Anderson Antônio Batista

PEIXES TROPICAIS NO SEU LIMITE DE DISTRIBUIÇÃO: DINÂMICA TEMPORAL DA ICTIOFAUNA RECIFAL NO SUL DO BRASIL

Tese submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Doutor em Ecologia. Orientador: Prof. Dr. Sergio Ricardo Floeter

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“**Peixes Tropicais no Seu Limite de Distribuição: Dinâmica Temporal da Ictiofauna Recifal no Sul do Brasil**”

Por
Anderson Antônio Batista

Tese julgada e aprovada em sua forma final pelos membros titulares da Banca Examinadora (023/PPGECO/2016) do Programa de Pós-Graduação em Ecologia - UFSC.

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Dedico este trabalho a minha esposa Manuela, que sempre esteve ao meu lado, nos melhores e piores momentos desta caminhada solitária.

Você, sempre você!

Agradeço ao Prof. Dr. Sergio Floeter pela oportunidade e parceria nestes oito anos de investigação, dedicados a esta porção da costa brasileira, belíssima, única, e extremamente generosa.

RESUMO

Monitoramentos de longo prazo das populações de peixes recifais constituem uma ferramenta valiosa para a compreensão dos processos ecológicos que governam as variações populacionais em sistemas de recifes marinhos. No presente trabalho, investigamos a composição, distribuição, estrutura, recrutamento e variações nas populações de peixes recifais, habitando seu limite meridional de distribuição. Nove anos de dados, coletados de 2006 a 2016, foram analisados resultando em uma tese dividida em três capítulos. Capítulo 1) a composição de peixes recifais do Estado de Santa Catarina. O trabalho resultou em uma lista de 278 espécies registrados ao longo da costa do estado de Santa Catarina. Doze novos registros de espécies para a região*: Acanthurus coeruleus, Acanthurus monroviae, Apogon americanus, Cantherhines macrocerus, Chaetodon sedentarius, Chromis flavicauda, Clepticus brasiliensis, Decapterus punctatus, Gymnothorax vicinus, Quasiremus ascensionis, Muraena retifera e Stegastes partitus. Stegastes partitus* é relatado pela primeira vez, para o Atlântico Sul ocidental, *Q. ascensionis* é relatada pela segunda vez, e *Acanthurus monroviae* é relatado pela terceira vez. Concluiu-se que as espécies apresentaram seletividade com relação à distribuição e uso do habitat, estrutura trófica e afinidades biogeográficas. Capítulo 2) variações temporais e espaciais de espécies dominantes. Neste capítulo apresentamos um esforço amostral de nove anos de monitoramento das variações na densidade e biomassa das principais espécies de peixe recifais, dentro e fora da única Reserva Biológica próxima da costa (Reserva Biológica Marinha do Arvoredo - REBIO Arvoredo). Este esforço cobriu 32.000 m² de recifes rochosos, onde 43.169 peixes foram contados, identificados, medidos e em seguida convertidos em dados de biomassa. Variações na densidade e biomassa, no espaço e no tempo foram detectados para a maioria das espécies. Vários fatores e mecanismos podem ter influenciado estas variações. Na escala espacial, predominantemente os mecanismos determinísticos, tais como complexidade estrutural do habitat, proteção contra pesca, podem ter influenciado com maior intensidade estas variações. Variações temporais (anuais), por outro lado, podem ter sido influenciadas pela proximidade das espécies à sua fronteira geográfica de distribuição, em sinergia com mecanismos dependentes da densidade e oscilações estocásticas de temperatura durante os invernos austrais. A REBIO Arvoredo parece influenciar positivamente a maioria das espécies com

relação às densidades e biomassa, de forma direta e indiretamente, no espaço e no tempo. Em contraste, um importante declínio no recrutamento de *E. marginatus*, alerta para resiliência da REBIO Arvoredo ao longo do tempo. Capítulo 3) variação influenciada por espécies invasoras: neste capítulo estudamos as colonizações do recifes rochosos de Santa Catarina pelo peixe Donzela dos Açores, *Chromis limbata*. Este pomacentrídeo é nativo dos arquipélagos da Macaronésia (Açores, Madeira e Canárias), e da costa ocidental da África, entre o Senegal e Angola. Durante os verões austrais de 2008 e 2009, esta espécie foi registrada pela primeira vez no Atlântico Sul Ocidental, na Ilha do Campeche e Ilha do Xavier, em Florianópolis, estado de Santa Catarina, Brasil. A população brasileira de *C. limbata* aumentou significativamente ao longo dos últimos cinco anos. Análises moleculares confirmaram a identidade da espécie, revelando ainda conectividade haplótipica entre os locais de estudo brasileiros. Mostrou baixa diversidade genética no Brasil quando comparada com as populações nativas originais. Quatro hipóteses poderiam explicar este evento colonizador: 1) vários espécimes de *C. limbata* foram descartados vivos no mar por aquaristas; 2) larvas ou juvenis foram transportados através de água de lastro de grandes embarcações; 3) a espécie veio acompanhando plataformas de petróleo; e 4) a espécie invasora cruzou o Atlântico através da dispersão larval normal ou acompanhando objetos à deriva (rafting). A terceira e quarta hipóteses pareceu-nos mais plausíveis, porém todas as quatro são prováveis e poderiam ter ocorrido combinadas. Eventos de colonização bem sucedidos são, muitas vezes, iniciados por um grande número de indivíduos, em vários eventos durante um longo período de tempo, evitando desta maneira a perda de diversidade genética na população recém fundada. A baixa diversidade genética detectada nas populações brasileiras de *C. limbata* sugere um pulso larval, ou a chegada de um grupo de indivíduos. Apesar das variações na densidade média entre sites para *C. multilineata* (seu congenere nativo), o aumento da população invasora (*C. limbata*) não parece, por enquanto, afetar as populações da congenere de forma direta. É importante notar que *C. multilineata* é uma espécie tropical que habita o seu limite sul de distribuição, enquanto que *C. limbata* habitar o seu ambiente ideal (recifes rochosos temperados). Dadas as suas preferências ecológicas no Atlântico oriental, prevemos que *C. limbata* será mais abundante do que *C. multilineata* na costa sul e sudeste do Brasil, e talvez, expandindo-se ainda mais para o sul, para o Uruguai e Argentina. Evidências da competição intra-específica não foram detectadas, até o momento. Mesmo *C. limbata* e *C. multilineata*

tendo uma dieta semelhante constituída, em sua maioria de zooplâncton, a alta produtividade das águas do Atlântico Sul, devido à alta produtividade de plâncton oriunda das ressurgências, indica que não há competição inter específica por recurso alimentar. Pequenos cardumes de *C. multilineata* e *C. limbata* alimentando-se juntos têm sido observados nos últimos quatro anos, em todos os locais estudados. Em contraste, o comportamento agressivo de *C. limbata* durante a reprodução pode afetar espécies territoriais locais (*e.g. Stegastes* spp., *Abudefduf saxatilis*). Locais adequados para proteção e nidificação, por exemplo, podem tornar-se um recurso limitante com o aumento das densidades de *C. limbata* em seu novo ambiente. No entanto, não houve nenhuma evidência de efeitos prejudiciais para as espécies nativas, até o momento. O monitoramento de longo prazo desta chegada recente será de suma importancia, podendo constituir ferramentas valiosas para uma melhor compreensão da genética, ecologia e impacto de expansões de espécies invasoras.

Palavras-chave: Áreas Marinhas Protegidas; Monitoramento de longo prazo; Espécies Invasoras; Recifes Rochosos do Sul do Brasil; Espécies alvo; Variações temporais; Estrutura populacional; Ecologia de recifes rochosos; Mecanismos dependentes da densidade

ABSTRACT

Long term monitoring of reef fish populations is a valuable tool to understand ecological processes that govern population's variations in marine reef systems. In the present work, we investigated the composition, distribution, structure, recruitment, and variations in rocky reef fish populations, inhabiting their southernmost limit of distribution. Nine years of data collected from 2006 to 2016, were analyzed. This work was divided in three chapters: 1) the composition of rocky reef fishes of the State of Santa Catarina: the work resulted in a checklist of 278 species recorded along the coastline of Santa Catarina State. Twelve new species records: *Acanthurus coeruleus, Acanthurus monroviae, Apogon americanus, Cantherhines macrocerus, Chaetodon sedentarius, Chromis flavicauda, Clepticus brasiliensis, Decapterus punctatus, Gymnothorax vicinus, Quasiremus ascensionis, Muraena retifera* and *Stegastes partitus. Stegastes partitus* is reported for the first time, for the Southwestern Atlantic, *Q. ascensionis* is reported for the second time, and *Acanthurus monroviae* is reported for the third time. Species presented selectivity regarding habitat distribution, trophic structure and biogeographic affinities. Chapter 2) temporal and spatial variations of dominant species: here we present a nine-year effort on monitoring the variations in densities and biomass of key rocky reef fish species, inside and outside the only no-entry near shore Brazilian Reserve (Arvoredo Biological Marine Reserve). Such effort covered 32.000 m² of rocky reefs, where 43.169 fish were counted, identified, measured and then converted into biomass data. Variations in specie's densities and biomass in space and time were detected for most species. Several factors and mechanisms may have influenced these variations: on spatial scale: deterministic mechanisms such as habitat structural complexity, protection from fisheries and aquarium trade may have influenced these variations. Temporal variations, otherwise, may have been influenced by the proximity of species to their distributional border, in synergy with density-dependent mechanisms and stochastic winter temperature oscillations. Arvoredo Marine Biological Reserve seem to influence positively most species densities and biomass directly and indirectly, in space and time. In contrast, a prominent decline in recruitment of *E. marginatus* lighten red alarms regarding Arvoredo Marine Biologic Reserve resilience over time. Chapter 3) variation influenced by invasive specie: here we studied the colonizations of Santa Catarina's rocky reefs

by the Azores Chromis *Chromis limbata*. This damselfish is native to the Macaronesian archipelagos (Azores, Madeira and Canaries), and the western coast of Africa between Senegal and Angola. During the austral summers of 2008 and 2009, the species was recorded for the first time in the southwestern Atlantic around Campeche and Xavier islands, in Florianópolis, Santa Catarina State, Brazil. The Brazilian population of *C. limbata* increased significantly over the past five years. The molecular analyses confirmed species identity, revealed strong haplotype connectivity among Brazilian study sites, and showed a low genetic diversity in Brazil when compared to the native populations. Four hypotheses could explain this colonizing event: 1) *C. limbata* was released by aquarium fish keepers; 2) larvae or juveniles were transported via ship ballast water; 3) the species has rafted alongside oilrigs; and 4) they crossed the Atlantic through normal larval dispersal or naturally rafting alongside drifting objects. We tend to favor the third and fourth hypotheses, but all four are plausible and could have happened in combination. Successful colonization events are often started by large numbers of individuals in multiple events during a long period avoiding loss of genetic diversity in the newly founded population. The low genetic diversity detected in Brazilian *C. limbata* suggests a small larval pulse, or the arrival of a small group of individuals. Despite significant differences in mean densities among sites for *C. multilineata* (the local congener species), it does not seem like they have been affected by the increase in the *C. limbata* population. It is important to note that *C. multilineata* is a tropical species inhabiting its southern limit of distribution, whereas *C. limbata* is inhabiting its optimum environment (subtropical, warm-temperate rocky reefs). Given its ecological preferences in the eastern Atlantic, we predict that *C. limbata* will be more abundant than *C. multilineata* in the south and southeastern coast of Brazil, and maybe, even expand further south to Uruguay and Argentina. Evidences of intra-specific competition have not been detect, so far. Even though *C. limbata* and *C. multilineata* have a similar zooplankton diet, the high productivity of south Atlantic waters due to upwelling and consequent high abundance of plankton, indicates that these species may not be competing for food. Schools of *C. multilineata* and *C. limbata* feeding together have been observed in the past two years in all studied sites. In contrast, *C. limbata* aggressive behavior during reproduction may affect local territorial species (*e.g. Stegastes* spp., *Abudefduf saxatilis*). Shelter for example may become a limiting resource

as their densities in the new environment increase. However, there has been no evidence of detrimental effects to native species, so far. Long term monitoring of this recent arrival will be important and could constitute a valuable tool for a better understanding the genetics, ecology, and impacts of species range expansions.

Keywords: Marine Protected Areas; Long-term monitoring; Invasive species; Southern Brazilian Rocky reefs; Targeted species; Temporal variations; Population structure; Reef fish ecology; density-dependent mechanisms

LISTA DE FIGURAS

Introdução:

Chapter 1)

Chapter 2)

Chapter 3)

LISTA DE TABELAS

Chapter 1)

Appendix 1

Chapter 2)

Chapter 3)

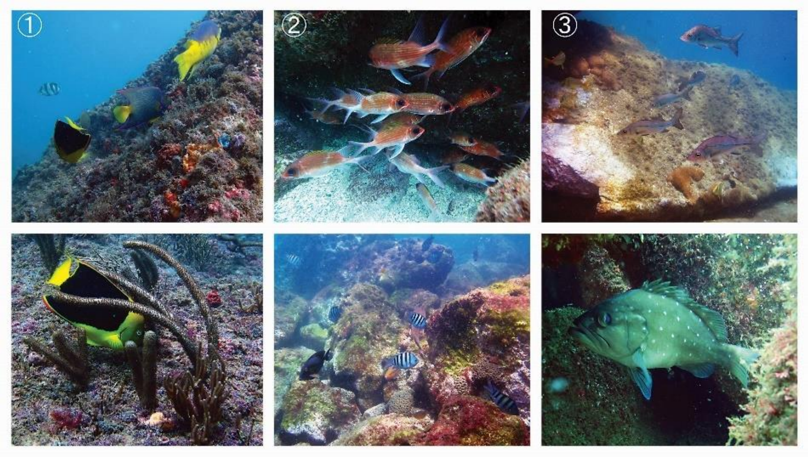
SUMÁRIO

INTRODUÇÃO

1.1 GEOMORFOLOGIA, PROCESSOS OCEANOGRÁFICOS E RELEVÂNCIA ECOLÓGICA

Recifes rochosos fornecem habitats para diversos grupos de organismos marinhos (BARROS *et al.*, 2001; ANDERSON *et al.*, 2015). No Sul do Brasil os costões rochosos de formação pré-cambriana estendem-se desde o litoral norte do Espírito Santo até o município de Torres, Rio Grande do Sul (DIEHL e HORN FILHO, 1996) (Figura 1). Neste ambientes marinhos, muitos estudos têm-se centrado no recrutamento, produtividade, comportamento e conservação das assembleias de peixes e animais bentônicos nestes sistemas (ANDRADE *et al.*, 2003; FLOETER *et al.*, 2005; FLOETER *et al.*, 2006, 2007, 2008; KOETTKER e FREIRE, 2006; ANDERSON *et al.*, 2015). A costa de Santa Catarina está inserida neste contexto geomorfológico, localizada entre as latitudes 25 ° 57'S e 29 ° 23'S, que representam cerca de 7% da costa brasileira (ANDERSON *et al.*, 2015).

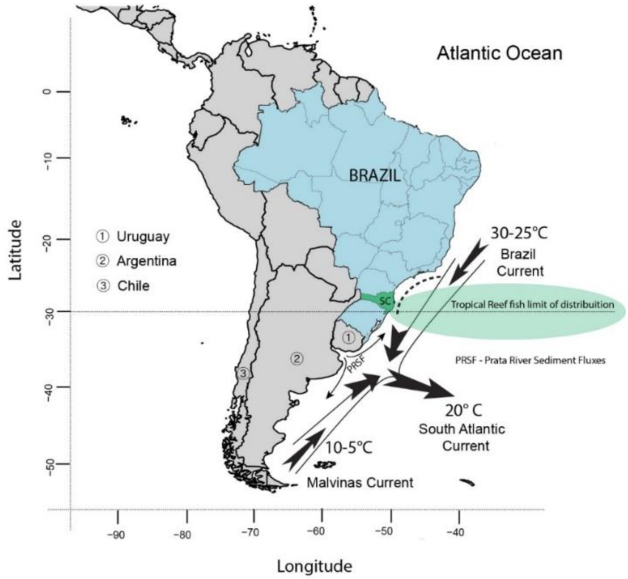
Figura 1: Feições dos costões rochosos pré-cambrianos do Sudeste e Sul do Brasil: 1) Costa Capixaba; 2) Costa Paulista e 3) Costa Catarinense. Imagens: Anderson, A. B.



O Estado possui geografia costeira complexa, incluindo numerosas ilhas costeiras. O litoral que recebe as descargas de água doce (em sua maioria carregadas de aportes de materiais de origem antrópica) de vários rios de pequeno e médio porte, resultando em vários tipos de ambientes (*e.g.* marismas, estuários, restingas, manguezais) (DIEHL e HORN FILHO, 1996; BARROS *et al.*, 2010; ANDERSON *et al.*, 2015). Esta riqueza de habitats traz consigo ainda características oceanográficas próprias e assembleias de espécies diferenciadas em cada ambiente (KOETTKER e FREIRE, 2006; WARREN *et al.*, 2008; BEGOSSI *et al.*, 2012; MARTINS *et al.*, 2013; ANDERSON *et al.*, 2015). Esta região é também influenciada por descargas continentais de rios de grande porte, carregadas de aportes de materiais de origem antrópica, na porção norte da costa (*e.g.* Rio Itapucu, Itajaí-açu, Tijucas e Tubarão) (KLEIN e MENEZES, 2001; HILLE *et al.*, 2008; CARVALHO *et al.*, 2010; MARTINS *et al.*, 2013; ANDERSON *et al.*, 2015). Na porção sul do estado, o fenômeno de ressurgência é o processo oceanográfico mais importante durante o verão austral (PIOLA *et al.*, 2000; PIOLA *et al.*, 2005; ANDERSON *et al.*, 2015). Durante os invernos austrais a influência da pluma de sedimentos oriunda do Rio da Prata (Plata River Sediment Flux- PRSF) e massas d’água originárias do Antártida (Subtropical Shelf Front) constituem os processos oceanográficos chaves (PIOLA *et al.*, 2000; MOLINA-SCHILLER, D. *et al.*, 2005; PIOLA *et al.*, 2005; ANDERSON *et al.*, 2015) (Figura 2).

Pode-se destacar neste contexto oceanográfico a influência importante exercida pela Corrente do Brasil a BC (Brazilian Current). Consiste de uma corrente oligotrófica, de contorno oeste, associada ao giro subtropical do Atlântico Sul (DA SILVEIRA *et al.*, 1994). Este, por sua vez, origina-se ao sul de 10 °S, na região onde o ramo mais ao sul da Corrente Sul Equatorial (South Equatorial Current-SEC) se bifurca e flui para o sul, bordejando toda a costa brasileira até a região da Convergência Subtropical (33 - 38°S), onde conflui com a Corrente das Malvinas e se afasta da costa (CASTRO *et al.*, 2006).

Figura 2: Mapa da América do Sul que mostra a influência de ambas as masss oceânicas tropicais quentes e frias ao longo da costa sul do Brasil. O estado Santa Catarina é representado em verde escuro (SC). A elipse verde clara representa o limite meridional da distribuição de peixes recifais tropicais. O arco tracejado representa o “Arco de Capricórnio” extraído e modificado de ANDERSON et al. (2015).



Ademais, a região da plataforma continental de Santa Catarina também sofre influência sazonal de águas mais frias e com baixa salinidade, provenientes do sul. Esta intrusão de águas mais frias e com baixas salinidades em direção ao norte durante o inverno tem sido descrita por diversos autores (CAMPOS *et al.*, 1999; PIOLA *et al.*, 2000; MÖLLER JR *et al.*, 2008). Piola e colaboradores (2000), com base em dados hidrográficos históricos ao longo da plataforma continental sul, sugerem que essa massa de água de baixa temperatura e baixa salinidade que flui em direção ao norte é formada pela descarga de água doce do Rio da Prata (~35 °S) e da Lagoa dos Patos (~ 32 °S), e sua distribuição horizontal apresenta uma forte variação sazonal. A plataforma continental da região sul apresenta alta heterogeneidade, tanto em escala espacial como temporal, com fortes gradientes horizontais e verticais. Essa complexidade física pode propiciar processos de fertilização da zona eufótica por tempo suficiente para o crescimento e o acúmulo da biomassa fitoplanctônica, tornando-a uma das áreas mais produtivas da plataforma continental brasileira (BRANDINI, 2006). Essas características conferem à região relevante importância ecológica, abarcando significativa biodiversidade marinha e representando o limite sul de distribuição da fauna e flora marinha tropical do Oceano Atlântico (FLOETER *et al.*, 2001, 2005, 2008; ANDERSON *et al.*, 2015). Por exemplo, cerca de 96,4% das espécies de peixes recifais tropicais que habitam a costa de Santa Catarina tem seu limite sul de distribuição nestas águas (ANDERSON *et al.*, 2015). A dinâmica oceanográfica da região confere alta produtividade pesqueira, levando o Estado ao posto de maior produtor de pescado nacional, Santa Catarina é responsável por 95% da produção nacional de mexilhões e ostras e abarca a maior frota pesqueira do país (PAULILO, 2002; BEGOSSI e SILVANO, 2008; CAVALLI e FERREIRA, 2010; SILVA *et al.*, 2013).

1.2 DIVERSIDADE ICTIOFAUNÍSTICA MARINHA RECIFAL DE SANTA CATARINA

Peixes recifais são organismos que habitam os recifes (biogênicos ou rochosos) em pelo menos uma de suas fazes ontogenéticas. São organismos fundamentais para a estruturação e resiliência de ecossistemas marinhos (GRAHAM *et al.*, 2007; ANDERSON *et al.*, 2014; ANDERSON *et al.*, 2015). Desta forma, podem ser considerados como excelentes modelos indicadores das condições ambientais, pela capacidade de refletir, em diferentes níveis, respostas causadas por inúmeras variações no habitat (FLOTEMERSCH *et al.*, 2006; ANDERSON *et al.*, 2014; ANDERSON *et al.*, 2015). Ademais, são bons indicadores de efeitos a curto, médio e longo prazo, devido à variabilidade dos ciclos biológicos e ontogenéticos (FLOTEMERSCH *et al.*, 2006; ANDERSON *et al.*, 2014).

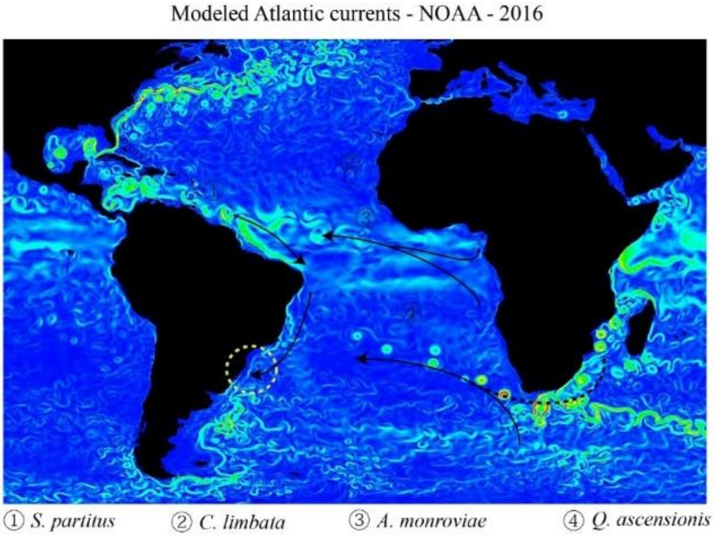
A costa Catarinense abriga cerca de 278 espécies de peixes recifais, distribuídos em 170 gêneros e 74 famílias, destes, 96,4% encontram-se em seu limite meridional de distribuição (ANDERSON *et al.*, 2015). Esta diversidade é caracterizada principalmente por espécies tropicais trazidas das águas quentes do norte por correntes oceânicas. Mesmo estando adaptadas às condições locais, as águas frias (<18ºC) que ocorrem durante o inverno austral, podem afetar a sobrevivência destas espécies, levando inclusive, à extirpação de populações (BOHNSACK, 1983; HSIEH *et al.*, 2008; ANDERSON *et al.*, 2015). Novos registros incomuns para o Brasil e principalmente para a costa Catarinense, indicam padrões peculiares de dispersão, com alta conectividade com costa Atlântica Oriental (ANDERSON *et al.*, 2015) (Figura 3).

1.3 PESQUISAS ENVOLVENDO PEIXES RECIFAIS EM SANTA CATARINA

A natureza da complexa dinâmica das comunidades dos organismos e sua capacidade de resiliência às diversas formas de perturbações no tempo permanece como uma das perguntas mais importantes para a ecologia, no que se refere ao manejo e conservação de ecossistemas (BEGON *et al.*, 2006). Para compreender tais questões, estudos com dados em escala temporal ampla são necessários (TAKEUCHI *et al.*, 2010). Nosso entendimento destas questões tem sido fundamentado sobre estudos que, em sua maioria, utilizam a composição de espécies, abundância relativa e biomassa, em uma pequena escala espacial e, principalmente, em uma pequena escala temporal (SALE, 1980; DOHERTY, 1983; JONES, 1987; CHOAT *et al.*, 1988; PLANES *et al.*, 2005).

As comunidades de peixes recifais altamente diversas e com relações ecológicas complexas têm sido alteradas ao longo do tempo por vários tipos fenômenos naturais, principalmente, pela atividade antrópica nos últimos séculos (ROBERTS, 2010; ANDERSON *et al.*, 2014). Ainda assim, pouco se sabe sobre os efeitos destas alterações nas comunidades de peixes recifais, pela carência de resultados obtidos a partir de trabalhos com seus desenhos amostrais projetados em escala temporal (CHOAT *et al.*, 1988; TAKEUCHI *et al.*, 2010; ANDERSON *et al.*, 2015). Grande parte dos estudos envolvendo estas comunidades de peixes recifais baseiam-se em variações espaciais (FLOETER *et al.*, 2004; ANDERSON *et al.*, 2015). Porém, trabalhos sobre as mudanças temporais na estrutura populacional das assembleias recifais ainda são escassos, inexistentes principalmente para a região sul do Brasil (ANDERSON *et al.*, 2015). Mudanças nos focos dos estudos envolvendo as comunidades marinhas nas últimas décadas podem resultar em efeitos favoráveis para a pesquisa e conservação nestes ambientes. Entre as décadas de 60 e 80 (por exemplo) a poluição foi o foco principal de preocupação dos cientistas, enquanto que nos anos 90 e o início do século 21 o foco voltou-se para os impactos da pesca (ROBERTS, 2010). Já na última década houve um incremento significativo na compreensão das consequências do impacto humano no ambiente marinho (ROBERTS, 2010). Futuros trabalhos desenvolvidos em escala temporal poderão ser ferramentas mais efetivas no que se refere à elaboração de modelos bem estruturados de cenários futuros voltados para a conservação dos sistemas marinos (CHOAT *et al.*, 1988; BRANDER, 2007; ANDERSON *et al.*, 2015).

Figura 3: Modelos dinâmico das correntes e giros oceânicos do Atlântico. O Sentido dos giros e correntes é sempre leste para oeste. As setas indicam as zonas de maior intensidade de correntes e giros. Os números indicam os expansões de área de ocorrência mais extremas para o Atlântico, em sua maioria exclusivas de Santa Catarina:1) Stegastes partitus (natural do Caribe) 1º registro para o Atlântico sul (costa Catrinense); 2) Chromis limbata (natural das Ilhas Canárias e Arquipélago dos Açores) população estabelecida em Santa Catarian desde 2009; 3) Acanthurus monroviae (natural da costa Africana) 2º registro para o Atlântico ocidental (Santa Catarina); 4) Quassiremus ascensionis (natural da Ilha de Ascensão, Santa Helena e Tristão da Cunha, 1º registro para o Atlântico sul ocidental (Santa Catarina) (ANDERSON et al., 2015). O Circulo amarelo pontilhado indica a costa de Santa Catarina.



Neste contexto, este trabalho possibilita uma análise temporal da estrutura de comunidades de peixes recifais em seu "*continuum*" ecológico. Ademais, foram selecionados dados de 2008 a 2016 totalizando 8 anos consecutivos que viabilizaram ainda, a análise dos potenciais padrões relacionados às variações temporais nas estruturas das comunidades de peixes recifais no seu limite sul de distribuição para a costa brasileira. Este trabalho constitui a primeira avaliação temporal das populações de espécies-chave de peixes recifais para a costa sul do Brasil e o trabalho com a série temporal mais longo para a costa do Brasil. Esta Tese foi subdividida em 3 capítulos. Capítulo 1: Brazilian tropical fishes in their southern limit of distribution: checklist of Santa Catarina's rocky reef ichthyofauna, remarks and new records. Neste capítulo foi analisada a composição ictiofaunística recifal da costa de Santa Catarina, com base em nove anos de dados de censos visuais subaquáticos, vouchers de museus brasileiros e revisão bibliográfica. Capítulo 2: Temporal variations of reef fish community in space and time: the first and longest temporal evaluation of rocky reef ichthyofauna of Brazilian coast. Neste capítulo foi avaliada a composição ictiofaunística em relação à sua variação especial e temporal dentro das áreas que compõem o desenho amostral. Ainda é avaliada a efetividade da Reserva Biológica Marinha do Arvoredo com base em nove anos de dados coletados, o que caracteriza este trabalho como a primeira avaliação temporal de efetividade de uma Reserva Biológica totalmente restrita em ambiente de costão rochoso da costa brasileira. Capítulo 3: The recent colonization of South Brazil by the Azores Chromis, *Chromis limbata* (Valenciennes, 1833). Neste capítulo é investigada a expansão biogeográfica e demográfica da espécie invasora *C. Limbata* na costa sul do Brasil, com base em nove anos de censos visuais subaquáticos e dados moleculares.

2 BRAZILIAN TROPICAL FISHES IN THEIR SOUTHERN LIMIT OF DISTRIBUTION: CHECKLIST OF SANTA CATARINA'S ROCKY REEF ICHTHYOFAUNA, REMARKS AND NEW RECORDS

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2.1 ABSTRACT

We present a checklist of 278 species of reef fishes recorded along the coastline of Santa Catarina state, the southernmost limit of distribution of tropical ichthyofauna on the coast of Brazil. Twelve new species records for this state are presented: *Acanthurus coeruleus, Acanthurus monroviae, Apogon americanus, Cantherhines macrocerus, Chaetodon sedentarius, Chromis flavicauda, Clepticus brasiliensis, Decapterus punctatus, Gymnothorax vicinus, Quassiremus ascensionis, Muraena retifera and Stegastes partitus. Stegastes partitus* and *Q. ascensionis* are reported for the first time, respectively, from the Southwestern Atlantic and for the coastal part of this region, while *Acanthurus monroviae* is reported for the second time for the Southwestern Atlantic. We present habitat distribution, trophic structure and comment on biogeographic affinities of this transitional region, discussing both remarkable species presences and absences.

Key words: rocky reefs, Southwestern Atlantic Shelf, Teleostei, Elasmobranchii, Atlantic Subtropical Convergence, upwelling

2.2 INTRODUCTION

The Brazilian reef ichthyofauna has been subject to considerable research in the past 30 years. This was especially due to the popularization of scuba diving among Brazilian scientists, and to the improvements in genetics and computational power (Floeter et al. 2001; Rocha et al. 2008; Bernardi et al. 2013; Pita et al. 2014). However, this region remains poorly studied in comparison to other biogeographic provinces in the world (Floeter et al. 2001).

The south and southeastern Brazilian coastline is characterized by granitic rocky reefs influenced by both warm tropical waters from the Brazil Current and cool waters from the South Atlantic Central Water (SACW). This water mass intrudes on the shallow coastal shelf of this region (Acha et al. 2004), especially during spring and summer northeastern winds, and features temperatures of ≤16°C (Carvalho et al. 1998). In the southernmost part of the Brazilian coast, the cold La Plata Plume Water (PPW) coming from the discharge of the La Plata River (at 35°S) reaches coastal areas during the winter (Möller Jr. et al. 2008). The low temperatures generated by these water masses affect the distribution of tropical marine organisms in the region (Boschi 2000; Floeter et al. 2001, 2008; Spalding et al. 2007; Barneche et al. 2009; Anderson et al. 2014a, 2014b), precluding some of them from establishing southwards. Mangrove forests (Sobrinho et al. 1969), corallith (Capel et al. 2012) and rhodolith beds (Gherardi 2004; Pascelli et al. 2013) are biological features of the landscape that reach their southern limit of distribution in the Southwestern Atlantic, precisely in the state of Santa Catarina. Coincidently, this state also represents the southern limit of occurrence of rocky reefs, with a large stretch of sandy beaches extending from it almost continuously to Uruguay. Therefore, for fishes and other organisms that inhabit hard substrates, Santa Catarina is the southernmost limit of the Brazilian biogeographic province (Floeter et al. 2008; Briggs and Bowen 2012).

There are recent taxonomic inventories from São Paulo (Luiz et al. 2008) and Paraná (Hackradt and Félix-Hackradt 2009) states in Brazil, as well as from the coast of Patagonia, in Argentina (Galván et al. 2009). However, despite its biogeographic importance, taxonomic knowledge on Santa Catarina reef fishes remains largely outdated (e.g., Lema 1976; Lema et al. 1980; Godoy1987).

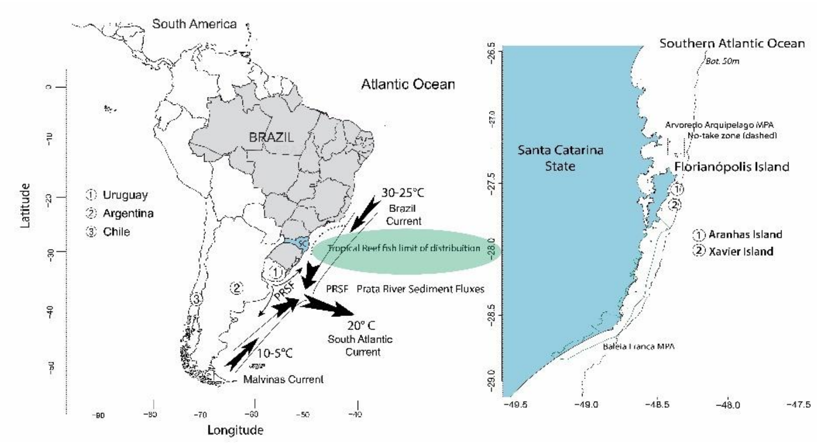

Figure 1. Map of South America showing the influence of both warm tropical and cool waters along the southern Brazilian coast. The Santa Catarina state is represented in light blue (SC). The green ellipse represents the southernmost limit of distribution for tropical reef fish. The dashed arc represents the “Arc of Capricorn” region. The dashed and green polygons and numbers represent most sampled areas.

2.3 MATERIALS AND METHODS

STUDY AREA

The coast of Santa Catarina is located between the latitudes 25°57′S and 29°23′S, representing approximately 7% of the Brazilian coast (Diehl and Horn Filho 1996) (Figure 1). This region is influenced by continental inputs from rivers in the northern part of the coast (i.e., Itapucu, Itajaí-açu, Tijucas and Tubarão Rivers) (Carvalho et al. 1998; Hille et al. 2008). In the southern portion of the state, the upwelling phenomenon during austral summer and the influence of the La Plata River Plume (see PRSF Figure 1) and Sub-Antarctic Water (Subtropical Shelf Front) during austral winter are key oceanographic processes (Piola et al. 2000; Piola et al. 2005). Complex coastal geography, including numerous coastal islands, and the output of various small to mediumsized rivers results in various types of environments, each having its own oceanographic features and species assemblages (Charrid 2011).

DATA

This work was based on over 12 years of underwater observations using free and scuba diving conducted by the authors (Anderson et al. 2014a; and Marine Macroecology and Biogeography Laboratory photo-graphic data bank), as well as museum vouchers and literature records (i.e., Godoy 1987; Carvalho-Filho 1999; Floeter et al. 2008; Hostim-Silva et al. 2006; Anderson et al. 2014a).

In this paper, we consider reef fish to be those species which are associated with hard substrates after their post-settlement stage, whose habitat includes the continental shelf and islands near the shore, and spend any part of their lifecycle associated with rocky reef systems, including occasional epipelagic and soft substrate species known to occasionally feed, shelter, reproduce or search for cleaning services in rock reefs. Species that have never been observed in reefs in the study region were not considered. This includes species from the families Achiridae, Atherinopsidae, Coryphaenydae, Cynoglossidae, Engraulidae, and some genera of Clupeidae and Scombridae. We consider here species that occur between the surface and depths to 50 m, acknowledging that, albeit deeper occurring species do indeed use reef habitat, we have not been able to adequately sample these depths.

Because of recent changes in the classification of fishes (e.g., Near et al. 2012; Faircloth et al. 2013), fish families are listed alphabetically. We adopted recent taxonomic changes in our classification: Westneat and Alfaro (2005); Craig and Hastings (2007); Smith and Craig (2007); Choat et al. (2012); Boehm et al. (2013); Frable et al. (2013); Knudsen and Clements (2013) and Silveira et al. (2014).

We also included the following information regarding species biology:

Habitat distribution. The physiognomy within a rocky reef where a species is usually recorded. We stipulated four different habitat types (Figure 2). The Reef slope (RS) is the zone associated with the presence of rocky substrate ranging from the surface to the point where sediments start to make up a substantial contribution to bottom cover.

This reef zone ranges from vertical to gently sloping surfaces and comprise depths varying from six to almost 30 m. The Sandy bottom (SB) is the zone covered essentially by sandy sediments (although silt and clay might also occur in extremely sheltered reefs) adjacent to the rocky reef slope. Carbonate is a minor contributor to these sediments except for a few rhodolith banks that occur in this region. Albeit this could be considered a different zone, fishes that occur in this zone are often the same that occur in sand sediments. Very sparsely scattered granitic boulders also occur in this zone. The Interface (INT) is the transitional zone between the complex rocky reef and the sandy bottom, characterized by hard structures, including some holes, surrounded by a matrix of sand. Water Column (WC) is represented by the pelagic environment adjacent to the rocky reef (adapted from Luiz et al. 2008).

Abundance indicator. Based on a diver's likelihood of recording a species in its usual habitat and depth range on any given dive (adapted from Feitoza et al. 2003; Luiz et al. 2008; Humann and DeLoach 2014), where CO = common (sightings are frequent); OC = occasional (sightings are not expected on a regular basis); UN = unusual (sightings occur less than occasionally); and RA = rare (sightings are exceptional).

Geographic range. The ranges of occurrence for species were based primarily in Floeter et al. (2008) and Carvalho-Filho (1999), with additional notes provided by Galván et al. (2009). Abbreviations are as follow CT = Circumtropical; CG = Circumglobal; AO = Atlantic Ocean; TA = Tropical Atlantic; EA = Eastern Atlantic; WA = Western Atlantic; SWA = Southwestern Atlantic; NWA = Northwestern Atlantic; MAR = Mid-Atlantic Ridge; MED = Mediterranean Sea; WIO = Western Indi-an Ocean; IP = Indo-Pacific Ocean; NWP = Northwestern Pacific; and TEP = Tropical Eastern Pacific (Froese and Pauly 2014). Brazilian Province endemics include species recorded from the southern tip of the Caribbean (Venezuela, Trinidad and Tobago and other islands of the Lesser Antilles), Cape Verde Archipelago and Ascension Island (Freitas et al. 2014), but which have 90% or more of its range in Brazil.

Trophic category. The diet of a species was based both in the literature (Randall 1967, 1996; Carvalho-Filho 1999; Ferreira et al. 2004; Luiz et al. 2008) and indirect observations performed by the authors, where MCAR = Macrocarnivores (species which feed mainly on mobile organisms, such as macroinvertebrates and fishes); MINV = Mobile Invertebrate Feeders (species which feed primarily on benthic mobile invertebrates, such as mollusks, crustaceans, and worms associated with hard or nearby unconsolidated substrate); OMNI = Omnivores (species which feed on a variety of resources, but that necessary include invertebrates and algae); PLANK = Planktivores (species which feed primarily on macro- and microplankton); HERB = Herbivores/ Detritivores (species, both nonterritorial and territorial herbivores, which include in their diet detritus and macroalgae) and SINV = Sessile Invertebrate Feeders (species which feed on sessile benthic invertebrates, such as cnidarians, bryozoans, ascidians and sponges).

Record type. The method by which species were recorded and documented: VOU = Museum Vouchers (the institutions and voucher numbers of specimens are provided in Appendix 1); LIT = Literature; PHO = Photographs and SIG = Sighting during underwater fieldwork.

Multivariate analysis. To describe associations of fish families to trophic categories and habitat distribution we employed a Correspondence Analysis (Nenadic and Greenacre 2007) based on species richness (i.e., number of species per family). To avoid distortions caused by highly over-dispersed data, a “Hellinger” transformation was applied before proceeding with statistical analysis (Greenacre 2007).

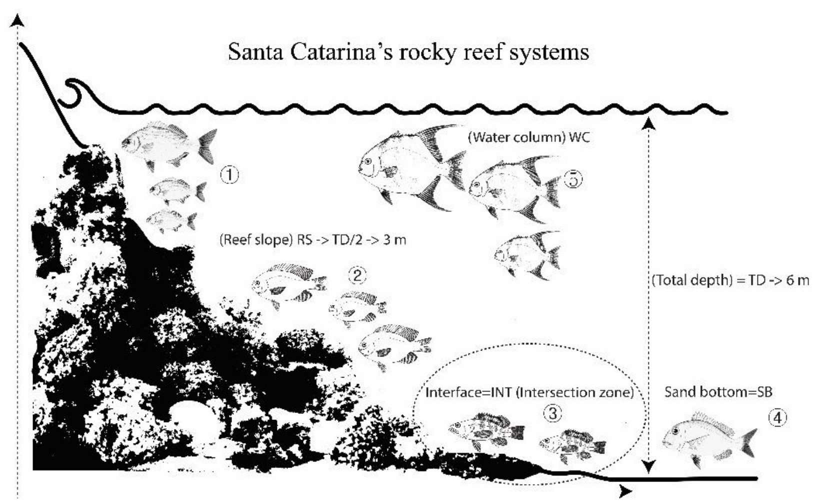

Figure 2. Hypothetical Santa Catarina rocky reef with examples of reef fish species typically associated with different zones. The Reef slope (RS) is associated to hard substrate, the Sandy bottom (SB) to sediments, the Interface (INT) is a transitional zone between the RS and the SB; and the Water column (WC) is absent on substrate. Examples of species commonly associated with a specific zone: (1) Kyphosus vaigiensis and (2) Stegastes fuscus (RS); (3) Serranus flaviventris (INT); (4) Calamus penna (SB) and (5) Chaetodipterus faber (WC).

2.3.4 RESULTS AND DISCUSSION

A total of 278 reef fish species in 170 genera and 74 families have been recorded along the coast of Santa Catarina during the past 12 years of underwater observations, as well as from the literature and museum vouchers (Table 1, Figure 3).

Based on species richness, the most representative families were Carangidae (20 species), Labridae (19 species), Carcharhinidae (11 species) and Epinephelidae (10 species). The most species-rich genera were *Carcharhinus* (eight species), followed by *Sphoeroides* and *Sparisoma* (five species). A total of 73 species were considered as “common” (CO = 26.3%), 69 species were considered “occasional” (OC = 24.8%), 132 species were considered “rare” (RA = 47.5%) (Figure 4), and four species were considered “unusual” (UN = 1.4%).

Some species are considered as “resident” organisms in the rocky reef systems, which means that they are dependent on the rocky reefs to complete their life cycles (62.6% or 174 species). All the others spend only part of their lives inhabiting the rocky reefs or adjacent habitats, and are able to survive using other habitats.

2.3.4.1 TROPHIC STRUCTURE

The two dominant trophic groups in this coastal region were the mobile invertebrate feeders (38.8%) and the macrocarnivores (32.4%), followed by planktivores (8.6%), omnivores (8.3%), herbivores/detritivores (7.6%) and sessile invertebrate feeders (4.3%) (Figure 5).

The high proportion of the mobile invertebrate feeders is a characteristic of reef fish assemblages worldwide (Ferreira et al. 2004; Luiz et al. 2008). The predators herein referred to as macrocarnivores include mainly Carcharhinidae (sharks), Carangidae (jacks and pompanos), Epinephelidae (groupers), Lutjanidae (snappers) and Scombridae (tunas and mackerels). In Santa Catarina, most planktivore species are Clupeidae and of the genus Chromis (Pomacentridae), as well as few species from other families. The herbivore/detritivores are mainly represented by Pomacentridae and Labridae-Scarini species. The sessile invertebrate feeders in this rocky environment are the generalists Chaetodontidae and Pomacanthidae, which consume a considerable amount of cnidarians and sponges, respectively. These families are also known to rely heavily on mobile invertebrates and algae, respectively.

2.3.4.2 HABITAT DISTRIBUTION AND THREATENED SPECIES

Distributions of rocky reef species within the habitat types, as evidenced herein by the Correspondence Analysis, mirror the classic ecological partitioning by fishes of the Brazilian rocky reef habitats (Sazima 1986). Specifically, apex predators, such as sharks, mesocarnivores, such as Carangidae and Scombridae, as well as Clupeidae and Engraulidae planktivores, all occupy the water column strata. Herbivores/ detritivores, omnivores, mobile invertebrate feeders and Epinephelidae mesocarnivores occupy the reef slope, while mullets and flat fishes dwell on the sandy bottom (Sazima 1986, Figure 6).

Several species are considered threatened according to the IUCN endangered species Red List (IUCN 2015). The relative proportion of threatened species has reached 8.3% (or 23 of 278 species) and encompasses mostly top predators, such as sharks (34.8%) and groupers (17.4%).

2.3.4.3 TAXONOMIC UPDATES

Following recent revisions of the families Kyphosidae (Knudsen and Clements 2013), Scaridae (Westneat and Alfaro 2005; Choat et al. 2012) and Serranidae (Craig and Hastings 2007; Smith and Craig 2007), and the genera *Hippocampus* (Boehm et al. 2013) and *Synodus* (Frable et al. 2013), some taxonomic updates shall be discussed. The whole family Scaridae is now recognized as a lineage of Labridae and now represents the Tribe Scarini (Westneat and Alfaro 2005; Choat et al. 2012). The family Epinephelidae was split from Serranidae, and the snowy grouper complex *Epinephelus niveatus* is now included in the previously invalidated genus Hyporthodus (i.e., *Hyporthodus niveatus*).

In the family Kyphosidae, the former species *Kyphosus incisor* (Cuvier, 1831), listed from Santa Catarina along with *Kyphosus sectatrix* (Linnaeus, 1758), both by Carvalho-Filho (1999) and Hostim-Silvaet al. (2006), is now revalidated as *Kyphosus vaigiensis* (Quoy & Gaimard, 1825) (Knudsen and Clements 2013). As this revision is recent, we could not determine wether the other Atlantic species, *K. cinerascens* and *K. bigibbus* do occur in Santa Catarina. In the genus *Hippocampus*, the Southwestern Atlantic species of the *H. erectus* complex is now considered to harbor two species, being *H. erectus* restricted to Brazil (Silveira et al. 2014), and the other ranging from Brazil to Uruguay and Argentina under the name of *Hippocampus patagonicus* Piacentino & Luzzatto, 2004 (Boehm et al. 2013; Silveira et al. 2014). In the *Synodus* genus, *Synodus foetens* (Linnaeus, 1766) may be considered restricted to nortwestern Atlantic (Frable et al. 2013). The species recorded for the southern part of Caribbean is now renamed as *Synodus bondi* Fowler, 1939. Although the authors suggest that the species which occur along Brazilian coast should be *S. bondi* (and we therefore consider it to), they did not possess a sufficient sampling of Brazilian individuals to avert the possibility that it is yet another species.

2.3.4.4 NEW RECORDS AND EXTREME RANGE EXTENSIONS

During this work, twelve species of reef fish were recorded for the first time for the coast of Santa Catarina: *Acanthurus coeruleus* (Bloch & Schneider, 1801); *Acanthurus monroviae* Steindachner, 1876; *Apogon americanus* (Castelnau 1855); *Cantherhines macrocerus* (Hollard, 1853); *Chaetodon sedentarius* (Poeyi, 1860); *Chromis flavicauda* (Günther, 1880); *Clepticus brasiliensis* (Heiser, Moura & Robertson, 2000); *Decapterus punctatus* (Cuvier, 1829); *Gymnothorax vicinus* (Castelnau, 1855); *Quassiremus ascensionis* (Studer, 1889); *Muraena retifera* Goode & Bean, 1882 and *Stegastes partitus* (Poey, 1868). For *S. partitus*, this is the first documented record for Southwestern Atlantic waters, and for *Q. ascensionis* this is the second record for the coastal Southwestern Atlantic (Figure 7). For *Acanthurus monroviae* Steindachner, 1876, this is also the third record for Southwestern Atlantic waters. Details on the new records are given below (ordered alphabetically by Order and then Family).

Table I. Checklist of reef fish species recorded at Santa Catarina State coast. The genera and species are arranged in alphabetical order within families. Additional information: **IUCN Status:** Extinct **(EX)** – No known individuals remaining; Extinct in the Wild **(EW)** – Known only to survive in captivity; Critically Endangered **(CR)** – extremely high risk of extinction in the wild; Endangered **(EN)** – high risk of extinction in the wild. Vulnerable **(VU)** – high risk of endangerment in the wild; Near Threatened **(NT)** – likely to become endangered in the near future. Least Concern **(LC)** – Lowest risk. Data Deficient **(DD)** – not enough data to make an assessment of its risk of extinction. Not Evaluated **(NE)** – not yet evaluated against the criteria. **Trophic Category: MCAR**=Carnivore; **MINV**=Mobile Invertebrate Feeder; **OMNI**=Omnivore; **PLANK**=Planktivores; **SINV**=Sessile Invertebrate Feeder; **HERB** = Algivores. **Habitat: RS** = Reef Slope; **INT**=Interface; **SB=**Sandy Bottom; **WC**=Water Column. RE: **Residence**= **R -** Rock reef; **T** – Transient fish. **Occurrence: CO**=Common; **OC**= Occasional; **RA**=Rare; **UN**=Unusual. **Geographic range: CT**=Circumtropical, **CG**=Circumglobal, **AO**=Atlantic Ocean, **TA**=Tropical Atlantic, **EA**=Eastern Atlantic, **WA**=Western Atlantic, **SWA**= Southwestern Atlantic, **SEA**= Southeastern Atlantic, **SEP**=Southeastern Pacific; **NWA**=Northwestern Atlantic, **MED**=Mediterranean Sea, **WIO**=Western Indian Ocean, **EIO**=Eastern Indian Ocean, **IP**=Indo-Pacific Ocean, **NWP**=Northwestern Pacific, **TEP**=Tropical Eastern Pacific, **EP**=Eastern Pacific **Record Type: LIT** = *in litteris*; **VOU**= Museum Voucher; **PHO** = Photograph; **UVC** = recorded during underwater visual censuses.

Photographic records:

1) Anderson et al. 2014a
2) Hostim-Silva et al. 2006
3) Marine Macroecology and Biogeography Lab, Photographic Databank
4) Souza 2000

	Species	Authority	IUCN	Trophic	Habitat	RE	Occur.	Geog. range	Rec.Type
Carcharhinidae	*Carcharhinus brevipinna*	(Müller & Henle, 1839)	NT	MCAR	WC		RA	WA/EA/MED /IP	VOU
	Carcharhinus isodon	(Müller & Henle, 1839)	LC	MCAR	WC		OC	WA	VOU
	Carcharhinus leucas	(Muller & Henle, 1839)	NT	MCAR	WC		RA	CT	LIT
	Carcharhinus limbatus	(Muller & Henle, 1839)	NT	MCAR	WC		RA	CT	LIT
	Carcharhinus obscurus	(LeSueur, 1818)	VU	MCAR	WC		RA	WA/EA/MED /IP	VOU
	Carcharhinus plumbeus	(Nardo, 1827)	VU	MCAR	WC		RA	CT	LIT/VOU
	Carcharhinus porosus	(Ranzani, 1839)	DD	MCAR	WC		RA	WA	VOU
	Carcharhinus signatus	(Poey, 1868)	VU	MCAR	WC		RA	WA/EA	VOU
	Galeocerdo cuvier	(Perón &LeSueur,1822)	NT	MCAR	WC		RA	CT	LIT
	Rhizoprionodon lalandii	(Müller & Henle, 1839)	DD	MCAR	WC		RA	WA	VOU
	Rhizoprionodon porosus	(Poey, 1861)	LC	MCAR	WC		RA	WA	LIT
Dasyatidae	*Dasyatis americana*	Hildebrand & Schroeder, 1928	DD	MINV	SB	R	RA	WA	LIT
	Dasyatis centroura	(Mitchill, 1815)	LC	MINV	SB		RA	WA/EA	SIG/LIT/PHO[3]
	Dasyatis guttata	(Bloch & Schneider, 1801)	DD	MINV	SB		RA	WA	SIG/LIT/PHO[1,3]
	Dasyatis hypostigma	Santos & Carvalho, 2004	LC	MINV	SB		RA	SWA	VOU
	Pteroplatytrygon violacea	(Bonaparte, 1832)	LC	MINV	SB		RA	CG	SIG/LIT/PHO[3]
Gymnuridae	*Gymnura altavela*	(Linnaeus, 1758)	VU	MINV	SB	R	RA	WA/EA	SIG/LIT/PHO[1]
Lamnidae	*Isurus oxyrhincus*	Rafinesque, 1810	VU	MCAR	WC		RA	CG	LIT
Myliobatidae	*Aetobatus narinari*	(Euphrasen, 1790)	NT	MINV	WC	R	RA	CT	SIG/LIT/PHO[1,2,3]
	Manta birostris	(Walbaum, 1792)	NT	PLANK	WC		UN	CG	LIT
	Mobula thurstoni	(Lloyd, 1908)	NT	PLANK	WC		UN	CG	LIT
Narcinidae	*Narcine brasiliensis*	(Olfers, 1831)	DD	MINV	SB	R	OC	WA	SIG/LIT/VOU/PHO[1,2,3]
Odontaspididae	*Carcharias taurus*	Rafinesque, 1810	VU	MCAR	WC/RS		RA	CG	LIT/PHO[4]
Rhinobatidae	*Rhinobatos sp.*			MINV	SB		RA	SWA	SIG/LIT/PHO[3]

	Rhinobatos percellens	(Walbaum, 1792)	NT	MINV	SB		RA	SWA/EA	LIT/VOU/PHO[3]
	Zapteryx brevirostris	(Muller & Henle, 1841)	VU	MINV	SB	R	RA	SWA	LIT/VOU
Rhincodontidae	*Rhincodon typus*	Smith, 1828	VU	PLANK	WC		RA	CT	LIT/PHO
Sphyrnidae	*Sphyrna lewini*	(Griffith & Smith, 1834)	EN	MCAR	WC		RA	CG	LIT/VOU
	Sphyrna tiburo	(Linnaeus, 1758)	LC	MCAR	WC		RA	WA/TEP	LIT
	Sphyrna zygaena	(Linnaeus, 1758)	VU	MCAR	WC		RA	CG	VOU
Acanthuridae	*Acanthurus bahianus+*	Castelnau, 1855	LC	HERB	RS/INT/SB	R	OC	SWA/MAR	SIG/LIT/VOU/PHO[1,2,3]
	Acanthurus chirurgus	(Bloch, 1787)	LC	HERB	RS/INT/SB	R	OC	AO	SIG/LIT/VOU/PHO[1,2,3]
	*Acanthurus coeruleus**	Bloch & Schneider, 1801	LC	HERB	RS/INT/SB	R	RA	WA/MAR	SIG/LIT/PHO[1,3]
	*Acanthurus monroviae**	Steindachner, 1876	LC	PLANK	WC/RS/INT		RA	EA	PHO[3]

Family	Species	Authority	IUCN	Trophic	Habitat	RE	Occur.	Geog. range	Rec.Type
Apogonidae	*Apogon americanus*+*	Castelnau, 1855	NE	PLANK	RS	R	OC	SWA	PHO[3]
	Apogon pseudomaculatus	Longley, 1932	NE	PLANK	RS	R	OC	WA/EA	SIG/LIT/PHO[1,2,3]
	Phaeoptyx pigmentaria	(Poey, 1860)	LC	PLANK	RS	R	OC	WA/EA	SIG/LIT/PHO[1,2,3]
Antennariidae	*Antennarius striatus*	(Shaw, 1794)	NE	MCAR	RS/INT	R	RA	CT	LIT
	Histrio histrio	(Linnaeus, 1758)	NE	MCAR	RS/INT		RA	CT	LIT
Ariidae	*Cathorops spixii*	(Agassiz, 1829)	NE	MCAR	SB		OC	WA	VOU
	Genidens barbus	(Lacepède, 1803)	NE	MCAR	SB		OC	SWA	VOU
	Genidens genidens	(Cuvier, 1829)	LC	MCAR	RS/INT/SB		RA	SWA	SIG/LIT/VOU/PHO[1,3]
Balistidae	*Balistes capriscus*	Gmelin, 1789	NE	MINV	RS/INT/SB	R	OC	WA/EA/MED	SIG/LIT/VOU
	Balistes vetula	Linnaeus, 1758	VU	MINV	RS/INT/SB	R	RA	AO	SIG/LIT/PHO[1,3]
Batrachoididae	*Porichthys porosissimus*	(Cuvier, 1829)	NE	MCAR	RS/INT/SB	R	CO	SWA	SIG/LIT/VOU/PHO[2,3]
	Thalassophryne montevidensis	(Berg, 1893)	NE	MCAR	SB/INT		RA	SWA	LIT
Belonidae	*Strongylura marina*	(Walbaum, 1792)	NE	OMNI	WC		OC	WA	VOU
	Tylosurus acus	(Lacepède, 1803)	NE	MCAR	WC		RA	CT	LIT

Blenniidae	*Hypleurochilus fissicornis*	(Quoy & Gaimard, 1824)	NE	MINV	RS/INT	R	CO	SWA/EA	SIG/LIT/VOU/PHO^{1,3}
	Hypleurochilus pseudoaequipinnis	Bath, 1994	NE	MINV	RS/INT	R	OC	WA	LIT/VOU
	Hypsoblennius invemar	Smith-Vaniz & Acero, 1980	NE	MINV	RS	R	CO	WA	SIG/LIT/VOU
	Ophioblennius trinitatis+	Miranda-Ribeiro, 1919	NE	HERB	RS	R	CO	SWA	SIG/LIT/VOU/PHO^{1,3}
	Parablennius marmoreus	(Poey, 1876)	NE	OMNI	RS/INT	R	CO	WA	SIG/LIT/VOU
	Parablennius pilicornis	(Cuvier, 1829)	NE	OMNI	RS/INT	R	CO	SWA/EA/MED/WIO	SIG/LIT/VOU
	Scartella cristata	(Linnaeus, 1758)	NE	HERB	RS	R	CO	WA/EA/NWP	SIG/LIT/VOU/PHO^{2,3}
Bothidae	*Bothus ocellatus*	(Agassiz, 1831)	NE	MINV	SB	R	OC	WA	SIG/LIT/VOU
	Bothus maculiferus	(Poey, 1860)	NE	MINV	SB		OC	WA/EA	SIG/LIT/PHO^{3}
Callionymidae	*Callionymus bairdi*	Jordan, 1888	NE	MINV	RS/INT/SB	R	RA	AO	LIT/VOU/PHO^{3}
Carangidae	*Alectis ciliaris*	(Bloch, 1787)	LC	MCAR	WC		RA	CT	SIG/LIT/PHO^{3}
	Caranx crysos	(Mitchill, 1815)	LC	MCAR	WC	R	OC	AO	SIG/LIT/VOU/PHO^{3}
	Caranx hippos	(Linnaeus, 1766)	NE	MCAR	WC	R	RA	WA/EA	SIG/LIT/VOU/PHO^{3}
	Caranx latus	Agassiz, 1831	NE	MCAR	WC	R	RA	AO	SIG/LIT/VOU/PHO^{1,3}
	Chloroscombrus chrysurus	(Linnaeus, 1766)	NE	PLANK	WC	R	RA	WA/EA	LIT/VOU
	Decapterus macarellus	(Cuvier, 1833)	NE	PLANK	WC		OC	CG	SIG/LIT/PHO^{3}
	*Decapterus punctatus**	(Cuvier, 1829)	NE	PLANK	WC		OC	AO	SIG/PHO^{3}
	Naucrates ductor	(Linnaeus, 1758)	NE	MCAR	WC		RA	CT	LIT
	Oligoplites saliens	(Bloch, 1793)	NE	PLANK	WC		RA	WA	SIG/LIT/VOU/PHO^{3}
	Oligoplites saurus	(Bloch & Schneider, 1801)	NE	MCAR	WC		RA	WA/TEP	LIT/VOU
	Pseudocaranx dentex	(Bloch & Schneider, 1801)	NE	PLANK	WC/SB	R	CO	CT	SIG/LIT/VOU
	Selene setapinnis	(Mitchill, 1815)	NE	MCAR	WC		RA	WA	VOU
	Selene vomer	(Linnaeus, 1758)	NE	MCAR	WC		OC	WA	SIG/LIT/VOU/PHO^{3}
	Seriola dumerili	(Risso, 1810)	NE	MCAR	WC	R	OC	CG	SIG/LIT/PHO^{1,2,3}
	Seriola lalandi	Valenciennes, 1833	NE	MCAR	WC	R	OC	CG	SIG/LIT/PHO^{1,3}
	Seriola rivoliana	Valenciennes, 1833	NE	MCAR	WC	R	OC	CG	SIG/LIT/PHO^{1,2,3}

Family	Species	Authority	IUCN	Trophic	Habitat	RE	Occur.	Geog. range	Rec.Type
	Trachinotus carolinus	(Linnaeus, 1766)	NE	MCAR	WC	R	OC	WA	SIG/LIT/VOU/PHO[3]
	Trachinotus falcatus	(Linnaeus, 1758)	NE	MCAR	WC	R	OC	WA	SIG/LIT/VOU/PHO[1,3]
	Trachinotus goodei	Jordan & Evermann, 1896	NE	MCAR	WC	R	OC	WA	SIG/LIT/PHO[1,3] SIG/LIT/PHO[1,3]
	Trachinotus marginatus	(Cuvier, 1832)	NE	MCAR	WC	R	CO	WA	SIG/LIT/VOU/PHO[3]
Centropomidae	*Centropomus undecimalis*	(Bloch, 1792)	NE	MCAR	RS/INT/SB	R	CO	WA	SIG/LIT/VOU
	Centropomus parallelus	Poey, 1860	NE	MCAR	RS/INT/SB	R	CO	WA	SIG/LIT/VOU/PHO[3]
Chaenopsidae	*Emblemariopsis signifer*	(Ginsburg, 1942)	LC	MINV	RS/INT	R	CO	WA	SIG/LIT/VOU
Chaetodontidae	*Chaetodon sedentarius**	Poey, 1860	LC	SINV	RS/INT/SB	R	RA	WA/EA	LIT/PHO[3]
	Chaetodon striatus	Linnaeus, 1758	LC	SINV	RS/INT/SB	R	CO	WA	SIG/LIT/VOU
	Prognathodes guyanensis	(Durand, 1960)	LC	SINV	RS/INT/SB	R	RA	WA	LIT/VOU
Cirrhitidae	*Amblycirrhitus pinos*	(Mowbray, 1927)	NE	MINV	RS/INT	R	RA	WA/MAR	LIT/PHO[1,2,3]
Clupeidae	*Harengula clupeola*	(Cuvier, 1829)	NE	PLANK	WC		CO	WA	VOU/PHO[1,3]
	Opisthonema oglinum	(LeSueur, 1818)	NE	PLANK	WC		RA	WA	LIT/VOU
	Sardinella aurita	Valenciennes, 1847	NE	PLANK	WC		RA	WA/EA	LIT
	Sardinella brasiliensis	(Steindachner, 1879)	NE	PLANK	WC		CO	WA	SIG/LIT/VOU/PHO[3]
Dactylopteridae	*Dactylopterus volitans*	(Linnaeus, 1758)	NE	MINV	INT/SB	R	OC	WA/EA	SIG/LIT/VOU
Dactyloscopidae	*Dactyloscopus crossotus*	Starks, 1913	NE	MINV	INT/SB		RA	WA	LIT/VOU
	Dactyloscopus foraminosus	Dawson, 1982	LC	MINV	INT/SB		RA	WA	LIT
	Dactyloscopus tridigitatus	Gill, 1859	LC	MINV	INT/SB		RA	WA	LIT
Diodontidae	*Chilomycterus reticulatus*	(Linnaeus, 1758)	NE	SINV	RS/INT/SB	R	RA	CG	SIG/LIT/VOU/PHO
	Chilomycterus spinosus	(Linnaeus, 1758)	NE	SINV	RS/INT/SB	R	OC	SWA	SIG/LIT/VOU/PHO[1,3]
	Diodon holocanthus	Linnaeus, 1758	NE	SINV	RS/INT/SB	R	OC	CT	SIG/LIT/PHO[3]
	Diodon hystrix	Linnaeus, 1758	NE	SINV	RS/INT/SB	R	OC	CT	SIG/LIT/PHO[1,3]
Echeneidae	*Echeneis naucrates*	Linnaeus, 1758	NE	MCAR	WC		RA	CT	LIT/VOU/PHO[2,3]

	Remora remora	(Linnaeus, 1758)	NE	MCAR	WC		RA	CT	LIT
Eleotridae	*Eleotris pisonis*	(Gmelin, 1789)	NE	MINV	RS/INT		RA	WA	LIT/VOU
Ephippidae	*Chaetodipterus faber*	(Broussonet, 1782)	NE	MINV	WC	R	CO	WA	SIG/LIT/VOU
Epinephelidae	*Epinephelus adscensionis*	(Osbeck, 1765)	LC	MCAR	RS/INT/SB	R	RA	AO	SIG/LIT
	Epinephelus itajara	(Lichtenstein, 1822)	CR	MCAR	RS/INT/SB	R	RA	WA/EA	LIT/PHO^{1,2,3}
	Epinephelus marginatus	(Lowe, 1834)	EN	MCAR	RS/INT/SB	R	CO	WA/EA	SIG/LIT/VOU
	Epinephelus morio	(Valenciennes, 1828)	NT	MCAR	RS/INT/SB	R	OC	WA	SIG/LIT/PHO^{1,3}
	Hyporthodus niveatus	(Valenciennes, 1828)	VU	MCAR	RS/INT/SB	R	CO	WA	SIG/LIT/VOU
	Mycteroperca acutirostris	(Valenciennes, 1828)	LC	MCAR	RS/INT/SB	R	CO	WA	SIG/LIT/VOU/PHO^{1,2,3}
	Mycteroperca bonaci	(Poey, 1860)	NT	MCAR	RS/INT/SB	R	OC	WA	SIG/LIT/VOU/PHO^{1,2,3}
	Mycteroperca interstitialis	(Poey, 1860)	VU	MCAR	RS/INT/SB	R	RA	WA	SIG/LIT/PHO^{1,3}
	Mycteroperca microlepis	(Goode & Bean, 1879)	LC	MCAR	RS/INT/SB	R	RA	WA	SIG/LIT/PHO^{3}
	Paranthias furcifer	(Valenciennes, 1828)	LC	PLANK	INT/SB	R	RA	WA/EA	SIG/LIT/PHO^{1,3}
Fistulariidae	*Fistularia petimba*	Lacepède, 1803	NE	MCAR	RS/INT/SB	R	RA	WA/EA/MED /IP	VOU
	Fistularia tabacaria	Linnaeus, 1758	NE	MCAR	RS/INT/SB	R	CO	WA/EA	SIG/LIT/VOU/PHO^{1,3}
Gerreidae	*Diapterus auratus*	Ranzani, 1842	NE	MINV	INT/SB		CO	WA	SIG/LIT/VOU/PHO^{3}
	Diapterus rhombeus	(Cuvier, 1829)	NE	MINV	INT/SB		OC	WA	VOU
	Eucinostomus argenteus	Baird & Girard, 1855	NE	MINV	INT/SB		OC	EP/WA/EA	VOU
	Eucinostomus gula	(Quoy & Gaimard, 1824)	NE	MINV	INT/SB		CO	WA	SIG/LIT/VOU/PHO^{3}
	Eucinostomus melanopterus	(Bleeker, 1863)	NE	MINV	INT/SB		CO	WA/EA	SIG/LIT/VOU/PHO^{3}
	Eugerres brasilianus	(Cuvier, 1830)	NE	MINV	INT/SB		CO	WA	SIG/LIT/VOU/PHO^{3}
Gobiesocidae	*Gobiesox barbatulus*	Starks, 1913	NE	MINV	RS		RA	WA	SIG/LIT/VOU/PHO^{3}
Family	*Species*	Authority	IUCN	Trophic	Habitat	RE	Occur.	Geog. range	Rec.Type
	Tomicodon australis	Briggs 1955	NE	MINV	RS		RA	WA	VOU

Gobiidae	*Barbulifer ceuthoecus*	(Jordan & Gilbert, 1884)	NE	MINV	INT/SB		RA	WA	LIT/VOU
	Bathygobius soporator	(Valenciennes, 1837)	NE	MINV	RS/INT/SB		CO	EA/WA/MED	SIG/LIT/VOU/PHO3
	Coryphopterus glaucofraenum	Gill, 1863	NE	OMNI	INT/SB	R	CO	WA	SIG/LIT/VOU
	Ctenogobius saepepallens	(Gilbert & Randall, 1968)	NE	MINV	INT/SB		RA	WA	SIG/LIT/PHO1,3
	Ctenogobius stigmaticus	(Poey, 1860)	NE	MINV	RS/INT/SB		RA	WA	LIT/VOU
	Elacatinus figaro+	Sazima, Moura & Rosa, 1996	NE	MINV	RS/INT/SB	R	RA	SWA	LIT/VOU
	Gnatholepis thompsoni	Jordan, 1904	NE	MINV	RS/INT/SB	R	RA	WA	SIG/LIT
	Gobiosoma hemigymnum	(Eingenmann & Eingenmann, 1888)	NE	MINV	RS/INT/SB		RA	WA	LIT/PHO3
	Microgobius meeki	Evermann & Marsh, 1899	NE	MINV	RS/INT/SB		RA	WA	LIT/VOU
Haemulidae	*Anisotremus surinamensis*	(Bloch, 1791)	NE	MINV	RS/INT	R	CO	WA	SIG/LIT/VOU
	Anisotremus virginicus	(Linnaeus, 1758)	NE	MINV	RS/INT	R	CO	WA	SIG/LIT/VOU
	Haemulon aurolineatum	Cuvier, 1830	NE	MINV	RS/INT/SB	R	CO	WA	SIG/LIT/VOU
	Haemulon steindachneri	(Jordan & Gilbert, 1882)	NE	MINV	RS/INT/SB	R	OC	WA	SIG/LIT/VOU/PHO3
	Haemulon parra	(Desmarest, 1823)	NE	MINV	RS/INT/SB	R	OC	WA	SIG/LIT/PHO3
	Orthopristis ruber	(Cuvier, 1830)	NE	MINV	RS/INT/SB	R	CO	WA	SIG/LIT/VOU
Hemiramphidae	*Hemiramphus brasiliensis*	(Linnaeus, 1758)	NE	OMNI	WC		OC	WA/EA	SIG/LIT/VOU/PHO3
	Hyporhamphus unifasciatus	(Ranzani, 1841)	NE	OMNI	WC		RA	WA	SIG/LIT/VOU/PHO3
Holocentridae	*Holocentrus adscensionis*	(Osbeck, 1765)	NE	MINV	RS/INT/SB	R	CO	AO	SIG/LIT/VOU
	Myripristis jacobus	Cuvier, 1829	NE	MINV	RS/INT	R	RA	AO	SIG/LIT/VOU
Kyphosidae	*Kyphosus sectatrix*	(Linnaeus, 1758)	NE	HERB	RS	R	CO	CT	SIG/LIT/PHO3
	Kyphosus vaigiensis	(Quoy & Gaimard, 1825)	NE	HERB	RS	R	CO	CT	SIG/LIT/VOU
Labridae - Hypsigeninae	*Bodianus pulchellus*	(Poey, 1860)	LC	MINV	RS/INT	R	OC	WA/EA	SIG/LIT/VOU
	Bodianus rufus	(Linnaeus, 1758)	LC	MINV	RS/INT	R	CO	WA	SIG/LIT/PHO1,2,3

Labridae - Julidinae	*Clepticus brasiliensis**+	Heiser, Moura & Robertson, 2000	LC	PLANK	RS/WC	R	RA	SWA	SIG/LIT/PHO1,3
	Doratonotus megalepis	Günther 1862	LC	MINV	RS	R	RA	WA	SIG/LIT
	Halichoeres brasiliensis+	(Bloch, 1791)	LC	MINV	RS/INT/SB	R	OC	SWA	SIG/LIT/PHO1,3
	Halichoeres dimidiatus	(Agassiz, 1831)	LC	MINV	RS/INT/SB	R	RA	SWA	SIG/LIT/PHO3
	Halichoeres poeyi	(Steindachner, 1867)	LC	MINV	RS/INT/SB	R	CO	WA	SIG/LIT/VOU
	Halichoeres sazimai+	Luiz, Ferreira & Rocha, 2009	NE	MINV	RS/INT/SB	R	RA	SWA	SIG/LIT/PHO3
	Thalassoma noronhanum+	(Boulenger, 1890)	LC	PLANK	RS/INT/SB	R	RA	SWA	SIG/LIT/PHO1,3
	Xyrichtys novacula	(Linnaeus, 1758)	LC	MINV	SB	R	RA	WA/EA	SIG/LIT/VOU/PHO1,3
Labridae - Scarini	*Cryptotomus roseus*	Cope, 1871	LC	HERB	RS/INT/SB	R	CO	WA/MAR	SIG/LIT/VOU/PHO1,2,3
	Nicholsina usta	Valenciennes, 1840	LC	HERB	RS/INT	R	RA	WA	SIG/LIT/PHO3
	Scarus trispinosus+	Valenciennes, 1840	EN	HERB	RS/INT/SB	R	RA	SWA	LIT/PHO1,3
	Scarus zelindae+	Moura, Figueiredo & Sazima, 2001	DD	HERB	RS/INT/SB	R	RA	SWA	SIG/LIT/PHO1,3
	Sparisoma amplum+	(Ranzani, 1841)	LC	HERB	RS/INT/SB	R	CO	SWA	SIG/LIT/PHO1,2,3
	Sparisoma axillare+	(Steindachner, 1878)	LC	HERB	RS/INT/SB	R	CO	SWA	SIG/LIT/PHO1,2,3
	Sparisoma frondosum+	(Agassiz, 1831)	DD	HERB	RS/INT/SB	R	CO	SWA/EA	SIG/LIT/PHO1,2,3
	Sparisoma radians	(Valenciennes, 1840)	LC	HERB	RS/INT/SB	R	CO	SWA	SIG/LIT/PHO1,3
	Sparisoma tuiupiranga+	Gasparini, Joyeux & Floeter, 2003	LC	HERB	RS/INT/SB	R	OC	SWA	SIG/LIT/PHO1,2,3
Labrisomidae	*Labrisomus cricota*+	Sazima, Gasparini & Moura, 2002	NE	MINV	RS/INT	R	RA	SWA	SIG/LIT/VOU/PHO3
Family	**Species**	**Authority**	**IUCN**	**Trophic**	**Habitat**	**RE**	**Occur.**	**Geog. range**	**Rec.Type**
	Labrisomus nuchipinnis	(Quoy & Gaimard, 1824)	NE	MINV	RS/INT	R	CO	WA/EA	SIG/LIT/VOU
	Malacoctenus delalandii	(Valenciennes, 1836)	NE	MINV	RS/INT	R	CO	WA	SIG/LIT/PHO^{1,2,3}
	Malacoctenus aff. triangulatus+		NE	MINV	RS/INT	R	RA	SWA	LIT/VOU
	Paraclinus rubicundus	(Starks, 1913)	LC	MINV	RS/INT	R	RA	SWA	LIT
	Paraclinus spectator+	Guimarães & Bacelar, 2002	NE	MINV	RS/INT	R	OC	SWA	SIG/LIT/PHO^{1,3}
	Starksia brasiliensis+	(Gilbert, 1900)	NE	MINV	RS/INT	R	OC	SWA	SIG/LIT/VOU/PHO^{3}
Lobotidae	*Lobotes surinamensis*	(Bloch, 1790)	NE	MCAR	RS/INT		RA	CT	LIT/PHO^{3}

Lutjanidae	*Lutjanus analis*	(Cuvier, 1828)	VU	MCAR	RS/INT/SB	R	RA	WA	SIG/LIT/VOU/PHO[1,3]
	Lutjanus cyanopterus	(Cuvier, 1828)	VU	MCAR	RS/INT/SB	R	RA	WA	SIG/LIT/PHO[3]
	Lutjanus jocu	(Bloch & Schneider, 1801)	NE	MCAR	RS/INT/SB	R	RA	WA/MAR	SIG/LIT/VOU/PHO[1,3]
	Rhomboplites aurorubens	(Cuvier, 1829)	NE	MCAR	RS/INT	R	OC	WA	SIG/LIT/PHO[1,3]
Malacanthidae	*Malacanthus plumieri*	(Bloch, 1786)	NE	MCAR	RS/INT/SB	R	OC	WA/MAR	SIG/LIT/VOU/PHO[1,3]
Microdesmidae	*Ptereleotris randalli+*	Gasparini, Rocha & Floeter, 2001	NE	MINV	SB	R	OC	SWA	SIG/LIT/PHO[1,3]
Monacanthidae	*Aluterus monoceros*	(Linnaeus, 1758)	NE	OMNI	RS/INT/SB	R	OC	CT	SIG/LIT/PHO[1,2,3]
	Aluterus scriptus	(Osbeck, 1765)	NE	OMNI	RS/INT/SB	R	RA	CT	PHO/LIT
	*Cantherhines macrocerus**	(Hollard, 1853)	NE	SINV	RS	R	RA	WA/EA	PHO
	Monacanthus ciliatus	(Mitchill, 1818)	NE	OMNI	RS/INT/SB	R	RA	WA	LIT/VOU
	Stephanolepis hispidus	(Linnaeus, 1766)	NE	OMNI	RS/INT/SB	R	CO	WA/EA	SIG/LIT/VOU
	Stephanolepis setifer	(Bennett, 1831)	NE	OMNI	RS/INT/SB	R	RA	WA	LIT
Mugilidae	*Mugil curema*	Valenciennes, 1836	NE	OMNI	INT/SB	R	CO	WA/EA/TEP	SIG/LIT/VOU
	Mugil liza	Valenciennes, 1836	NE	OMNI	INT/SB		CO	WA	SIG/LIT/VOU/PHO[3]
Mullidae	*Pseudupeneus maculatus*	(Bloch, 1793)	NE	MINV	RS/INT/SB	R	CO	WA	SIG/LIT/VOU
	Upeneus parvus	Poey, 1852	NE	MINV	RS/INT/SB		RA	WA	LIT/PHO
Muraenidae	*Echidna catenata*	(Bloch, 1795)	NE	MCAR	RS	R	RA	WA/MAR	LIT/VOU
	Gymnothorax funebris	Ranzani, 1839	NE	MCAR	RS	R	OC	WA	SIG/LIT/PHO[1,2,3]
	Gymnothorax moringa	(Cuvier,1829)	NE	MCAR	RS	R	CO	WA/MAR	SIG/LIT/VOU
	Gymnothorax ocellatus	Agassiz, 1831	NE	MCAR	RS		RA	AO	VOU
	*Gymnothorax vicinus**	(Castelnau, 1855)	NE	MCAR	RS	R	OC	TA	PHO[3]
	*Muraena retifera**	Goode & Bean, 1882	NE	MCAR	INT/SB	R	RA	WA	PHO
Ogcocephalidae	*Ogcocephalus vespertilio*	(Linnaeus, 1758)	NE	MINV	RS/INT/SB	R	CO	WA	SIG/LIT/VOU
Ophichthidae	*Ahlia egmontis*	(Jordan, 1884)	NE	MINV	RS/INT/SB	R	RA	WA	LIT
	Myrichthys breviceps	(Richardson, 1848)	NE	MINV	RS/INT	R	OC	WA	SIG/LIT/VOU
	Myrichthys ocellatus	(LeSueur, 1825)	NE	MINV	RS/INT	R	CO	WA	SIG/LIT/VOU

Family	Species	Authority	IUCN	Trophic	Habitat	RE	Occur.	Geog. range	Rec.Type
	Myrophis punctatus	Lütken, 1852	NE	MINV	RS/INT/SB		RA	WA	LIT
	*Quassiremus ascensionis**	(Richardson, 1848)	NE	MINV	INT/SB	R	UN	EA	SIG/PHO[3]
	Ophichthus ophis	(Castelnau, 1855)	NE	MINV	INT/SB		RA	WA	PHO
Ophidiidae	*Genipterus brasiliensis*	Regan, 1903	NE	MINV	SB/INT		RA	SWA	LIT
	Ophidion holbrooki	Putnam, 1874	NE	MINV	SB/INT		RA	WA	LIT/VOU
	Raneya brasiliensis	(Kaup, 1856)	NE	MINV	SB/INT		RA	SWA	LIT
Ostraciidae	*Acanthostracion polygonius*	Poey, 1876	NE	OMNI	RS/INT/SB	R	OC	WA	SIG/LIT/PHO[1,2,3]
	Acanthostracion quadricornis	(Linnaeus, 1758)	NE	OMNI	RS/INT/SB	R	OC	WA/EA	SIG/LIT/VOU
	Lactophys trigonus	(Linnaeus, 1758)	NE	OMNI	RS/INT/SB		RA	WA	LIT/VOU
Paralichthyidae	*Cyclopsetta fimbriata*	(Goode & Bean, 1885)	NE	MINV	SB		OC	WA	SIG/LIT/PHO[3]
	Paralichthys brasiliensis	(Ranzani, 1842)	NE	MINV	SB		OC	SWA	LIT/VOU
	Syacium micrurum	Ranzani, 1842	NE	MINV	SB		RA	WA	VOU
	Syacium papillosum	(Linnaeus, 1758)	NE	MINV	SB		RA	WA/MAR	LIT
Pempheridae	*Pempheris schomburgki*	Müller & Troschel, 1848	NE	PLANK	RS/INT	R	CO	WA	SIG/LIT/VOU
Polynemidae	*Polydactylus oligodon*	(Günther, 1860)	NE	OMNI	INT/SB		RA	WA	LIT
	Polydactylus virginicus	(Linnaeus, 1758)	NE	OMNI	INT/SB		RA	WA	LIT/VOU
Pomacanthidae	*Centropyge aurantanotus*	Burgess, 1974	LC	HERB	RS/INT	R	RA	WA/EA	SIG/LIT/PHO[3]
	Holacanthus ciliaris	(Linnaeus, 1758)	LC	SINV	RS/INT/SB	R	RA	WA	SIG/LIT/VOU
	Holacanthus tricolor	(Bloch, 1795)	LC	SINV	RS/INT/SB	R	RA	WA	SIG/LIT/PHO[1,2,3]
	Pomacanthus arcuatus	(Linnaeus, 1758)	LC	SINV	RS/INT/SB	R	RA	WA	SIG/LIT/PHO[1,3]
	Pomacanthus paru	(Bloch, 1787)	LC	SINV	RS/INT/SB	R	CO	WA/MAR	SIG/LIT/VOU
Pomacentridae	*Abudefduf saxatilis*	(Linnaeus, 1758)	NE	OMNI	RS/INT/SB	R	CO	AO	SIG/LIT/VOU
	*Chromis flavicauda**	(Günther, 1880)	DD	PLANK	RS/INT	R	RA	WA/EA	SIG/LIT/PHO[3]

	Chromis jubauna+	Moura, 1995	NE	PLANK	RS/INT	R	RA	SWA	SIG/LIT/VOU/PHO[1,3]
	Chromis limbata	(Valenciennes, 1833)	NE	PLANK	RS/INT	R	CO	WA/EA	SIG/LIT/PHO[1,3]
	Chromis multilineata	(Guichenot, 1853)	NE	PLANK	RS/INT	R	CO	AO	SIG/LIT/VOU
	Stegastes fuscus+	(Cuvier, 1830)	LC	HERB	RS/INT	R	CO	SWA	SIG/LIT/VOU
	*Stegastes partitus**	(Poey, 1868)	NE	HERB	RS/INT	R	UN	NWA	SIG/PHO[3]
	Stegastes pictus+	(Castelnau, 1855)	NE	HERB	RS/INT	R	CO	SWA	SIG/LIT/VOU
	Stegastes variabilis	(Castelnau, 1855)	NE	HERB	RS/INT	R	CO	SWA	SIG/LIT/VOU
Pomatomidae	*Pomatomus saltatrix*	(Linnaeus, 1766)	NE	MCAR	WC	R	CO	CG	SIG/LIT/VOU
Priacanthidae	*Cookeolus japonicus*	(Cuvier, 1829)	NE	MINV	RS/INT	R	RA	CG	LIT/VOU
	Priacanthus arenatus	Cuvier, 1829	NE	MINV	RS/INT	R	OC	WA/EA	SIG/LIT/VOU/PHO[1,3]
Rachycentridae	*Rachycentron canadum*	(Linnaeus 1766)	NE	MCAR	RS/INT/SB		RA	CT	LIT/VOU
Sciaenidae	*Menticirrhus americanus*	(Linnaeus, 1758)	NE	MINV	INT/SB		CO	WA	LIT/VOU/PHO
	Menticirrhus littoralis	(Holbrook, 1847)	NE	MINV	INT/SB		OC	WA	VOU
	Micropogonias furnieri	(Desmarest, 1823)	NE	MINV	INT/SB		CO	WA	LIT/VOU/PHO
	Odontoscion dentex	(Cuvier, 1830)	NE	MCAR	RS/INT	R	CO	WA	SIG/LIT/VOU
	Pareques acuminatus	(Bloch & Schneider, 1801)	NE	MINV	RS/INT/SB	R	CO	WA	SIG/LIT/VOU
Scombridae	*Acanthocybium solandri*	(Cuvier, 1832)	LC	MCAR	WC		OC	CT	LIT
	Euthynnus alletteratus	(Rafinesque, 1810)	LC	MCAR	WC		OC	AO	LIT/PHO[3]
	Scomberomorus brasiliensis	Collette, Russo & Zavala-Camin, 1978	LC	MCAR	WC		OC	WA	LIT/VOU
	Scomberomorus cavalla	(Cuvier, 1829)	LC	MCAR	WC		OC	WA/EA	LIT
Scorpaenidae	*Scorpaena brasiliensis*	Cuvier, 1829	NE	MCAR	RS/INT/SB	R	OC	WA	SIG/LIT/PHO[1,3]
	Scorpaena isthmensis	Meek & Hildebrand, 1928	NE	MCAR	RS/INT/SB	R	OC	WA	VOU
	Scorpaena plumieri	Bloch, 1789	NE	MCAR	RS/INT/SB	R	OC	WA/MAR	SIG/LIT/VOU/PHO[1,3]
Serranidae	*Diplectrum formosum*	(Linnaeus, 1766)	NE	MCAR	SB	R	CO	WA	SIG/LIT/VOU/PHO[1,3]
	Diplectrum radiale	(Quoy & Gaimard, 1824)	NE	MCAR	SB	R	CO	WA	SIG/LIT/VOU/PHO[1,3]

Family	Species	Authority	IUCN	Trophic	Habitat	RE	Occur.	Geog. range	Rec.Type
	Dules auriga	Cuvier, 1829	NE	MCAR	INT/SB	R	CO	SWA	SIG/LIT/PHO[1,2,3]
	Rypticus randalli	Courtenay, 1967	NE	MCAR	RS/INT		RA	WA/EA	LIT/VOU
	Rypticus saponaceus	(Bloch & Schneider, 1801)	NE	MCAR	RS/INT	R	RA	AO	LIT
	Serranus atrobranchus	(Cuvier, 1829)	NE	MINV	INT/SB	R	CO	WA	SIG/LIT/PHO[1,2,3]
	Serranus baldwini	(Evermann & Marsch, 1899)	NE	MINV	INT/SB	R	CO	WA	SIG/LIT/PHO[1,2,3]
	Serranus flaviventris	(Cuvier, 1829)	NE	MINV	INT/SB	R	CO	WA	SIG/LIT/VOU
Sparidae	*Archosargus probatocephalus*	(Walbaum, 1792)	NE	MINV	RS/INT	R	OC	WA	LIT
	Archosargus rhomboidalis	(Linnaeus, 1758)	NE	OMNI	RS/INT/SB	R	RA	WA	SIG/LIT/VOU/PHO[3]
	Calamus penna	(Valenciennes, 1830)	NE	MINV	INT/SB	R	RA	WA	SIG/LIT/PHO[1,3]
	Calamus pennatula	Guichenot, 1868	NE	MINV	INT/SB	R	RA	WA	SIG/LIT/VOU/PHO[3]
	Diplodus argenteus	(Valenciennes, 1830)	NE	OMNI	RS/INT/SB	R	CO	SWA	SIG/LIT/VOU
	Pagrus pagrus	(Linnaeus, 1758)	EN	MCAR	RS/INT/SB		RA	WA	LIT/VOU
Sphyraenidae	*Sphyraena barracuda*	(Edwards, 1771)	NE	MCAR	RS/INT/SB	R	RA	CT	SIG/LIT/PHO[2,3]
	Sphyraena guachancho	Cuvier, 1829	NE	MCAR	RS/INT/SB	R	OC	WA/EA	SIG/LIT/VOU/PHO[3]
	Sphyraena tome	Fowler, 1903	NE	MCAR	RS/INT/SB	R	OC	SWA	VOU
Syngnathidae	*Halicampus crinitus*	(Jenyns, 1842)	NE	MINV	RS/INT	R	OC	WA	SIG/LIT/PHO[1,2,3]
	Hippocampus erectus	Perry, 1810	VU	MINV	RS/INT	R	OC	WA/MAR	SIG/LIT/VOU
	Hippocampus patagonicus	Piacentino & Luzzato, 2004	VU	MINV	RS/INT	R	OC	SWA	SIG/LIT/VOU/PHO[3]
	Hippocampus reidi	Ginsburg, 1933	VU	MINV	RS/INT	R	OC	WA	SIG/LIT/VOU
	Microphis lineatus	(Kaup, 1856)	NE	MINV	RS/INT		RA	WA	VOU
	Syngnathus folletti	Herald, 1942	NE	MINV	RS/INT		RA	SWA	VOU
Synodontidae	*Synodus intermedius*	(Spix & Agassiz, 1829)	NE	MCAR	RS/INT/SB	R	RA	WA	LIT/PHO[3]
	Synodus bondi	Fowler, 1939	NE	MCAR	INT/SB		RA	WA	LIT/VOU/PHO[3]
	Synodus synodus	(Linnaeus, 1758)	NE	MCAR	RS/INT/SB	R	CO	AO	SIG/LIT/PHO[1,2,3]
	Trachynocephalus myops	(Forster, 1801)	DD	MCAR	INT/SB		RA	AO	LIT

Tetraodontidae	*Canthigaster figueiredoi+*	Moura & Castro, 2002	NE	OMNI	RS/INT/SB	R	OC	WA	SIG/LIT/VOU
	Lagocephalus laevigatus	(Linnaeus, 1766)	NE	OMNI	SB		OC	WA/EA	LIT/VOU
	Sphoeroides greeleyi	Gilbert, 1900	NE	MINV	RS/INT/SB	R	CO	WA	VOU
	Sphoeroides pachygaster	(Müller & Troschel, 1848)	NE	MINV	RS/INT/SB		RA	CG	LIT
	Sphoeroides spengleri	(Bloch, 1785)	NE	MINV	RS/INT/SB	R	CO	WA/EA	SIG/LIT/VOU
	Sphoeroides testudineus	(Linnaeus, 1758)	NE	MINV	RS/INT/SB	R	CO	WA	SIG/LIT/VOU
	Sphoeroides tyleri	Shipp, 1972	NE	MINV	RS/INT/SB		RA	WA	LIT/VOU
Triglidae	*Prionotus nudigula*	Ginsburg, 1950	NE	MINV	INT/SB		RA	SWA	VOU
	Prionotus punctatus	(Bloch, 1793)	NE	MINV	INT/SB		RA	WA	LIT/VOU
Uranoscopidae	*Astroscopus y-graecum*	(Cuvier, 1829)	DD	MCAR	INT/SB		RA	WA	LIT/PHO[3]

Figure 3. Examples reef fish considered "common" in reefs of Santa Catarina, Southern Brazil. (**A**) The Tomtate Grunt, *Haemulon aurolineatum*; (**B**) Sergeant Major, *Abudefduf saxatilis*; (**C**) Porkfish, *Anisotremus virginicus*; (**D**) Banded Butterflyfish, *Chaetodon striatus*; (**E**) Reef Croaker, *Odontoscion dentex*; (**F**) Dusky Grouper, *Epinephelus marginatus*; (**G**) South American Silver Porgy, *Diplodus argenteus*; (**H**) Bandtail Puffer, *Sphoeroides spengleri*.

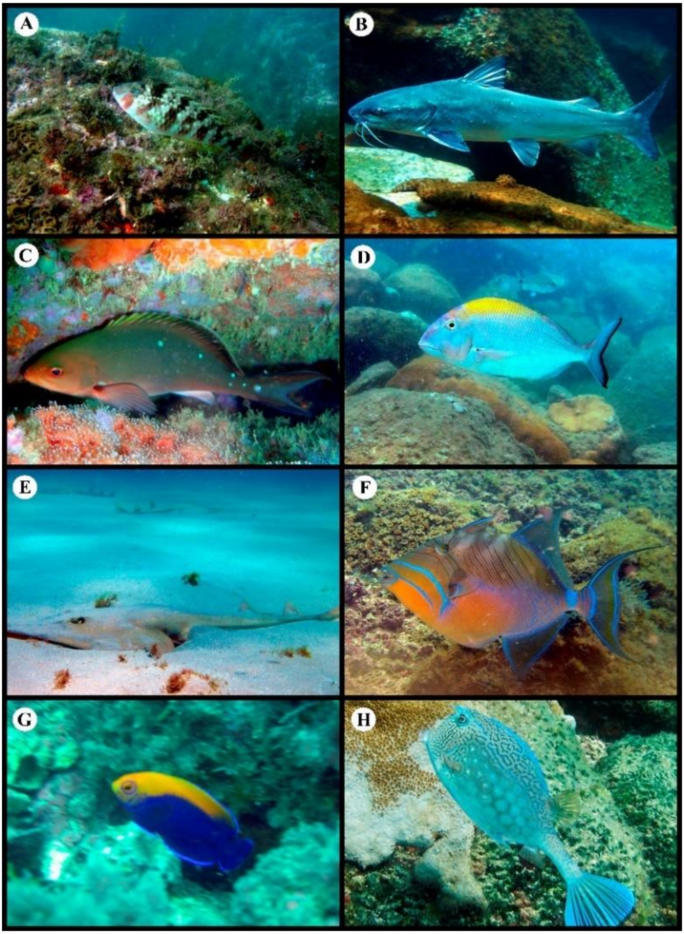

Figure 4. Examples of reef fish species considered as “rare”in reefs of Santa Catarina, Southern Brazil. (A) Emerald Parrotfish, *Nicholsina usta*; (B) Guri Sea Catfish, *Genidens genidens*; (C) Creole-fish, *Paranthias furcifer*; (D) Sheepshead Porgy, *Calamus penna*; (E) Brazilian Guitarfish, *Rhinobatos* sp.; (F) Queen Triggerfish, *Balistes vetula*; (G) Flameback Angelfish, *Centropyge aurantonotus*; (H) Honeycomb Cowfish, *Acanthostracion polygonius*.

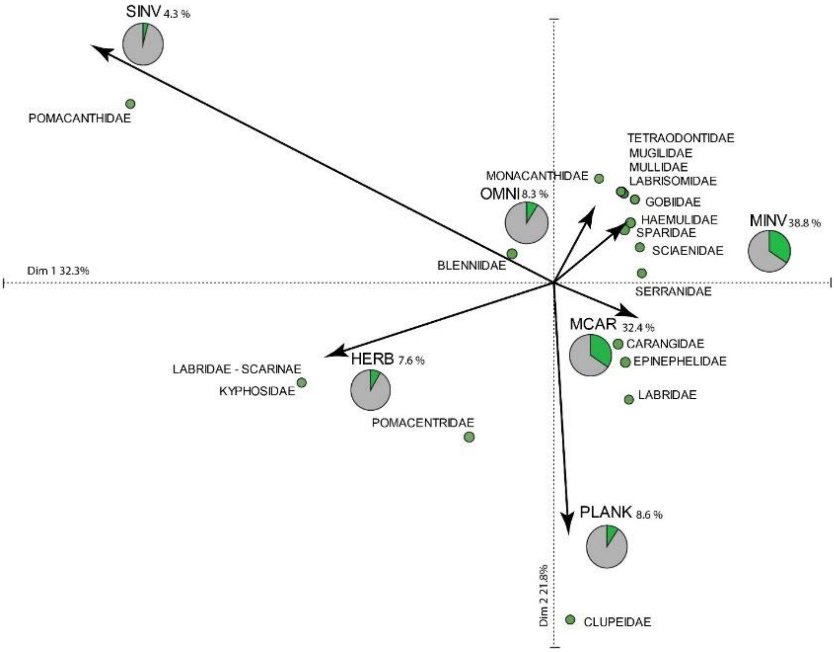

Figure 4. Correspondence analysis based on species richness showing the trophic structure of reef fish ichthyofauna in Santa Catarina’s rocky reef systems. Vectors indicate the feeding habits of species: MINV = mobile invertebrate feeders, MCAR = macrocarnivores, PLANK = planktivores, OMNI = omnivores, HERB = herbivores/detritivores, SINV = sessile invertebrate feeders. Green circles mark the positions of the families. Grey/green circles represent the relative proportion of species for each trophic group.

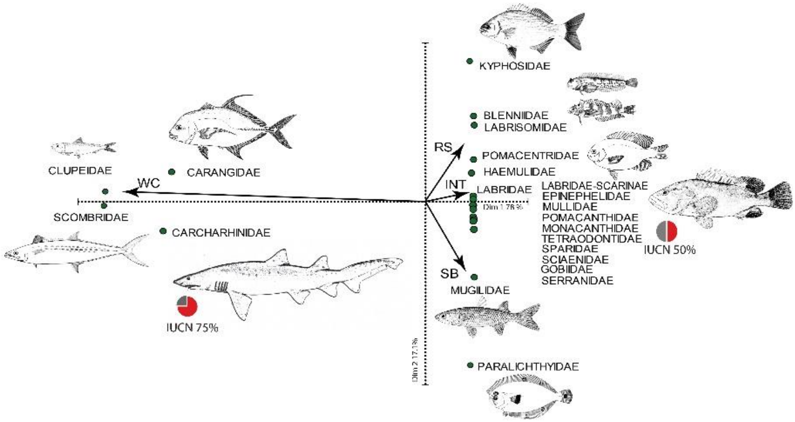

Figure 5. Habitat distribution of reef fish in Santa Catarina's rocky reef systems. The vectors indicate the reef's ecological zones: RS = Reef Slope zone, INT = interface, SB = sandy bottom, WC = water column. Green circles indicate the position of respective families in the rocky reef system (CA). Grey/ red circles indicate the relative quantity of threatened species within the families of sharks, tunas and groupers, which are the most threatened groups.

Order Anguilliformes, Family Muraenidae

Gymnothorax vicinus (Castelnau, 1855) (Figure 7A). One individual was recorded at the approximate depth of 7 m, Arvoredo Marine Biological Reserve, Santa Catarina in 2008. *Remarks:* Previous southernmost record was the state of Paraná (Hackradt and Félix-Hackradt 2009).

Muraena retifera Goode & Bean, 1882 (Figure 7B). One adult individual was recorded at Xavier Island and another one at Aranhas Island in February 2015 both at the approximate depth of 8 m. *Remarks:* Previous southernmost record was the state of São Paulo (Carvalho-Filho 1999).

Order Anguilliformes, Family Ophichthidae

Quassiremus ascensionis (Studer, 1889) (Figure 7C and 7D). One large individual (around 90 cm) was recorded at Rancho Norte, Arvoredo Marine Biological Reserve in February 2014, at the approximate depth of 7 m, and another one smaller (around 40 cm) was recorded from Deserta Island, Arvoredo Marine Biological Reserve in May 2014.These two individuals were observed patrolling rhodolith banks that exist at these two locations. *Remarks:* These individuals represent the second record for the coastal Western Atlantic Ocean. Its native geographic range is the Eastern Atlantic, Ascension and Santa Helena Islands, but it has been recently reported to occur also on Saint Peter and Saint Paul Archipelago (Wirtzet al. 2015). Therefore, this is the second report of this species for the Southwestern Atlantic and the first one for the coastal part of this region.

Order Perciformes, Family Acanthuridae

Acanthurus coeruleus Bloch & Schneider, 1801 (Figure 7E). One juvenile individual was recorded at the approximate depth of 8 m, Deserta Island, Arvoredo Marine Biological Reserve, Santa Catarina in 2010, and one adult (ca. 30 cm total length) was recorded at a depth of 12 m at Saco do Farol, Arvoredo Island in March 2014. *Remarks:* Previous southernmost record for this species wasin the state of São Paulo (Carvalho-Filho 1999; Moura et al. 1999).

Acanthurus monroviae Steindachner, 1876. One individual, an adult male, was recorded at the approximate depth of 7 m at Parcel da Deserta, Arvoredo Marine Biological Reserve, Santa Catarina in February 2015. *Remarks:* This individual represents the second record for the Western Atlantic Ocean, being previously recorded for Laje de Santos, in the state of São Paulo (Luiz et al. 2004, 2010). Its native range is in the Eastern Atlantic.

Family Apogonidae

Apogon americanus (Castelnau 1855) (Figure 7F). One individual was recorded at a depth of 10 m at Saco do Farol, Arvoredo Island in February 2014. *Remarks:* Previous southernmost record was in the state of São Paulo (Carvalho-Filho 1999).

Family Carangidae

Decapterus punctatus (Cuvier, 1829). Many individuals were seen and photographed at 10–15 m deep, at Deserta Island, Santa Catarina, 2015.

Remarks: The previous southernmost record was in the state of São Paulo (Carvalho-Filho 1999).

Family Chaetodontidae

Chaetodon sedentarius Poey, 1860 (Figure 8A). One individual was recorded at the approximate depth of 9 m, Arvoredo Marine Biological Reserve, Santa Catarina in 2010. *Remarks:* Previous southernmost record was in the state of São Paulo (Carvalho-Filho 1999).

Family Labridae

Clepticus brasiliensis Heiser, Moura & Robertson, 2000 (Figure 8B). One individual was recorded at the approximate depth of 6 m, Deserta Island, Arvoredo Marine Biological Reserve, Santa Catarina, in April 2011. *Remarks:* The previous southernmost record was in the state of São Paulo (Carvalho-Filho 1999).

Family Pomacentridae

Chromis flavicauda (Günther, 1880) (Figure 8E). Three individuals were recorded at the approximate depth of 10 m, Xavier Island, Santa Catarina in February 2011. One of these individuals was resighted in April of the same year. *Remarks:* Previous southernmost record was in the state of São Paulo (Carvalho-Filho 1999).

Stegastes partitus (Poey, 1868) (Figure 8C and 8D). One individual was recorded at the approximate depth of 6 m, Galé Island, Arvoredo Marine Biological Reserve, Santa Catarina in February 2013. *Remarks:* The individual recorded represents the first record for the Southern Atlantic Ocean. Its native range is in the Northwestern Atlantic, south to Venezuela (Cervigón 1993).

Order Tetraodontiformes, Family Monacanthidae

Cantherhines macrocerus (Hollard, 1853) (Figure 8F). One individualrecorded being cleaned by a juvenile of *Pomacanthus paru* at the approximate depth of 2 m at Praia da Sepultura, Bombinhas, Santa Catarina in March 2015. *Remarks:* Previous southernmost record was in the state of São Paulo (Carvalho-Filho 1999).

A growing number of reef fishes have been detected outside of their native range in the Atlantic (Freitas et al. 2013; Luiz et al. 2013), with at least three recent examples reaching south-southeastern Brazil: the

Azores Chromis, *Chromis limbata* (Valenciennes, 1833), the West African Tang, *Acanthurus monroviae* Steindachner, 1876, and the Bannerfish, *Heniochus acuminatus* (Linnaeus, 1758). The first two species are known from the Eastern Atlantic and have reached the Brazilian coast after breaching the Mid-Atlantic Barrier (Luiz et al. 2004; Leite et al. 2009). The Bannerfish is distributed all over the Indo-Pacific and it is controversial whether its arrival in Brazil means a long dispersal via South Africa or an aquarium release (Luiz et al. 2014). From these three species, only *C. limbata* has successfully established populations in the Southwestern Atlantic (Anderson *et al*. pers. obs.). Of the new records presented by this work, the Bicolor Damselfish, *Stegastes partitus*, and the Ornate Snake Eel, *Quassiremus ascensionis*, are considerably unnusual not only because they expand species´ known geographic range by several thousands of kilometers, but also because of large environmental differences between their place of origin and the Santa Catarina coast.

The Bicolor Damselfish is a Northwestern Atlantic endemic species, ranging from Florida to Venezuela (Humannn and Deloach 2014). This species is heavily associated with coral reefs, even when occurs in cooler upwelling Caribbean locations, such as the Venezuelan coast, and therefore its occurrence on a transitional zone with no coral reef builders (see Castro and Pires 2001, for distribution of coral reefs in Brazil) is at least intriguing. Introduction via ship's ballast water is unlikely because most fish larvae do not survive for long periods in that environment (Carlton 1985). Aquarium trade is also unlikely because this species is not commonly exported from the Caribbean, and there are no records of it being commercialized in the study region. The building of new platforms and intense oil industry activity seems to be the more likely form of artificial introduction because movement of these structures is intensifying worldwide and adults from some species are known to have been transported through those means (Dulcic and Dragicevic 2013). However, the possibility of a natural colonization cannot be dismissed and only future monitoring of this species presence along the Brazilian coast could clarify this range extension causes.

The Ornate Snake Eel is considered to be endemic to the Eastern Atlantic and islands of Santa Helena, Ascension and Saint Paul´s Rocks (Wirtz et al. 2015), none of which is located less than 3,700 km from Santa Catarina coast. Although no ecological information concerning this species was found in the literature, in the two occasions it was encountered in Santa Catarina, it wandered through shallow rhodolith beds. Contrary to *Stegastes partitus*, it is highly unlikely that this species was artificially introduced at Santa Catarina coast and, so, natural dispersal might account for its presence there. The first and most likely hypothesis is that it is also present in other places along the Brazilian coast, but was overlooked due to its cryptic nature and, especially, to its poorly sampled habitat (rhodolith beds), for which Santa Catarina is the southernmost limit (Gherardi 2004; Pascelli et al. 2013). The alternative hypothesis is that it represents another case of extreme dispersal event driven by Brazil Current.

Zoogeography, tropical affinities and remarkable absences

Most of the recorded species (162 species or 58.3%) are known to occur only in the Western Atlantic Ocean. Species occurring on both sides of the Atlantic Ocean (Western and Eastern Atlantic, 60 species) total 21.6% of the richness. Circumtropical cosmopolitan species (24 species) totaling 8.6% and 15 species were considered circumglobal cosmopolitan species (5.4%) (Floeter et al. 2008; Froese and Pauly 2014). Also, 23 of the recorded species (8.3%) are endemic to the Brazilian Province (Figure 9), a little lower than the number for the whole Brazilian coast (10.5%; Floeter et al. 2008). This might be due to the fact that many endemic Brazilian species possess tropical affinities, with some attaining their southern limit of occurrence northwards, in the states of Rio de Janeiro or São Paulo (Carvalho-Filho 1999; Luiz et al. 2009). In fact, all these localities are part of the Southwestern Atlantic Shelf (Matano et al. 2010) and are affected by seasonal cool waters that can restrict the occurrence of tropical species. Examples of endemic tropical species that do not reach Santa Catarina are *Haemulon squamipinna*, *Halichoeres penrosei*, and *Lutjanus alexandrei*, just to mention a few.

Despite some tropical reef fish species that do not occur southward to Santa Catarina state, many do and overall its faunal domain can be considered tropical with the enrichment of temperate elements. These temperate elements are, however, less important for species composition than its relatively high latitude would predict. This is particularly true when comparing to southeastern region reefs that are heavily affected by upwelling, such as Arraial do Cabo and Ilha Rasa in Rio de Janeiro state, and Laje de Santos in São Paulo state (Luiz et al. 2008; Carvalho-Filho et al. 2009; Bertonciniet al. 2013). In these places, temperate species that occur in deep waters throughout the Brazilian shelf have been recorded for shallow waters associated with frequent upwelling events.

This upwelling of deep water/temperate species includes the occurrence of *Dules auriga* Cuvier, 1829, *Pagrus pagrus* (Linnaeus, 1758), *Pinguipes brasilianus* Cuvier, 1829, *Halichoeres sazimai* Luiz, Ferreira & Rocha, 2009, *Acanthistius brasilianus* (Cuvier, 1828) and *Pronotogrammus martinicensis* (Guichenot, 1868) for depths shallower than 40 m (Irigoyen et al. 2008; Luiz et al. 2008; Carvalho-Filho et al. 2009; Bertonciniet al. 2013). The first three species are common in shallow Argentine reefs (Irigoyen and Galván 2010), *H. sazimai* have its southern distribution limit at Santa Catarina (Barneche et al. 2009), but *P. martinicensis* have its only known shallow water population in these upwelling areas along the “Arc of Capricorn” (Carvalho-Filho et al. 2009) and *A. brasilianus* in this region and also Uruguay (Irigoyen et al. 2008; Irigoyen et al. 2010). *Dules auriga* is commonly found in Santa Catarina southward from Xavier Island (27°36′ S, 048°23′ W), while *H. sazimai* and *Pagrus pagrus* are rare or uncommon, even in shallow habitats in the southern part of the state (RM pers obs). But the most intriguing issue is that *Pinguipes brasilianus, Acanthistius brasilianus* and *Pronotogrammus martinicensis* have never been recorded for the shallow reefs despite relatively wide geographic sampling and the fact that the higher latitude reefs of Santa Catarina are exposed to temperatures sometimes as low as these upwelling places northward. Recently, *Pronotogrammus martinicensis* was recorded from Santa Catarina at a depth of 130 m, associated with the sunken German submarine U-513 (Figure 10). This suggests that other temperate species might also be present in deep reefs, and may be confirmed by more observations and further sampling of these habitats.

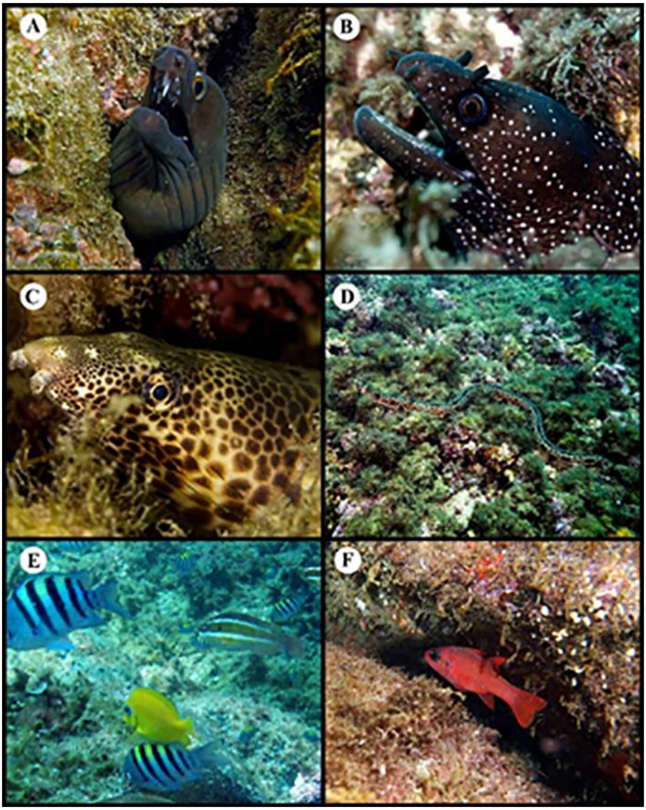

Figure 6. Examples of new records of reef fish species to the state of Santa Catarina, Southern Brazil. (**A**) Purplemouth Moray, *Gymnothorax vicinus*; (**B**) Reticulate Moray, *Muraena retifera*; (**C** & **D**) Ornate Snake Eel, *Quassiremus ascensionis*; (**E**) Blue Tang Surgeonfish, *Acanthurus coeruleus*; (**F**) Brazilian Flamefish, *Apogon americanus.*

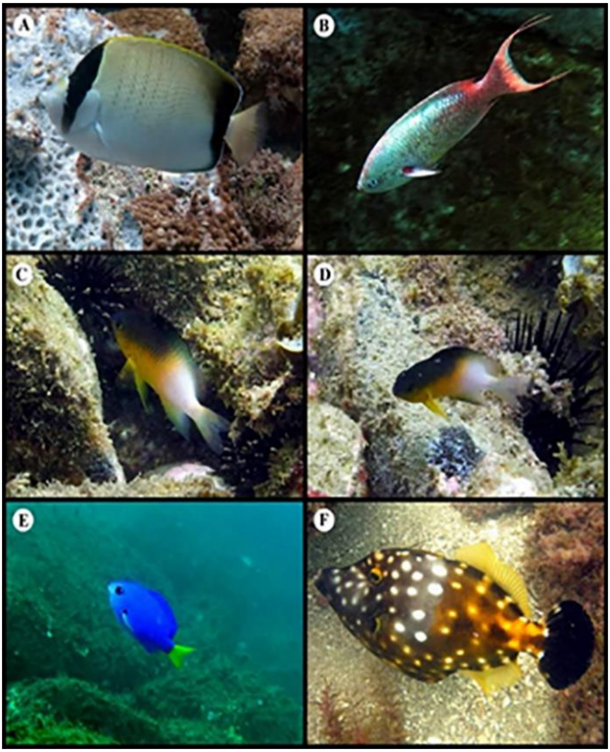

Figure 7. Examples of new records of reef fish species to the state of Santa Catarina, Southern Brazil. (**A**) Reef Butterflyfish, *Chaetodon sedentarius*; (**B**) Brazilian Creolewrasse, *Clepticus brasiliensis*; (**C** and **D**) Bicolor Damselfish, *Stegastes partitus*; (**E**) Cobalt Chromis, *Chromis flavicauda*; (**F**) Whitespotted Filefish, *Cantherhines macrocerus*.

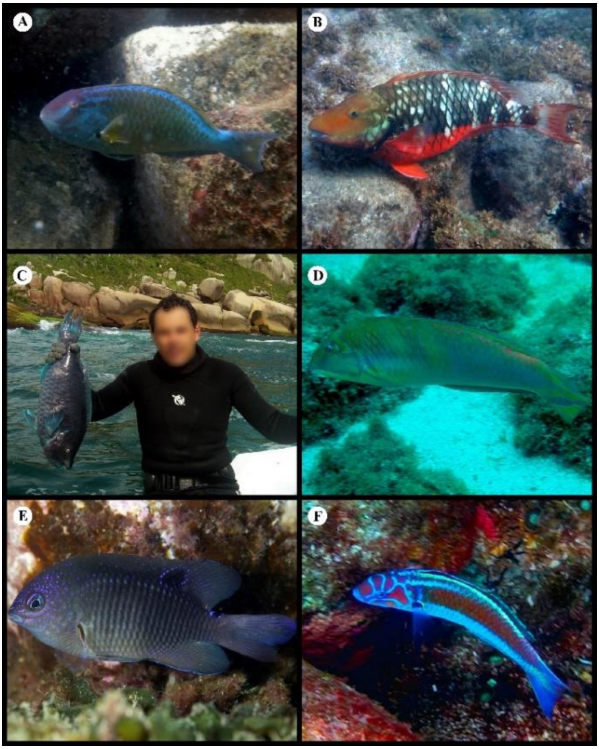

Figure 8. Examples of endemic Brazilian reef fish species observed in reefs of Santa Catarina, Southern Brazil. (**A**) Striped Parrotfish, *Scarus zelindae;* (**B**) Reef Parrotfish, *Sparisoma amplum*; (**C**) Greenback Parrotfish, *Scarus trispinosus*; (**D**) Brazilian Dartfish, *Ptereleotris randalli*; (**E**) Brazilian Dusky Damselfish, *Stegastes fuscus*; (**F**) Noronha Wrasse, *Thalassoma noronhanum*.

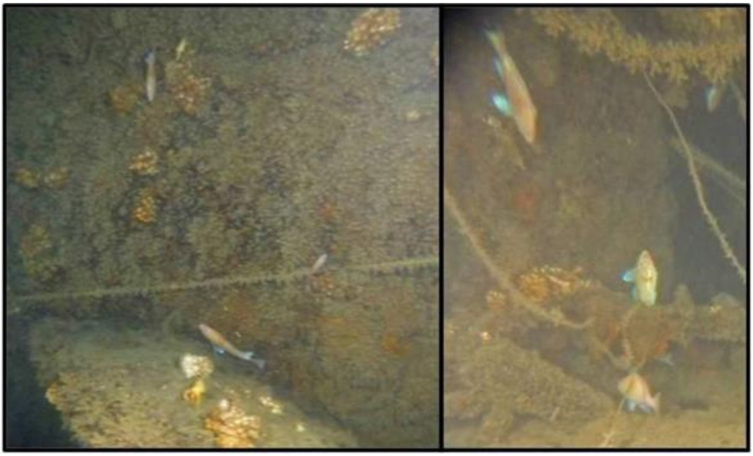

Figure 9. *Pronotogrammus martinicensis* recorded at 130 m depth associated with the sunken German submarine U-513 off Santa Catarina, Southern Brazil.

2.4 CONCLUSIONS

The ichthyofauna of Santa Catarina state is mostly characterized by tropical species brought from the northern warm waters by oceanic currents. Nevertheless, the cold waters in the austral winter sea surface temperature can affect the survival of such species, leading to the extirpation of populations (cf. Bohnsack 1983; Hsieh et al. 2008). The unusual new records presented in this work indicates that long-term monitoring studies will allow a better understanding of connectivity patterns along the coast of Santa Catarina as well as the possible establishment of new populations at their southernmost limit of distribution. Of interest also are cold-water related species whose reasons for the disjunct observed distributions, which exclude Santa

Catarina, are not clear. Further sampling efforts on deeper habitats might reveal novel insights concerning their distribution status.

2.5 ACKNOWLEDGEMENTS

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Appendix 1

Table A1. Vouchers specimens from MZUSP (Museu de Zoologia da Universidade de São Paulo, Brazil); vouchers from NEMAR (Center of Sea Studies of Universidade Federal de Santa Catarina UFSC / Brazil); vouchers from CIUFSC (Ichthyological collection of Universidade Federal de Santa Catarina, UFSC / Brazil); voucher from USNM (National Museum of Natural History; Smithsonian Institution; Washington, DC) and voucher from UFRGS (Universidade Federal do Rio Grande do Sul). Names in parenthesis are the previous recognized as valid for the area.

Family	**Species**	**MZUSP**	**CIUFSC**	**NEMAR**
Acanthuridae	*Acanthurus bahianus*	MZUSP55397	CUFSC1391	-
Acanthuridae	*Acanthurus chirurgus*	MZUSP55341	-	-
Ariidae	*Cathorops spixii*	-	CIUFSC251	ARII 1982.001.191
Ariidae	*Genidens barbus*	-	CIUFSC1079	ARII 1992.029.219
Ariidae	*Genidens genidens*	-	CIUFSC1329	ARII 1982.002.192
Balistidae	*Balistes capriscus*	-	CIUFSC814	BALIS 1981.002.1186
Batrachoididae	*Porichthys porosissimus*	-	CIUFSC779	BATRA 1982.001.101
Belonidae	*Strongylura marina*	-	-	BELO 1992.011.138
Blenniidae	*Hypleurochilus fissicornis*	MZUSP55318	-	BLEN 1984.002.121
Blenniidae	*Hypleurochilus pseudoequipinnis*	MZUSP55320	-	-
Blenniidae	*Hypsoblennius invemar*	MZUSP55319	-	-
Blenniidae	*Ophioblennius trinitatis*	MZUSP55452	-	-
Blenniidae	*Parablennius marmoreus*	MZUSP55451	-	-
Blenniidae	*Parablennius pilicornis*	-	CIUFSC605	BLEN 1989.004.123
Blenniidae	*Scartella cristata*	MZUSP55440	CIUFSC1574	BLEN 1979.001.120
Bothidae	*Bothus ocellatus*	MZUSP55378	-	-

Callionymidae	*Callionymus bairdi*	MZUSP55455	-	-
Carangidae	*Caranx crysos*	MZUSP55363	-	-
Carangidae	*Caranx hippos*	-	CIUFSC1311	CARA 1984.012.416
Carangidae	*Caranx latus*	-	CIUFSC734	CARA 1989.051.455
Carangidae	*Chloroscombrus chrysurus*	-	CIUFSC1309	CARA 1980.002.406
Carangidae	*Oligoplites saliens*	-	-	CARA 1988.033.437
Carangidae	*Oligoplites saurus*	-	CIUFSC727	CARA 2005.072.476
Carangidae	*Pseudocaranx dentex*	MZUSP55438	-	-
Carangidae	*Selene setapinnis*	-	CIUFSC379	CARA 2003.073.477
Carangidae	*Selene vomer*	-	CIUFSC371	-
Carangidae	*Trachinotus carolinus*	-	CIUFSC723	CARA 2005.077.713
Carangidae	*Trachinotus falcatus*	-	CIUFSC735	CARA 1988.045.449
Carangidae	*Trachinotus marginatus*	-	-	CARA 1989.056.460
Carcharhinidae	*Carcharhinus brevipinna*	-	CIUFSC1357	-
Carcharhinidae	*Carcharhinus isodon*	-	CIUFSC1139	-
Carcharhinidae	*Carcharhinus obscurus*	-	CIUFSC 468	-
Carcharhinidae	*Carcharhinus plumbeus*	-	CIUFSC1162	-
Carcharhinidae	*Carcharhinus porosus*	-	CIUFSC481	-
Carcharhinidae	*Carcharhinus signatus*		CIUFSC1152	-
Carcharhinidae	*Rhizoprionodon lalandii*	-	CIUFSC1376	-
Centropomidae	*Centropomus undecimalis*	-	CIUFSC679	CENTRO 1998.018.157
Centropomidae	*Centropomus parallelus*	-	CIUFSC1513	CENTRO 2002.027.166
Chaenopsidae	*Emblemariopsis signifer*	MZUSP55448	CIUFSC608	-
Chaetodontidae	*Chaetodon striatus*	MZUSP55342	CIUFSC1370	-
Chaetodontidae	*Prognathodes guyanensis*	MZUSP49096	-	-

Family	**Species**	**MZUSP**	**CIUFSC**	**NEMAR**
Clupeidae	*Harengula clupeola*	-	CIUFSC545	CLUP 1980.001.788
Clupeidae	*Opisthonema oglinum*	-	CIUFSC55	CLUP 2005.042.829
Clupeidae	*Sardinella brasiliensis*	-	CIUFSC1064	CLUP 1982.004.491
Dactylopteridae	*Dactylopterus volitans*	MZUSP55431	-	DACTY 1989.003.390
Dactyloscopidae	*Dactyloscopus crossotus*	MZUSP46668	-	-
Dasyatidae	*Dasyatis hypostigma (say)*	-	CIUFSC511	-
Diodontidae	*Chilomycterus reticulatus*	-	CIUFSC259	-
Diodontidae	*Chilomycterus spinosus spinosus*	MZUSP940	-	DIODS 1999.002.1104
Echeneidae	*Echeneis naucrates*	-	CIUFSC578	-
Eleotridae	*Eleotris pisonis*	-	CIUFSC1652	-
Ephippidae	*Chaetodipterus faber*	MZUSP13314	CIUFSC771	EPHI 1988.006.401
Epinephelidae	*Epinephelus marginatus*	MZUSP55334	CIUFSC797	-
Epinephelidae	*Hyporthodus niveatus*	-	CIUFSC1063	-
Epinephelidae	*Mycteroperca acutirostris*	MZUSP55325	-	-
Epinephelidae	*Mycteroperca bonaci*	MZUSP55423	-	-
Fistulariidae	*Fistularia petimba*	-	CIUFSC778	-
Fistulariidae	*Fistularia tabacaria*	-	CIUFSC530	FISTU 1993.001.787
Gerreidae	*Diapterus auratus*	-	CIUFSC115	GERRE 2010.065.1031
Gerreidae	*Diapterus rhombeus*	-	CIUFSC62	GERRE 1997.041.1007
Gerreidae	*Eucinostomus argenteus*	-	CIUFSC639	GERRE 1988.024.990
Gerreidae	*Eucinostomus gula*	-	CIUFSC247	GERRE 1987.019.985

Gerreidae	*Eucinostomus melanopterus*	-	CIUFSC1816	GERRE 1988.010.976
Gerreidae	*Eugerres brasilianus*	-	CIUFSC1555	GERRE 1984.008.974
Gobiesocidae	*Gobiesox barbatulus (strumosus)*	-	CIUFSC1383	GOBIE 1993.001.111
Gobiesocidae	*Tomicodonaustralis (fasciatus)*	USNM 88042*	CIUFSC536	-
Gobiidae	*Barbulifer ceuthoecus*	MZUSP55331	-	-
Gobiidae	*Bathygobius soporator*	-	CIUFSC675	GOBI 1986.019.1051
Gobiidae	*Coryphopterus glaucofraenum*	MZUSP55332	-	-
Gobiidae	*Ctenogobius stigmaticus*	-	-	GOBI 1988.036.1068
Gobiidae	*Elacatinus figaro*	MZUSP49139	-	-
Gobiidae	*Microgobius meeki*	-	-	GOBI 1982.002.1034
Haemulidae	*Anisotremus surinamensis*	MZUSP67863	CIUFSC628	HAEMU 1993.017.1156
Haemulidae	*Anisotremus virginicus*	-	CIUFSC647	-
Haemulidae	*Haemulon aurolineatum*	MZUSP55357	CIUFSC645	HAEMU 1984.004.1143
Haemulidae	*Haemulon bonariense*	MZUSP55354	-	-
Haemulidae	*Orthopristis ruber*	-	CIUFSC396	HAEMU 1988.006.1145
Haemulidae	*Pomadasys corvinaeformis*	-	CIUFSC400	HAEMU 2010.024.1163
Hemiramphidae	*Hemiramphus brasiliensis*	-	CIUFSC780	HEMI 1988.004.1170
Hemiramphidae	*Hyporhamphus unifasciatus*	-	CIUFSC1070	HEMI 1986.001.1167
Holocentridae	*Holocentrus adscensionis*	MZUSP55390	CIUFSC762	-
Holocentridae	*Myripristis jacobus*	MZUSP55388	CIUFSC759	-
Kyphosidae	*Kyphosus vaigiensis*	MZUSP55335	CIUFSC753	-
Labridae	*Bodianus pulchellus*	MZUSP55398	-	-
Labridae	*Halichoeres poeyi*	-	CIUFSC823	-
Labridae	*Xyrichtys novacula*	-	CIUFSC1058	-
Labridae -Scarine	*Cryptotomus roseus*	MZUSP55425	-	-
Labrisomidae	*Labrisomus cricota*	MZUSP55339	-	-

Family	Species	MZUSP	CIUFSC	NEMAR
Labrisomidae	*Labrisomus nuchipinnis*	MZUSP55379	CIUFSC599	LABRE 1994.001.1166
Labrisomidae	*Malacoctenus aff. triangulatus*	MZUSP55450	-	-
Labrisomidae	*Starksia brasiliensis*	MZUSP55367	-	-
Lutjanidae	*Lutjanus analis*	-	-	LUTJA 1989.002.1178
Lutjanidae	*Lutjanus jocu*	-	-	LUTJA 1987.001.1177
Malacanthidae	*Malacanthus plumieri*	MZUSP55430	-	-
Monacanthidae	*Monacanthus ciliatus*	-	-	MONA 1992.006.1192
Monacanthidae	*Stephanolepis hispidus*	MZUSP55326	CIUFSC815	MONA 1987.001.1187
Mugilidae	*Mugil curema*	-	CIUFSC1067	MUGI 1986.001.716
Mugilidae	*Mugil liza*	-	CIUFSC1967	MUGI 1987.010.725
Mullidae	*Pseudupeneus maculatus*	MZUSP55344	CIUFSC810	-
Muraenidae	*Echidna catenata*	MZUSP16623	-	-
Muraenidae	*Gymnothorax moringa*	-	CIUFSC556	-
Muraenidae	*Gymnothorax ocellatus*	-	CIUFSC541	MURAE 1984.001.1199
Muraenidae	*Gymnothorax vicinus*	-	CIUFSC554	-
Narcinidae	*Narcine brasiliensis*	-	CIUFSC576	NARCI 1991.001.1279
Ogcocephalidae	*Ogcocephalus vespertilio*	MZUSP55433	CIUFSC575	OGCOC 1990.001.1276
Ophichthidae	*Myrichthys breviceps*	MZUSP55337	-	-
Ophichthidae	*Myrichthys ocellatus*	-	CIUFSC557	-
Ophidiidae	*Ophidion holbrooki*	-	CIUFSC1524	-

Ostraciidae	*Acanthostracion quadricornis*	MZUSP49101	CIUFSC531	-
Ostraciidae	*Lactophrys trigonus*	MZUSP55428	-	OSTRA 2001.001.1124
Paralichthyidae	*Paralichthys brasiliensis*	-	CIUFSC437	-
Paralichthyidae	*Syacium micrurum*	-	CIUFSC806	-
Pempheridae	*Pempheris schomburgki*	-	CIUFSC1060	-
Polynemidae	*Polydactylus virginicus*	-	-	POLY 2011.001.1218
Pomacanthidae	*Holacanthus ciliaris*	MZUSP55392	CIUFSC1061	-
Pomacanthidae	*Pomacanthus paru*	MZUSP55458	CIUFSC822	-
Pomacentridae	*Abudefduf saxatilis*	-	CIUFSC1368	POMAC 1991.001.1112
Pomacentridae	*Chromis jubauna*	MZUSP55432	-	-
Pomacentridae	*Chromis multilineata*	-	CIUFSC1059	-
Pomacentridae	*Stegastes fuscus*	MZUSP55343	CIUFSC620	-
Pomacentridae	*Stegastes pictus*	MZUSP55346	-	-
Pomacentridae	*Stegastes variabilis*	MZUSP55400	CIUFSC610	-
Pomatomidae	*Pomatomus saltatrix*	-	CIUFSC1545	POMA 1991.018.1101
Priacanthidae	*Cookeolus japonicus*	-	-	PRIAC 2005.002.1174
Priacanthidae	*Priacanthus arenatus*	-	CIUFSC769	PRIAC 2011.004.1176
Rachycentridae	*Rachycentron canadum*	-	CIUFSC1491	-
Rhinobatidae	*Rhinobatos percellens*	-	-	RHINO 2005.002.1279
Rhinobatidae	*Zapteryx brevirostris*	-	CIUFSC503	RHINO 2005.003.1280
Sciaenidae	*Menticirrhus americanus*	-	CIUFSC1965	SCIA 1999.110.612
Sciaenidae	*Menticirrhus littoralis*	-	CIUFSC683	SCIA 1991.100.592
Sciaenidae	*Micropogonias furnieri*	-	CIUFSC1831	SCIA 1988.084.576
Sciaenidae	*Odontoscion dentex*	MZUSP55345	CIUFSC710	-
Sciaenidae	*Pareques acuminatus*	MZUSP55386	CIUFSC601	-
Scombridae	*Scomberomorus brasiliensis*	-	-	SCOMB 2011.001.1194

Scorpaenidae	*Scorpaena isthmensis*	-	-	SCORP 1982.001.1136
Scorpaenidae	*Scorpaena plumieri*	-	CIUFSC1373	SCORP 1987.002.1137
Serranidae	*Diplectrum formosum*	-	-	SERRA 1986.003.1285
Serranidae	*Diplectrum radiale*	-	-	SERRA 1982.001.1283
Serranidae	*Rypticus randalli*	MZUSP46648(1)	-	-
Serranidae	*Serranus flaviventris*	MZUSP55429	-	-
Sparidae	*Archosargus rhomboidalis*	-	CIUFSC1072	SPAR 1989.012.774
Sparidae	*Calamus pennatula*	MZUSP69960	-	-
Sparidae	*Diplodus argenteus*	MZUSP66545	CIUFSC1366	SPAR 1988.006.768
Sparidae	*Pagrus pagrus*	MZUSP70093	CIUFSC624	-
Sphyraenidae	*Sphyraena guachancho*	-	CIUFSC1840	SPHYR 1983.001.165
Sphyraenidae	*Sphyraena tome*	-	UFRGS 04429	-
Sphyrnidae	*Sphyrna lewini*	-	CIUFSC1134	-
Sphyrnidae	*Sphyrna zygaena*	-	CIUFSC1155	-
Syngnathidae	*Hippocampus patagonicus*	-	CIUFSC315	-
Syngnathidae	*Hippocampus reidi*	MZUSP55456	-	SYNG 1981.001.488
Syngnathidae	*Microphis lineatus*	-	CIUFSC275	-
Syngnathidae	*Sgnathus folleti*	-	-	SYNG 1989.002.489
Synodontidae	*Synodus bondi (foetens)*	-	-	SYNO 1983.001.478
Tetraodontidae	*Canthigaster figueiredoi*	MZUSP55355	-	-
Tetraodontidae	*Lagocephalus laevigatus*	-	CIUFSC1365	TETRA 1991.019.1238
Tetraodontidae	*Sphoeroides greeleyi*	-	CIUFSC245	TETRA 1980.001.1220
Tetraodontidae	*Sphoeroides spengleri*	MZUSP55338	CIUFSC552	TETRA 2010.031.1250
Tetraodontidae	*Sphoeroides testudineus*	-	CIUFSC388	TETRA 1980.004.1223
Tetraodontidae	*Sphoeroides tyleri*	-	-	TETRA 2004.028.1247
Triglidae	*Prionotus nudigula*	-	-	TRIGL 2010.024.1275

Triglidae	*Prionotus punctatus*	-	CIUFSC1966	TRGL 1989.017.1268

* *Tomicodon australis* holotype is from São Francisco do Sul, SC, Brazil.

3 ROCKY REEF FISH COMMUNITY VARIATION IN SPACE AND TIME: A NINE YEAR STUDY IN SOUTH BRAZIL

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3.1 ABSTRACT

Long term monitoring of reef fish populations is a valuable tool to understand ecological processes that govern population's variations in marine reef systems. Southern Brazilian rocky reefs are the southernmost limit of distribution for 96% of tropical ichthyofauna. Most research in the area to date is focused on spatial variations, leaving a severe gap regarding the ecological *continuum* (variations in time). In this work, we present a nine-year effort on monitoring the variations in densities and biomass of key rocky reef fish species, inhabiting their threshold of distribution, inside and outside the only no-entry near shore Brazilian Biologic Reserve. The rocky reef fish ichthyofauna was studied with the use of underwater visual censuses (UVC) method, during SCUBA diving expeditions from 2006 to 2016. All samples were conducted in the morning during the austral summers. Such effort covered 32.000 m² of rocky reefs, where 43.169 fish were counted, identified, measured, then converted to biomass data. Variations in specie's densities and biomass in space and time were detected for most species. Several factors and mechanisms may have influenced these variations. On spatial scale: deterministic mechanisms such as habitat structural complexity and protection from fisheries may have influenced these variations. Temporal variations, otherwise, may have been influenced by the proximity of species to their distributional border (*e.g.* species at their distributional border are physiologically stressed by hash environmental consitions), in synergy with density-dependent mechanisms and stochastic winter temperature oscillations. Arvoredo Marine Biological Reserve (AMBR) seems to influence positively all species densities and biomass directly and indirectly, in space and time. In contrast, a prominent decline in recruitment of *E. marginatus* lighten red alarms regarding AMBR effectivness over time.

Key words Rocky reef systems, Southern Atlantic, Long term monitoring, Marine Protected Areas

3.3 INTRODUCTION

Southern Brazilian rocky reefs are the threshold of distribution for approximately 96% of tropical reef fishes (Anderson et al. 2015). Such peculiar region, a transitional climatic zone, influenced by both warm tropical waters from the Brazil Current (BC) and cool waters from the South Atlantic Central Water (SACW), is regarded as “The Arc of Capricorn” by local scientists (Acha et al. 2004; Anderson et al. 2014; 2015). During the past decade, this region have been subjected to a considerable scientific effort to study marine biota (Andrade et al. 2003; Koettker and Freire 2006; Hackradt et al. 2011; Begossi et al. 2012; Anderson et al. 2014; Anderson et al. 2015). Despite the positive results, most works focused on the *momentum*, leaving a severe gap regarding the ecological *continuum* (*e.g.* evaluations of temporal variations on marine populations) (Andrade et al. 2003; Hackradt et al. 2011; Begossi et al. 2012; Anderson et al. 2014; Anderson et al. 2015). Moreover, the mechanisms responsible for temporal variations in reef fish densities and biomass are a matter of controversy and debate (Choat et al. 1988; Sale 2013). To understand the rocky reefs dynamics of southern Brazilian coast a long-term monitoring program was created in 2006. The database management and sampling effort was centered at the Biogeography and Macroecology Laboratory, located at the Federal University of Santa Catarina, Brazil.

This study reports the results of a nine-year monitoring programme of key species of reef fish, inside and outside Arvoredo Marine Biologic Reserve (AMBR), the only near shore Brazilian Biologic Reserve totally restricted from fisheries (No-Entry Area: NE-A) (Koettker and Freire 2006; Anderson et al. 2014). The AMBR (17.600 ha) was created in 1990 to protect the high level of biodiversity, which is subsidized by high primary productivity, resulted from confluence of northern warm tropical and southern cold waters in the region (Acha et al. 2004; Koettker and Freire 2006; Anderson et al. 2015). Scientists recorded 278 species of reef fish inhabiting this environment, so far (Anderson et al. 2015). Such ecological, oceanographic and geographic peculiarities, qualifies AMBR as one the most important Marine Protected Areas in the world, and a potential natural laboratory for climate change studies using species population’s and communities variations as models (Green et al. 2007; McLeod et al. 2009; Anderson et al. 2015).

A high level of spatial and temporal variations has been detected considering species densities and biomass. Several factors and mechanisms could account to the probable sorts of variations: on spatial scale, variations may be governed by deterministic mechanisms such as habitat structural complexity, protection from fisheries and aquarium trade. Annual variations may be influenced by the proximity to species distributional border, density-dependent mechanisms and stochastic temperature oscillations (Sale 1978; Sale 1980; Doherty 2002; Almada and Faria 2004; Begon et al. 2006).

Arvoredo Marine Biological Reserve seem to influence positively all species densities and biomass directly and indirectly, in space and time. Likewise, the positive effects on densities and biomass of trophic groups is evident (Watson et al. 2007;Babcock et al. 2010; Anderson et al. 2014; Mellin et al. 2016).

A prominent decline in recruitment of *E. marginatus* lighten red alarms regarding Arvoredo MPA effectiveness over time (Botsford et al. 2009; Pujolar et al. 2013). Urgent policies and projects for conservation and restoration of nursery adjacent habitats and optimized management programs (*i.e.* enforcements to prevent frequent illegal fisheries) (Anderson et al. 2014) are necessary to improve the effectivness of AMBR over time, and the direct and indirect effects on all local species favored by its existence.

3.4 MATERIALS AND METHODS

Study area

The present study was conducted on four subtropical Islands bordering on the north and east side of Florianópolis Island (27° 35’ 41.08”S 48° 32’ 38.96”W), Santa Catarina State, South Brazil. The geomorphology Southern Brazilian rocky reefs is characterized in its major portion by steep granitic rocky reefs ending in sandy bottoms, usually starting from 12 to15 m deep (Hostim-Silva et al. 2006; Anderson et al. 2014; Anderson et al. 2015). In addition, these rocky reefs are regarded as the southernmost limit of distribution of tropical reef fish species, which inhabit the north portion of the Brazilian coast (Anderson et al. 2014; Anderson et al. 2015).

For the sampling design four Islands were selected: Deserta Island (1) (27º16’25”S 48º 19’36.49”W) located inside the limits of AMBR. Galé Island (2) (27°14'43.97"S 48°25'41.57"W) also located inside the limits of AMBR. Arvoredo Island (3) (the south portion) located outside the limits of AMBR (27°17'20.34"S 48°22'7.92"W). Xavier Island (4) (27°36'33.95"S 48°23'11.39"W) located outside the limits of AMBR. Both sites inside AMBR: Deserta Island and Galé Island were grouped and treated as one specific area (No-Entry Area), and both sites outside AMBR: Arvoredo Island and Xavier Island were also grouped and treated as one specific area (No-Protected Area). Both areas were compared to highlight variations of distribution of species’ density and biomass, in space and time, regarding the effectiveness of the No-Entry Area (Figure 1).

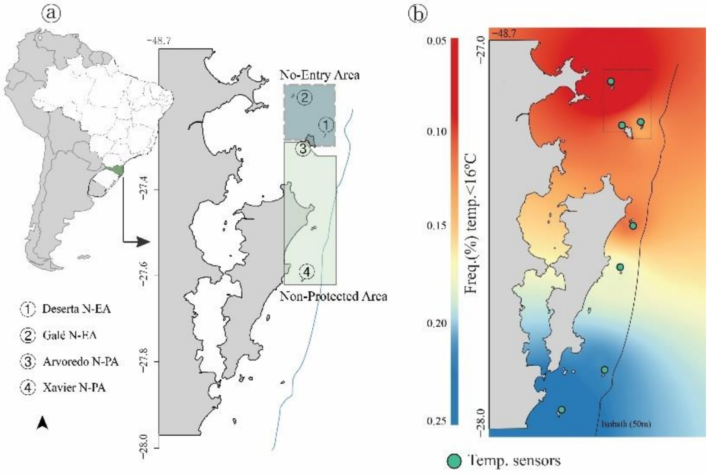

Figure 1. a) Map of the studied sites. Santa Catarina State is represented in green. The dashed dark green polygon represent Arvoredo Biologic Marine Reserve [AMBR: No-Entry Area (N-EA)], the light green polygon represent the area where fisheries are allowed [Non-Protected Area (N-PA)] and circles with numbers represent sampled sites (Islands). b) Interpolated map of temperature frequencies < 16ºC during the Austral winter. Green circles represent the sites where temperature sensors were deployed.

Arvoredo Marine Biological Reserve designated as a no-take Marine Protected Area in 1990 encompassing 17800 ha (43985 acres) is constituted by three major Islands: Arvoredo, Deserta and Galé. Fishing, harvesting and human presence are strictly forbidden by law, admitting scientific research only. It is the unique of its category in the south-southeast coast of Brazil, conserving fragments of the Atlantic Rainforest and a rich marine biodiversity (Hostim-Silva et al. 2006; Anderson et al. 2014). Approximately 278 species of marine fish inhabit the Archipelago (Anderson et al. 2015).

Dominant species

Santa Catarina's coast is the habitat of 278 rocky reef fish species. To infer variations in density and biomass, in space and time, 18 species were selected as proxies [due to their dominance among sites in density and biomass (they account for 70% of total biomass recorded for the past nine years)] (Anderson et al. 2015). Species are listed in alphabetical order: *Abudefduf saxatilis* (Linnaeus, 1758), *Anisotremus virginicus* (Linnaeus, 1758), *Bodianus rufus* (Linnaeus, 1758), *Chaetodon striatus* Linnaeus, 1758, *Chromis limbata* (Valenciennes, 1833), *Chromis multilineata* (Guichenot, 1853), *Diplodus argenteus argenteus* (Valenciennes, 1830), *Epinephelus marginatus* (Lowe, 1834), *Haemulon aurolineatum* Cuvier, 1830, *Halichoeres poeyi* (Steindachner, 1867), *Mycteroperca acutirostris* (Valenciennes, 1828), *Parablennius marmoreus* (Poey, 1876), *Parablennius pilicornis* (Cuvier, 1829), *Pomacanthus paru* (Bloch, 1787), *Sparisoma axillare* (Steindachner, 1878), *Sparisoma frondosum* (Agassiz, 1831), *Stegastes fuscus* (Cuvier, 1830) and *Stegastes variabilis* (Castelnau, 1855).

In addition, to infer variations in space and time regarding functional roles, 16 dominant species were divided in eight trophic categories (Ferreira et al. 2004; Luiz et al. 2008; Anderson et al. 2015): (HERB) species which include in their diet mostly macroalgae, represented by *S. axillare* and *S. frondosum*. Macrocarnivores (MCAR) species which feed mainly on macroinvertebrates and fishes, represented by *E. marginatus* and *M. acutirostris*. Mobile Invertebrate Feeders (MINV) species which feed primarily on benthic mobile invertebrates such as mollusks, crustaceans and worms associated with hard or nearby unconsolidated substrate, represented by *H. aurolineatum* and *A. virginicus*. Cryptic macroinvertebrates feeders (MINVC) species which present a cryptic behavior, also feed primarily on benthic mobile invertebrates such as mollusks, crustaceans and worms associated with hard or nearby unconsolidated substrate, represented by *P. marmoreus* and *P. pilicornis*. Omnivores (OMNI) species which feed on a variety of resources (*i.e.* detritus, small fish, macroalgae, mollusks, etc.), represented by *A. saxatilis* and *D. argenteus*. Planktivores (PLANK) species which feed primarily on micro and macroplankton, represented by *C. limbata* and *C. multilineata*. Sessile Invertebrate Feeders (SINV) species which feed on sessile benthic invertebrates (*i.e.* cnidarians, bryozoans, ascidians and sponges), represented by *C. striatus* and *P. paru*. Territorial herbivores (THER) species which include in their diet mostly macroalgae, cultivated in a restricted area, aggressively defended, represented by *S. fuscus* and *S. variabilis* (Ferreira et al. 2004; Luiz et al. 2008; Anderson et al. 2015).

Data collection of fish density and biomass

This work was based on nine years of underwater observations using scuba diving conducted by the authors and accessing the Marine Macroecology and Biogeography Laboratory data bank. Over 4,000 underwater visual censuses taken from 2008 to 2016 were analyzed.

To collect and quantify data of density reef fishes populations, underwater visual census method (UVC: 20 × 2 m strip transects =40 m^2) was applied. The diver swam 1 m above substratum along the transect, while unrolling a measuring tape, all fish individuals found were recorded, identified, measured and separated into 5 cm categories (Floeter et al. 2007). All sampling campaigns were conducted in the morning, during the Austral summers.

The biomass of fishes was accessed using the following equation: $\mathbf{W = a \times TL^b}$ (published weight-length relationships) in which **“W”** is the total wet weight in grams, **“a”** and **“b”** are species-specific parameters of the relationship, and TL is the total size in cm (Anderson et al. 2014; Froese and Pauly 2016).

Data collection of topographic variables

The same method with different width and length (UVC: 30 × 4 m strip transects =120 m^2) was applied to explore the topographic patterns of the sites (*i.e.* complexity, shelter availability and inclination of the reef) (Anderson 2012). Eighteen transects were executed, totaling

2160 m² sampled for each of the four sampled sites. The diver recorded environmental data, stopping at every 5 m along the length of 30 m, totaling six environmental datasets sampled per transect. Environmental variables included (1) complexity: the diver counted the number of small rocks [radius (r) <10 cm)], medium rocks [radius (r) = 10-50 cm)], and large rocks [radius (r) > 50 cm)]; (2) shelter availability: the diver counted the number of small holes/shelters [opening (o) <10 cm], medium [opening (o) = 10-50 cm] and large holes/shelters [opening (o) >50 cm]; (3) inclination of the rocky reef: the diver inferred the inclination of the reef at every 5 m along the transect using a plastic protractor (Anderson 2012).

Temperature data

Temperature data was inferred with data loggers (HOBO® Data Logger UA-002) deployed on the rocky reefs by divers during sampling expeditions. Each data logger was fixed on the bottom with epoxy resin. Fourteen data loggers were installed: [six on the "shallow" (Slope) stratum and six on the "intermediate" (Interface)] (Figure 1).

Fish community structure sampling design

Two depth strata were sampled in each site: slope and interface. Slope (S) was considered the area between the water surface and half (1/2) of the total depth (TD) (*i.e.* if TD = 12 m, the slope will be = 0-6 m). The interface (I) consists of the transition zone between the rocky reef (slope) and the non-consolidated substratum (Anderson et al. 2015; Floeter et al. 2008). To ensure a symmetric and balanced design among sites, 20 censuses were selected randomly for each site, per year, per strata (*i.e.* n=10 censuses surveyed at the Slope (S) strata (400m²) and n=10 at the Interface (I) strata (400m²) year/site), totalling 800 m² surveyed per year, per site.

Recruitment

Along each transect, the diver swam at constant speed (approximately 4 meters/min.), identifying and recording the number and size of each fish encountered. Fish size (total length: TL) was recorded within 2-cm size classes for most of the species, and within 5-cm size classes for large-sized species such as *E. marginatus* (Guidetti et al.

2014). Small recruits were considered as specimens smaller than 5cm. These individuals were excluded from the population analyses then analyzed separately to infer recruitment rates variations in space and time.

Data analyses

Differences in space and time in density and biomass of species, among trophic groups, size classes, and recruitment were analyzed using ANOVA (analysis of variance) with site and time interval being treated as fixed factors (Lefèvre and Bellwood 2015). When significant differences were found, Tukey HSD post-hoc test was used to verify sources of variation. Before the analyses, assumptions of normality and homoscedasticity were assessed with the Shapiro-Wilks, Kolmogorov-Smirnov/Lilliefors and Bartlett's tests and (Underwood 1981; Zar 1999). All data was submitted to logarithm transformation [Log (X+1)]. Analyses of variance were run in environment R with the package Agricolae (de Mendiburu 2013).

Canonical Correspondence Analysis (CCA) was used to explore and highlight tendencies and patterns of species distribution. Fish biomass means for each site were correlated with environmental variables. Such statistical method allows direct correlations among population and environmental variations, once the ordination axes are chosen with respect to the variables (Ter Braak 1986; Ter Braak 1987; Legendre and Legendre 2012). Variance inflation factor (VIF) was also calculated to test the redundancy of environmental variables in the analysis. A large VIF implies that the variable is redundant with other variables in the data set (Oksanen et al. 2010). Canonical Correspondence Analysis was carried out using the R Package Vegan (Oksanen et al. 2007).

3.5 RESULTS

Spatial and temporal variations of dominant species

Nine years of UVC samples were analyzed during this work. We selected randomly 800 UVCs among four sites (20 censuses per site/per year, during eight years). Such amount of effort covered 32.000 m² of rocky reefs, where 43.169 fish were counted, identified and measured *(in situ*), then converted to biomass data (Table 1).

Most species showed significant variations (ANOVA) in density and biomass among area and time (Table 1, Appendix 1, Figs. 1, 2 and 3). Amongst the 18 species selected in this work, six showed dominance in density and biomass: *A. saxatilis, A. virginicus, D. argenteus, E. marginatus, H. aurolineatum* and *S. fuscus* (species listed in alphabetical order) (Table 1, Appendix 1, Figs. 2 and 3).

The omnivorous (OMNI) Pomacentridae *A. saxatilis* (Sergeant major) showed no significant variations in density and biomass among area [N-EA (No-Entry Area) and N-PA (Non-Protected Area)]. The factor time (Year) showed significant variations for the year 2010, considering the variables density and biomass. Interactions between the factors area and time showed significant variations in density for the N-EA and the year 2011(Table 1, Appendix 1, Fig. 3).

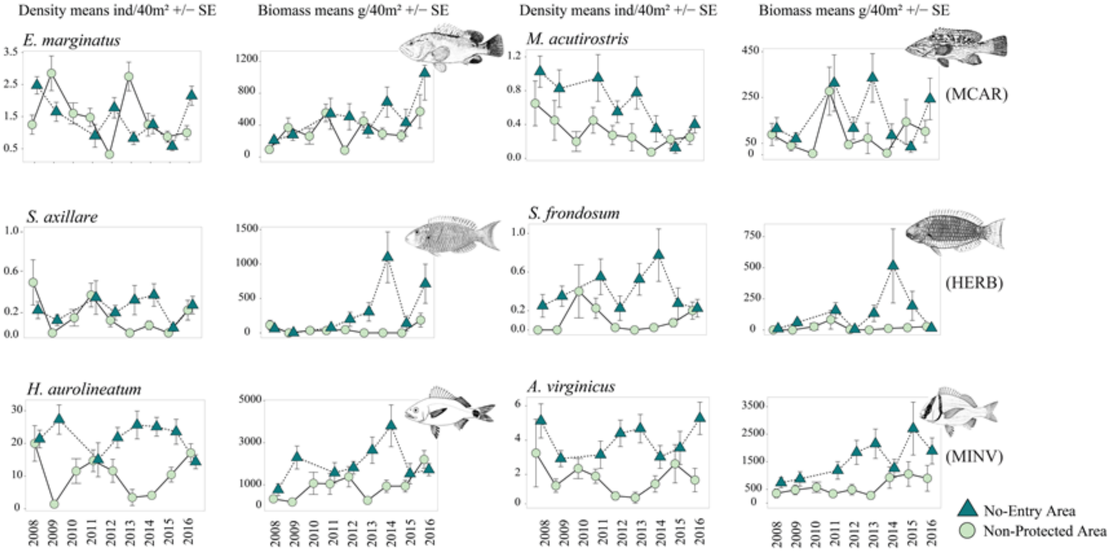

Figure 2. Dominant species mean densities and mean biomasses variations in space and time. Light green circles represent the Non-protected area (N-PA) located outside the MPA, where fisheries are allowed. Dark green triangles represent the No-Entry Area (N-EA) located inside the MPA, totally restricted from fisheries. The acronym MCAR stands for macrocarnivore species, HERB stands for herbivorous species and MINV stands for macro-invertebrate feeders.

The macro-invertebrate feeder (MINV) Haemulidae *A. virginicus* (Porkfish) showed significant variations in density among area. Densities of *A. virginicus* were significantly different inside the N-EA. The factor time (Year) showed no significant variations in density and biomass. Interactions between the factors area and time showed significant variations in biomass for the N-EA and the year 2013 (Table 1, Appendix 1, Fig. 2).

The omnivorous (OMNI) Sparidae *D. argenteus* (South American silver porgy) showed significant variations in density among area (N-EA). The factor time (Year), showed significant variations in density and biomass. Densities and biomass of *D. argenteus* were significantly different inside the N-EA and the year 2009. Interactions between the factors showed significant variations in density for the N-EA and the years 2011 and 2013, and the biomass varied significantly for the N-EA and the years 2012 and 2013(Table 1, Appendix 1, Fig. 3).

The macro-invertebrate feeder (MINV) Haemulidae *H. aurolineatum* (Tomtate grunt) showed significant variations in density and biomass among area (N-EA). The factor time (Year), showed no significant variations in density and biomass. Interactions between the factors showed significant variations in density for the N-EA and the years 2009, 2012, 2013 and 2014; the biomass varied significantly for the N-EA and the years 2012 and 2014 (Table 1, Appendix 1, Fig. 2).

Table 1: Analysis of Variance of dominant species.

Species	Model anova(lm) α=0.05	Significance	Df	Sum sq	Mean sq	F value	P value	Signif. codes	Interactions (Area:Year)
A. saxatilis	Density~Area * Year	Area	1	4.1200	4.1200	2.1805	0.1403	ns	
		Year	8	49.4300	6.1800	3.2701	0.0012	**	
		Area:Year	7	40.7500	5.8200	3.0807	0.0034	**	NE-A: 2011
	Biomass~Area * Year	Area	1	12.1000	12.0500	1.0718	0.3010	ns	
		Year	8	176.5000	22.0630	1.9624	0.0490	*	
		Area:Year	7	117.2000	16.7470	1.4896	0.1682	ns	
A. virginicus	Density~Area * Year	Area	1	60.9000	60.9000	88.1895	0.0000	***	
		Year	8	7.9800	1.0000	1.4451	0.1747	ns	
		Area:Year	7	9.0500	1.2900	1.8722	0.0718	ns	
	Biomass~Area * Year	Area	1	770.9000	770.8900	73.5200	0.0000	***	
		Year	8	30.8000	3.8600	0.3678	0.9375	ns	
		Area:Year	7	169.8000	24.2600	2.3138	0.0248	*	NE-A: 2013
B. rufus	Density~Area * Year	Area	1	0.4750	0.4746	3.2448	0.0722	ns	
		Year	8	3.7230	0.4700	3.1812	0.0015	**	

		Area:Year	7	2.1240	0.3034	2.0743	0.0445	*	NE-A:2019
	Biomass~Area * Year	Area	1	39.7200	39.7170	8.0325	0.0048	**	
		Year	8	36.6500	4.5810	0.9266	0.4938	ns	
		Area:Year	7	71.2300	10.1800	2.0579	0.0463	*	NE-A:2014
C. striatus	Density~Area * Year	Area	1	5.5690	5.5686	18.2577	0.0000	***	
		Year	8	14.4540	1.8067	5.9237	0.0000	***	
		Area:Year	7	1.8860	0.2695	0.8835	0.5191	ns	
	Biomass~Area * Year	Area	1	56.0900	56.0940	15.3357	0.0001	***	
		Year	8	76.4000	9.5500	2.6110	0.0082	**	
		Area:Year	7	33.0900	4.7270	1.2924	0.2516	ns	
C. limbata	Density~Area * Year	Area	1	8.5210	8.5206	17.8135	0.0000	***	
		Year	8	34.9590	4.3700	9.1357	0.0000	***	
		Area:Year	7	7.4470	1.0639	2.2241	0.0309	*	NE-A:2016
	Biomass~Area * Year	Area	1	17.6500	17.6487	8.4473	0.0038	**	
		Year	8	154.0000	19.2497	9.2136	0.0000	***	
		Area:Year	7	17.7700	2.5382	1.2149	0.2923	ns	
C. multilineata	Density~Area * Year	Area	1	4.3860	4.3900	12.0068	0.0006	***	

		Year	8	6.1450	0.7681	2.1025	0.0338	*	
		Area:Year	7	2.2670	0.3239	0.8865	0.5167	ns	
	Biomass~Area * Year	Area	1	7.7500	7.7541	2.8475	0.0921	ns	
		Year	8	44.3100	5.5400	2.0340	0.0406	*	
		Area:Year	7	30.5700	4.3674	1.6038	0.1316	ns	
D. argenteus	Density~Area * Year	Area	1	4.1200	4.1181	5.0223	0.0254	*	
		Year	8	124.9600	15.6195	19.0489	0.0000	***	
		Area:Year	7	35.9200	5.1321	6.2588	0.0000	***	N-EA:2011,2013
	Biomass~Area * Year	Area	1	0.1000	0.0630	0.0075	0.9312	ns	
		Year	8	475.8000	59.4720	7.0259	0.0000	***	
		Area:Year	7	317.9000	45.4170	5.3655	0.0000	***	NE-A: 2012,2013
E. marginatus	Density~Area * Year	Area	1	0.7780	0.7776	2.1732	0.1410	ns	
		Year	8	17.0580	2.1323	5.9592	0.0000	***	
		Area:Year	7	24.2970	3.4710	9.7006	0.0000	***	NE-A:2009,2011,2013,2014,2015
	Biomass~Area * Year	Area	1	17.3000	17.2940	1.9663	0.1614	ns	
		Year	8	170.0000	21.2510	2.4162	0.0143	*	
		Area:Year	7	371.6000	53.1000	6.0365	0.0000	***	NE-A:2009,2011,2013,2015
H. aurolineatum	Density~Area * Year	Area	1	152.6800	152.6830	78.5552	0.0000	***	

		Year	8	18.7800	2.3500	1.2079	0.2918	ns	
		Area:Year	7	83.4300	11.9190	6.1321	0.0000	***	NE-A:2009,2012,2013,2014
	Biomass~Area * Year	Area	1	410.5000	410.4600	39.9726	0.0000	***	
		Year	8	147.1000	18.3900	1.7913	0.0761	ns	
		Area:Year	7	207.9000	29.7000	2.8919	0.0056	**	NE-A:2012,2014
H. poeyi	Density~Area * Year	Area	1	0.9270	0.9300	6.4069	0.0116	*	
		Year	8	2.5040	0.3100	2.1633	0.0287	*	
		Area:Year	7	0.6470	0.0900	0.6384	0.7242	ns	
	Biomass~Area * Year	Area	1	7.3800	7.3800	2.0051	0.1573	ns	
		Year	8	33.7200	4.2200	1.1454	0.3308	ns	
		Area:Year	7	14.3300	2.0500	0.5565	0.7913	ns	
M. acutirostris	Density~Area * Year	Area	1	3.8870	3.8900	21.5899	0.0000	***	
		Year	8	7.4080	0.9300	5.1433	0.0000	***	
		Area:Year	7	1.1990	0.1700	0.9513	0.4663	ns	
	Biomass~Area * Year	Area	1	68.2900	68.2900	12.3685	0.0005	***	
		Year	8	163.0200	20.3800	3.6904	0.0003	***	
		Area:Year	7	37.9700	5.4200	0.9823	0.4431	ns	

P. marmoreus	Density~Area * Year	Area	1	2.2200	2.2200	3.4271	0.0647	ns	
		Year	8	36.5800	4.5700	7.0489	0.0000	***	
		Area:Year	7	49.0800	7.0100	10.8103	0.0000	***	NE-A:2009,2011,2013,2014,2015
	Biomass~Area * Year	Area	1	1.6700	1.6700	1.0510	0.3057	ns	
		Year	8	50.2200	6.2800	3.9598	0.0001	***	
		Area:Year	7	71.9400	10.2800	6.4833	0.0000	***	NE-A:2009,2011,2012,2013,2014,2015
P. pilicornis	Density~Area * Year	Area	1	0.4100	0.4100	0.5900	0.4427	ns	
		Year	8	20.5000	2.5600	3.7036	0.0003	***	
		Area:Year	7	23.0800	3.3000	4.7654	0.0000	***	NE-A:2009,2011,2012,2014,2015
	Biomass~Area * Year	Area	1	0.0000	0.0000	0.0002	0.9890	ns	
		Year	8	61.6200	7.7000	4.3782	0.0000	***	
		Area:Year	7	55.2300	7.8900	4.4846	0.0001	***	NE-A:2009,2011,2012,2014,2015
P. paru	Density~Area * Year	Area	1	2.1540	2.1500	18.1182	0.0000	***	
		Year	8	0.4170	0.0500	0.4381	0.8982	ns	
		Area:Year	7	1.6340	0.2300	1.9641	0.0579	ns	
	Biomass~Area * Year	Area	1	139.7400	139.7400	27.5994	0.0000	***	
		Year	8	10.7800	1.3500	0.2662	0.9765	ns	

		Area:Year	7	53.7800	7.6800	1.5173	0.1586	ns	
S. axillare	Density~Area * Year	Area	1	0.3170	0.3200	3.4985	0.0619	ns	
		Year	8	2.1450	0.2700	2.9559	0.0030	**	
		Area:Year	7	0.9990	0.1400	1.5736	0.1405	ns	
	Biomass~Area * Year	Area	1	43.9200	43.9200	9.7598	0.0019	**	
		Year	8	99.2200	12.4000	2.7562	0.0054	**	
		Area:Year	7	51.6100	7.3700	1.6385	0.1219	ns	
S. frondosum	Density~Area * Year	Area	1	2.7280	2.7300	21.6445	0.0000	***	
		Year	8	1.5700	0.2000	1.5573	0.1347	ns	
		Area:Year	7	1.2450	0.1800	1.4110	0.1981	ns	
	Biomass~Area * Year	Area	1	64.3200	64.3200	20.7731	0.0000	***	
		Year	8	43.2500	5.4100	1.7459	0.0852	ns	
		Area:Year	7	40.2700	5.7500	1.8580	0.0742	ns	
S. fuscus	Density~Area * Year	Area	1	17.0500	17.0500	14.0356	0.0002	***	
		Year	8	36.0700	4.5100	3.7116	0.0003	***	
		Area:Year	7	45.9700	6.5700	5.4053	0.0000	***	NE-A:2011
	Biomass~Area * Year	Area	1	21.3700	21.3700	5.0770	0.0246	*	
		Year	8	186.0600	23.2600	5.5252	0.0000	***	

		Area:Year	7	140.2000	20.0300	4.7581	0.0000	***	NE-A:2011,2015
S. variabilis	Density~Area * Year	Area	1	1.9790	1.9800	7.9288	0.0050	**	
		Year	8	7.8260	0.9800	3.9185	0.0002	***	
		Area:Year	7	1.8360	0.2600	1.0504	0.3946	ns	
	Biomass~Area * Year	Area	1	5.2200	5.2200	3.3253	0.0688	ns	
		Year	8	24.7500	3.0900	1.9698	0.0481	*	
		Area:Year	7	20.3800	2.9100	1.8539	0.0749	ns	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

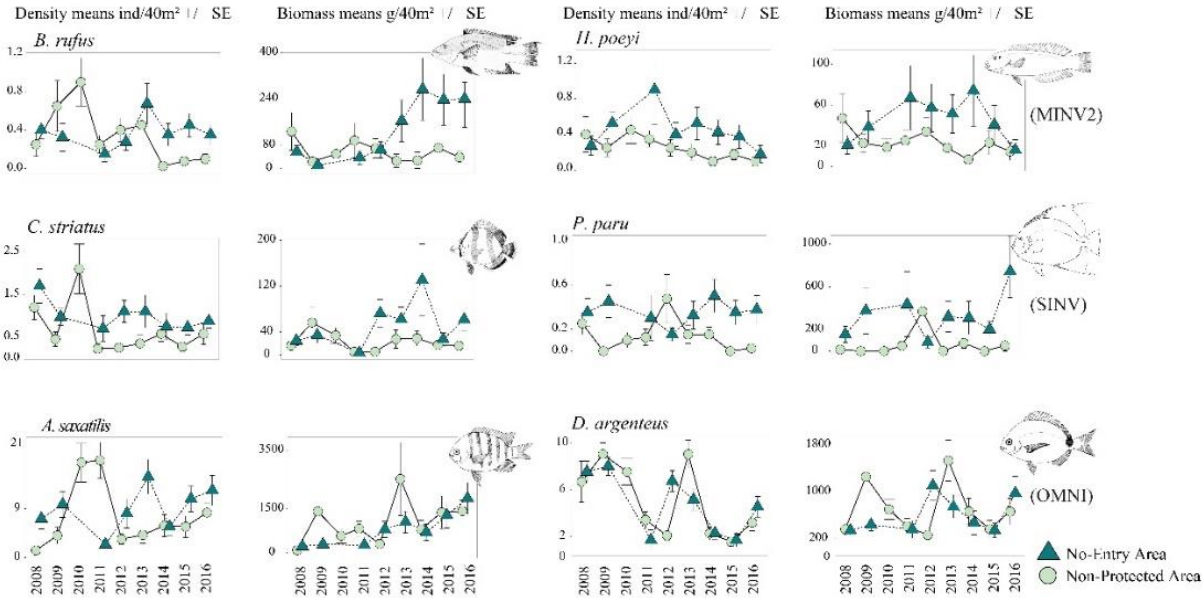

Figure 3. Dominant species mean densities and mean biomasses variations in space and time. Light green circles represent the Non-protected area (N-PA) located outside the MPA, where fisheries are allowed. Dark green triangles represent the No-Entry Area (N-EA) located inside the MPA, totally restricted from fisheries. The acronym MINV2 stands for macro-invertebrate feeders, SINV stands for sessile invertebrate feeders and OMNI stands for omnivorous species.

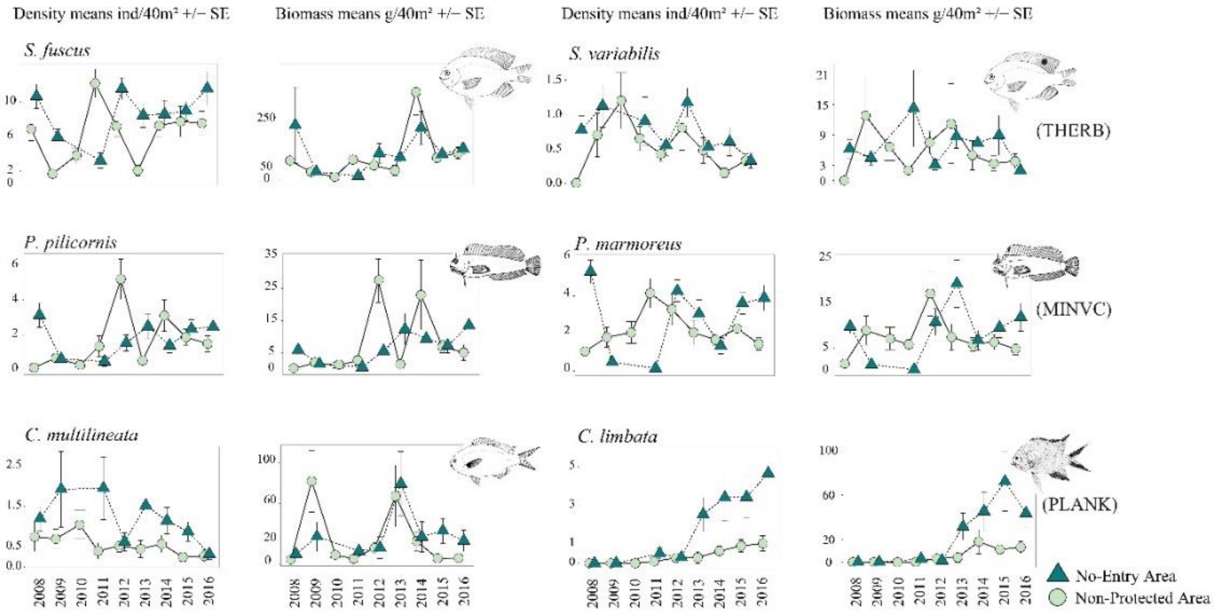

Figure 4. Dominant species mean densities and mean biomasses variations in space and time. Light green circles represent the Non-protected area (N-PA) located outside the MPA, where fisheries are allowed. Dark green triangles represent the No-Entry Area (N-EA) located inside the MPA, totally restricted from fisheries. The acronym THERB stands for territorial herbivores, MINVC stands for cryptic macro-invertebrate feeders and PLANK stands for planktivores species.

The territorial herbivore (THERB) Pomacentridae *S. fuscus* (Brazilian damsel) showed significant variations in density and biomass among area (N-EA). The factor time (Year) also showed significant variations in density and biomass. Density varied significantly for the years 2008, 2009, 2011 and 2012. Biomass varied significantly for the years 2008, 2009, 2011, 2013 and 2014. Interactions between the factors showed significant variations in density for the N-EA and the year 2011; biomass varied significantly for the N-EA and the years 2011 and 2015 (Table 1, Appendix 1, Fig. 4).

Spatial and temporal variations of trophic groups

Most groups showed significant variations of density and biomass among area and time (ANOVA) (Table 2, Appendix 2. Fig. 5). When species were grouped into trophic groups responses to spatial distribution and annual population variations seem to show similar patterns as shown by species analyzed isolatedly.

Macrocarnivores/ piscivores (MCAR) represented by *E. marginatus* and *M. acutirostris*, varied significantly in density and biomass according to the factor area (Space) (NE-A). In addition, densities and biomass of MCARs varied according to the factor time (Year). Densities decreased in time from 2008 to 2015. In 2016, densities shows modest signs of recovery. Otherwise, biomass of MCARs increased in time from 2008 to 2016. Interactions between the factors showed significant variations in space (NE-A) and time (years: 2009, 2011, 2013, 2014, and 2015). The biomass of MCARs also showed significant variations in space (NE-A) and time (years: 2009, 2011, 2013, and 2015) (Table 2, Appendix 2. Fig. 5).

Herbivorous fish (HERB) represented here by the parrotfishes *S. axillare* and *S. frondosum*, also showed significant variations of density and biomass in space and time. Density and biomass varied significantly for the factors area (NE-A) and time (Years: 2011, 2014 and 2015). Interactions between the factors showed significant variations for the NE-A and the years 2013 and 2014. The biomass showed the same pattern of variation for the NE-A and the years 2011, 2013 and 2014 (Table 2, Appendix 2. Figs. 1, 5 and 9).

Grunts [macroinvertebrates feeders (MINV)], positioned in the central region of the marine food web (mesoconsumers) in this work, are represented by *H. aurolineatum* and *A. virginicus* showed higher densities and biomass among other species studied in this work. Moreover, density varied significantly for the factor area (NE-A) and time (Year). Biomass varied significantly only in space (NE-A). Interactions between the factors showed significant variations in space (NE-A) and time (years: 2009, 2012, 2013 and 2014). Biomass seems to be increasing in time for both NE-A and NP-A (Table 2, Appendix 2. Fig 5).

Table 2: Analysis of variance species grouped by Trophic levels.

Trophic level	Model anova(lm) α=0.05	Significance	Df	Sum sq	Mean sq	F value	P value	Signif. codes	Interactions (Area:Year)
Macrocarnivores/piscivores	Density~Area * Year	Area	1	4.2890	4.2890	11.1258	0.0009	***	
(MCAR)		Year	8	25.3100	3.1638	8.2070	0.0000	***	
		Area:Year	7	19.4510	2.7787	7.2079	0.0000	***	N-EA: 2009,2011,2013,2014,2015
	Biomass~Area * Year	Area	1	52.2000	52.1660	6.1334	0.0136	*	
		Year	8	197.9000	24.7430	2.9091	0.0035	**	
		Area:Year	7	274.8000	39.2570	4.6156	0.0000	***	N-EA: 2009,2011,2013,2015
Herbivores	Density~Area * Year	Area	1	4.2050	4.2053	21.7657	0.0000	***	
(HERB)		Year	8	4.6690	0.5837	3.0210	0.0025	**	
		Area:Year	7	3.2180	0.4596	2.3791	0.0210	*	N-EA: 2013,2014
	Biomass~Area * Year	Area	1	161.7000	161.6570	26.3840	0.0000	***	
		Year	8	136.8000	17.1000	2.7910	0.0049	**	
		Area:Year	7	114.8000	16.4030	2.6771	0.0098	**	N-EA: 2011,2013,2014
Macroinvertebrates feeders	Density~Area * Year	Area	1	195.4100	195.4050	122.2790	0.0000	***	
(MINV)		Year	8	28.9500	3.6190	2.2646	0.0218	*	
		Area:Year	7	47.7000	6.8150	4.2644	0.0001	***	N-EA: 2009,2012,2013,2014
	Biomass~Area * Year	Area	1	579.5000	579.4700	70.3972	0.0000	***	
		Year	8	124.6000	15.5800	1.8928	0.0588	ns	
		Area:Year	7	50.3000	7.1900	0.8737	0.5270	ns	

Sessile invertebrates feeders	Density~Area * Year	Area	1	11.0490	11.0492	30.7136	0.0000	***	
(SINV)		Year	8	13.5200	1.6900	4.6976	0.0000	***	
		Area:Year	7	1.8820	0.2689	0.7475	0.6317	ns	
	Biomass~Area * Year	Area	1	227.9000	227.8770	35.2035	0.0000	***	
		Year	8	62.9000	7.8650	1.2150	0.2876	ns	
		Area:Year	7	57.0000	8.1460	1.2584	0.2689	ns	
Omnivores	Density~Area * Year	Area	1	5.8600	5.8575	4.0274	0.0453	*	
(OMNI)		Year	8	77.4100	9.6757	6.6526	0.0000	***	
		Area:Year	7	42.8700	6.1246	4.2110	0.0002	***	N-EA: 2011
	Biomass~Area * Year	Area	1	0.3000	0.2520	0.0299	0.8627	ns	
		Year	8	184.4000	23.0530	2.7394	0.0057	**	
		Area:Year	7	283.4000	40.4930	4.8119	0.0000	***	N-EA: 2012
Cryptic macroinvertebrates feeders	Density~Area * Year	Area	1	2.5300	2.5342	2.7928	0.0952	ns	
(MINVC)		Year	8	43.4700	5.4335	5.9880	0.0000	***	
		Area:Year	7	64.3000	9.1854	10.1229	0.0000	***	N-EA: 2009,2011,2012,2013,2014,2015
	Biomass~Area * Year	Area	1	1.4200	1.4239	0.6792	0.4102	ns	
		Year	8	71.1700	8.8968	4.2441	0.0001	***	
		Area:Year	7	108.9100	15.5585	7.4219	0.0000	***	N-EA: 2009,2011,2012,2013,2014,2015
Territorial herbivores	Density~Area * Year	Area	1	20.4400	20.4422	17.0175	0.0000	***	
(THERB)		Year	8	23.5700	2.9458	2.4523	0.0129	*	

		Area:Year	7	43.0400	6.1490	5.1188	0.0000	***	N-EA: 2011
	Biomass~Area * Year	Area	1	19.5900	19.5908	4.9443	0.0266	*	
		Year	8	104.3700	13.0464	3.2927	0.0011	**	
		Area:Year	7	89.7300	12.8185	3.2352	0.0023	**	N-EA: 2011
Planktivores	Density~Area * Year	Area	1	20.3100	20.3082	28.3178	0.0000	***	
(PLANK)		Year	8	14.5900	1.8237	2.5430	0.0100	**	
		Area:Year	7	8.5300	1.2181	1.6986	0.1067	ns	
	Biomass~Area * Year	Area	1	34.6000	34.6030	9.1818	0.0026	**	
		Year	8	98.7200	12.3410	3.2745	0.0012	**	
		Area:Year	7	59.6300	8.5180	2.2603	0.0283	*	N-EA: 2013

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

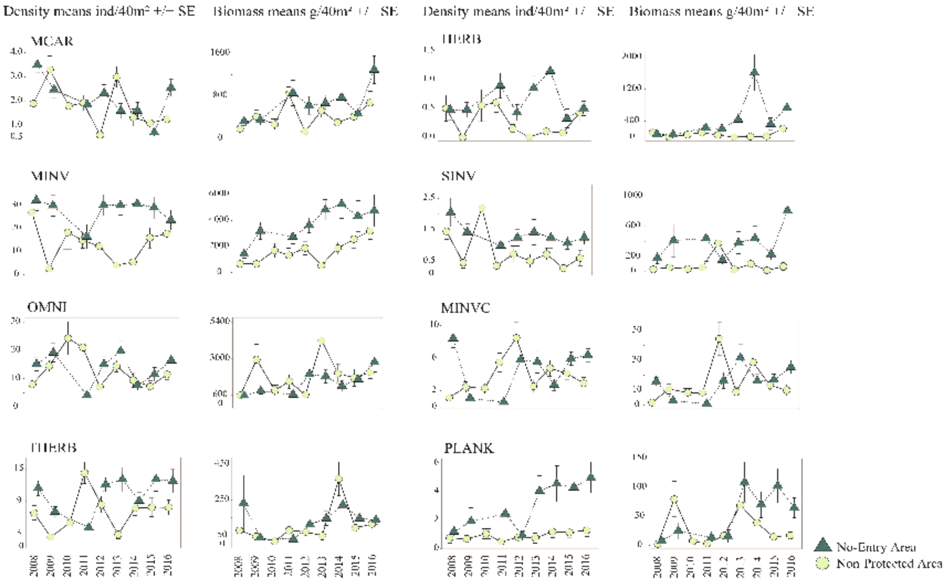

Figure 5. Functional trophic groups mean densities and mean biomasses variations in space and time. Light green circles represent the Non-protected area (N-PA) located outside the MPA, where fisheries are allowed. Dark green triangles represent the No-Entry Area (N-EA) located inside the MPA, totally restricted from fisheries. The acronym MCAR stands for macrocarnivore species, HERB herbivorous species, MINV macro-invertebrate feeders, SINV stands for sessile invertebrate, OMNI omnivorous species, MINVC cryptic macro-invertebrate feeders THERB territorial herbivores and PLANK planktivores species.

Sessile invertebrates feeders (SINV) (*i.e.* angelfishes and butterfly fishes), in this work represented by *P. paru* and *C. striatus* showed significant variations in density for the factors area (NE-A) and time (Year). Interactions between the factors showed no significant variations. The biomass of SINVs varied only for the factor area (NE-A). No interactions between the factors were found (Table 2, Appendix 2. Figs. 1, 5 and 9).

Omnivores (OMNI) also positioned in the central region of the marine food web (mesoconsumers) represented by *A. saxatilis* and *D. argenteus*, showed significant variations in density for the factors area (NE-A) and time (Year). Interactions between the factors showed significant variations for the NE-A and the year 2011. Their biomass varied significantly for the factor time (Year), biomass showed no significance for the factor area. Interactions between the factors showed significant variations for the NE-A and the year 2012 (Figs 1, 5 and 9).

Cryptic macroinvertebrates feeders (MINVC - *P. marmoreus* and *P. pilicornis*) and Territorial herbivores (THERB - *S. fuscus* and *S. variabilis*), are regarded as the basis of the food web. MINVCs populations densities did not varied significantly for the actor area. Their densities varied significantly for the factor time. Interactions between the factors showed significant variations in densities for the NE-A and the years: 2009, 2011, 2012, 2013, 2014, and 2015 (Table 2, Appendix 2, Figs. 5 and 9). Biomass of MINVCs varied significantly on for the factor time (Year). Interactions between the factors showed significant variations in biomass for N-EA and years: 2009, 2011, 2012, 2013, 2014 and 2015. THERBs densities varied significantly for the factor area (NE-A) and showed modest variations in time. Interactions between the factors showed significant variations in densities for NE-A and the year 2011. Biomass showed low significant variations for the factor area (NE-A) and year. Interactions between the factors showed significant variations in biomass for NE-A and the year 2011(Table 2, Appendix 2, Figs. 5 and 9).

Planktivores Pomacentridae (PLANK - *C. limbata* and *C. multilineata*) are also regarded as the basis of the food web. Their densities and biomass showed significant variations for both factors area (NE-A) and time. Interactions between the factors showed no significant variations in densities. Also, interactions between the factors showed modest significant variations in Biomass (Table 2, Appendix 2, Figs. 5).

Dominant species population structure’s spatial variations

Among all dominant species only *A. virginicus* and *H. aurolineatum* varied significantly (ANOVA) for the factor area (NE-A). The biomass of *A. virginicus* also showed significant variation of biomass for the factor area (NE-A) (Table 3, Appendix 3, Figs.6 and 9). Considering the interactions between the factors (*e.g.* biomass~size.class * area) only *E. marginatus* showed significant variations for species larger than 60 cm and the NE-A (Table 3, Appendix 3, Figs.6 and 9).

All populations of reef fish on southern Brazilian rocky reefs showed significant variations in size classes, regarding the intermediate sizes (sub-adults) for all species (Table 3, Appendix 3, Figs.6).

Table 3. Analysis of variance of dominant species subdivided in size classes.

Species	Model anova(lm) α=0.05	Significance	Df	Sum sq	Mean sq	F value	P value	Signif. codes	Interactions (Area:Size.class)
A. saxatilis	Density~Size.class * Area	Area	1	0.0714	0.0714	0.1396	0.7184	ns	
		Size.class	3	20.3159	6.7720	13.2429	0.0018	**	
		Area:Size.class	3	0.5075	0.1692	0.3308	0.8035	ns	
	Biomass~Size.class * Area	Area	1	0.2996	0.2996	0.3029	0.5971	ns	
		Size.class	3	26.0988	8.6996	8.7957	0.0065	**	
		Area:Size.class	3	1.0159	0.3386	0.3424	0.7956	ns	
A. virginicus	Density~Size.class *Area	Area	1	1.5233	1.5233	13.9789	0.0022	**	
		Size.class	6	18.3879	3.0646	28.1233	0.0000	***	
		Area:Size.class	6	1.0122	0.1687	1.5481	0.2340	ns	
	Biomass~Size.class * Area	Area	1	10.1950	10.1950	6.8305	0.0204	*	
		Size.class	6	232.4580	38.7430	25.9572	0.0000	***	
		Area:Size.class	6	12.0640	2.0110	1.3471	0.3010	ns	
D. argenteus	Density~Size.class * Area	Area	1	0.1719	0.1719	1.6867	0.2184	ns	
		Size.class	5	24.6708	4.9342	48.4068	0.0000	***	
		Area:Size.class	5	0.9768	0.1954	1.9166	0.1651	ns	
	Biomass~Size.class * Area	Area	1	0.0260	0.0260	0.0812	0.7806	ns	

		Size.class	5	181.1620	36.2320	112.1100	0.0000	***	
		Area:Size.class	5	1.6260	0.3250	1.0064	0.4549	ns	
E. marginatus	Density~Size.class * Area	Area	1	0.2825	0.2825	3.8700	0.0693	ns	
		Size.class	6	6.0647	1.0108	13.8470	0.0000	***	
		Area:Size.class	6	0.1314	0.0219	0.3000	0.9267	ns	
	Biomass~Size.class * Area	Area	1	9.5800	9.5801	45.5970	0.0000	***	
		Size.class	6	130.5850	21.7641	103.5880	0.0000	***	
		Area:Size.class	6	29.9950	4.9992	23.7940	0.0000	***	N-EA: 60>
H. aurolineatum	Density~Size.class * Area	Area	1	1.9420	1.9423	9.7595	0.0108	*	
		Size.class	4	52.1060	13.0265	65.4527	0.0000	***	
		Area:Size.class	4	1.2450	0.3113	1.5640	0.2576	ns	
	Biomass~Size.class * Area	Area	1	5.4030	5.4030	4.5682	0.0583	ns	
		Size.class	4	157.7460	39.4360	33.3423	0.0000	***	
		Area:Size.class	4	2.8670	0.7170	0.6060	0.6674	ns	
S. fuscus	Density~Size.class * Area	Area	1	0.2425	0.2425	2.0005	0.2070	ns	
		Size.class	2	8.9399	4.4700	36.8824	0.0004	***	
		Area:Size.class	2	0.1516	0.0758	0.6256	0.5665	ns	
	Biomass~Size.class * Area	Area	1	0.3324	0.3324	1.5046	0.2659	ns	
		Size.class	2	12.6424	6.3212	28.6139	0.0009	***	

Area:Size.class	2	0.1548	0.0774	0.3504	0.7179	ns

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

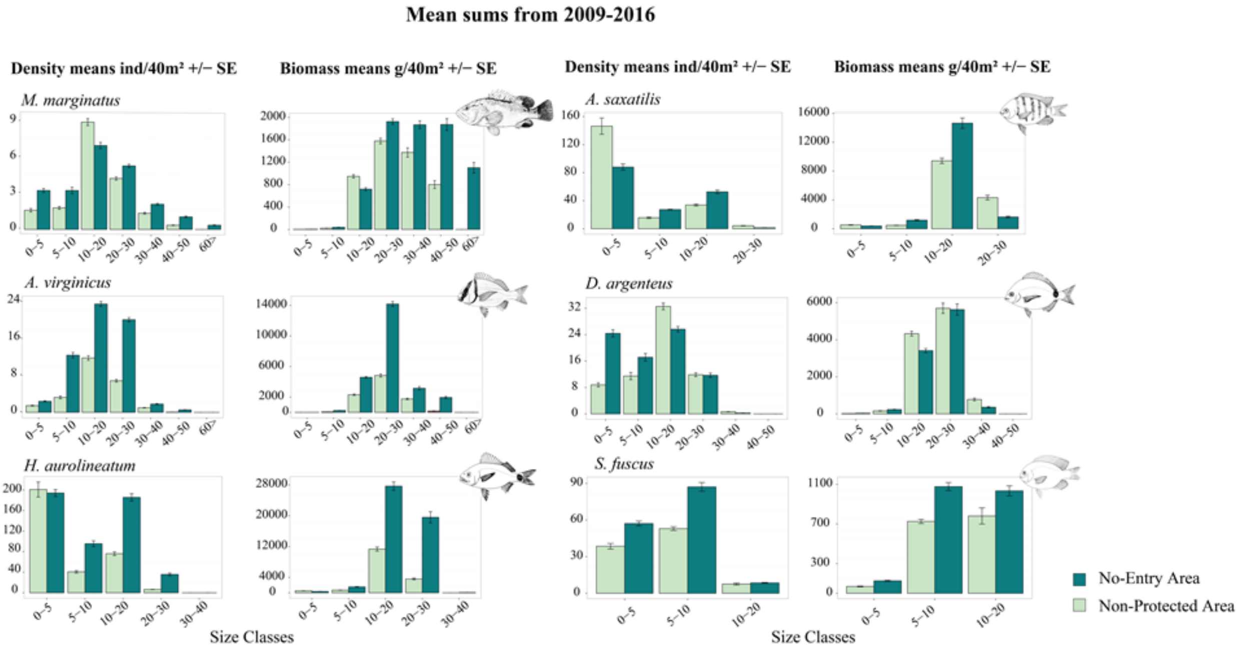

Figure 6. Dominant species mean densities sums and mean biomasses sums (2009-2016) variations in space according to their size classes. Light green bars represent the Non-protected area (N-PA) located outside the MPA, where fisheries are allowed. Dark green bars represent the No-Entry Area (N-EA) located inside the MPA, totally restricted from fisheries.

Recruitment of dominant species in space and time

Recruitment rates showed significant variations for *D. argenteus* for the factors area (NE-A) and year. Densities of *E. marginatus* varied significantly for area (NE-A) and year. Interactions among factors showed significant variations for area (NE-A) and the years 2009, 2011, 2013, 2014, 2015 and 2016. The damselfish *S. fuscus* showed significant variations only for the factor year. Others show no significant variations in recruitment in space and time (Table 4, Appendix 4, and Fig. 7).

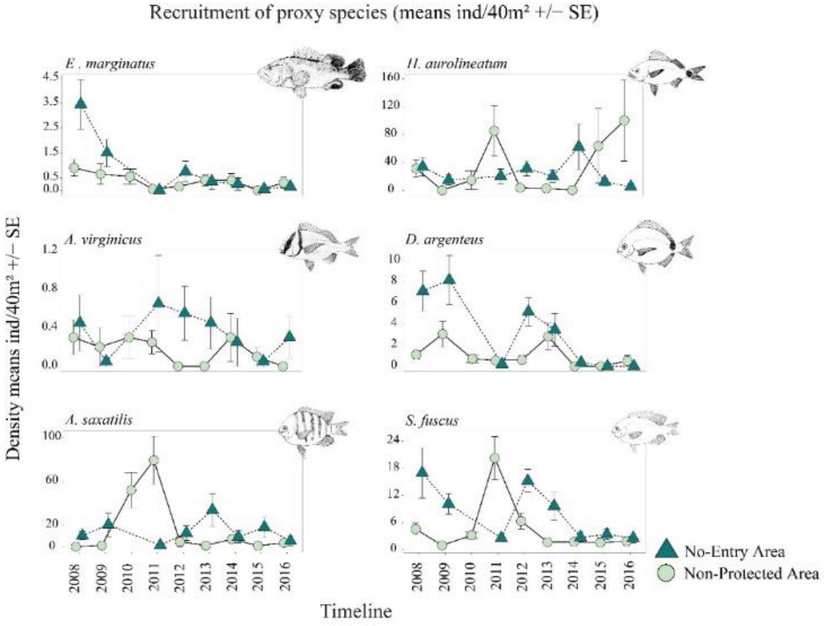

Figure 7. Recruitment of dominant species mean densities and mean biomasses variations in space and time. Light green circles represent the Non-protected area (N-PA) located outside the MPA, where fisheries are allowed. Dark green triangles represent the No-Entry Area (N-EA) located inside the MPA, totally restricted from fisheries.

Table 4: Analyses of variance: recruitment of dominant species.

Species	**Model anova(lm) α=0.05**	**Significance**	**Df**	**Sum sq**	**Mean sq**	**F value**	**P value**	Signif. codes	**Interactions (Area : Year)**
A. saxatilis	Density~Area * Year	Area	1	1.1200	1.1200	1.5240	0.2406	ns	
		Year	8	13.1797	1.6475	2.2418	0.1003	ns	
		Area : Year	7	9.4864	1.3552	1.8441	0.1678	ns	
A. virginicus	Density~Area * Year	Area	1	0.0299	0.0300	2.2540	0.1591	ns	
		Year	8	0.1583	0.0198	1.4892	0.2575	ns	
		Area : Year	7	0.1721	0.0246	1.8499	0.1667	ns	
D. argenteus	Density~Area * Year	Area	1	0.9065	0.9065	14.2909	0.0026	**	
		Year	8	7.9979	0.9997	15.7601	0.0000	***	
		Area : Year	7	1.2906	0.1844	2.9066	0.0504	ns	
E. marginatus	Density~Area * Year	Area	1	0.0773	0.0774	12.8538	0.0037	**	
		Year	8	1.9493	0.2437	40.4792	0.0000	***	
		Area : Year	7	0.1688	0.0241	4.0061	0.0173	*	N-EA:2009, 2011, 2013, 2014, 2015, 2016
H. aurolineatum	Density~Area * Year	Area	1	1.1756	1.1756	0.5110	0.4884	ns	
		Year	8	8.5093	1.0637	0.4623	0.8601	ns	
		Area : Year	7	22.5104	3.2158	1.3977	0.2910	ns	
S. fuscus	Density~Area * Year	Area	1	0.8078	0.8078	4.5771	0.0536	ns	
		Year	8	8.3857	1.0482	5.9394	0.0032	**	

Area : Year	7	2.1729	0.3104	1.7589	0.1862	ns

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

3.6 DISCUSSION

Spatial and temporal variations of dominant species

The spatial variations detected in this work are more likely to be influenced by deterministic mechanisms such as evolutive history (habitat affinity), habitat heterogeneity of rocky substrate availability, cyclic seasonal temperature oscillations, protection factor (e.g. *E. marginatus* and *M. acutirostris*) (Leirs et al. 1997; Ault and Johnson 1998; García-Charton and Pérez-Ruzafa 2001; Kuffner et al. 2007; Anderson et al. 2014). Whereas, observed annual dynamic variations in populations may be affected by nonlinear density-dependent components (*i.e.* higher predation rates induced by warmer austral summers), coupled with deterministic (habitat heterogeneity) and stochastic seasonal components (*i.e.* random seasonal temperature oscillations) (Leirs et al. 1997; Ault and Johnson 1998; García-Charton and Pérez-Ruzafa 2001; Kuffner et al. 2007) (Fig. 2, 3, 4 and 9).

Some species, such as, *A. saxatilis*, *D. argenteus*, *H. aurolineatum*, *P. pilicornis*, which seem more acclimated to stochastic seasonal temperature oscillations, in south western Atlântic, tend to present more homogeneous distributions among areas (Figs 1and 9). Such pattern could indicate a connection with an evolutive process (Rocha 2003; Rocha et al. 2005) in which these species could have acclimated more rapidly than others to temperature oscillations (Donelson et al. 2011). Otherwise, their population variations in time could be influenced mainly by density-dependent mechanisms [*i.e.* decrease: recruits post-settlement survival rates, predation of sub-adult and adults; increase: removal of predator by fisheries, high level of larval production and recruitment (density-dependent facilitation-Allee effect)], coupled with the deterministic mechanisms mentioned above (Carr 1991; Carr and Hixon 1995; Leirs et al. 1997; Begon et al. 2006).

Other species, differently, seem to be more sensitive to stochastic seasonal temperature oscillations than others (*i.e. A. virginicus, H. poeyi, P. marmoreus, S. axillare* and S. *fromdosum*). Consequently, their spatial distributions tend to be higher in areas where lower austral winter temperatures are less likely to occur (Figs. 1, 8 and 9). Their annual variations seem to be governed also by the same density-dependent mechanisms mentioned above, working in synergy with deterministic mechanisms, also mentioned before (Carr 1991; Carr and Hixon 1995;

Leirs et al. 1997; Begon et al. 2006) (Figs. 2, 3, 8 and 9). In extreme cases of low temperatures during harsh austral winters, the metabolism of herbivorous parrotfishes (for example) is not enough to provide energy for normal diurnal activities. The fish lay numb by the cold on the reef substrate, and they must be probably preyed (Anderson & Floeter, pers. obs.).

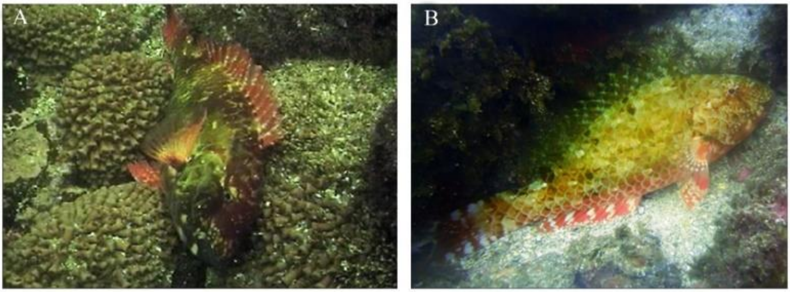

Figure 8. Herbivorous fish in a state of diurnal torpor induced by the cold (sea temperature <18ºC). A) *S. frondosum*, Arvoredo Island (NP-A), austral winter 2010; B) *S. axillare*, Xavier Island (NP-A), austral winter, 2012.Picture A taken by Dalben, A. and picure B taken by Anderson, A.B.

The torpor induced by cold temperatures in parrot fishes from southern Brazil may also have roots on their evaluative Caribbean past (Rocha 2003; Rocha et al. 2005). Moreover, according to Almada & Faria (2008), for many rocky reef species of teleost fishes that are near or on their distributional limits (Anderson et al. 2015), fluctuations in abundance are frequent (Almada and Faria 2004).

Some species in this work (*i.e. C. limbata*, *C. multilineata*, *C. striatus, S. fuscus* and *S. variabilis*) tend to have their spatial distribution highly influenced deterministic mechanisms such as shelter and nursery environmental availability (Figs.3, 4 and 9). Pomacentrids are notorious to display aggressive farming, foraging and reproductive behavior (Leal et al. 2013; Osório et al. 2006; Pereira and Padovani Ferreira 2012). Therefore, spatial complexity may be a very important driver on their spatial distribution (Figs.3, 4 and 9). In contrast, their annual population variations may vary governed by stochastic mechanisms such as harsh austral winter temperature oscillations, which tend to influence farming (Field et al. 1998; Raven and Geider 1988; Hata and Kato 2004). Moreover, density-dependent mechanisms such as intra-specific and inter-specific competition, predation may operate important influence on their annual variations (Carr 1991, Carr & Hixon 1995, Leirs et al. 1997, Begon et al. 2006) (Figs.3, 4 and 9).

Spatial and temporal variations of trophic groups

Macrocarnivores (MCAR) biomass seem to vary in space favored by the restrictions from fisheries of the NE-A (Palumbi 2004; Maggs et al. 2013; Anderson et al. 2014; Mellin et al. 2016). The effectiveness of the MPA is evident, specially protecting the old, big and furtive matrices (*i.e* long-living individuals can reach 60 years and their biomass tend to increase in time) (Reñones et al. 2002) (Fig. 6). Old and large individuals are responsible for most of high quality larval production and repopulation of adjacent areas (Palumbi 2004, Maggs et al. 2013). In contrast, their densities variations in space seem to be more influenced by spawning and recruitment rates (Fig. 5), which has been decreasing in time over the past nine years (Fig.7). Tidal pools are regarded as nursery habitat for grouper recruits on southern Brazilian rocky reefs (Andrade et al. 2003; Cunha et al. 2007). Small post-spawning grouper recruits are often seen living on tidal pools (Andrade et al. 2003). Anthropic pressure on these microhabitats may have influenced the low recruitment rates on MCARs (Giraldes et al. 2015).

Density and biomass of HERB fishes shows a discrete pattern of stability, which may be due to their low density and biomass (Fig. 5). These species are also, very sensitive to low temperatures, which seem to occur more frequently on the sites outside the NE-A (Figs. 1, 5, 8 and 9). Both variables: protection from fisheries and temperature, acting synergically, seems to govern the distributions (densities) and growth rates (biomass) (Figs. 1, 5, 8 and 9). The numbness induced by cold austral winter water temperatures on HERBs may be very important phenomena, regarding the mortality of herbivores in Brazilian southern rocky reefs (Fig.8). The periods these fishes remain numb is unknown. Local researchers call these phenomena “the long sleep of the southern parrotfish” (Anderson & Floeter, pers. obs) (Fig.8). Such patterns may indicate variations influenced by stochastic mechanisms (*i.e.* density-dependent mortality factor mediated by climatic oscillations) (Sale 1978; Sale 1980; Doherty 2002; Almada and Faria 2004).

Despite the low commercial interest in MINVs (Begossi et al. 2012; Martins et al. 2013), their biomass is higher inside the NE-A. Such unexpected response from non-targeted species, corroborates Mellin et al. (2016), regarding the indirect benefits promoted by Marine Protected Areas on the marine ecosystem as a whole (Babcock et al. 2010; Mellin et al. 2016).

The indirect benefits promoted by the MPA (Babcock et al. 2010; Mellin et al. 2016), the environmental complexity (Hackradt et al. 2011), may have influenced SINVs spatial distribution, once there are targeted by aquarium trade (Gasparini et al. 2005). Stochastic temperature oscillations during the austral winters in synergy with density-dependent mechanisms seem to govern the annual variations of densities and biomass of SINVs (Sale 1978; Sale 1980; Doherty 2002; Almada and Faria 2004; Begon et al. 2006) (Fig. 1, 5 and 9).

Omnivores non-targeted from fisheries or aquarium trade (Gasparini et al. 2005; Begossi et al. 2012; Martins et al. 2013) also seem to have their densities and biomass spatial distributions favored by the indirect benefits promoted by the MPA (*e.g.* populations with better fitness induced by the presence of larger number of predators) (Begon et al. 2006; Babcock et al. 2010; Mellin et al. 2016) (Figs. 5 and 9). In addition, OMNIs spatial distribution seem to be linked with microhabitats where temperature oscillations are more likely to occur (Figs 1, 5 and 9). OMNIs annual variations may also indicate influences driven by stochastic mechanisms (*i.e.* density-dependent mortality factor mediated by climatic oscillations, intra-specific competition for shelter and predation) (Sale 1978, 1980, Doherty 2002, Almada & Faria 2004).

Cryptic macroinvertebrates feeders (MINVC) have a short life spam (*i.e.* approx. 4 years) (Carlson 1992; Longenecker and Langston 2005). Aggressive territorial herbivores (THERB) (Osório et al. 2006) otherwise, have a long life spam (*i.e.* up to 15 years) (Schwamborn and Ferreira 2002; Osório et al. 2006). Despite strong morphological and ecological differences, on southern Brazilian rocky reefs, both trophic groups play similar roles. They transfer energy (as preys) to higher levels of the food web (Shpigel and Fishelson 1989; Mumby et al. 2012). Moreover, they show similar patterns of spatial and temporal variations (Fig. 5). The stability and of these trophic groups may be directly influenced by deterministic mechanisms, such as, structural complexity of the rocky reef (*e.g.* shelter availability and farming) and density-dependent mortality mechanisms, mediated by stochastic temperature oscillations (Sale 1978; Sale 1980; Doherty 2002; Almada and Faria 2004) (Figs. 1, 5 and 9).

Plankton feeders (PLANK) in this particular case have their spatial and temporal distributions influenced by the invasion and colonization of the rocky reefs of southern Brazil by Azores chromis (*Chromis limbata*) (Chown et al. 2015; Anderson et al. 2016). As other trophic groups mentioned before, deterministic, stochastic and density-dependent mechanisms may have also, very important influence on distributions and structure of PLANKs populations of southern Brazilian rocky reefs (Sale 1978; Sale 1980; Almada and Faria 2004; Doherty 2002; Begon et al. 2006). Otherwise, increasing variations in annual densities of PLANKs may have been directly influenced by invasive species patterns of population growth (Neubert and Caswell 2000; Allendorf and Lundquist 2003; Anderson et al. 2016) (Figs. 1, 5 and 9).

Species population structure’s spatial variations

The dominantion of species population’s structure by sub-adult individuals (*i.e.* intermediary size-classes) may evidence high mortality rates in initial stages (Sale 1978, 1980, Doherty 2002, Almada & Faria 2004) (Fig. 6). Stochastic dispersal of larvae (Cocheret de la Morinière et al. 2002), fear effect (Preisser and Bolnick 2008), predation, mediated by stochastic temperature oscillations may explain such patterns (Fig. 6). Moreover, younglings grow faster after populations being reduced by their natural predators, resulting in lower intra-specific competition (Carr and Hixon 1995).

The protection factor of the MPA seem to have influenced positively the survival of large individuals of highly targeted groupers (>60 cm), inside its restriction area, which corroborates its protection effectiveness of overexploited species described in previous works (Anderson et al. 2014) (Fig. 6).

Recruitment in space and time

Most species showed a clear pattern of decline in time regarding recruitment rates. The anthropic pressure on adjacent nursery areas (Andrade et al. 2003; Cunha et al. 2007; Magris and Barreto 2010) (*e.g.*

mangroves and tidal-pools), could account to such dangerous decline in recruitment rates (Fig.7).

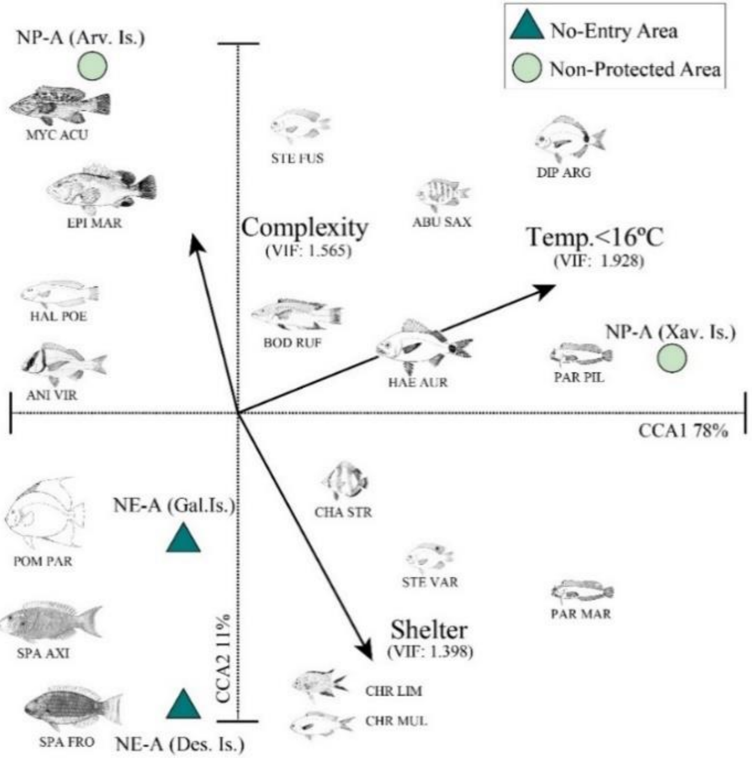

Figure 9. Canonical Correspondence Analysis (CCA) showing distribution of species according to their total mean densities and biomasses (2009-2016) and environmental variables (cumulative % of variance = 89). Light green circles represent the Non-protected area (N-PA) located outside the MPA, where fisheries are allowed. Dark green triangles represent the No-Entry Area (N-EA) located inside the MPA, totally restricted from fisheries. The arrow vectors represent environmental variables.

The decline in recruitment of *E. marginatus* for example, raises very important questions about MPAs true effectiveness over time (Botsford et al. 2009; Pujolar et al. 2013). The “spill over” (Harmelin-Vivien et al. 2008) and connectivity among populations is crucial to maintain a genetically healthy population inside the MPA (Saenz-Agudelo et al. 2011; Pujolar et al. 2013). So far, grouper populations inside Arvoredo Marine Biological Reserve, and exportation of larvae and adults to adjacent areas seem to be subsidized by the big old matrices (*i.e.* individuals >60 cm) which can be found only inside the MPA (Reñones et al. 2002; Palumbi 2004; Maggs et al. 2013; Anderson et al. 2014). When these large, very productive mothers perish, and considering the actual declining recruitment rate, the future of Arvoredo Marine Biological Reserve may be doomed. Protection and restoration of nursery habitats are urgent to ensure the future of the only near shore, no-entry Marine Protected Area, as well as the rocky reef fish communities on the southern Brazilian coast (Lotze et al. 2006; Halpern et al. 2007; Barbier et al. 2011; Sundblad et al. 2014).

3.7 CONCLUSIONS

Most studied species in this work are at the southernmost limit of their distribution (Anderson et al. 2015). According to Almada & Faria (2004), for many rocky reef species of teleost fishes that are near or on their distributional limits, fluctuations in abundance are frequent (Almada and Faria 2004). The proximity to their distributional border, deterministic mechanisms, density-dependent mechanisms and stochastic temperature oscillations may constitute the main drivers of population’s variations on rocky reef ichthyofauna in southern Brazilian rocky reefs (Sale 1978; Sale 1980, Doherty 2002; Almada and Faria 2004; Begon et al. 2006). Variations on spatial distribution may be governed by deterministic mechanisms such as habitat structural complexity, protection from fisheries and aquarium trade. In contrast, annual variations may be influenced by density-dependent mechanisms such as predation, competition and stochastic mechanisms such as larval dispersion, harsh austral winter temperature oscillations (Thomson and Lehner 1976; Sale 1978; Sale 1980; Grossman 1982; Doherty 2002; Almada and Faria 2004; Begon et al. 2006). Thomson & Lehner (1976) emphasized that sporadic episodes of high mortality may occur for fishes that are near their distribution limits, when unexpected extreme physical conditions occur, such as cold-water intrusion in subtropical fishes.

Arvoredo Marine Biological Reserve seem to influence positively all species densities and biomass directly (*e.g.* targeted species) and indirectly. Likewise, the positive effects on densities and biomass of trophic groups is evident. Such patterns corroborates Watson et al. (2007), Babcock et al. (2010) and Mellin et al. (2016), when they affirm that MPAs affect positively (*i.e.* increasing densities and biomass) all reef fish species in system. Otherwise, considering the severe decline in species recruitment, specially top predators, no policy or projects for conservation and restoration of nursery habitats and very poor management (*i.e.* frequent illegal fisheries) (Anderson et al. 2014), the future of Arvoredo MPA and the rocky reef ichthyofauna is uncertain.

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Appendix1: Tukey HSD dominant species

Variable: Density	T.HSD α=0.05	Species: ***A. saxatilis***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2010	a	2.0907
2011	ab	1.6149
2016	ab	1.4627
2013	ab	1.4263
2015	ab	1.2105
2009	ab	1.2086
2008	ab	1.0350
2014	b	1.0205
2012	b	0.9281

Variable: Biomass	T.HSD α=0.05	Species: ***A. saxatilis***
Area	Groups	Means (Log X+1)
N-EA	a	1.2291
N-PA	b	0.5806
Year	Groups	Means (Log X+1)
2010	a	2.0907
2011	ab	1.6149
2016	ab	1.4627
2013	ab	1.4263
2015	ab	1.2105
2009	ab	1.2086
2008	ab	1.0350
2014	b	1.0205
2012	b	0.9281

Variable: Density	T.HSD α=0.05	Species: ***A. virginicus***
Area	Groups	Means (Log X+1)
N-EA	a	1.2291
N-PA	b	0.5806
Year	ns	ns

Variable: Biomass	T.HSD α=0.05	Species: ***A. virginicus***
Area	Groups	Means (Log X+1)
N-EA	a	5.0874
N-PA	b	2.7803
Year	ns	ns

Variable: Density	T.HSD α=0.05	Species: ***B. rufus***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2010	a	0.4938
2013	ab	0.2973
2008	ab	0.2282
2009	ab	0.2145
2012	ab	0.2037
2015	b	0.1589
2016	b	0.1437
2011	b	0.1358
2014	b	0.1126

Variable: Biomass	T.HSD α=0.05	Species: ***B.rufus***
Area	Groups	Means (Log X+1)
N-EA	a	1.3370
N-PA	b	0.8133

Year	ns	ns
Variable: Density	T.HSD α=0.05	Species: ***C. striatus***
Area	Groups	Means (Log X+1)
N-EA	a	0.4676
N-PA	b	0.2715
Year	Groups	Means (Log X+1)
2010	a	0.8029
2008	a	0.7135
2009	ab	0.4216
2016	b	0.3641
2013	b	0.3371
2012	b	0.3268
2014	b	0.2959
2015	b	0.2737
2011	b	0.1847
Variable: Biomass	T.HSD α=0.05	Species: ***C. striatus***
Area	Groups	Means (Log X+1)
N-EA	a	1.5466
N-PA	b	0.9243
Year	Groups	Means (Log X+1)
2008	a	1.9691
2010	ab	1.9287
2009	ab	1.4295
2016	ab	1.3993
2013	ab	1.2068
2014	ab	1.1569
2012	ab	1.1173
2015	ab	1.0554

2011	b	0.4929
Variable: Density	T.HSD α=0.05	Species: ***C. limbata***
Area	Groups	Means (Log X+1)
N-EA	a	0.4194
N-PA	b	0.1769
Year	Groups	Means (Log X+1)
2016	a	0.6660
2015	a	0.5304
2014	ab	0.4624
2013	ab	0.3970
2012	bc	0.1458
2011	bc	0.1192
2008	c	0.0000
2009	c	0.0000
2010	c	0.0000
Variable: Biomass	T.HSD α=0.05	Species: ***C. limbata***
Area	Groups	Means (Log X+1)
N-EA	a	0.7973
N-PA	b	0.4483
Year	Groups	Means (Log X+1)
2015	a	1.2862
2016	a	1.2686
2014	ab	0.9760
2013	abc	0.7448
2012	bc	0.3204
2011	c	0.1980
2008	c	0.0000
2009	c	0.0000
2010	c	0.0000

Variable: Density	T.HSD α=0.05	Species: ***C. multilineata***
Area	Groups	Means (Log X+1)
N-EA	a	0.4219
N-PA	b	0.2479
Year	Groups	Means (Log X+1)
2010	a	0.5158
2009	a	0.4605
2008	a	0.4526
2013	a	0.4495
2014	a	0.3619
2011	a	0.3015
2012	a	0.2844
2015	a	0.2749
2016	a	0.1517

Variable: Biomass	T.HSD α=0.05	Species: ***C. multilineata***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2013	a	1.4578
2009	ab	1.2223
2010	ab	1.0635
2014	ab	1.0234
2015	ab	0.8608
2012	ab	0.8149
2008	ab	0.7726
2016	b	0.5421
2011	b	0.5055

Variable: Density	T.HSD α=0.05	Species: ***D. argenteus***

Area	Groups	Means (Log X+1)
N-EA	a	1.2895
N-PA	b	1.1209
Year	Groups	Means (Log X+1)
2009	a	2.0378
2010	ab	1.8725
2008	ab	1.7045
2013	ab	1.5742
2012	bc	1.2356
2016	cd	1.0787
2011	cde	0.8258
2014	de	0.7762
2015	e	0.5934
Variable: Biomass	T.HSD α=0.05	Species: ***D. argenteus***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2009	a	5.4110
2010	ab	5.1499
2013	ab	4.8092
2008	abc	4.0494
2016	abc	3.8851
2012	bc	3.8344
2014	bc	3.0915
2011	bc	2.8569
2015	c	2.5695
Variable: Density	T.HSD α=0.05	Species: ***E. marginatus***
Area	Groups	Means (Log X+1)

N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2008	a	0.9591
2009	ab	0.8815
2010	abc	0.7997
2016	abc	0.7411
2013	abc	0.6694
2011	bc	0.6030
2014	c	0.5532
2012	c	0.4930
2015	c	0.4095

Variable: Biomass	T.HSD α=0.05	Species: ***E. marginatus***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2016	a	4.1574
2010	ab	3.7765
2009	ab	3.6361
2011	ab	3.5886
2008	ab	3.4381
2013	ab	3.2514
2014	ab	3.1185
2015	b	2.6313
2012	b	2.4982

Variable: Density	T.HSD α=0.05	Species: ***H. aurolineatum***
Area	Groups	Means (Log X+1)
N-EA	a	2.4663

N-PA	b	1.4395
Year	ns	ns
Variable: Biomass	T.HSD α=0.05	Species: ***H. aurolineatum***
Area	Groups	Means (Log X+1)
N-EA	a	5.4486
N-PA	b	3.7652
Year	ns	ns
Variable: Density	T.HSD α=0.05	Species: ***H. poeyi***
Area	Groups	Means (Log X+1)
N-EA	a	0.2292
N-PA	b	0.1491
Year	Groups	Means (Log X+1)
2011	a	0.2896
2010	ab	0.2831
2009	ab	0.2696
2013	ab	0.2203
2012	ab	0.1891
2008	ab	0.1772
2015	ab	0.1652
2014	ab	0.1530
2016	b	0.0840
Variable: Biomass	T.HSD α=0.05	Species: ***H. poeyi***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Year	ns	ns
Variable: Density	T.HSD α=0.05	Species: ***M. acutirostris***

Area	Groups	Means (Log X+1)
N-EA	a	0.3298
N-PA	b	0.1660
Year	Groups	Means (Log X+1)
2008	a	0.4902
2009	ab	0.3551
2011	abc	0.3330
2013	abcd	0.3158
2012	bcd	0.2447
2016	bcd	0.2072
2010	bcd	0.1242
2014	cd	0.1141
2015	d	0.1003
Variable: Biomass	T.HSD α=0.05	Species: ***M. acutirostris***
Area	Groups	Means (Log X+1)
N-EA	a	1.6613
N-PA	b	0.9746
Year	Groups	Means (Log X+1)
2011	a	2.0776
2008	a	1.9644
2013	a	1.8822
2016	ab	1.5216
2009	ab	1.3555
2012	ab	1.3158
2015	b	0.6319
2014	b	0.6126
2010	b	0.3980
Variable: Density	T.HSD α=0.05	Species: ***P. marmoreus***
Area	Groups	Means (Log X+1)

N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2008	a	1.2560
2012	ab	1.1224
2015	ab	1.0461
2016	abc	0.9429
2011	abcd	0.8083
2013	bcd	0.7865
2010	bcd	0.7860
2014	cd	0.6193
2009	d	0.3945

Variable: Biomass	T.HSD α=0.05	Species: ***P. marmoreus***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2012	a	1.5871
2008	a	1.5629
2015	a	1.4600
2016	a	1.4083
2013	ab	1.2756
2010	ab	1.2174
2014	ab	1.0781
2011	ab	0.9442
2009	b	0.6474

Variable: Density	T.HSD α=0.05	Species: ***P. pilicornis***
Area	Groups	Means (Log X+1)
N-EA	ns	ns

N-PA	ns	ns
Year	Groups	Means (Log X+1)
2012	a	0.7947
2016	ab	0.7351
2015	abc	0.7252
2014	abc	0.6395
2008	abc	0.6081
2013	abc	0.5179
2011	bc	0.3152
2009	c	0.2863
2010	c	0.1589
Variable: Biomass	T.HSD α=0.05	Species: ***P. pilicornis***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2012	a	1.2289
2014	a	1.1828
2016	a	1.1763
2015	ab	1.0993
2008	ab	0.7502
2013	ab	0.7406
2009	b	0.4587
2011	b	0.3949
2010	b	0.2942
Variable: Density	T.HSD α=0.05	Species: ***P. paru***
Area	Groups	Means (Log X+1)
N-EA	a	0.2012
N-PA	b	0.0793

Year	ns	ns
Variable: Biomass	T.HSD α=0.05	Species: ***P. paru***
Area	Groups	Means (Log X+1)
N-EA	a	1.3977
N-PA	b	0.4154
Year	ns	ns
Variable: Density	T.HSD α=0.05	Species: ***S. axillare***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2011	a	0.2166
2008	a	0.1857
2016	ab	0.1517
2014	ab	0.1379
2013	ab	0.1126
2012	ab	0.1054
2010	ab	0.1039
2009	ab	0.0577
2015	b	0.0173
Variable: Biomass	T.HSD α=0.05	Species: ***S. axillare***
Area	Groups	Means (Log X+1)
N-EA	a	1.0842
N-PA	b	0.5336
Year	Groups	Means (Log X+1)
2016	a	1.2819
2011	ab	1.1202

2014	ab	1.1018
2008	ab	1.0455
2012	ab	0.8322
2013	ab	0.7693
2010	ab	0.7164
2015	b	0.1933
2009	b	0.1918
Variable: Density	T.HSD α=0.05	Species: ***S. frondosum***
Area	Groups	Means (Log X+1)
N-EA	a	0.1955
N-PA	b	0.0583
Year	ns	ns
Variable: Biomass	T.HSD α=0.05	Species: ***S. frondosum***
Area	Groups	Means (Log X+1)
N-EA	a	0.9589
N-PA	b	0.2925
Year	ns	ns
Variable: Density	T.HSD α=0.05	Species: ***S. fuscus***
Area	Groups	Means (Log X+1)
N-EA	a	1.7985
N-PA	b	1.4554
Year	Groups	Means (Log X+1)
2008	a	2.0341
2012	ab	1.8638
2011	abc	1.7818
2016	abc	1.7077
2015	abc	1.6279
2014	abc	1.5391

2013	bc	1.3295
2009	c	1.2411
2010	c	1.2401
Variable: Biomass	T.HSD α=0.05	Species: ***S. fuscus***
Area	Groups	Means (Log X+1)
N-EA	a	3.2004
N-PA	b	2.8162
Year	Groups	Means (Log X+1)
2008	a	3.7490
2014	ab	3.5068
2016	ab	3.4702
2015	ab	3.1756
2012	ab	3.0737
2011	abc	2.7503
2013	bc	2.4230
2009	c	1.973
2010	c	1.8388
Variable: Density	T.HSD α=0.05	Species: ***S. variabilis***
Area	Groups	Means (Log X+1)
N-EA	a	0.3706
N-PA	b	0.2537
Year	Groups	Means (Log X+1)
2013	a	0.5350
2010	ab	0.5249
2009	ab	0.4446
2011	ab	0.3705
2012	ab	0.2823
2008	ab	0.2664
2014	b	0.2627

2016	b	0.1965
2015	b	0.1927

Variable: Biomass	T.HSD α=0.05	Species: ***S. variabilis***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2013	a	1.2072
2010	ab	1.0538
2009	ab	0.9615
2012	ab	0.7881
2011	ab	0.7806
2014	ab	0.6682
2008	ab	0.6574
2015	ab	0.6002
2016	b	0.4951

Appendix 2. Tukey HSD Trophic levels

Variable: Density	T.HSD α=0.05	Trophic level: **MCAR**
Area	Groups	Means (Log X+1)
N-EA	a	0.8994
N-PA	b	0.7273
Year	Groups	Means (Log X+1)
2008	a	1.1951
2009	ab	1.1205
2013	abc	0.8976
2016	bc	0.8582
2011	bc	0.8516

2010	bcd	0.8423
2012	cd	0.6614
2014	cd	0.6392
2015	d	0.5004
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	a	4.2188
N-PA	b	3.6187
Year	Groups	Means (Log X+1)
2011	a	4.7182
2016	a	4.6864
2013	ab	4.2979
2009	ab	4.1859
2008	ab	4.0242
2010	ab	3.7900
2014	ab	3.5334
2012	ab	3.2482
2015	b	3.1508
Variable: Density	T.HSD $\alpha=0.05$	Trophic level: **HERB**
Area	Groups	Means (Log X+1)
N-EA	a	0.3182
N-PA	b	0.1478
Year	Groups	Means (Log X+1)
2011	a	0.3840
2014	ab	0.2906
2013	ab	0.2722
2016	ab	0.2651
2010	ab	0.2649
2008	ab	0.2478
2009	ab	0.1839

2012	ab	0.1652
2015	b	0.1073
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	a	1.8362
N-PA	b	0.7796
Year	Groups	Means (Log X+1)
2011	a	1.9103
2014	a	1.7937
2016	a	1.7491
2013	a	1.3977
2008	a	1.1492
2010	a	1.1309
2012	a	1.0082
2015	a	0.8285
2009	a	0.8122
Variable: Density	T.HSD α=0.05	Trophic level: **MINV**
Area	Groups	Means (Log X+1)
N-EA	a	2.8542
N-PA	b	1.6819
Year	Groups	Means (Log X+1)
2008	a	2.8762
2016	ab	2.4453
2015	ab	2.3393
2010	ab	2.3227
2013	ab	2.3081
2009	ab	2.2753
2012	b	2.1616
2014	b	2.0689
2011	b	1.9183

Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	a	6.9935
N-PA	b	4.9748
Year	Groups	Means (Log X+1)
ns	ns	ns
Variable: Density	T.HSD α=0.05	Trophic level: **SINV**
Area	Groups	Means (Log X+1)
N-EA	a	0.6150
N-PA	b	0.3388
Year	Groups	Means (Log X+1)
2008	a	0.8324
2010	ab	0.8231
2009	abc	0.5358
2013	bc	0.4618
2014	bc	0.4565
2016	bc	0.4504
2012	bc	0.4464
2015	bc	0.3590
2011	c	0.2692
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	a	2.5422
N-PA	b	1.2878
Year	Groups	Means (Log X+1)
ns	ns	ns
Variable: Density	T.HSD α=0.05	Trophic level: **OMNI**
Area	Groups	Means (Log X+1)

N-EA	a	2.0569
N-PA	b	1.8542
Year	Groups	Means (Log X+1)
2010	a	2.8225
2009	a	2.5537
2013	ab	2.3547
2008	abc	2.1371
2016	abc	1.9974
2011	abc	1.9195
2012	bc	1.7955
2015	c	1.5261
2014	c	1.5031
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2009	a	6.2665
2013	a	5.9979
2010	a	5.8767
2016	a	5.7653
2008	a	4.9517
2012	a	4.9067
2014	a	4.8618
2015	a	4.7835
2011	a	4.6786
Variable: Density	T.HSD α=0.05	Trophic level: **MINVC**
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns

Year	Groups	Means (Log X+1)
2008	a	1.5007
2012	a	1.4418
2015	a	1.3972
2016	a	1.3248
2014	ab	1.0237
2013	ab	1.0153
2011	ab	1.0068
2010	ab	0.8424
2009	b	0.6199
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	ns	ns
N-PA	ns	ns
Year	Groups	Means (Log X+1)
2012	a	2.0095
2016	a	1.9776
2015	ab	1.9332
2008	ab	1.8368
2014	ab	1.8056
2013	abc	1.5408
2010	abc	1.3226
2011	bc	1.1870
2009	c	0.9793
Variable: Density	T.HSD α=0.05	Trophic level: **THERB**
Area	Groups	Means (Log X+1)
N-EA	a	1.9590
N-PA	b	1.5824
Year	Groups	Means (Log X+1)
2008	a	2.1054

2012	ab	1.9525
2011	ab	1.9483
2016	ab	1.7873
2015	ab	1.7686
2014	ab	1.6259
2013	ab	1.6148
2010	ab	1.5783
2009	b	1.4635
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	a	3.4702
N-PA	b	3.1015
Year	Groups	Means (Log X+1)
2008	a	3.8779
2014	a	3.6740
2016	a	3.5748
2015	ab	3.4997
2012	ab	3.2765
2011	ab	2.9970
2013	ab	2.9302
2010	ab	2.5026
2009	b	2.4883
Variable: Density	T.HSD $\alpha=0.05$	Trophic level: **PLANK**
Area	Groups	Means (Log X+1)
N-EA	a	0.7659
N-PA	b	0.3914
Year	Groups	Means (Log X+1)
2016	a	0.7557
2013	a	0.7279
2015	a	0.7277

2014	a	0.7139
2010	a	0.5158
2009	a	0.4606
2008	a	0.4527
2011	a	0.4114
2012	a	0.3765
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	a	1.5670
N-PA	b	1.0782
Year	Groups	Means (Log X+1)
2013	a	1.8595
2015	a	1.8241
2014	ab	1.6188
2016	ab	1.5672
2009	ab	1.2223
2010	ab	1.0635
2012	ab	0.9657
2008	ab	0.7726
2011	b	0.6901

Appendix 3: Tukey HSD tests. Species grouped by size classes.

Variable: Density	T.HSD α=0.05	Species: ***A. saxatilis***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Size class	Groups	Means (Log X+1)
0-5	a	3.7961

10-20	a	3.0509
5-10	a	2.4216
20-30	b	0.7423
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	ns	ns
N-PA	ns	ns
Size class	Groups	Means (Log X+1)
10-20	a	8.6259
20-30	ab	6.6835
5-10	b	5.9177
0-5	b	5.2042
Variable: Density	Groups	Species: ***A. virginicus***
Area		Means (Log X+1)
N-EA	a	1.2032
N-PA	b	0.7367
Size class	Groups	Means (Log X+1)
10-20	a	2.1943
20-30	a	1.9191
5-10	ab	1.4201
0-5	bc	0.6578
30-40	c	0.4673
40-50	c	0.1313
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	a	5.1900
N-PA	b	3.9832
Size class	Groups	Means (Log X+1)
20-30	a	8.2838
10-20	ab	7.3359
30-40	abc	6.6077

40-50	bc	4.6819
5-10	cd	3.9858
0-5	de	1.2110
Variable: Density	Groups	Species: ***D. argenteus***
Area		Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Size class	Groups	Means (Log X+1)
10-20	a	2.6855
5-10	ab	2.0758
0-5	ab	2.0709
20-30	b	1.9110
30-40	c	0.2014
40-50	c	0.0000
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	ns	ns
N-PA	ns	ns
Size class	Groups	Means (Log X+1)
10-20	a	2.6855
5-10	ab	2.0758
0-5	ab	2.0709
20-30	b	1.9110
30-40	c	0.2014
40-50	c	0.0000
Variable: Density	Groups	Species: ***E. marginatus***
Area		Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Size class	Groups	Means (Log X+1)
10-20	a	1.5435

20-30	ab	1.1918
5-10	bc	0.8005
0-5	bc	0.7536
30-40	bcd	0.6144
40-50	cd	0.2799
60>	d	0.0796
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	5.217688	a
N-PA	4.04782	b
Size class	Groups	Means (Log X+1)
20-30	a	6.7227
30-40	a	6.6763
40-50	a	6.2960
10-20	a	5.9486
60>	b	3.1061
5-10	b	2.7546
0-5	c	0.9251
Variable: Density	Groups	Species: ***H. aurolineatum***
Area		Means (Log X+1)
N-EA	a	3.1414
N-PA	b	2.5181
Size class	Groups	Means (Log X+1)
0-5	a	4.4866
10-20	a	4.0371
5-10	a	3.4714
20-30	b	2.1416
30-40	c	0.0122
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	ns	ns

N-PA	ns	ns
Size class	Groups	Means (Log X+1)
10-20	a	9.0223
20-30	ab	8.2790
5-10	bc	6.2390
0-5	c	5.1779
30-40	d	1.0619
Variable: Density	T.HSD α=0.05	Species: ***S. fuscus***
Area	Groups	Means (Log X+1)
N-EA	ns	ns
N-PA	ns	ns
Size class	Groups	Means (Log X+1)
5-10	a	3.5353
0-5	a	3.1899
10-20	b	1.5562
Variable: Biomass	Groups	Means (Log X+1)
Area		
N-EA	ns	ns
N-PA	ns	ns
Size class	Groups	Means (Log X+1)
5-10	a	6.0793
10-20	a	5.9826
0-5	b	3.8552

Appendix 4: Tukey HSD tests. Temporal variations of species recruitment.

Variable: Density	T.HSD α=0.05	Species: ***A. saxatilis***
	Groups	Means (Log X+1)

Area	ns	ns
Year	ns	ns

Variable: Density	T.HSD α=0.05	Species: ***A. virginicus***
	Groups	Means (Log X+1)
Area	ns	ns
Year	ns	ns

Variable: Density	T.HSD α=0.05	Species: ***D. argenteus***
Area	Groups	Means (Log X+1)
NE-A	a	0.7372
N-PA	b	0.3834
Year		
2009	a	1.5473
2008	ab	1.2554
2013	ab	1.0770
2012	bc	0.7205
2010	bcd	0.5306
2011	cd	0.2226
2016	cd	0.1014
2014	cd	0.0750
2015	d	0.0000

Variable: Density	T.HSD α=0.05	Species: ***E. marginatus***
Area	Groups	Means (Log X+1)
NE-A	a	0.2993
N-PA	b	0.1959
Year		
2008	a	a
2009	b	b
2010	bc	bc
2013	cd	cd

2012	cd	cd
2014	cd	cd
2016	d	d
2011	d	d
2015	d	d

Variable: Density	T.HSD α=0.05	Species: ***H. aurolineatum***
	Groups	Means (Log X+1)
Area	ns	ns
Year	ns	ns

Variable: Density	T.HSD α=0.05	Species: ***S. fuscus***
Area	Groups	Means (Log X+1)
NE-A	ns	ns
N-PA	ns	ns
Year		
2008	a	2.0591
2011	a	1.9952
2012	ab	1.7436
2013	ab	1.4690
2010	ab	1.4231
2009	ab	1.4015
2015	b	0.7526
2014	b	0.7042
2016	b	0.6526

4 THE RECENT COLONIZATION OF SOUTH BRAZIL BY THE AZORES CHROMIS, *CHROMIS LIMBATA* (VALENCIENNES, 1833)

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4.1 ABSTRACT

Species range expansions (natural or human mediated) constituteone of the major drivers of environmental change, affecting nutrient cycling, food webs, and changing evolutionary trajectories via hybridization. The damselfish *Chromis limbata* is native to the Macaronesian archipelagos (Azores, Madeira and Canaries), and the western coast of Africa between Senegal and Angola. During the austral summers of 2008 and 2009 the species was recorded for the first time in the southwestern Atlantic around Campeche and Xavier islands, in Florianópolis, Santa Catarina State, Brazil. To monitor the progression of *C. limbata* in Southern Brazilian waters, underwater visual censuses were carried out from 2009 to 2014. In addition, tissue samples were collected and the mtDNA control region sequenced and analyzed to infer relationships between the Brazilian and Macaronesian populations. The Brazilian population of *C. limbata* increased significantly over the past five years. The molecular analyses confirmed species identity, revealed strong haplotype connectivity among Brazilian study sites, and showed a low genetic diversity in Brazil when compared to the native populations. Four hypotheses could explain this colonizing event: 1) *C. limbata* was released by aquarium fish keepers; 2) larvae or juveniles were transported via ship ballast water; 3) the species has rafted alongside oilrigs; and 4) they crossed the Atlantic through normal larval dispersal or naturally rafting alongside drifting objects. We tend to favor the third and fourth hypotheses, but all four are plausible and could have happened in combination.

Key words
Biogeography; Dispersal; Invasive species; Invasion genetics; Southwestern Atlantic; Reef fishes.

4.2 INTRODUCTION

Biological invasions are considered one of the main threats to biodiversity worldwide, with detrimental consequences for native community ecology and local economies (Elton, 1958; Cardinale *et al.*, 2006; Lurgi *et al.*, 2014). Many alien species constitute drivers of major environmental change, affecting nutrient cycling, food webs, and even causing changes in evolutionary trajectories (Strauss *et al.*, 2006; McDonald *et al.*, 2008; Chown *et al.*, 2015). Therefore, much attention has been given to understanding the invasion process and the mechanisms that are involved in each stage of human-mediated invasions (*i.e.* transport, colonization, and establishment) (Blackburn *et al.*, 2011; Chown *et al.*, 2015). Natural range expansions however, are poorly understood, mostly because they are rare and hard to detect and monitor (Gillespie *et al.*, 2012).

The zooplanktivore damselfish *Chromis limbata* (Valenciennes, 1833), the Azores Chromis, is native to the Macaronesian islands (Azores, Madeira, and Canaries) and the western coast of Africa between Senegal and Angola (Wood, 1977; Edwards, 1986; Domingues *et al.*, 2006; Wirtz, 2012). This species inhabits rocky reefs from 3 to 50 m depth, where it forms aggregations in the water column and feeds on zooplankton (Domingues *et al.*, 2006; Leite *et al.*, 2009). During the summer, nesting males defend territories and take care of eggs, which are attached to the substratum (Domingues *et al.*, 2006; Leite *et al.*, 2009). The duration of *C. limbata*’s larval stage is unknown, but it lasts 18-19 days in the closely related *Chromis chromis* (Linnaeus, 1758) (Domingues *et al.*, 2006; Leite *et al.*, 2009).

In March and April of 2008 two individuals of *C. limbata* were repeatedly observed at Campeche Island (27º70’38” S; 48º46’83” W), state of Santa Catarina, Southern Brazil by Leite *et al.* (2009). All encounters occurred in the same 12 m^2 boulder area, suggesting a small home range. Both specimens were observed feeding together with a single individual of *Chromis multilineata* (Guichenot, 1853), a look-alike species native to the area. In December 2008 and March 2009, three to five individuals were observed at Xavier Island (27º41’57”S; 48º28’05”W) located 12 km north of Campeche Island, 3 km from the east coast of Florianópolis Island, Santa Catarina State (Leite *et al.*, 2009).

The increasing number of records of *C. limbata* at Santa Catarina since 2009 indicated the witnessing of an important ecological event (Anderson *et al.*, 2015). Here we try to answer two main questions about this new arrival to Brazil: 1) what is the relationship between Brazilian *C. limbata* and the west African populations? 2) has the Brazilian *C. limbata* persisted over this period and are their populations expanding in space and time? We used a combined population genetic and underwater visual census approach to answer these questions.

4.3 MATERIALS AND METHODS

STUDY AREA

This study was carried out on subtropical reefs at Florianópolis, Santa Catarina, southern Brazil (27°35’41.08” S; 48°32’38.96” W). Reefs in the area are mostly composed of steep granitic rocks, interfacing with sandy bottoms, generally 10-15 m deep (Anderson *et al.*, 2014). The study was conducted during austral summers, from 2010 to 2016. During this period, water temperatures ranged from 22ºC to 28°C and underwater visibility ranged from 4 to 15 m.

C. limbata was recorded on eight islands: Arvoredo, Deserta, Galé, Aranhas, Xavier, Campeche, Moleques do Sul, and Corais (Fig. 1). To infer the progress of the *C. limbata* colonization and study its population genetics, five islands were selected for sampling: Arvoredo, Deserta, Galé, Aranhas and Xavier. These islands were selected for logistical reasons (*e.g.* diving operations and short distance from the shore). The abundance of the native look-alike congener (*C. multilineata*) was also estimated across these sites.

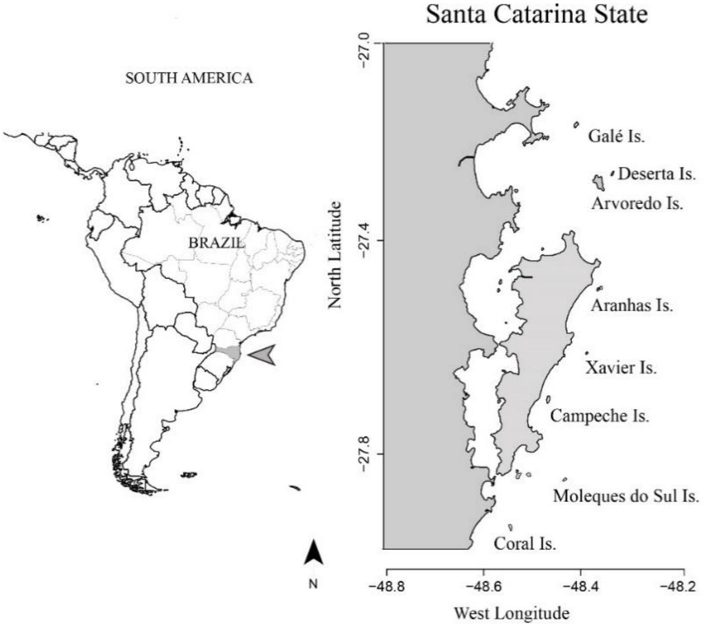

Fig. 1 Location of sampling sites in the state of Santa Catarina, Southern Brazil.

DATA COLLECTION

Underwater visual censuses [20 x 2 m strip transects (40 m²)] were used to quantify fish density across the five sites. For this methodology, a scuba diver swam 1 m above the substratum along 20 m, recording fish 1 m to each side of the transect. At each study site, two depth strata were sampled: Slope and Interface. Slope (S) was considered the area comprising the water surface and half of the total depth (TD). Thus, if TD = 12 m, the slope would be = from 0 to 6 m [*i.e.* TD (12 m depth) divided by 2 (stratum) = slope (6 m)]. The interface (I) corresponded to the transition zone between the rocky reef and the non-consolidated substratum, typically sandy bottom (Anderson *et al.*, 2015). Total depth (TD) varied from 7 m at Arvoredo to 24 m at Xavier. For each depth stratum, 15 transects were carried out each year, totaling 30 transects (1.200 m²) per year per site.

POPULATION DENSITY ANALYSIS

To test the effect of time (year) on the density of *C. limbata* and its close relative and potential competitor *C. multilineata*, two-way ANOVA was used. Density per site was used as a dependent variable, and time and site as the fixed factors. Two-way ANOVA was also used to evaluate differences in species vertical distribution (depth effect) in two depth strata [slope (S) and interface (I)]. In this case, the sum of mean densities of species in all islands was used as response variables and strata as fixed factor. To evaluate differences in the combined mean densities of *C. limbata* and *C. multilineata* across the five islands, and throughout the years, a mixed design ANOVA was used. Mean densities of both species were used as response variables and year and island (space and time) as fixed factors. When significant differences were found, the Tukey HSD post-hoc test was used to verify sources of variation. Before the analyses, assumptions of normality and homoscedasticity were assessed with Kolmogorov-Smirnov/Lilliefors and Bartlett's tests (Underwood, 1981; Snedecor & Cochran, 1989; Zar, 1999). Analyses were perfomed in R environment with the package Agricolae (De Mendiburu, 2016).

SPECIMEN COLLECTION, DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

In 2012 and 2013, 29 specimens of *C. limbata* were collected with a spear while scuba diving. The left pectoral fin of each individual was removed, labeled, and preserved in 95% ethanol. The samples were stored at -4º C until DNA extraction. Genomic DNA was extracted using a standard phenol-chloroform protocol (Sambrook & Russell, 2006). A fragment of the mitochondrial DNA control region (d-loop) was amplified using universal primers CR-A and CR-B (Lee *et al.*, 1995). PCR products were visualized on 1% agarose gel, purified with ExoSapIT and cycle-sequenced in both the forward and reverse direction on an ABI 3130 automated sequencer (Applied Biosystems, Foster, CA). PCR amplification was performed in 15 ul reactions using approximately 10 ng of template DNA, 1.5 ul of 10x PCR buffer, 0.75 MgCl2 (50mM), 0.3 ul of each forward and reverse primers (10uM), 0.75 ul of 10mM dNTP and 0.3 ul of DNA polymerase (Invitrogen; 5 units/ul). PCR conditions were as follows: initial denaturation at 94º C for 2 minutes, followed by 30 cycles of denaturing at 94º C for 60 seconds, 54º C annealing for 60 s, 72º C extension for 2 minutes and a final extension of 72º C for 10 min.

GENETIC ANALYSES

Analyses were performed using samples collected by our team as well as sequences downloaded from GenBank (*C. limbata* d-loop sequences from eastern Atlantic locations and a sequence of *C. chromis*, from Domingues *et al.*, 2006). Sequences were aligned and trimmed to 328 bp in Geneious version 5.4 (Kearse *et al.*, 2012) using ClustalW (Thompson *et al.*, 1994) with free end gaps and an IUB cost matrix. A Bayesian tree was estimated using the MrBayes (Ronquist & Huelsenbeck, 2003) plug-in available in Geneious with *C. chromis* as an outgroup, and the following settings: 1,000,000 MCMC chain length, subsampling frequency 1,000, burn-in length 50,000, 4 heated chains, and temperature 0.2. jModelTest (Guindon & Gascuel, 2003) was used to explore the most likely model of evolution, which was TrN+G. Since this model is not available in MrBayes, the second most likely model HKY+G was used. Population genetic parameters (including haplotype and nucleotide diversity) of *C. limbata* were calculated using Arlequin ver 3.5.1.2 (Excoffier & Lischer, 2010). A haplotype network was created using the R package “Pegas” (Paradis, 2010) to illustrate the relationships among haplotypes.

4.4 RESULTS

POPULATION STRUCTURE

A total of 480 transects were performed from 2010 to 2014 in all sites, covering an area of 19,200 m², and corresponding to approximately 64 hours of underwater observation. *C. limbata* populations grew significantly over time, according to the two-way ANOVA ($F=12.40$, $p<0.05$). This analysis revealed an increase in populations of *C. limbata* in all five sites during the past five years (Sites: $F=2.55$, $p=0.038$; Time: $F=12.40$, $p<0.05$) (Appendix 1 and Fig. 2).

The analyzes revealed significant differences of *C. limbata* in space and time: regarding the factor “Site”, highly significant differences were detected only between two islands: Deserta (highest total density: F=12.39, p<0.05) and Arvoredo (lowest: F=6.98, p<0.05; Fig. 2). Mean densities of *C. limbata* and *C. multilineata* during the period of five years showed significant differences for the year 2014 according to the mixed design ANOVA (F=37.79, p<0.05; Appendix 1 and Fig. 2). Exponential population growth was detected for *C. limbata* populations in all five sites.

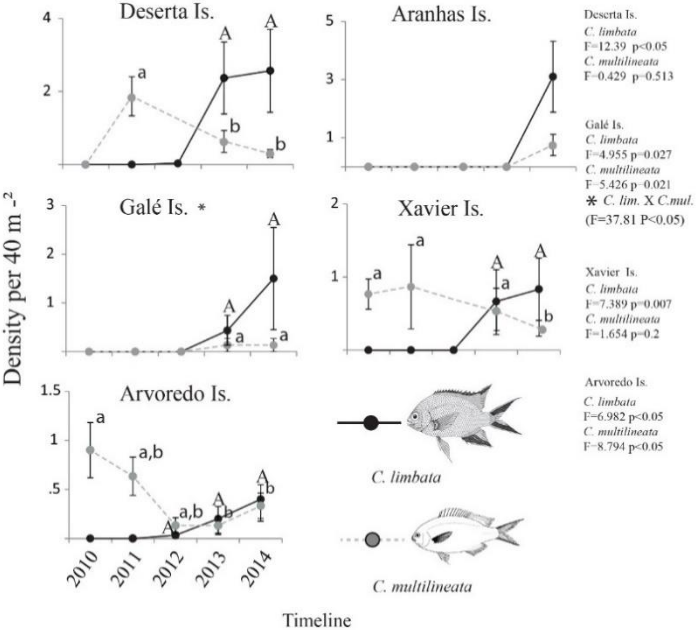

Fig. 2 Temporal variations (ANOVA) in density (mean ± SE) of *C. limbata* (black circles) and native *C. multilineata* (grey circles). Letters above bars indicate significant differences within species in time (upper case indicate *C. limbata* and lower case *C. multilineata*) (Tukey HSD, p<0.05). Asterisks show significant differences between species in time per site (Tukey HSD, p < 0.05).

C. limbata densities were only significantly different at one depth strata, the “interface”. The analyses of total sums of species density means in time and the two depth strata biotopes (slope and interface) as factors showed significant differences only for *C. limbata* at the interface (F=38.12, p<0.05; Fig. 3). *Chromis limbata* showed significant preference for deeper and colder waters (>10 m deep and 2º C below SST) mostly when searching for shelter and during reproduction. It did not differ from the native *C. multilineata* in the slope. Both species were observed feeding together in large schools in shallow water.

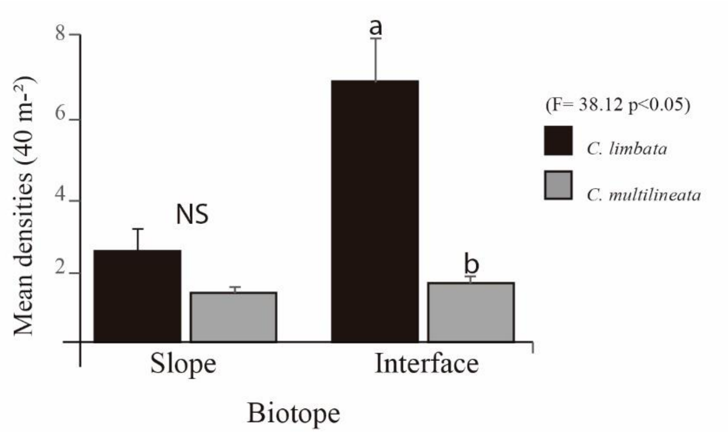

Fig. 3 Mean densities (+ SE) of *C. limbata* (black bars) and *C. multilineata* (grey bars) in the sampled biotopes. Letters above bars indicate significant differences (Tukey HSD, p < 0.05).

GENETIC ANALYSES

The mitochondrial control region of 29 individuals from Brazilian islands was sequenced and compared to 26 sequences from the Azores, 18 from Madeira, and 17 from the Canaries, totaling 90 sequences (Table I). The 29 samples from Southern Brazil were confirmed as *C. limbata*, with close relatives in Macaronesian islands (Fig. 4). GenBank accession numbers will be provided when the manuscript is accepted.

Table I. Sampled sites used in the present study and diversity indexes for mitochondrial control region of *C. limbata*

Islands	N (ind)	Private haplotypes	Shared haplotypes	Total haplotypes	Haplotype diversity (Hd) (± SD)	Nucleotide diversity (π) (average over loci) (± SD)
Azores (Portugal)	26	12	0	12	0.914 ± 0.023	0.036 ± 0.019
Madeira (Portugal)	18	17	0	17	0.993 ± 0.021	0.058 ± 0.030
Canaries (Spain)	17	17	0	17	1.000 ± 0.017	0.050 ± 0.026
Deserta (Brazil)	1	0	1	1	1.000 ± 0.000	0.000 ± 0.000
Aranhas (Brazil)	3	0	2	2	0.667 ± 0.314	0.033 ± 0.026
Galé (Brazil)	8	0	3	3	0.714 ± 0.123	0.029 ± 0.017
Xavier (Brazil)	12	0	3	3	0.667 ± 0.091	0.027 ± 0.015
Arvoredo (Brazil)	5	0	3	3	0.700 ± 0.218	0.029 ± 0.019
Macaronesian	61	46	0	46	0.984 ± 0.007	0.049 ± 0.025
Brazilian	29	3	0	3	0.638 ± 0.056	0.026 ± 0.139

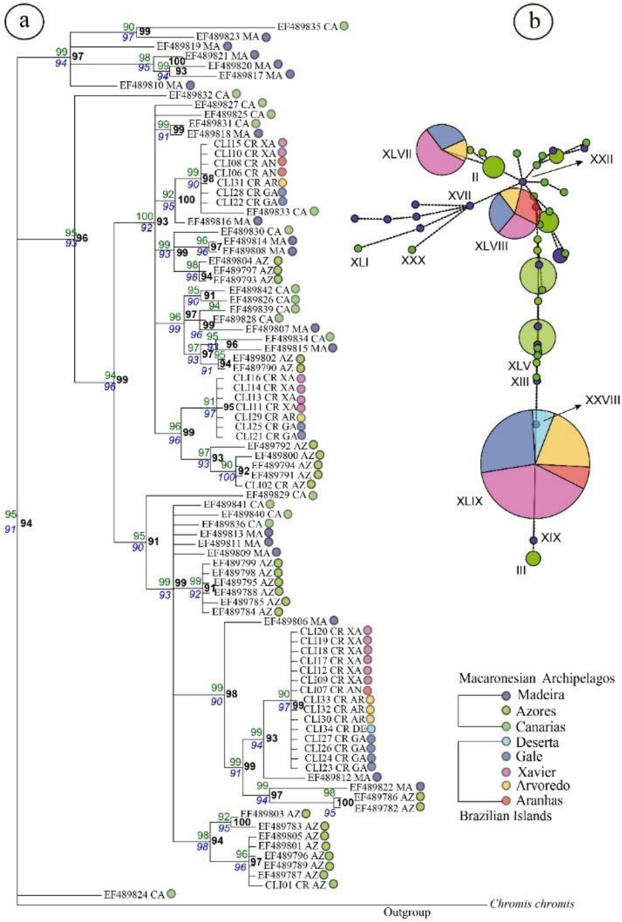

Fig. 4 a) Bayesian tree showing relationships among *C. limbata* haplotypes from the Macaronesian islands and Brazil. The numbers listed at each fork in the tree report posterior probability; b) haplotype network showing the spatial distribution among populations and haplotype sharing. Circles represent the haplotypes, and their sizes are proportional to the number of individuals with that haplotype. The three biggest circles and their colors represent the haplotypes shared among Brazilian sites.

Only three haplotypes were detected in Southern Brazil, a number much lower than that observed in the original *C. limbata* range (46 haplotypes). Such low haplotype diversity is consistent with the hypothesis of dispersal consisting of just a few individuals (Table I, Fig. 4). As expected due to proximity, Southern Brazilian populations showed a high level of connectivity among sites, and all three haplotypes are shared among Galé, Xavier and Arvoredo (Table I, Fig. 4).

4.5 DISCUSSION

The success of a new population depends on several factors such as mating success, new mutations, elimination of deleterious alleles, and repeated inflow of new genotypes, which may reduce the effects of inbreeding and further loss of genetic variation (Kaňuch *et al.*, 2014). Successful colonizations are often started by large numbers of individuals in multiple events during a long period avoiding loss of genetic diversity in the newly founded population (Roman, 2006; Dlugosch & Parker, 2008; Kaňuch *et al.*, 2014). The low genetic diversity detected in Brazilian *C. limbata* suggests a small larval pulse, or the arrival of a small group of individuals (Table I; Fig. 4). Four hypotheses could explain this colonization event: 1) *C. limbata* was released by aquarium fish keepers; 2) larvae may have been transported in ship ballast water; 3) the species might have rafted alongside oil rigs; and 4) natural colonization via larval transport and/or natural rafting across the Atlantic.

All four hypotheses may be possible but two of them seem more plausible than the others. Aquarium release is an unlikely source since this species is not particularly appealing to aquarists, very rarely exported from the Northeastern Atlantic and was never seen for sale in Brazil; also, considering the number of haplotypes found in Brazilian populations, a release of a large number of individuals (>160 according to the calculations based on table I) would be necessary to establish this population. Introduction via ship ballast water is also unlikely since most fish larvae (especially those of demersal pomacentrids) do not survive for long periods in such environment (Carlton, 1996; David *et al.*, 2007).

The transport of larvae and adults rafting alongside oilrigs seems plausible, and it has been responsible for several odd occurrences worldwide (Langeneck *et al.*, 2012; Dulčić & Dragičević, 2013; Pajuelo *et al.*, 2016). Moreover, the commerce and trade of oil and infra-structure involved on drilling operations and oil refining among Brazil, the Macaronesian Archipelago and African countries is frequent since 2003 (Frynas & Paulo, 2007). Specimens of *C. limbata* have recently (April,

2016) been detected in São Tomé, Principe, and Angola (Vasco-Rodrigues *et al.*, 2016), indicating that this species might have a wider range in the eastern Atlantic, and more potential source populations.

The natural dispersal hypotheses also seems plausible considering that *C. limbata* has been observed rafting associated with patches of algae and debris (Bortone *et al.*, 1994). In addition, the closely related *C. multilineata* also shows a history of successful long distance dispersal. The African populations of this species are unique, but date back to only a few tens of thousands of years, indicating that they crossed the Atlantic recently (Rocha *et al.*, 2008), albeit in the opposite direction that *C. limbata* did now. The sister species of *C. limbata*, *C. chromis* also rafts alongside floating objects in the open ocean (Bortone *et al.*, 1994), and species that can raft are generally better dispersers (Luiz *et al.*, 2015).

Long distance dispersal events are common in reef fishes in the Atlantic and other species from the Eastern Atlantic have recently been detected in southern Brazilian waters (*e.g. Acanthurus monroviae* Steindachner, 1876, the Monrovia surgeonfish native from south Morocco to Angola; (Luiz -Júnior *et al.*, 2004; Anderson *et al.*, 2015). Recently, the Caribbean invasive lionfish *Pterois volitans* (Linnaeus, 1758) was detected in Brazil, and it seems to have arrived as the result of natural dispersal from Caribbean waters (Ferreira *et al.*, 2015).

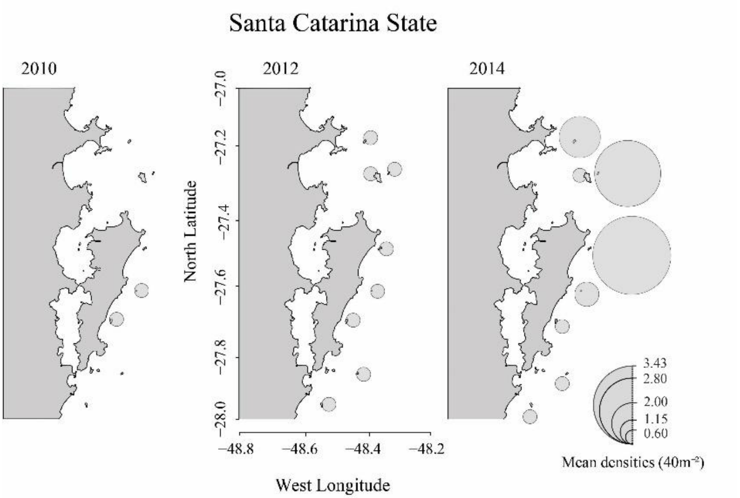

Fig. 5 Range expansion of *C. limbata* into southwestern Atlantic reefs from 2010 to 2014 (circle sizes are proportional to abundance).

Oceanic currents play an important role in the dispersal of marine organisms (Lumpkin & Garzoli, 2005; Cunha *et al.*, 2014). The surface circulation in the South Atlantic is complex and consists of an equatorial gyre formed by the North Equatorial Counter Current (NECC), the Guinea Current and three branches (north, central and south) of the South Equatorial Current (SEC), which form the North Brazil Current (NBC) and the Brazil Current (BC) (Lumpkin & Garzoli, 2005; Cunha *et al.*, 2014). These currents, which generally bring water from Africa towards Brazil and then from North to South below the equator (Matano, 1993; Molina-Schiller *et al.*, 2005; Matano *et al.*, 2010), may help larvae and rafters cross the Atlantic and also may be driving the unusual colonization events discussed here.

Other examples of disjunct distributions that were possibly driven by these same oceanographic processes include *Epinephelus marginatus* (Lowe, 1834) and *Parablennius pilicornis* (Cuvier, 1829). Their current distributions reflect what is seen in *C. limbata*: the northeastern Atlantic (including the Macaronesian islands) and southern Brazil (Froese & Pauly, 2016). Such similarity in distributional patterns may suggest that, during their range expansion across the Atlantic, these species may have dispersed using similar routes, and that in the future, *C. limbata* may establish a permanent population in Brazil.

POTENTIAL IMPACTS

Despite significant differences in mean densities among sites for *C. multilineata*, it does not seem like they have been affected by the increase in the *C. limbata* population (Fig. 2). It is important to note that *C. multilineata* is a tropical species inhabiting its southern limit of distribution, whereas *C. limbata* is inhabiting its optimum environment (subtropical, warm-temperate rocky reefs). Given its ecological preferences in the eastern Atlantic, we predict that *C. limbata* will be more abundant than *C. multilineata* in the south and southeastern coast of Brazil, and maybe, even expand further south to Uruguay and Argentina. The dusky grouper (*Epinephelus marginatus*), for example, expanded southwards recently (Irigoyen *et al.*, 2005).

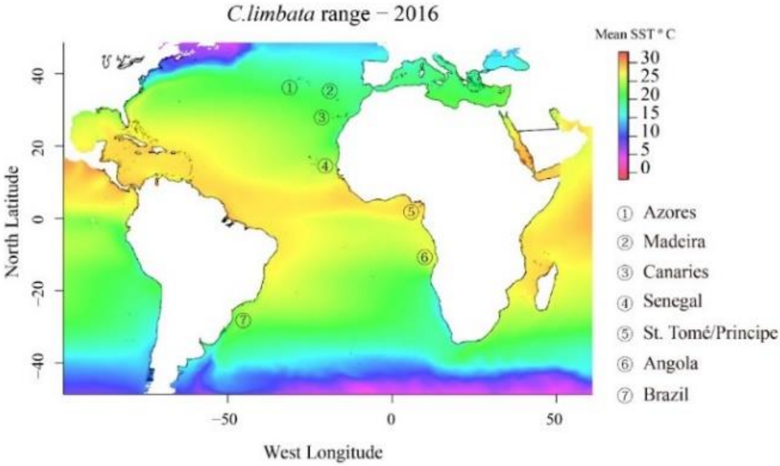

Fig. 6 Distribution of *C. limbata* and mean sea surface temperature (raster source Bio-ORACLE; Tyberghein et al. 2015).

Even though *C. limbata* and *C. multilineata* have a similar zooplankton diet (Froese & Pauly, 2016), the high productivity of south Atlantic waters due to upwelling and consequent high abundance of plankton (Barua, 2005), indicates that these species may not be competing for food (Fig. 7d; Green *et al.*, 2012; Elleouet *et al.*, 2014; Anderson *et al.*, 2015; Chown *et al.*, 2015). Schools of *C. multilineata* and *C. limbata* feeding together have been observed in the past two years in all studied sites. In addition to *C. multilineata, C. limbata* also interacts with other natives, and its aggressive behavior during reproduction (Fig. 7 c) may affect local territorial species [*e.g. Stegates spp*., *Abudefduf saxatilis* (Linnaeus 1758)]. Shelter for example may become a limiting resource as their densities in the new environment increase (Green *et al.*, 2012; Elleouet *et al.*, 2014; Chown *et al.*, 2015).

Fig. 7 Behavior of *C. limbata* in the Southwestern Atlantic: a) Schools in Galé Is., January, 2014; b) Juvenile aprox. 3 cm TL using a sea urchin as shelter, Deserta Is. February 2014; c) Large blue male (aprox. 15 cm TL) defending his nest, Xavier Is. May, 2014; d) *C. limbata* and *C. multilineata* feeding together, Xavier Is. May, 2014; e) School in Aranhas Is., April, 2014 and f) Juveniles (aprox. 5 cm TL) at Arvoredo Is., 2013.

However, so far there has been no evidence of detrimental effects to native species. Long term monitoring of this recent arrival will be important and could constitute a valuable tool for a better understanding the genetics, ecology, and impacts of species range expansions.

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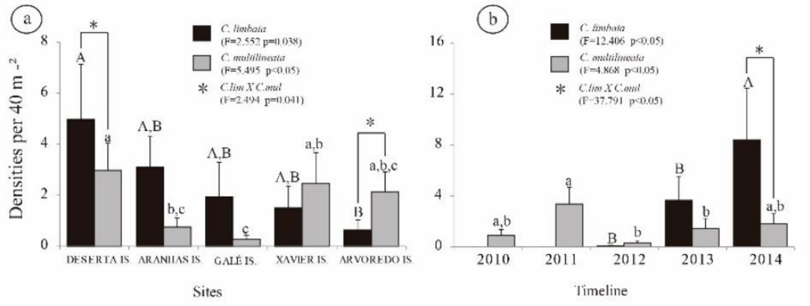
Appendix 01:



Appendix 1: A) Spatial variations in sum of mean densities (+ SE) and B) temporal variations of mean densities of *C. limbata* (black bars) and *C. multilineata* (grey bars). Letters above bars indicate significant differences (upper case letters indicate comparisons in *C. limbata* and lower case in *C. multilineata*); asterisks denote significant differences among species (Tukey HSD, $p < 0.05$).

5 CONCLUSÕES E CONSIDERAÇÕES FINAIS

A ictiofauna do estado de Santa Catarina é caracterizada por 278 espécies tropicais trazidas pelas águas quentes oriundas das correntes oceânicas quentes do Norte (Brazilian current - BC). No entanto, as águas frias que ocorrem durante o inverno Austral afetam a fisiologia das espécies, podendo inclusive, promover o desaparecimento de populações (BOHNSACK, 1983; HSIEH *et al.*, 2008; ANDERSON *et al.*, 2014; ANDERSON *et al.*, 2015). Cerca de 96.4% das espécies estudadas neste trabalho habitam seu limite meridional de distribuição (ANDERSON *et al.*, 2015).

Estas populações apresentam alta variabilidade com relação à distribuição espacial e altíssima variabilidade com relação à densidade e biomassa em escala temporal (anual). De acordo com ALMADA e FARIA (2004), para muitas espécies de peixes teleósteos que habitam recifes rochosos localizados próximo, ou em seu limite de distribuição, as flutuações populacionais são consideradas fenômenos frequentes (ALMADA e FARIA, 2004). *Em suma*, a proximidade com os seus limites de distribuição, mecanismos determinísticos, dispersão larval estocástica, os mecanismos dependentes de densidade e oscilações estocásticas de temperatura, podem constituir os principais fatores que influenciam as variações populacionais da ictiofauna que habita os recifes rochosos do sul do Brasil (SALE, 1978; 1980; DOHERTY, 1983; ALMADA e FARIA, 2004; BEGON *et al.*, 2006; SALE, 2013).

Por outro lado, as variações da distribuição em escala espacial podem ser governadas por mecanismos determinísticos, como a complexidade estrutural do habitat, a seletividade (afinidade) de habitat, a proteção contra pesca e comércio espécies ornamentais (CHOAT *et al.*, 1988; WATSON *et al.*, 2007; BABCOCK *et al.*, 2010; ABURTO-OROPEZA *et al.*, 2011; ANDERSON *et al.*, 2014; MELLIN *et al.*, 2016). Nesse contexto, a Reserva Biológica Marinhado Arvoredo parece influenciar de forma direta e indiretamente as variações de densidades e biomassa de todas as espécies. Da mesma forma, os efeitos positivos sobre a densidade e biomassa dos grupos tróficos é evidente. Tais padrões corroboram com os estudos de Watson e colaboradores (2007), Babcock e colaboradores (2010) e Mellin e colaboradores (2016), quando afirmam que as AMP afetam positivamente (e.g. aumento da densidade e biomassa) todas as espécies de peixes que habitam estes sistemas. Porém, considerando o grave declínio no recrutamento de espécies, especialmente os predadores de topo (e.g. *E. marginatus*), aliado ao fato de que não há nenhuma política ou projetos para a conservação e restauração de habitats considerados como berçários, e a má gestão (i.e., pesca ilegal frequente) (Anderson et al. 2014), qualificam como incerto, o futuro das populações de garoupas da REBIO Arvoredo, e das demais espécies que nela habitam.

Os registros incomuns para a região de Santa Catarina descritos neste trabalho confirmam a forte influência exercida pelas correntes oceânicas, nesta parte da costa Brasileira (MATANO, 1993; CUNHA *et al.*, 2007; MATANO *et al.*, 2010; ANDERSON *et al.*, 2015). Estas correntes, que geralmente trazem água da costa da África para a costa do

Brasil e, em seguida, de norte para o sul abaixo do equador, podem auxiliar no transporte das espécies através do Atlântico (MATANO, 1993; MOLINA-SCHILLER, DANIZA *et al.*, 2005; MATANO *et al.*, 2010).

A espécie invasora *C. limbata* após extensivo estudo de sua variação populacional em escala temporal e espacial, apresenta padrões de espécie em processo de colonização (CARLTON, 1996). No entanto, até agora não houve nenhuma evidência de efeitos prejudiciais para espécies nativas.

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