of a linear mixed model with reef fish standing biomass from Southwestern Atlantic reefs. All coefficients are from standardized variables.

Parameter	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.8047	0.1319	13.686	<0.0001
sstmean	0.1696	0.1182	1.435	0.1513
topind	0.1243	0.0518	2.397	0.0165
funclhd	0.4698	0.0944	4.978	<0.0001
funcllc	1.6525	0.0944	17.51	<0.0001
funcomn	1.1992	0.0944	12.707	<0.0001
funcshd	0.7909	0.0944	8.38	<0.0001
funczpk	0.0897	0.0944	0.951	0.3418
lndiscoast	0.6469	0.1177	5.498	<0.0001
protind	0.0939	0.1033	0.909	0.3634
funclhd:lndiscoast	-0.0258	0.1002	0.257	0.797
funcllc:lndiscoast	-0.5712	0.1002	5.703	<0.0001
funcomn:lndiscoast	-0.4094	0.1002	4.088	<0.0001
funcshd:lndiscoast	-0.6435	0.1002	6.425	<0.0001
funczpk:lndiscoast	-0.1819	0.1002	1.816	0.0693
funclhd:protind	-0.0365	0.1002	0.364	0.7156

Parameter	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
funcllc:protind	-0.1181	0.1002	1.179	0.2385
funcomn:protind	-0.2597	0.1002	2.593	0.0095
funcshd:protind	0.0455	0.1002	0.455	0.6493
funczpk:protind	-0.2583	0.1002	2.579	0.0099