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Padrões e processos espaço-temporais da diversidade taxonômica e funcional de peixes recifais em uma zona de transição de temperatura

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Tese submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina como requisito parcial para a obtenção do título de Doutora em Ecologia.

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Fernanda Carolina da Silva

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O presente trabalho em nível de Doutorado foi avaliado e aprovado, em 11 de julho de 2023, pela banca examinadora composta pelos seguintes membros:

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À minha mãe e ao meu pai,
Meus alicerces.

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“Lembrete:

Se procurar bem você acaba encontrando.
Não a explicação (duvidosa) da vida,
Mas a poesia (inexplicável) da vida.”

(*Carlos Drummond de Andrade*)

RESUMO

Zonas de transição são consideradas laboratórios naturais para explorar os efeitos das mudanças climáticas sobre a organização das comunidades ao longo do tempo. Estas zonas são influenciadas pelas condições ambientais de clima tanto quente quanto frio, o que reflete na presença de faunas adaptadas para ambas as condições. Apesar da relevância, zonas de transição têm sido relativamente pouco estudadas em áreas costeiras e poucos tem sido os estudos explorando mudanças temporais baseadas em aspectos taxonômicos e funcionais. Abordagens baseadas em atributos podem ser complementares às taxonômicas ajudando a detectar respostas da comunidade frente a mudanças ambientais, pois refletem os requisitos de recursos e habitat das espécies. O objetivo deste estudo foi avaliar a diversidade taxonômica e funcional de peixes recifais em sete ilhas do sudoeste do Atlântico no espaço e o tempo. Mais especificamente, este estudo buscou entender (i) como as comunidades de peixes recifais são estruturadas no espaço em termos de riqueza, densidade, biomassa, tolerância térmica e grupos tróficos; (ii) se existem indícios de homogeneização das comunidades ao longo do tempo dada às diferenças espaciais na composição de espécies; e (iii) quais atributos das comunidades tem variado ao longo do tempo dado as mudanças na temperatura do mar nos últimos 15 anos. Para tanto, foram compilados atributos de história de vida para as espécies de peixes recifais e 15 anos de monitoramento delas em sete ilhas de Santa Catarina - zona de transição do Atlântico Sudoeste. Os resultados desta compilação foram publicados dos artigos na revista Ecology. Os resultados espaciais apontam uma separação das comunidades de peixes recifais entre as ilhas do norte e sul tanto em termos taxonômicos quanto de tolerância térmica, com uma predominância de espécies mais adaptadas a climas quentes ao norte e a climas amenos ao sul. Contrariamente às expectativas, não foram observados sinais de homogeneização destas comunidades ao longo do tempo. Embora a composição taxonômica tenha variado temporalmente, a composição de atributos é geralmente mais conservada, destacando a redundância funcional presente na região. Foi detectada uma gradual reorganização de atributos ao longo do tempo com assembleias dominadas por espécies grandes e de alto nível trófico no início da série para uma comunidade com alta abundância de espécies menores e criptobênticas nos anos mais recentes. Tal dinâmica foi relacionada a variações na temperatura superficial do mar no verão, o que resulta em implicações ecológicas de rápida substituição de espécies, afetando a complexidade das cadeias tróficas e a vulnerabilidade das comunidades a perturbações (Capítulo publicado em Marine Ecology Progress Series). Este estudo destaca que esforços de conservação em escala local podem ser particularmente eficazes na proteção de espécies e funções ecológicas em áreas experienciando variações climáticas constantes (e. g. zonas de transição). Finalmente, a integração de dados temporais incorporando abundância e abordagens funcionais em diferentes escalas consiste em uma poderosa ferramenta para o entendimento da dinâmica dos recifes e das respostas da comunidade às variações ambientais, incluindo o aumento da temperatura.

Palavras-chave: Peixes recifais; tolerância térmica; zonas de transição; reorganização funcional; α-diversidade; β-diversidade; variações temporais; mudanças climáticas; estrutura de comunidades.

ABSTRACT

Transition zones are considered natural laboratories for exploring the effects of climate change on community organization over time. These zones are influenced by both warm and cold climate conditions, which is reflected in the presence of fauna adapted to both conditions. Despite their relevance, transition zones have been relatively understudied in coastal areas, and few studies have explored temporal changes based on taxonomic and functional aspects. Trait-based approaches can complement taxonomy in detecting community responses to environmental changes, as they reflect the resource requirements of species. The objective of this study was to evaluate the taxonomic and functional diversity of reef fish in seven islands in the southwestern Atlantic in space and time. Specifically, this study aimed to understand (i) how reef fish communities are structured in terms of richness, density, biomass, thermal tolerance, and trophic groups in space; (ii) if there is evidence of community homogenization over time given the spatial differences in species composition; and (iii) which traits have varied over time due to changes in sea temperature over the past 15 years. To do so, life history attributes for reef fish species and 15 years of monitoring data were compiled for seven islands in Santa Catarina - a transition zone in the southwestern Atlantic. The results of this compilation were published in Ecology journal. The spatial results indicate a separation of reef fish communities between the northern and southern islands, both in terms of taxonomy and thermal tolerance, with a predominance of species adapted to warmer climates in the north and colder climates in the south. Contrary to expectations, there were no signs of homogenization of these communities over time. Although taxonomic composition varied temporally, trait composition was generally more conserved, highlighting the functional redundancy present in the region. A gradual reorganization of attributes over time was detected, with assemblages initially dominated by large, high trophic-level species transitioning to a community with high abundance of small and cryptobenthic species in more recent years. This dynamic was related to variations in summer sea surface temperature, resulting in ecological implications such as fast species turnover, affecting the complexity of trophic chains, and the vulnerability of communities to disturbances (Chapter published in Marine Ecology Progress Series journal). This study emphasizes that conservation efforts at the local scale can be particularly effective in protecting species and ecological functions in areas experiencing constant climate variations (e.g., transition zones). Finally, the integration of temporal data incorporating abundance and trait-based approaches at different scales represents a powerful tool for understanding reef dynamics and community responses to environmental variations, including increasing temperatures.

Keywords: Reef fish; thermal tolerance; transition zones; functional reorganization; α-diversity; β-diversity; temporal variation; climate change; community structure.

LISTA DE FIGURAS

INTRODUÇÃO GERAL

CAPÍTULO I

CAPÍTULO II

CAPÍTULO III

LISTA DE TABELAS

CAPÍTULO I

CAPÍTULO II

CAPÍTULO III

SUMÁRIO

INTRODUÇÃO GERAL

Biodiversidade

A vida na Terra não se distribui homogeneamente e é caracterizada por variações no número de espécies, abundância dos indivíduos, características de história de vida e história evolutiva (LAWTON, 1999). Tais variações ocorrem no espaço e tempo e têm despertado a curiosidade de pesquisadores por décadas (VON HUMBOLDT, 1849). Nesse sentido, a criação do termo biodiversidade vem de encontro à necessidade de descrever as variações entre espécies, comunidades e ecossistemas (HEYWOOD, 1992; NORSE, 1986). Biodiversidade biológica ou simplesmente biodiversidade (WILSON, 1988) são, portanto, termos amplamente utilizados na literatura científica e popular que definem a variedade e abundância das espécies em uma área de estudo definida (MAGURRAN, 2004). A fim de facilitar o entendimento dos sistemas naturais, uma organização hierarquizada da biodiversidade foi proposta definindo indivíduo como um organismo único; indivíduos da mesma espécie como populações; populações de diferentes espécies como comunidades; e diferentes comunidades somadas aos componentes abióticos de ecossistemas (HEYWOOD, 1992). Tal organização facilita a identificação dos padrões existentes nos ecossistemas bem como o entendimento de suas causas. Neste estudo, o conceito de biodiversidade será associado ao conjunto de espécies presente em um determinado local.

A biodiversidade pode ser quantificada de diferentes formas e em múltiplas escalas. Whittaker em 1972 reconheceu que as escalas espaciais determinam a composição de espécies em determinado local, pois de acordo com a Teoria de Biogeografia de ilhas, a riqueza tende a aumentar com a área amostrada (MACARTHUR; WILSON, 1967). Ele propôs três níveis de organização: α, β e γ, onde α e γ correspondem à diversidade em escala local e regional, respectivamente, e β à diferença de biodiversidade entre áreas (WHITTAKER, 1972). Ainda que existam outros níveis de organização, a diversidade α e β são as mais amplamente exploradas no espaço e tempo (BARWELL; ISAAC; KUNIN, 2015; DORNELAS et al., 2014; VILLEGER et al., 2012) e são o foco dos capítulos apresentados nesta tese. Apesar do termo biodiversidade ser frequentemente atribuído à riqueza (ou número) de espécies em determinado local (TITTENSOR et al., 2010), outros fatores como a frequência em que determinada espécie ocorre também caracteriza biodiversidade. Desta forma, a diversidade α se torna um conceito bidimensional que descreve a riqueza de espécies e suas distribuições de abundância (BEGON;

HARPER; TOWNSEND, 2006). Por sua vez, índices que consideram a abundância relativa das espécies nas unidades amostrais informam sobre a uniformidade das distribuições dos indivíduos (*evenness*), onde altos valores refletem abundâncias similares entre espécies e valores baixos refletem alta dominância de espécies em particular (PIELOU, 1977). Por outro lado, para acessar a heterogeneidade ou diferenciação entre amostras deve-se considerar medidas de β diversidade (BASELGA; LEPRIEUR, 2015). A diversidade β pode ser particionada em dois componentes: substituição ou *turnover* e aninhamento ou *nestedness*, visto que a heterogeneidade entre amostras pode ocorrer tanto por diferenças no número de espécies quanto pela identidade das mesmas (BASELGA, 2010).

Apesar de estimativas da riqueza de espécies (também referida como riqueza taxonômica) promoverem informações relevantes sobre a estruturação das comunidades, elas assumem que os indivíduos contribuem de maneira igual no funcionamento dos ecossistemas (MAGURRAN, 2004). Assim, a riqueza taxonômica muitas vezes promove uma visão incompleta das comunidades porque não considera a identidade biológica das espécies e seus papeis efetivos no ambiente (VILLÉGER et al., 2010). Abordagens funcionais surgem nesse contexto incorporando atributos das espécies, auxiliando no entendimento do funcionamento e estruturação dos ecossistemas (PETCHEY; GASTON, 2006; VIOLLE et al., 2007). Um atributo é definido como uma característica morfológica, fisiológica ou fenológica de um indivíduo (VIOLLE et al., 2007). Por sua vez, o conjunto destes atributos determina onde um organismo vive e qual seu desempenho no ambiente, por exemplo: a posição trófica que se relaciona com transferência de energia e biomassa; e a herbivoria, que em peixes controla populações de macroalgas e corais (MUMBY, 2006). As estimativas dos atributos das espécies e suas abundâncias numa comunidade refere-se à diversidade funcional (MOUILLOT et al., 2013) e diversos autores demonstram sua contribuição significativa no entendimento de processos ecossistêmicos como produtividade, regulação no fluxo de energia e resiliência (BELLWOOD et al., 2004; HOOPER et al., 2005).

A caracterização da biodiversidade considerando aspectos taxonômicos e funcionais tem trazido avanços no conhecimento em diferentes esferas. Exemplos incluem a investigação de dinâmicas em escalas locais (PINHEIRO et al., 2015), padrões globais biogeográficos (TITTENSOR et al., 2010), respostas das comunidades frente a distúrbios (VAN DENDEREN et al., 2014), regras de montagem de comunidades (PECUCHET; TÖRNROOS; LINDEGREN, 2016) e funcionamento dos ecossistemas (BRANDL et al., 2019). Todas as métricas mencionadas acima (diversidade α, β, γ e funcional), além de serem utilizadas para comparações entre localidades ou regiões, também são aplicadas em escala temporal, investigando padrões mensais, sazonais ou anuais de comunidades (DORNELAS et al., 2014; MCLEAN et al., 2019; PECUCHET et al., 2020).

Padrões e Processos

O termo "padrão" de biodiversidade, por definição, se refere às regularidades observadas na natureza ou tendências amplamente observadas (WHITTAKER, 1975). Ecólogos buscam identificar "leis" e "regras" como princípios dos padrões encontrados na natureza da mesma forma que esportes possuem regras para que todos joguem da mesma forma (LAWTON, 1999). Por outro lado, os mecanismos que geram tais padrões correspondem aos "processos", e são eles os responsáveis pela criação dos fenômenos identificados (LAWTON, 1999). Um dos padrões mais bem estabelecidos refere-se ao Gradiente Latitudinal de Diversidade de espécies (GLD), que define um aumento da riqueza de espécies em regiões tropicais de baixas latitudes, e um decréscimo em direção aos polos e altas latitudes (CONDAMINE et al., 2012; WILLIG; KAUFMAN; STEVENS, 2003). Este padrão é bem estabelecido para diversos táxons como aves, plantas, mamíferos e peixes (BLOWES; BELMAKER; CHASE, 2017; GASTON, 2000; MITTELBACH et al., 2007). Uma das teorias ecológicas que explica tal padrão relaciona a estabilidade climática de baixas latitudes com as características de vida das espécies, ou seja, o nicho individual (PIANKA, 1966). Por exemplo, espécies habitando ambientes tropicais experienciam pouca sazonalidade e, portanto, vivem longe de seu ótimo térmico pela temperatura anual relativamente constante (WILLIG; KAUFMAN; STEVENS, 2003). Essas características permitem alta riqueza de espécies, contrariamente a regiões com invernos rigorosos que demandam adaptações especiais (WILLIG; KAUFMAN; STEVENS, 2003).

Entender os padrões gerais, bem como os mecanismos que os governam em escala espacial e temporal constitui um dos maiores desafios da ecologia (MCGILL et al., 2006; SIMBERLOFF, 2004). Além da importância para a ecologia teórica em si, o estudo destes mecanismos promove ideias de como as comunidades devem responder às variações ambientais no futuro (OVASKAINEN et al., 2017). No entanto, para alguns ambientes, a identificação dos padrões e a contribuição relativa dos processos locais e regionais que geram variações na estrutura das comunidades ainda permanece incompreendida (MITTELBACH; SCHEMSKE, 2015).

Ameaças aos padrões de biodiversidade

Estressores regionais e locais têm dramaticamente ameaçado os ecossistemas naturais, principalmente os oriundos das atividades humanas (FIGUEROA-PICO; TORTOSA; CARPIO, 2021). Quando comparamos a atual diversidade e abundância de peixes com a diversidade de décadas passadas é possível perceber um drástico declínio tanto em águas costeiras, como oceânicas, rasas e profundas (ROBERTS, 2007). Tal mudança deve-se à combinação sinergética de ameaças como poluição, pesca e aquecimento global (SOARES, 2018). Embora a pesca constitua um importante fator na modificação da estrutura das comunidades, ela não constitui o foco deste trabalho pela falta de dados disponíveis e extensivas revisões sobre seus impactos podem ser encontradas em (FLOETER; HALPERN; FERREIRA, 2006; MUMBY et al., 2012; YOUNG; FOALE; BELLWOOD, 2014).

Outra forte ameaça à biodiversidade refere-se ao aquecimento global e seus impactos têm ganhado destaque nas últimas décadas devido ao aumento das emissões de gases do efeito estufa (HUGHES, 2000). Modelos climáticos têm projetado variações na temperatura dos oceanos de um aumento de 1,5ºC em diferentes partes do mundo até 2011 (IPCC, 2018). Sabe-se que o aquecimento altera diferentes aspectos oceanográficos como padrões de circulação (FRANCO et al., 2020) e acidificação (RUMMER; MUNDAY, 2017), consequentemente afetando a disponibilidade de hábitat e nicho para a manutenção das populações (DONEY et al., 2012). Por sua vez, os efeitos das mudanças de temperatura em peixes a nível de indivíduo e de comunidades tem sido relatados por diversos autores (DONEY et al., 2012; HUGHES, 2000; MUNDAY et al., 2013; PINSKY et al., 2013; PINSKY; SELDEN; KITCHEL, 2020). Alguns deles incluem: (i) o aumento da concentração de CO2 graças ao aquecimento e emissão de gases, que prejudica a performance das espécies, acidificando os tecidos e elevando os custos metabólicos (MUNDAY et al., 2008); (ii) a diminuição do período de duração larval (Pelagic Larval Duration – PLD), redução do sobrevivência (fitness), crescimento, reprodução e diversidade funcional como um todo (HUGHES, 2000; JOURDAN et al., 2018; WALTHER et al., 2002); e (iii) alterações nos padrões de abundância e distribuição, influenciando a presença ou ausência dos atributos funcionais nas comunidades (ARAÚJO; NEW, 2007; TEICHERT; LEPAGE; LOBRY, 2018; THOMAS et al., 2004; YEAGER et al., 2017). Apesar da relevância, pouco se sabe sobre a dinâmica espacial e temporal da estrutura das comunidades associadas aos impactos globais de aumento da temperatura, principalmente em áreas de variação climática natural.

Efeitos da temperatura em peixes recifais

Um dos grupos mais interessantes para modelo de estudo de estrutura de comunidades refere-se aos peixes recifais. Isto se deve à sua alta diversidade (cerca de 6.500 espécies), taxonomia bem resolvida, distribuição biogeográfica bem documentada e alto valor econômico para populações humanas (KULBICKI et al., 2013; MORA et al., 2011). Sua riqueza e distribuição variam no tempo e espaço, e são determinadas tanto por processos evolutivos de especiação e extinção, como fisiológicos e ecológicos incluindo disponibilidade de habitat (FLOETER et al., 2018; PARRAVICINI et al., 2013). Peixes recifais apresentam ainda uma grande variedade de interações (e.g., competição, predação, mutualismo e facilitação), contribuindo na ciclagem de nutrientes e em modificações físicas no ambiente (BELLWOOD et al., 2004; HOLMLUND; HAMMER, 1999). Entretanto, distúrbios ambientais como o aquecimento global têm influenciado e modificado cada vez mais os padrões de distribuição e as interações nas assembleias de peixes, comprometendo os processos ecológicos e as funções ecossistêmicas prestadas por elas (BELLWOOD; HOEY; HUGHES, 2012).

Atributos de história de vida podem diferir drasticamente em populações de peixes recifais influenciadas por diferentes regimes de temperatura e disponibilidade de recursos (MUNDAY et al., 2008). O tamanho corporal por exemplo, pode ser afetado e reduzido em função de altas temperaturas devido ao custo metabólico para crescimento (BARNECHE et al., 2014). Consequentemente, é esperado que a idade de maturação das espécies também seja reduzida, visto que a idade de maturação é correlacionada com o tamanho máximo atingido pela espécie (MUNDAY et al., 2008). Na Grande Barreira de Corais da Austrália, por exemplo, peixes papagaio tendem a crescer mais lentamente, apresentar altas taxas de mortalidade e mudar de sexo precocemente sob altas temperaturas (GUST, 2004; GUST; CHOAT; ACKERMAN, 2002). Exceções a estes padrões são reportadas por outros autores onde temperaturas elevadas associadas a outras variáveis como disponibilidade de recursos podem aumentar a taxa de crescimento entre populações (MUNDAY et al., 2008). Neste sentido, um crescimento mais rápido pode resultar em aumento da taxa de recrutamento, como visto em *Stegastes partitus* no Caribe (WILSON; MEEKAN, 2002). Porém, apesar de favorecer o recrutamento, pequenas alterações de temperatura podem resultar em redução da produção de ovos por estresse fisiológico, bem como do número de larvas que entram na fase pelágica de seu desenvolvimento (MUNDAY et al., 2008).

A resposta das espécies ao aumento da temperatura também varia conforme outros atributos, como a mobilidade e o acesso à refúgios térmicos; o que pode interferir na distribuição geográfica dos organismos (PINSKY; SELDEN; KITCHEL, 2020). Novas áreas podem ser colonizadas através da dispersão de espécies sensíveis às variações do ambiente, as quais imediatamente buscam novos habitats com condições favoráveis à sua sobrevivência. Tal evento foi observado para peixes herbívoros tropicais (e.g. *Siganus fuscescens*; *Kyphosus bigibbus*) na costa do Japão (KUMAGAI et al., 2018). Assim, mudanças de distribuição são, portanto, uma consequência emergente das interações entre os organismos e o ambiente, moldadas pela variabilidade climática e o aquecimento global (PINSKY; SELDEN; KITCHEL, 2020). Dada a diversidade (FLOETER et al., 2008) e diferentes respostas a variações de temperatura (PRATCHETT et al., 2011; VERGÉS et al., 2014), peixes recifais foram escolhidos como o grupo focal desta tese.

Zonas de transição no contexto de alterações climáticas

Zonas de transição são regiões exibindo combinações de características provenientes de dois ambientes distintos (MORRONE, 2023). Essas características podem se referir a gradual variação em termos de aspectos físicos da paisagem, da composição de espécies ou de condições ambientais e climáticas (FERRO; MORRONE, 2014). Em termos climáticos, zonas de transição podem se referir a regiões com mudança gradual de ambientes tropicais para subtropicais/temperados (SOMMER et al., 2017). O oceano Atlântico apresenta pelo menos quatro zonas de transição marinha de altas latitudes, onde espécies com diferentes afinidades de temperatura se encontram, estas zonas incluem o leste dos Estados Unidos, o oeste da Europa, o sul do Brasil e o sudeste da África.

Uma zona de destaque constitui a zona de transição marinha do sul Brasil, localizada na região da plataforma continental do estado de Santa Catarina e caracterizada pela proximidade com a região da confluência da Corrente do Brasil (CB) com a Corrente das Malvinas (CM) (DE MAHIQUES et al., 2021). Esta região sofre influência sazonal de águas frias e com baixa salinidade, provenientes da descarga de água doce do Rio da Prata (~35°S) e da Lagoa dos Patos (~ 32°S) durante o inverno fluindo sentido norte (MÖLLER et al., 2008; PIOLA et al., 2000, 2008). Tais características conferem à região relevante importância ecológica dada à presença de espécies marinhas tropicais em seu limite sul de distribuição (ANDERSON et al., 2015). Em geral, zonas de transição marinhas abrigam uma mistura de faunas tanto adaptadas a temperaturas quentes quanto a temperaturas frias (EBELING; HIXON, 1991). Por este motivo, essas áreas são consideradas *hotspots* de biodiversidade com alta resiliência à pequenas variações climáticas dada as oscilações que naturalmente ocorrem nos parâmetros oceanográficos regionais (HORTA E COSTA et al., 2014). Além de serem expostas à altas flutuações ambientais, espécies de recifes de altas latitudes vivem próximas aos seus limites de temperatura, habitat e disponibilidade de nutrientes (GUINOTTE; BUDDEMEIER; KLEYPAS, 2003). Assim, considerando que recifes de altas latitudes e em zonas de transição são suscetíveis às mudanças de temperatura globais, espera-se que nessas regiões ocorra também modificações nas distribuições das espécies que os habitam (YAMANO; SUGIHARA; NOMURA, 2011). Expansões nos limites de distribuição geográfica de peixes recifais já vêm sido observadas na zona de transição da Austrália (VERGÉS et al., 2014), o que faz com que recifes destas áreas atuem como bons sentinelas das mudanças climáticas (SOMMER et al., 2014).

Objetivos da tese

Diante da importância de avaliar a estrutura das comunidades de peixes recifais em zonas de transição expostas às variações climáticas, esta tese teve como objetivo explorar em escala espacial e temporal as variações das comunidades de peixes considerando diferentes aspectos da biodiversidade como riqueza taxonômica e de atributos (Fig. 1). Mais especificamente, este estudo buscou entender (i) como as comunidades de peixes recifais são estruturadas no espaço em termos de tolerância térmica, riqueza, densidade, biomassa e grupos tróficos em 7 ilhas da zona de transição do Atlântico Sul (Capítulo 1); (ii) se existem indícios de homogeneização das comunidades ao longo do tempo dada às diferenças espaciais na composição de espécies nesta região (Capítulo 2); e (iii) quais atributos das espécies presentes nas comunidades tem variado ao longo do tempo dado as mudanças na temperatura do mar nos últimos 15 anos (Capítulo 3). Considerando o gradiente latitudinal em que se encontram, espera-se que as comunidades presentes nas ilhas sejam segregadas de acordo com sua tolerância térmica, apresentando afinidade a temperaturas mais altas ao norte e mais frias ao sul, refletindo também em padrões diferenciados para as outras métricas. Temporalmente, espera-se que as comunidades se tornem cada vez mais similares em termos taxonômicos e funcionais em função do aumento da temperatura superficial do oceano, refletindo inclusive em variações nos atributos funcionais ao longo do tempo.

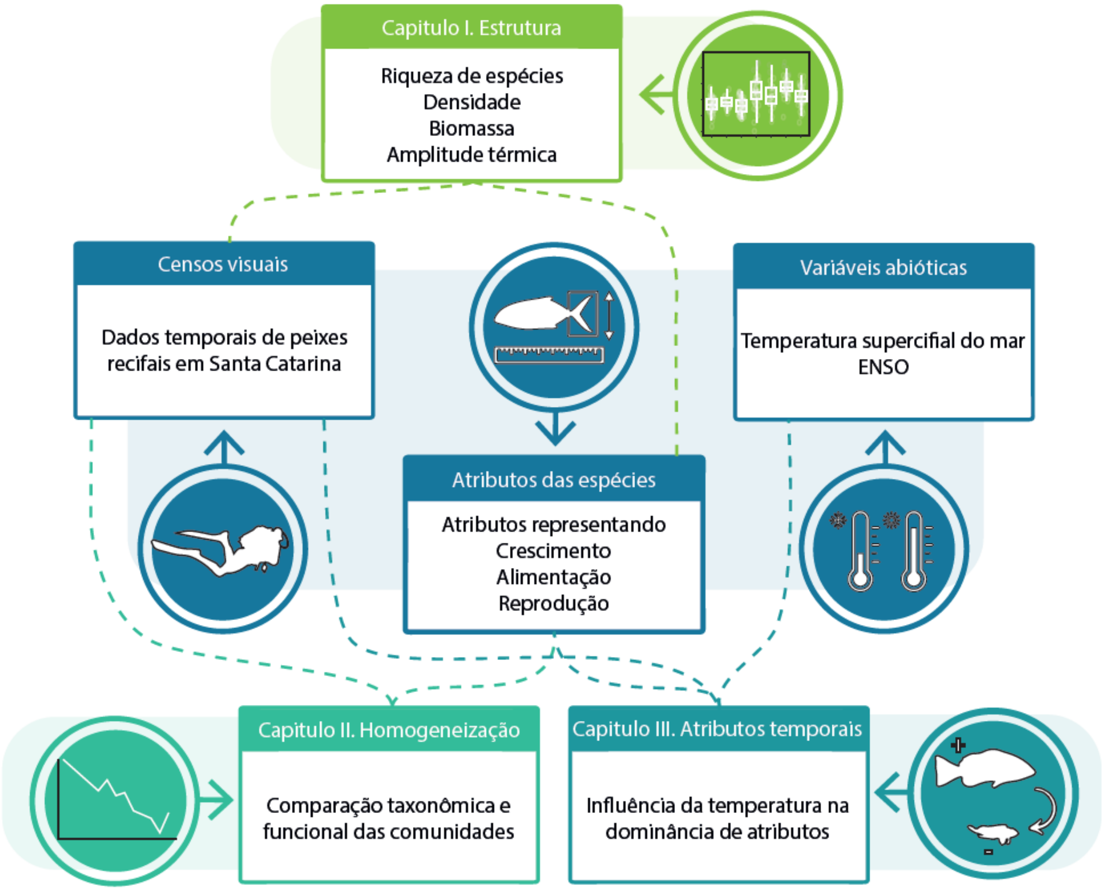

Figura 1. Figura conceitual representando os três artigos científicos desenvolvidos nesta tese em escala espacial (capítulo I) e temporal (capítulos II e III). Foram utilizados três bancos de dados referentes a riqueza e abundância de peixes recifais em Santa Catarina, aos atributos de história de vida destas espécies, e dados de temperatura do mar na região de estudo.

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CAPÍTULO I

Reef fish community structure across an ecological transition zone

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Reef fish community structure across an ecological transition zone

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Abstract

Transition zones exhibit a unique combination of abiotic characteristics derived from the merging of two distinct areas, hosting communities with different thermal tolerance and distribution ranges. Given these characteristics, these zones are key to unmasking the effects of climate change on biodiversity since rapid changes in the sea temperature can favor some populations more than others. This study aimed to investigate the community structure of reef fish in seven islands of the southwestern Atlantic in a transition zone. Our results revealed distinct patterns of thermal affinity separating north to south islands, indicating a higher tolerance for species experiencing colder and seasonal temperatures. We also found that common species abundance distribution pattern corresponds to the presence of many rare and few dominant species. Planktivores were the most abundant trophic group in the north islands, while omnivores prevail in the south islands, potentially due to differences in the oceanographic conditions of the region, such as water transparency. Our findings underscore the importance of understanding how communities differ or shift in space, which is crucial for predicting the consequences of environmental changes on biodiversity and ecosystem functioning.

Introduction

One of the primary challenges in ecology is to identify general patterns and processes observed in communities (Lawton 1999; Simberloff 2004; McGill et al. 2006). Species distribution patterns can be shaped by environmental conditions and ecological interactions (Hubbell 2001; Chase and Leibold 2003). Some environmental conditions that drive biodiversity patterns include temperature, depth, and habitat complexity, whereas competition and predation are some ecological interactions that can module natural communities on a local scale (Macneil et al. 2009; Samoilys et al. 2019). Additionally, anthropogenic activities have gained strength in recent years as important factors that affect biodiversity, since activities such as fishing, pollution, and the introduction of species can alter the equilibrium among habitats and communities and therefore impact ecosystem functioning (McGill et al. 2015). Therefore, identifying how communities are spatially structured and how these can respond to environmental and human disturbances are the first steps to understanding biodiversity within the Anthropocene.

Biodiversity in local scales has been explored classically through species richness, taxonomic composition, and abundance (Levin, 2001). Although these metrics have been important in elucidating population trends in abundance and obtaining essential information regarding communities, they do not reflect the differences among species and their contributions to the functioning ecosystems. Thus, the inclusion of metrics associated with nutrient cycling (e.g., biomass) and how species occupied a niche given their traits (e.g., diet, body size) are key to revealing the biodiversity patterns (Bacheler et al. 2017). For instance, studies have shown that marine areas with high fish biomass produce more energy and maintain stability within habitats (McClanahan et al. 2019). On the other hand, a recent study showed that the variations in community structure could be attributed to the response of species tracking temperature fluctuations and changing their range distributions (Sommer et al. 2017; Vergés et al. 2019). Furthermore, the species classification within trophic groups could provide extra tools to evaluate community structure because these might be associated with environmental conditions such as turbidity, benthic composition, wave exposure, and temperature (Floeter et al. 2007; Maia et al. 2018). Locations with low turbidity have a high abundance of planktivores whereas locations with high topography complexity favor a higher richness of mobile invertebrate feeders (Morais et al. 2017). Hence, to gain a complete understanding of the emergent community patterns is essential to combine different metrics which offer a more complete perspective of communities.

Transition zones offer unique opportunities to investigate and analyze community structure patterns using different metrics (Williams 1996; Horta E Costa et al. 2014). In particular, these zones are intriguing due to their distinctive combination of characteristics resulting from the merging of two areas with different environmental conditions (Ferro and Morrone 2014). In marine ecosystems, temperature transition zones support communities that consist of species overlapping distribution ranges between the northern and southern regions (Horta E Costa et al. 2014). This overlap can largely be attributed to the species' niche and ability to tolerate a wider range of temperatures, making them well-suited for the cyclic oscillations of oceanographic conditions found in these zones (Bernhardt and Leslie 2013). Studying these zones presents an excellent opportunity to understand the spatial patterns of community structure since species distribution are linked to the individual ecological niche and are projected to shift in response to environmental change (Sexton et al. 2009).

Here, we compile 1,837 underwater visual censuses of reef fish communities to investigate the community structure of reef fishes in the (sub)tropical-warm temperate transition zone of the southwestern Atlantic. Specifically, we aim to address the following research questions: (i) Is there a gradient of thermal tolerance among fish communities across the islands? (ii) Do fish communities exhibit differences in assemblage metrics (richness, density, and biomass) based on island and depth? (iii) Are there variations in the occurrence frequency, abundance, and biomass of reef fish species among the different islands? (iv) Do the islands show variations in the distribution of trophic groups within their communities? Considering that global warming is promoting the expansion of species with tropical affinity within subtropical areas (Pinsky et al. 2020, Vergés et al. 2017), we expected differences in reef fish communities from the north and south islands due to the distinct species thermal tolerance. The Southwestern Atlantic represents the limit of distribution for reef fish species (Anderson et al. 2015, 2020), resulting in lower species richness at higher latitudes due to a cold climatic barrier that prevents the entry of species. This leads to an uneven distribution of species ranges. Furthermore, we anticipate that this uneven distribution will result in distinct variations in the abundance, biomass, and trophic group distribution among the islands. Warm-affinity species are likely to be more abundant and contribute to higher biomass estimates at lower latitudes, influenced by the warmer temperatures that affect their physiology and growth rates. Consequently, we can expect a higher frequency of warm-affinity species in lower latitudes (warmer waters), as well as increased density and biomass, particularly within specific trophic groups. For instance, a greater presence of herbivores in the low latitude islands due to the influence of temperature on feeding rates (Longo et al. 2014; Vergés et al. 2018; Bosch et al. 2022). The opposite is hypothesized for the cold-affinity species, which tend to be less abundant and have lower biomass in lower latitudes within the study region.

Material and methods

Study area

We sampled reef fish assemblages in seven coastal islands located in the subtropical-warm temperate transition zone of the Southwestern Atlantic. These islands were Galé, Arvoredo, Deserta, Aranhas, Xavier, Campeche and Moleques do Sul (Fig. 1). The northernmost islands experience generally higher mean temperatures, whereas the southernmost experience cooler conditions (Silva et al. 2023). On the other hand, Galé, Arvoredo, Deserta are located inside the Arvoredo Marine Protected Area (MPA), while Aranhas, Xavier, Campeche and Moleques do Sul are located outside the MPA and are therefore exposed to higher human pressures, including both artisanal and recreational fishing. The rocky reefs in all islands are characterized by steep granitic formations, covered mainly by algal turfs, erect macroalgae, and zoanthids (Aued et al. 2018).

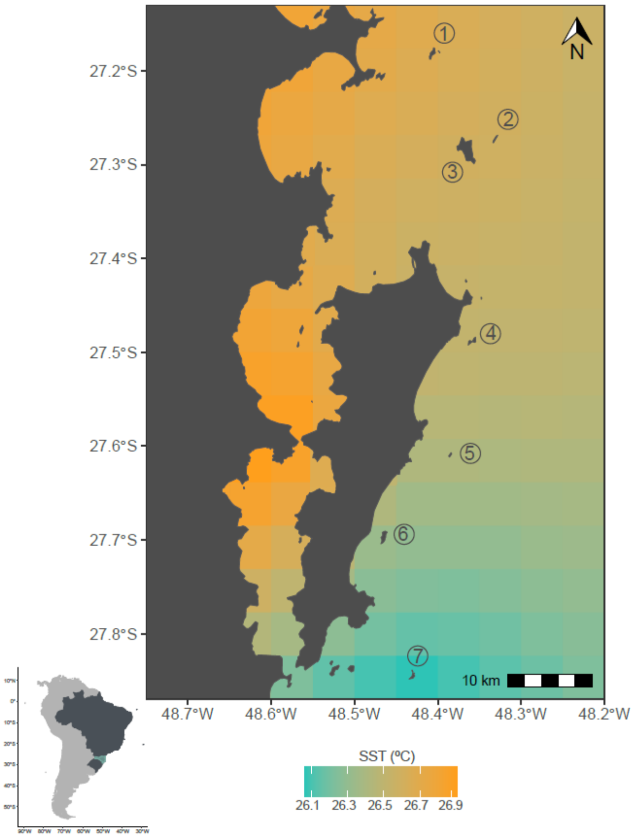

Figure 1. Map of the study area, including the seven sampled islands across the transition zone. The color range represents the Sea Surface Temperature (SST°C) gradient during one day of the austral summer, serving as an example of differential thermal conditions across the study area. Galé (1), Arvoredo (2), Deserta (3), Aranhas (4), Xavier (5), Campeche (6), and Moleques do Sul (7).

Underwater visual censuses survey data

Reef fish species occurrences and abundance were obtained from 1,837 Underwater Visual Censuses (UVCs) carried out during the austral summers between 2008-2022 time period (Fig. S1). The data is freely available in Quimbayo et al. (2023), and the number of UVCs per island during the time period sampled varied from 40 to 683. The UVC method involves the identification and counting of all ray-finned fish species found within a transect of 40 m2 (20 x 2 m). During each survey, the diver visually identifies, counts, and estimates the total length (rounded to the nearest centimeter) of all species present in the water column while unwinding a measuring tape. On the return, the diver applies the same procedure to smaller and concealed species, typically found near the bottom (Morais et al. 2017). The UVC surveys were conducted at shallow depths ranging from 3 to 15 meters below the surface.

Calculation of diversity metrics

To evaluate changes in community structure, we estimated thermal tolerance, species richness, density, biomass, and trophic group for each island. Due to the heterogeneity in sampling effort, Species Accumulation Curves (SACs) were used to standardize the number of surveys across locations ensuring comparable representations of the underlying communities. Using the "vegan" package in R (Oksanen et al. 2016), seven SAC were estimated (one per island, Fig. S2) and fitted by Michaelis-Menten functions (Maureaud et al. 2020). Then we estimated the asymptotic species richness based on all available samples for each island (Table S1). We randomly re-sampled 99 times (with replacement) the number of UVCs needed to reach 75% of the asymptotic species richness for each island (94 for Galé, 83 for Deserta, 150 for Arvoredo, 40 for Aranhas, 106 for Xavier, 34 for Campeche, and 18 for Moleques do Sul). In each permutation, we calculated the diversity metrics per island using the respective number of UVCs needed to achieve 75% of biodiversity, as well as the linear models and other statistical analysis to account for differences among diversity metrics. Mean values of all permutations were used as input for the graphs and tables.

Thermal tolerance of communities was evaluated through thermal breadth, a metric representing how many degrees of temperature the species can support and therefore providing a measure of response to temperature variations (Schuster et al. 2022). First, we compiled the realized thermal range of all species recorded in the seven islands of our case study based on global occurrence data available in the Global Biodiversity Information Facility (GBIF: http://www.gbif.org). We collected data on the full geographic range coverage of each species and matched the geographical coordinate of species presence with the respective monthly sea surface temperature in the occurrence location from Global Ocean Data Assimilation System (GODAS) - NOAA (1980 – 2020, 0.33 x 1 degree grid resolution). Species thermal breadth was then calculated as the subtraction of the lower and upper percentile (5th and 95th percentile) of the temperature distribution experienced across a species geographic range to avoid extremes and rare values.

Fish biomass was calculated using the following equation: $W = a * TL^b$, where W is the weight in grams, a and b represent species-specific constants for length-weight relationships, and TL represents the total length estimated in the UVCs. Length–weight constants were obtained for each species from Quimbayo et al. (2021; 2023). When coefficients were unavailable, we used the values of congeneric species that are phylogenetically close and morphologically similar. Density and biomass values were transformed by Log_e (x + 1) to improve the assumptions of linear models.

Community structure was evaluated in terms of linear relationships between occurrence frequency and density/biomass, and by trophic groups. All observed fishes were classified following the trophic groups described in Quimbayo et al. (2021; 2023): herbivore−detritivore (feed on epilithic algal matrix), macroalgivore (feed on macroalgae >1 cm high or seagrass), macrocarnivore (feed on fishes and cephalopods), mobile invertebrates (feed on crustaceans, annelids, echinoderms, mollusks), omnivore (feed on animal and plant and/or detrital material), planktivore (feed on zooplankton, coelenterates, detrital aggregates on the water column, etc.), and sessile invertebrate feeder (feed corals, sponges, ascidians). Density and biomass were calculated for each trophic group per island.

Data analysis

To test whether thermal breadth differed between islands, we performed a cluster analysis using a continuous distance similarity matrix based in the Bray-Curtis index. Specifically, we used Ward linkage method to build the cluster. P-values for cluster nodes were calculated using bootstrap resampling with 999 replicates using the “Pvclust” package (Suzuki and Shimodaira, 2006) to assess their reliability. Linear Mixed Models (LMMs) were used to test differences among islands and the effect of depth in the thermal community structure since UVCs were conducted in different depths. Year was considered as a random factor in the models to account for a possible temporal effect on the community structure. To compare reef fish communities in terms of the other metrics (response variables: species richness, density, and biomass) among islands, we also used LMMs. We examined the effect the depth on these metrics, considering location and depth as fixed factors and year as a random factor in the models. The models were constructed using function lmer within the “lme4” package (Bates et al. 2015). At each simulation step, we used the number of UVCs needed to reach 75% of the biodiversity for each island, built the model, retained the parameter estimates (e.g., p and t coefficients from LMM), and then used their mean overall 99 steps as a measure of their effect on each response variable. The simulation process utilizing UVCs is similar to sample-based rarefaction curves, as it permits the assessment of the effect of each variable on reef fish community metrics while accounting for variations in sample size (Gotelli and Colwell 2001).

To examine the community, specifically the dominance and rarity of species on each island, we used linear regressions to assess the correlation between occurrence frequency and the variables of density and biomass. By obtaining a separate slope for each island, we were able to compare the observed trends. Regarding trophic groups, we evaluated the differences among islands through two approaches: i) Permutational Multivariate Analyses of Variance (PERMANOVAS) using islands (factor) and depth (numeric) as explanatory variables. The PERMANOVAS were performed using the function adonis within the “vegan” package (Oksanen et al. 2016) with a Bray-Curtis dissimilarity distance matrix and were conducted using the number of UVCs needed to reach 75% of the biodiversity for each island in each permutation as in LMMs. The statistical significance was tested with 999 permutations; and ii) Non-Metric Multidimensional Scaling (NMDS) analysis to graphically explore the patterns emerged from the above analysis. We did not consider depth in NMDS since the variation of this metric is missed during resampling method. All analysis were conducted in the R environment (R Core Team 2020).

Results

Thermal tolerance

Our study revealed differences in fish composition since species from the northern islands (Galé, Deserta, and Arvoredo) presented 3.5 ºC of thermal breadth and varied from 2.1 to 5.2 ºC. These values were lower if compared to the average of species from the southern islands (Aranhas, Xavier, Campeche, and Moleques), which was 4.3 ºC and varied from 2.3 ºC to 6.2 ºC. Specifically, the north islands, exhibited narrower temperature ranges, indicating lower tolerance for temperature fluctuations (i.e., more tropical species). On the other hand, the southern islands demonstrated a higher capacity to withstand temperature oscillations, as indicated by their broader temperature ranges (Fig. 2). These findings were further supported by both the cluster analysis and the models employed which clearly showed a distinct separation between the islands situated at different latitudes (Table 1). This separation was evident in the form of two distinct branches in the analysis, highlighting the contrasting thermal characteristics of these island groups. The depth variable did not have a significant influence on thermal breadth, as indicated by the model results.

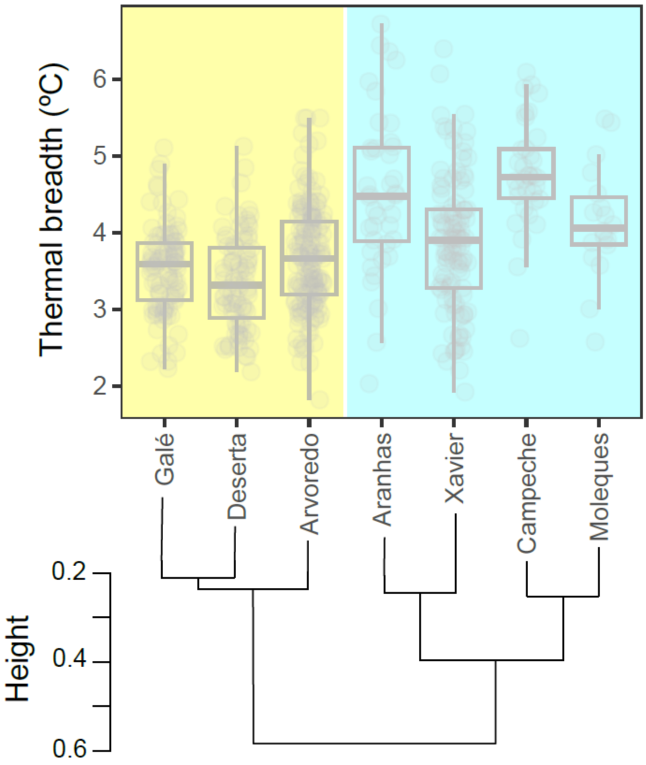

Figure 2. Variation in thermal breadth of fish communities per island. The boxplots are based on values obtained from each of the 99 permutations. The cluster analysis on the bottom reveal a separation of the islands in two main branches, also indiceted by the yellow and blue color panels.

Diversity metrics

A total of 142 species belonging to 47 families were observed in the seven islands of the studied transition zone. On average, ten species were observed per transect in all islands and varied from 2 to17 species (Fig. 3). Deserta Island exhibited a notably higher richness (mean 11 ± 2 species) compared to Aranhas Island (mean 7 ± 3 species), which displayed the lowest value. In terms of density and biomass, the island showing higher values was also Deserta (mean 2.9 ± 1 individuals per m^2; 241 ± 86 grams per m^2). In contrast, Aranhas had the lowest number of individuals and biomass (mean 0.7 ± 0.7 individuals per m^2; 66.9 ± 147 grams per m^2); revealing a predominance of smaller individuals. Our findings showed notable variations in the southwestern Atlantic transition zone, indicating that the islands located in lower latitudes (Galé, Deserta and Arvoredo) differ in terms of richness and other metrics when compared to the remaining islands (Figure 1; Table 1). Differences in density were found for all islands except Aranhas and Moleques, while biomass found in Moleques were distinct to the others. Our results also showed that depth negatively influence species richness, density, and biomass (Table 1).

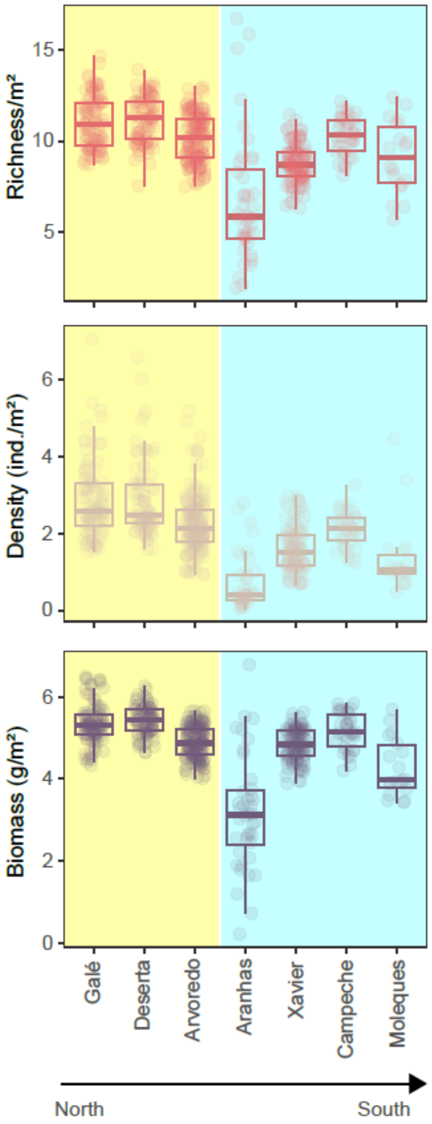

Figure 3. Comparative variation in species richness (a), density (b) and biomass (c) of fish communities per island. The boxplots are based on values obtained from each of the 99 permutations. Biomass was Log_e (x + 1) transformed to improve visualization of the values. Yellow and blue backgrounds were included to promote better visualization of the islands located at different latitudes (north and south of the study region).

Table 1. Mean effects of islands as factors and depth on the fish assemblage metrics (species richness, density, biomass and thermal breadth) of southwestern Atlantic transition zone. The values derived from 99 permutations and significant values ($p < 0.05$) are highlighted in bold.

Island	Parameter	Richness	Density	Biomass	Thermal breadth
Aranhas	Estimate	9.53	0.16	4.17	0.97
	t	13.03	2.88	83.41	6.18
	p	**<0.01**	0.41	**<0.01**	**<0.01**
Arvoredo	Estimate	3.28	1.12	1.13	0.20
	t	5.14	18.54	22.48	2.02
	p	**<0.01**	**<0.01**	**<0.01**	**0.04**
Campeche	Estimate	2.44	1.23	1.58	1.07
	t	2.75	18.15	27.64	7.35
	p	**0.03**	**<0.01**	**<0.01**	**<0.01**
Deserta	Estimate	5.06	1.56	1.70	-0.15
	t	7.14	26.01	33.53	-1.26
	p	**<0.01**	**<0.01**	**<0.01**	0.21
Galé	Estimate	4.26	1.44	1.58	3.35
	t	6.32	23.91	31.91	25.00
	p	**<0.01**	**<0.01**	**<0.01**	**<0.01**
Moleques	Estimate	1.30	0.67	0.83	0.26
	t	1.19	3.86	12.27	1.26
	p	0.31	0.06	0.09	0.21
Xavier	Estimate	2.10	0.76	1.09	0.58
	t	3.05	13.23	21.62	5.18
	p	**0.01**	**<0.01**	**<0.01**	**<0.01**
Depth	Estimate	-0.40	-0.08	-0.06	0.01
	t	-8.04	-7.45	-4.51	1.18
	p	**<0.01**	**<0.01**	**0.01**	0.24
Year (Random effect SD)	Estimate	1.09	0.38	0.52	0.71

Community structure

We observed flat trends for Galé, Deserta and Arvoredo islands (north region, lower latitudes) between the density and biomass with the frequency of occurrence, while for higher latitudes (south region), either positive or flat trends emerged. This indicates that, in south, some species increase in density and biomass while simultaneously increasing in frequency of occurrence. The most frequent species were *Haemulon aurolineatum*, *Orthopristis ruber*, *Diplodus argenteus, Abudefduf saxatilis*, and *Kyphosus* spp., which also exhibited high or moderate density and biomass (Fig. 3). However, despite their common occurrence, certain species, such as *Stegastes fuscus, Coryphopterus glaucofraenum, Parablennius marmoreus*, *P. pilicornis*, and *Epinephelus marginatus*, did not demonstrate high density or biomass. Some species with higher density or biomass values were found to be rare in most reefs of the islands, including *Pempheris schomburgkii, Mugil curema*, and *Calamus pena*.

Examples of rare species both in terms of occurrence frequency and density/biomass include *Acanthurus bahianus* in Campeche Island and *Sparisoma radians* in Deserta. The individual regressions and their respective parameters are in supplementary material (Fig. S3 and S4).

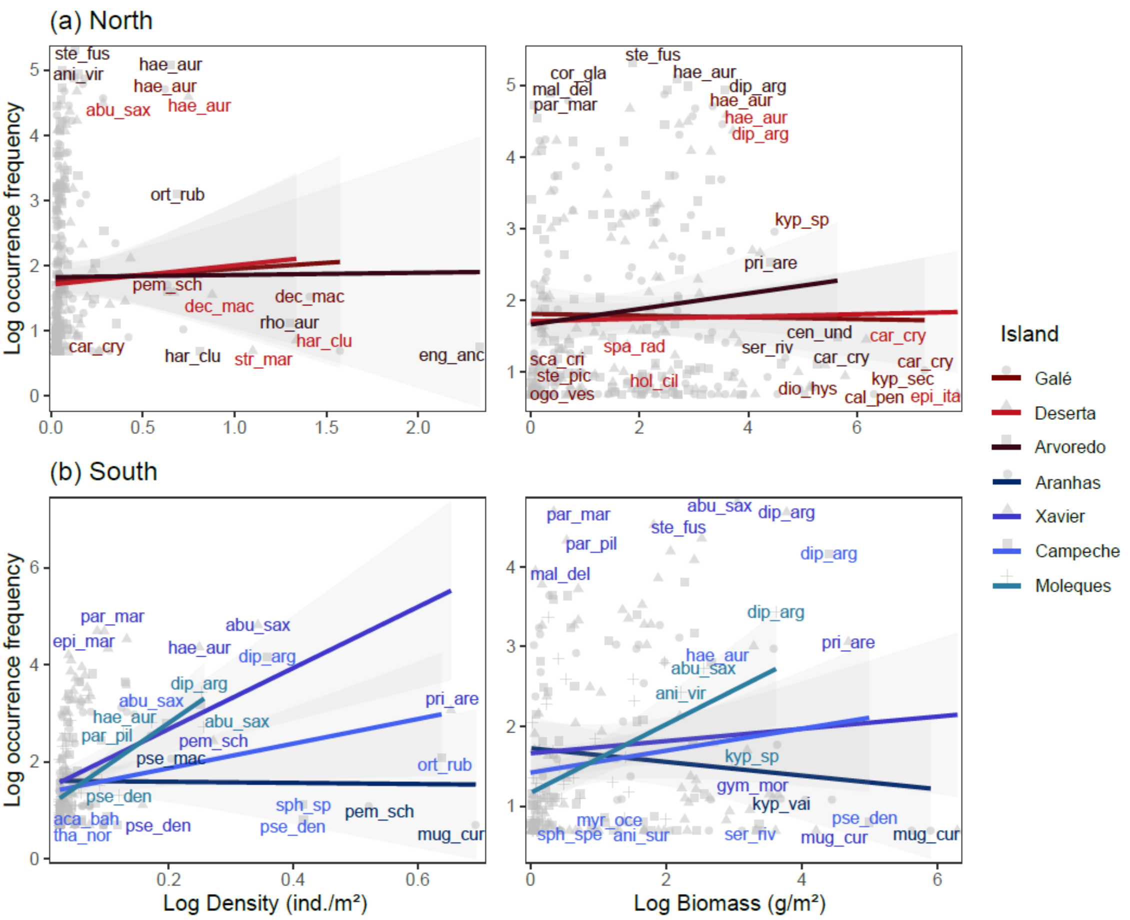

Figure 4. Relationship between occurrence frequency and density/biomass of reef fish in the seven islands sampled. For convenience, separate plots were created for islands in lower latitudes, north region (a) and in higher latitudes, south region (b), which are represented by red and blue color gradients and icons. The solid lines show the trends derived from linear regressions.

Trophic groups

We observed primarily mobile invertebrate feeders in terms of their richness, density, and biomass (Fig. 5), which were represented by species of genus *Haemulon*. Additionally, omnivores and planktivores were also trophic groups with high density and biomass. *Abudefduf saxatilis* and *Diplodus argenteus* are the most representative omnivores species in the communities, while *Azurina multilineata* and juveniles of *Haemulon aurolineatum* enhanced the values of planktivores. Omnivores were most abundant on the south islands (Campeche and Moleques), while planktivores were more prevalent on the north islands (Galé, Deserta, Arvoredo). Some trophic groups including herbivore/detritivore, macroalgivore, macrocarnivore and sessile invertivore did not show high values for richness. The most representative species of these groups are likely rare or less abundant in the reefs, corresponding to genus *Stegastes, Sparisoma, Kyphosus, Epinephelus, Caranx, Sphoeroides* and *Chaetodon*, respectively. The rarity and representativeness in terms of abundance reflects the patterns found for density and biomass observed in the regression analysis (Fig. 4), for example, macroalgivores and macrocarnivores showing high biomass despite low density.

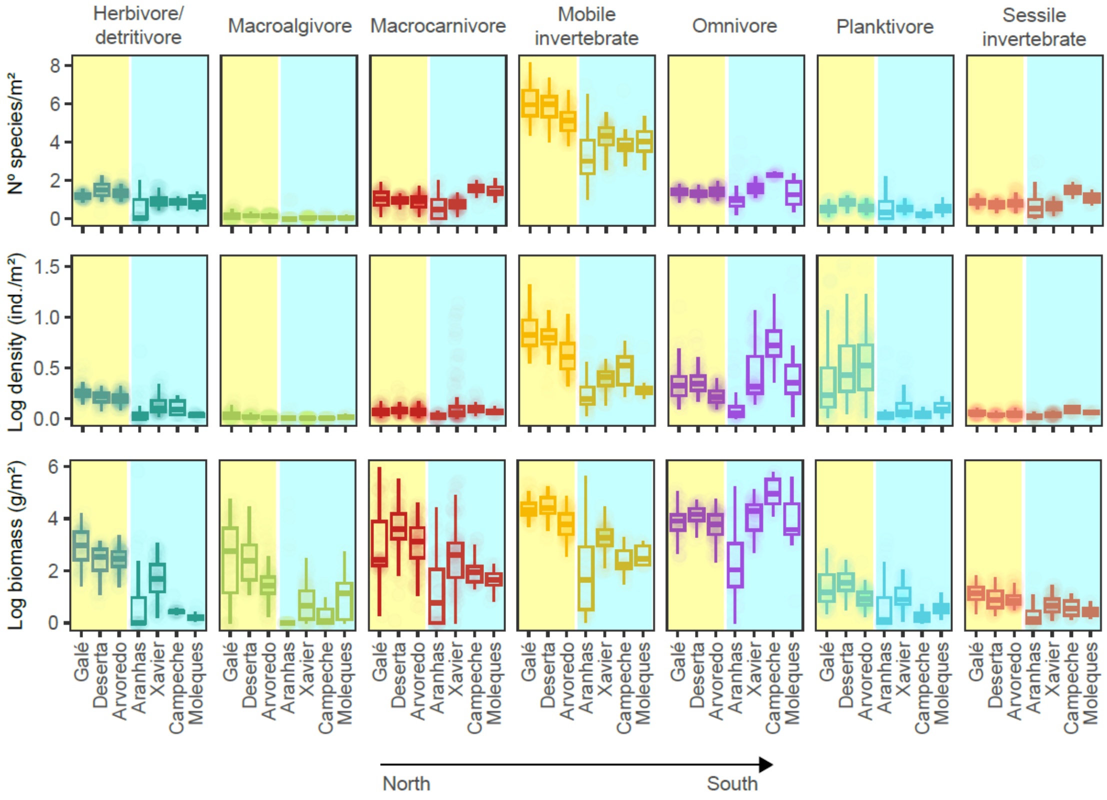

Figure 5. Variation of number of species, density and biomass of trophic groups (columns) in the sampled islands. Each dot represent one value per transect from each of the 99 permutations. Yellow and blue backgrounds were included to promote better visualization of the islands located at different latitudes (north and south of the study region).

Our findings demonstrate that the number of species, density, and biomass varied across trophic groups, islands, and depths (Table 2). However, the specific effects and their direction differ among the islands. For instance, the number of species of planktivores and mobile invertebrate feeders is higher in Deserta and Galés islands (NMDS stress = 0.11, Fig. 6a). The density of omnivores on Xavier, Campeche and Moleques was higher to that of other trophic groups, while macrocarnivores and macroalgivores were more abundant on Arvoredo, Galé and Deserta (NMDS stress = 0.13, Fig. 6b). Furthermore, the biomass of macroalgivore was notable in Arvoredo and Galé, while omnivores dominated in Xavier and Moleques (NMDS stress = 0.17).

Table 2. Outputs of PERMANOVAS evaluating differences in species richness, density, and biomass of the trophic groups across islands and according to their depth. Significant values ($p < 0.05$) in bold.

	Richness				Density (ind./m^2)				Biomass (g/m^2)			
	df	SS	F	*p*	*df*	SS	F	*p*	*df*	SS	F	*p*
Island	6	1.30	6.05	**0.01**	6	6.26	7.13	**0.01**	6	14.62	10.58	**0.01**
Troph. group	6	96.17	446.58	**0.01**	6	106.59	121.33	**0.01**	6	89.89	65.04	**0.01**
Depth	1	0.89	24.79	**0.01**	1	9.42	64.33	**0.01**	1	3.30	14.30	**0.01**

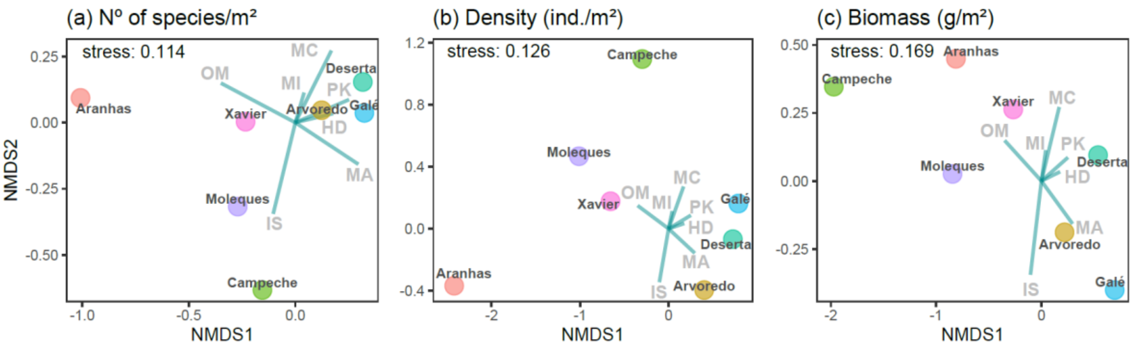

Figure 6. Non-metric multidimensional scaling (NMDS) showing the influence of richness (a), density (b) and biomass (c) of each trophic group and depth in the different islands sampled. Trophic groups: herbivores-detritivores (HD), macroalgae-feeder (MA), sessile invertebrate feeders (IS), mobile invertebrate feeders (IM), planktivores (PK), macrocarnivores (MC) and omnivores (OM).

Discussion

Our study showed that reef fish communities in the southwestern Atlantic transition zone exhibited a distinct division between north and south islands. This division was found based on thermal breadth, providing support for our hypothesis that the temperature gradient influences the species distribution. Our findings also suggest that the warmer conditions in the north regions and cooler conditions in the south have a significant influence on the thermal tolerance of species in this area. These effects extend to various fish assemblage metrics, including species richness density and biomass. In general, these metrics exhibit higher values in the northern islands, indicating that temperature plays a pivotal role in shaping species physiology. This leads to increased richness, abundance, and consequently, biomass of warm-affinity species in islands with warmer conditions, specifically in lower latitudes – the northern region. Furthermore, the density and biomass patterns of trophic groups align with species dominance/rarity patterns and are potentially influenced by local environmental conditions. As hypothesized, we observed a higher occurrence frequency of warm-affinity species in north islands, while cold-affinity in south. In this context, temperature appears to be a key factor shaping the observed patterns reflected in specific trophic groups, such as high biomass of herbivores in northern islands and omnivores in the south.

A clear distinction was found between the northern and southern communities regarding thermal affinity. Even on a local scale, we were able to identify islands with species exhibiting higher thermal tolerance (indicated by a broader thermal breadth) located at higher latitudes and experiencing colder waters. In contrast, the other islands comprised species with lower thermal tolerance, inhabiting warmer conditions. It is well known that temperature act as a driver of biodiversity patterns, as it influences the physiology, growth, reproduction rate, and range distribution of species (Munday et al. 2008; Pinsky et al. 2013). Thus, the observed patterns likely result from species actively tracking suitable thermal conditions in space to ensure their survival (Burrows et al. 2019). The region's seasonality potentially plays a crucial role in shaping communities because the species must have traits adapted to cyclic environmental conditions to endure the challenges of overwintering (Beukhof et al. 2019). It’s well described that thermal ranges of species can predict changes in the structure of communities during disturbances (Stuart-Smith et al. 2015; Day et al. 2018). Thus, our results suggest that communities in the south islands would exhibit higher resilience in the face of warming events due to their high tolerance to temperature fluctuations.

The total fish richness observed in the study area (n = 142) is relatively lower when compared to the Southeastern and Northeastern Brazilian coast, as well as the Caribbean (Floeter et al. 2004, 2008). This difference can be attributed to the geographic position of the islands, in the very limit of the distribution of tropical reef-associated species (Floeter et al. 2004; Anderson et al. 2015). Besides, this low species richness can also be associated with temperature oscillations in this area (Piola et al. 2008; Matano et al. 2010). The sea surface temperature in this transition zone varies from 18 to 26ºC due to the meeting of warmer tropical waters from the Brazil current and colder waters from the Prata River, as well as the wind interchange from the northeast and south (Segal et al. 2017). Consequently, the seasonality typical of subtropical systems acts as a limiting factor for the geographical distribution of species, which explains the overall patterns of richness in the area. This also elucidates why the north islands (Galé, Deserta, and Arvoredo) exhibit higher species richness compared to the other islands.

Based in our initial hypothesis, we observed discernible patterns between the north and south islands in terms of density and biomass. Species living at their optimal temperature achieve maximal abundance (Wladock et al. 2019). Consequently, on the northernmost islands, the increased diversity of species, coupled with their physiological preference for warmer temperatures, results in a greater population density. This, in turn, may trigger a cascading effect, potentially leading to elevated biomass levels in the north, while the southernmost islands may exhibit lower species richness and abundance. Additional variables than temperature (e.g., fishing, benthic composition, wave exposure) specific to each site may interact synergistically with mechanisms of coexistence, influencing resource and niche suitability for species to inhabit (Hutchinson 1957; Ricklefs 1987; Hubert et al. 2011). Therefore, it is plausible that other factors contribute to the distinct patterns observed, as different species may exhibit diverse responses to the surrounding abiotic and biotic conditions and presenting different values of density and biomass. Level of protection could also play a role in the patterns of density and biomass, since we observed higher values of these metrics in Deserta, an island inside Marine Protected area. It's been recognized the positive effects of protection in reef fish communities promoting higher rates of growth and survival (Turnbull et al. 2018; Karlovic et al. 2021) and we acknowledge that the MPA are contributing for the maintenance of populations in this area. The depth variable displayed statistical significance in models assessing richness, density, and biomass, as well as in PERMANOVAs. However, it's important to note that it didn't reveal substantial variations in species presence or absence across different depths. Instead, it highlighted differences in the frequencies of occurrence, with all species being present across all depths. This outcome aligns with expectations, given that benthic composition (and fish community associated) tends to remain relatively constant across the depths studied (Aued et al. 2018).

Our study uncovered significant heterogeneity in terms of frequency of occurrence and density/biomass across of the seven islands. While there was a certain degree of similarity in terms of species richness among all the islands, we observed a distinct pattern in terms of dominance when analyzing islands separately. A few species were found to be highly abundant, while many species were rarely present. For instance, in the north region, *H. aurolineatum* emerged as the dominant species, whereas in the southern region, *D. argenteus* and *A. saxatilis* were the most representative species. These findings align with the commonly investigated assemblage-level properties, specifically the species abundance distribution that predicts a prevalence of low commonness and high rarity among species (Connolly et al. 2005, 2014; McGill et al. 2007). We emphasize that the dominant species observed in the south are likely better adapted to cold conditions, confirming our earlier hypothesis of an environmental response. Additionally, we observed the presence of schooling and shoaling behaviors among oceanic and rare species, particularly *M. curema* and *D. macarellus*. Even rare, these species have the potential to emerge within reef ecosystems, leading to notable increases in both density and biomass and influencing the dynamic of communities. Furthermore, our results indicate that the community structure exhibits variations when comparing islands separately, highlighting the importance of considering local scales in understanding the dynamics of ecosystems (Garcia et al. 2018).

Despite variations among islands, our study indicates that mobile invertebrate feeders exhibit higher richness, density, and biomass values overall. In the north islands, planktivores dominate, while omnivores prevail in the south islands. This distribution pattern aligns with the oceanographic conditions of the region, characterized by clearer waters in the north that facilitate the development of plankton (Lopes et al. 2006) and consequently, populations of *A. multilineata* and juvenile of haemulids (abundant and common species). Therefore, we highlight the crucial role of planktivores in reef food webs, which is consistent with similar findings in other temperate rocky reefs (Truong et al., 2017; Maia et al., 2018). The observed density and biomass patterns of omnivores could likely be influenced by the benthic composition of Campeche and Moleques do Sul islands, characterized by a substantial presence of turf algae, macroalgae, and sponges (Bouzon et al. 2012; Aued et al. 2018), as well as oceanographic conditions, such as the input of cold and freshwater from Prata River (de Mahiques et al. 2021). The lower values of richness and density and comparatively higher biomass of herbivores/detritivores, macroalgivores, macrocarnivores and sessile invertebrate feeders reflect the rarity of species present in these groups (*M. curema*, *Kyphosus* sp., *E. marginatus* and *C. striatus*). These findings are aligned with other research, showing that these trophic groups are less representative in coral reef assemblages when compared to planktivores and omnivores (Stergiou and Karpouzi 2002; Siqueira et al. 2021). As expected, a higher biomass of herbivores was found in north islands, corroborating with previous studies showing that the presence and feeding behavior of herbivores is enhanced by higher temperatures (Longo et al. 2014; Vergés et al. 2018; Bosch et al. 2022). When examining trophic groups, it is important to consider the ontogenetic diet variation observed for certain species. One example is *H. aurolineatum*, which feeds on plankton during its juvenile stage but transitions into a mobile invertebrate feeder as an adult (Pereira et al. 2015). This species holds significant importance throughout the entirety of the Brazilian province's reefs (Ferreira et al. 2004) thereby contributing to the patterns of two distinct trophic groups. Consequently, understanding the dietary preferences across different life stages of species becomes a valuable tool for characterizing community structure in terms of trophic groups.

Finally, our study contributes to the understanding of community structure metrics in the seven islands of the southwestern Atlantic. Because the prevalence of dominant and rare species differs between islands, understanding whether and how communities differ or shift in space is critically important for predicting consequences of environmental changes for biodiversity and ecosystem functioning (Connolly et al. 2005). While acknowledging the limitations of our study, particularly the absence of data on habitat composition and oceanographic parameters to explore the underlying drivers of the observed patterns, we believe that our findings provide insights for future research. Integrating additional perspectives and scales, such as investigating temporal dynamics and incorporating the use of functional traits, will help unravel the general patterns and processes occurring in transition zones.

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Suplemmentary material

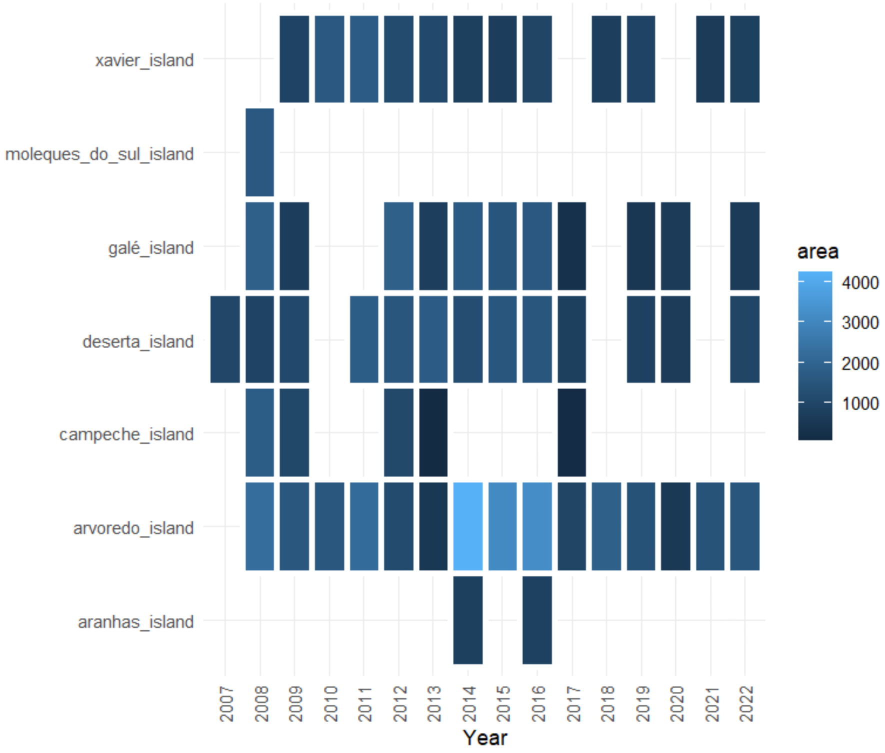

Figure S1. Community data available for each year and island sampled. The color gradient represents the sampling effort in square meters. The gaps in the figure represent the absence of sampling.

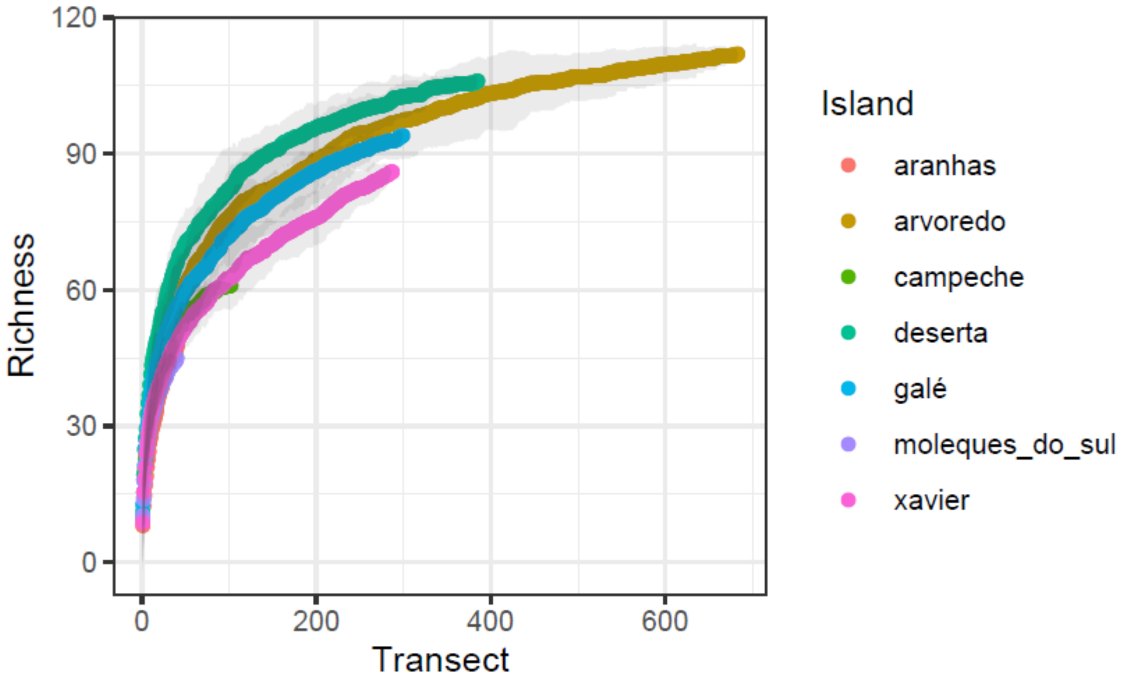

Figure S2. Sampling effort heterogeneity between islands (i.e., number of Underwater Visual Census – UVC in each sampling unit) as shown by species accumulation curves, where species richness is a function of the number of UVCs within sample units.

Table S1. Table derived from Species Accumulation Curves (SAC) showing: Island = islands where samples were made; n.census = number of Underwater Visual census (UVC) done per sample unit; n.census.min = minimal number of UVC done per sample unit; keep = if the sample unit should be kept in the analysis considering species richness sampled; sr = species richness; chao = extrapolated species richness using Chao equation; limit0.8/ limit0.75/ limit0.65 = percentage richness of 80%, 75%, and 65% respectively reached if using n.census.min in the analysis; aympt = mean value of the coefficients from the species accumulation model.

Island	n.census	n.census.min	keep	sr	chao	limit0.8	limit0.75	limit0.65	asympt
Aranhas	41	22	YES	48	71	NA	40	25	60.754
Arvoredo	683	45	YES	112	121	200	150	93	115.8027
Campeche	102	23	YES	61	63	46	34	21	66.60481
Deserta	385	41	YES	106	116	111	83	52	110.0603
Galé	299	38	YES	94	106	125	94	58	99.1492
Moleques	40	16	YES	45	51	24	18	12	50.19567
Xavier	287	35	YES	86	110	141	106	66	89.76145

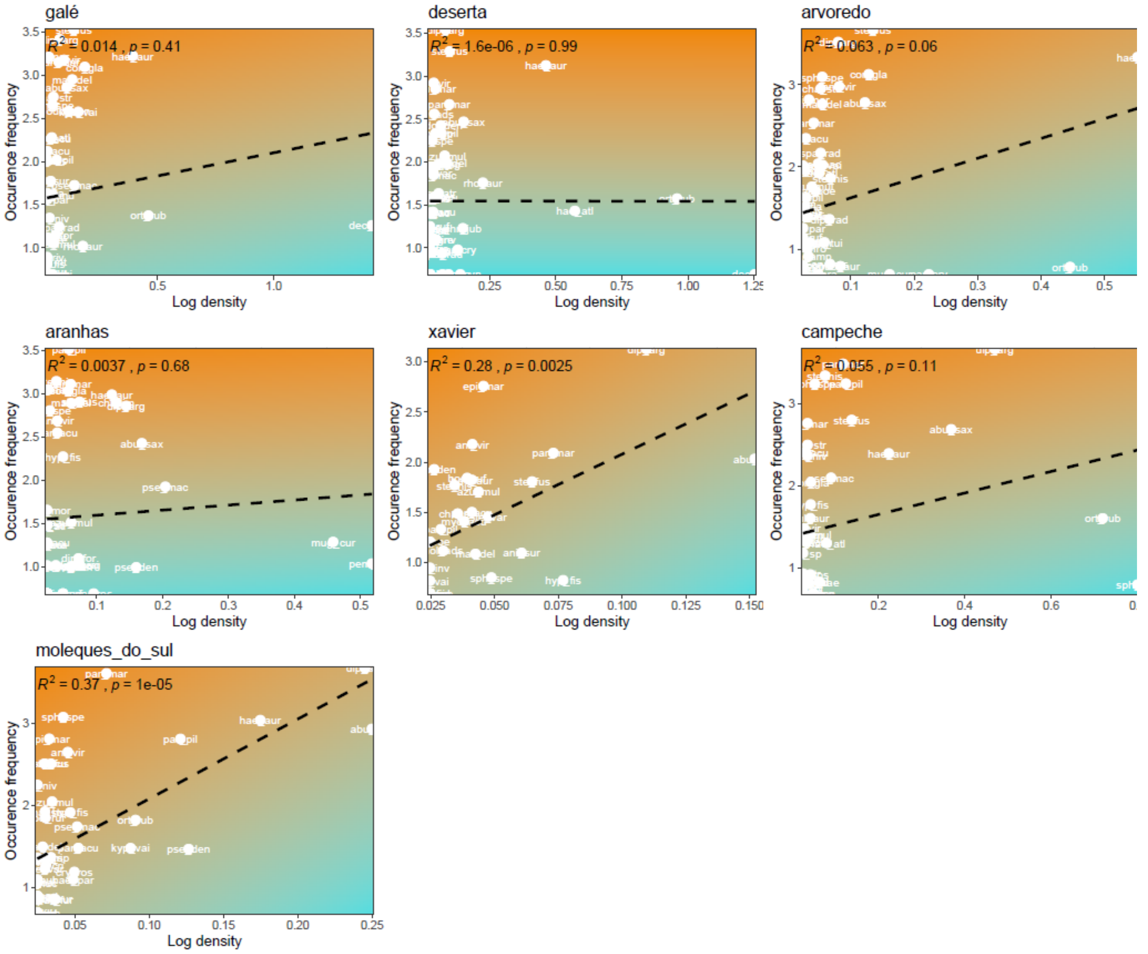

Figure S3. Relationship between occurrence frequency and density of reef fish in the seven islands sampled separately. The dashed lines show the trends derived from linear regressions.

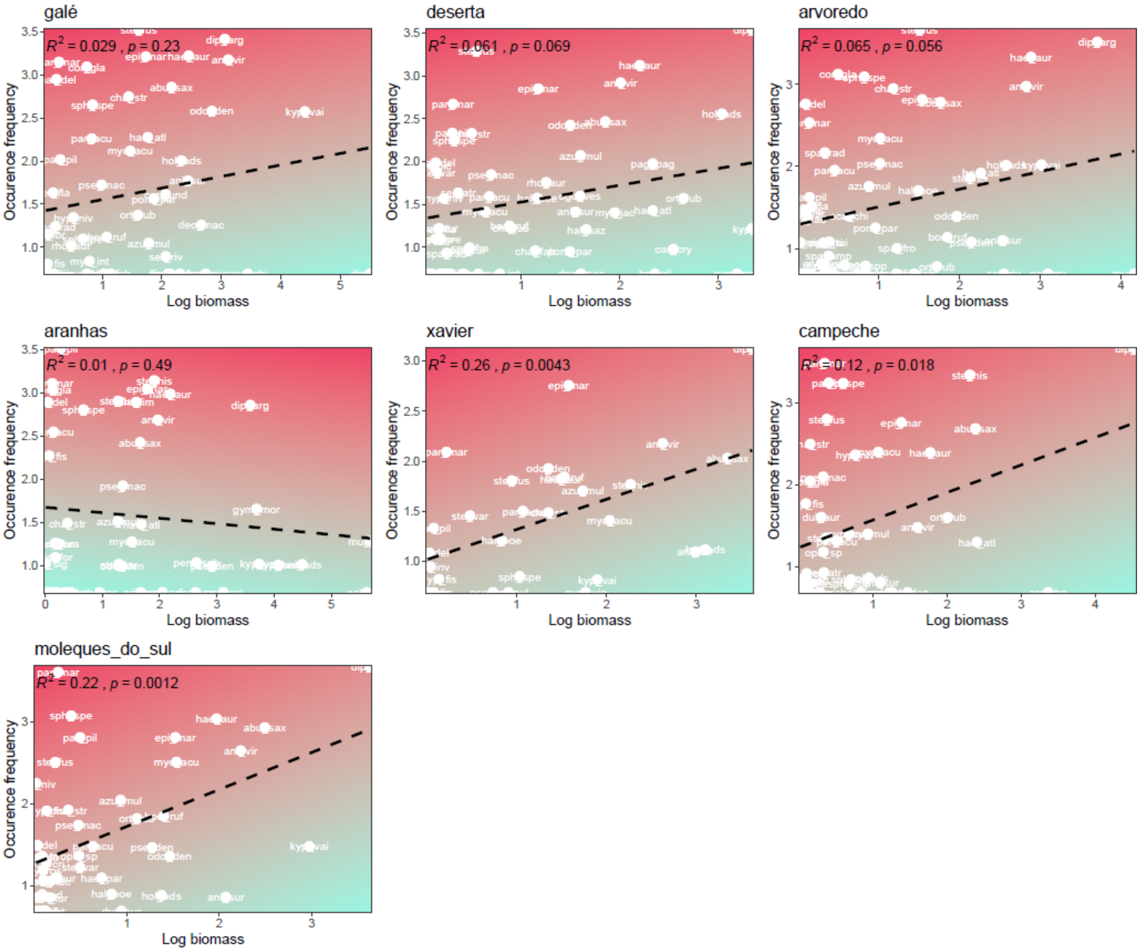

Figure S4. Relationship between occurrence frequency and biomass of reef fish in the seven islands sampled separately. The dashed lines show the trends derived from linear regressions.

CAPÍTULO II

Local turnover but no sign of homogenization in reef fish communities across an ecological transition zone exposed to warming

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Local turnover but no sign of homogenization in reef fish communities across an ecological transition zone exposed to warming

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Abstract

Marine organisms are responding to warming by altering their distribution ranges, causing biogeographic range-shifts and in some cases, favoring the community homogenization. Transition zones can be natural laboratories to explore the effects of homogenization, however these habitats are relatively poorly studied in coastal areas. In this study we aimed to investigate homogenization and changes in community composition from both a taxonomic and functional perspective. We used a long-term survey data set of reef fish species abundances and traits sampled across seven islands in the Southwestern Atlantic transition zone as an illustrative case study. Contrary to previous expectations, we found no sign of homogenization. The colder islands (southern) experienced a decrease in taxonomic and trait richness metrics, whereas for the warmer islands (northern), the taxonomic and trait richness fluctuated without any significant temporal trends. While taxonomic composition may change over time, the trait composition is generally more conserved, highlighting the trait redundancy in southwestern Atlantic communities and supporting the idea that these communities can maintain a range of ecological processes despite changes in taxonomic composition. Finally, the study revealed that despite non-homogenization, the species that contribute most to variation, especially in the south, have common trait combinations indicating an increase in the functional redundancy of fish communities over time. We underline that local-scale conservation efforts may be particularly effective in preserving and protecting species and ecological functions in areas experiencing unique and fast changes in biodiversity.

Introduction

Marine organisms worldwide have shown pronounced alterations in their distribution ranges in response to warming (Pinsky et al. 2020, Lenoir et al. 2020). Species may respond to warming by moving either poleward, deeper or decreasing in abundance (Perry 2005, McLean et al. 2021). One well-known consequence of such climate-driven range shifts includes tropicalization, caused by warm-affinity species expanding their distribution and increasing in proportion in more temperate locations (Vergés et al. 2016). In concert with tropicalization, climate-driven range shifts are expected to lead to an overall homogenization of communities (Pradervand et al. 2014, Stewart et al. 2018). The homogenization process is primarily a result of fast-growing, generalist species increasing both in terms of distribution and abundances, largely thanks to their broad thermal tolerance and ability to colonize new habitats (Clavel et al. 2011). In contrast, more specialized species, which typically have particular feeding and habitat affinities, slower growth and lower fecundity, may be less capable to adapt or shift their distribution and thus render them more susceptible to climate-induced variations (Graham et al. 2011). Taken together, the decrease and replacement of specialists by more abundant and widespread generalist species may contribute to greater similarity in species and trait composition, thus leading to homogenization and a resulting decline in diversity (Clavel et al. 2011, Pool & Olden 2012, Zwiener et al. 2018). Furthermore, the underlying processes contributing to species range shifts and homogenization can have important implications also in terms of the structure and functioning of ecosystems (Beger et al. 2014, Vergés et al. 2019, Maureaud et al. 2020). For instance, in Australian reefs, warming led to an increase in tropical herbivorous fish species and the decline of temperate planktivorous species, which in turn modified the community structure and energy flux (Smith et al. 2021). Therefore, the consideration of both species and traits in diversity studies is key to better understand the underlying processes contributing to community changes (including homogenization) and their variability in space and time (Bellwood et al. 2002, Swenson et al. 2011, Soininen et al. 2016, Richardson et al. 2018).

Empirical studies have shown that regional diversity may be partitioned into multiple components (Cavender-Bares et al. 2009). One of these components encompass beta diversity, which describe the turnover in species composition across space and time (Loreau 2000, Maxwell et al. 2022). Studies using beta-diversity have shown signs of homogenizations in both marine and terrestrial taxa, e.g., birds, fish, marine meiofauna, mammals, and plants (Pool & Olden 2012, Davey et al. 2012, Zwiener et al. 2018, Brustolin et al. 2019, Hidasi-Neto et al. 2019). However, the degree to which homogenization affects both the taxonomic and functional structure of communities is poorly known, especially when accounting for species abundances (Pool & Olden 2012).

Transition zones where environmental conditions change markedly, even over limited geographical distances may act as natural laboratories allowing us to explore the effects of homogenization. This because sharp environmental gradients favor communities characterized by species adapted to different conditions (Ferro & Morrone 2014). The study of transition zones may provide key test cases to study the effect of global warming on regional-scale responses of communities in general. This because species in these areas are close to their physiological tolerance limits (Sommer et al. 2017) and therefore changes in regional abiotic patterns may play an important role affecting species distributions and community composition.

Despite their potential to provide new insights regarding community changes and responses to warming, transition zones are relatively poorly studied, at least in marine ecosystems (Vergés et al. 2016, Iknayan & Beissinger 2020).

In this study, we investigate signs of homogenization and potential changes in community composition from both a taxonomic and functional perspective, using a unique, long-term survey data set of reef fish species abundances and traits sampled across the Southwestern Atlantic transition zone as an illustrative case study. More specifically, we aim to investigate and compare long-term changes in richness and turnover among reef fish communities in islands from two regions exposed to warming; but characterized by generally warmer or colder water masses, as well as differences in the level of exploitation. To achieve this overall aim, we pursued the following research questions: (i) How is the overall species- and trait richness changing over time in each region? (ii) To what extent have potential changes in richness been accompanied by underlying alterations in composition and abundances? (iii) Have changes in community composition and abundances led to increased taxonomic or functional homogenization between regions over time?

Material and methods

Study área

The study area encompasses reef fish assemblages sampled in seven continental islands located in the subtropical-warm temperate transition zone of the Southwestern Atlantic (Fig. 1). The islands can be divided into a Northern warm region (Galé, Arvoredo, and Deserta), and a Southern temperate region (Aranhas, Xavier, Campeche and Moleques do Sul islands). The northern islands show generally higher mean temperatures, whereas the southernmost islands experience cooler conditions. Both areas are exposed to similar regional variation in temperature dynamics, which plays an important role in shaping ecological communities due to fast temperature change (Beger et al. 2014). This warming trend is evident in terms of the mean observed sea surface temperatures (SST; North mean SST: $p = 0.01$, $r^2 = 0.41$; South mean SST: $p = 0.01$, $r^2 = 0.42$). Furthermore, the northern islands are located inside the Arvoredo Marine Protected Area (MPA), while the southern islands are located outside the MPA and are therefore exposed to higher human pressures, including both artisanal and recreational fishing. The rocky reefs in all localities are covered mainly by algal turfs, erect macroalgae, and zoanthids (Aued et al. 2018).

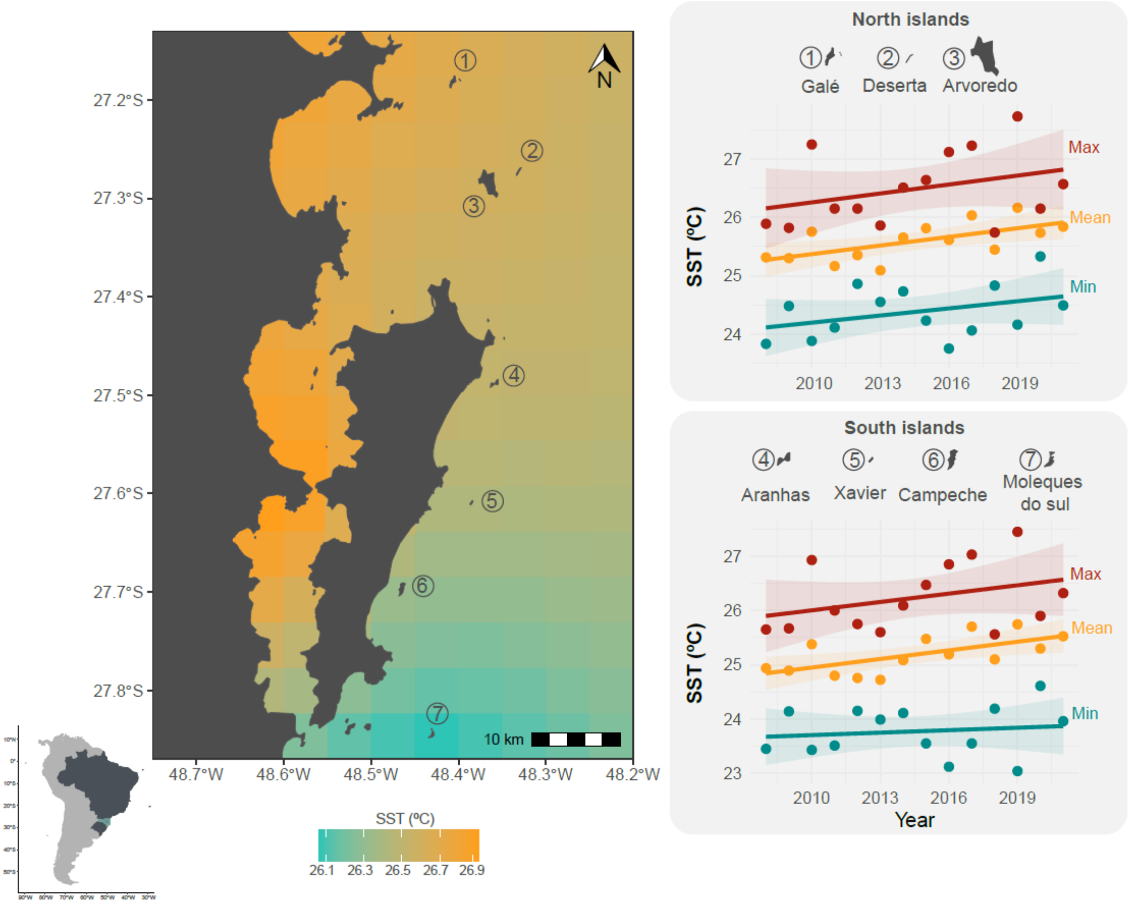

Figure 7. Map of the study area, including the northern (1-3) and southern (4-7) islands across the transition zone. The color range represent the mean Sea Surface Temperature (SST°C) gradient during the austral summer. The right panel shows time series and trends in the mean, minimum and maximum SST for both regions.

Underwater visual censuses survey data

Reef fish species occurrences and abundance were obtained from 1,306 Underwater Visual Censuses (UVCs) carried out during summers from 2008 to 2022 (Fig. S1). The sampling protocol consists of identifying and counting all actinopterygian (ray-finned) fish species observed within a belt transect of 40 m^2 (20 x 2 m). At each transect the diver visually identified, counted, and estimated the total length (to the nearest centimeter bin) of all species in the water column while unwinding a measuring tape. When retracting the tape on the way back, the diver follows the same protocol for smaller and cryptic species, usually associated with the bottom (Morais et al. 2017). The UVCs were carried out at shallow depths ranging between 1.5 – 16 m depth (95% CI, Fig. S2). All fish account data available in (Quimbayo et al. 2023).

Life history traits

In order to reflect the general ecology of all species recorded in the UVCs (N=142), a set of biological traits broadly characterizing their morphological, physiological, or behavioral adaptations related to feeding, growth, and survival were considered (Table 1). The classification and selection of traits builds on previous trait-based descriptions of marine organisms (Litchman & Klausmeier 2008, Litchman et al. 2013), adopted in recent studies on marine fish community structure and changes (e.g., Dencker et al. 2017, Pecuchet et al. 2017, Beukhof et al. 2019, Silva et al. 2023). All trait information was compiled through a review of published checklists, online repositories, local reports, books, and monographs compiled by Quimbayo et al. (2021).

Table 3. Life-history traits and their definitions, as provided by Quimbayo et al. (2021). Categorical and numerical traits characterizing the main ecological aspects of species were compiled to conduct the analysis.

Trait	**Definition and categories**	**Category**	**Levels**	**Class**	**Reference**
Activity	Period of the day that species feed and breed	Categoric	Day, night or both	Feeding/resource acquisition	(Robertson & Allen 2016, Robertson & Van-Tassell 2019, Froese & Pauly 2021)
Level water	Position in water column	Categoric	Bottom (staying at the bottom all the time, low (live slightly above the bottom, occasionally rest on the bottom) or high (several meters above the bottom)		(Robertson & Allen 2016, Robertson & Van-Tassell 2019, Froese & Pauly 2021)
Mouth position	Anatomic jaw position	Categoric	Superior (lower jaw protruding upwards), terminal (upper and lower jaws equal in length), subterminal (upper jaw protruding downwards), inferior (mouth in ventral position), tubular (enlargement of mouth cavity) or elongated (long snout due to the increase in the bones premaxillary, maxillary and dental)		(Froese & Pauly 2021)
PLD	Pelagic larval duration measured in days	Discrete	-	Growth/Reproduction	(Luiz et al. 2013)
Maximum body size	Length of the largest individual of the species observed in the census	Numeric	-		(Robertson & Allen 2016, Robertson & Van-Tassell

					2019, Froese & Pauly 2021)
Spawning	The way that species deposit eggs in water	Categoric	Attach to objects, demersal (deposit directly on the substrate), live (birth without external larval stage), oral (parental care when female or male keep the eggs in their mouth) or pelagic		(Froese & Pauly 2021)
Trophic level	Position in the food web based on diet composition and mean trophic level of food items	Numeric	-		(Froese & Pauly 2021)
Body shape	Morphological specialization for swimming	Categoric	Box shaped (globular as in Diodontidae), compressed (flattened laterally), depressed (flattened dorsoventrally), eel-like (elongated, snake-like shape and locomotion), elongated (long in relation to length) or fusiform (spindle shap, most hydrodynamic form)		(Froese & Pauly 2021)
Caudal fin aspect ratio	An indicative value of species activity calculated from the squared height of caudal fin (h) divided by its surface (s) area (h^2/s)	Numeric	-	Survival/ predator avoidance	(Froese & Pauly 2021)
Group size	Gregariousness behavior	Categoric	Solitary, pairing, small groups (3-20 individuals), medium groups (20-50 individuals) or large groups (>50 individuals)		(Froese & Pauly 2021)
Mobility	Area of activity	Categoric	Sedentary, territorial, mobile or very mobile		(Froese & Pauly 2021)

Standardization of sampling effort

Sampling effort was not uniform across years and islands (Fig. S1) and this heterogeneity can lead to biased estimates of diversity and composition (Chao & Jost 2012). To account for such differences in sampling effort we constructed species accumulation curves (SACs, Fig. S3) for each island and year to assess the level of taxonomic completeness of sampling using the "vegan" package in R (Oksanen et al. 2016). For each estimated SAC, we then fitted Michaelis-Menten functions (Maureaud et al. 2020) and estimated the asymptotic species richness based on all available samples for each year-island combination (Table S1). Subsequently, we estimated the number of samples needed to achieve 75% completeness of the estimated asymptotic species richness (i.e., here ranging from 9 to 67 samples). Only one island-year combination had insufficient sampling to reach the required number of samples for the desired level of completeness and was therefore removed from the analysis (Table S1).

Calculation of species and trait richness and turnover

To investigate changes in species richness and composition in the Northern and Southern region, we randomly re-sampled the number of UVCs needed to reach 75% of the asymptotic species richness for each year-island combination. For each of the 99 permutations (with replacement) we calculated taxonomic and trait diversity metrics, both weighted and non-weighted by species abundances. The α-diversity metrics included Species richness (SRic), trait-based richness (functional richness, FRic), as well as species and functional evenness estimated through the vegan and FD packages (Laliberté et al. 2015, Oksanen et al. 2016). To account for temporal shifts in the taxonomic composition within each region we calculated β-diversity using Jaccard dissimilarity index for presence/absence data and Bray-Curtis dissimilarity index for abundance data using the "betapart" package (Baselga & Orme 2012). In terms of traits, we calculated β-diversity for presence/absence data by using Gower's distance, capable of accounting for both continuous and categorical variables (Gower 1971). Subsequently, a PCoA was built using the three first axes of the resulting distance matrix (Laliberté & Legendre 2010), as they cumulatively explained more than 50% of the variation in traits. The trait β-diversity weighted by abundances was calculated using kernel density n-dimensional hypervolumes as implemented in the "BAT" package (Cardoso et al. 2015). Community trait hypervolume was constructed for each year-island combination with the "hypervolume" package (Blonder et al. 2022) incorporating categorical variables through Gower dissimilarity and keeping three orthogonal axes. We estimated trait β-diversity following Mammola & Cardoso (2020), i.e. by computing the overall differentiation among kernel hypervolumes.

To reflect temporal turnover throughout the time period all the β-indices above were calculated for North and South separately by comparing the start year (first year of the time series) to all subsequent years with increasing temporal distance. As an addition to the calculations above we used the similarity percentage analysis (SIMPER) to identify species contributing the most to the estimated dissimilarities in composition between the starting and end year for each region. To better explore the trait composition of the identified species and assess to what extent the species contributing to compositional changes are predominately generalists or specialists, we also calculated the functional distinctiveness of species within each region according to Murgier et al. (2021). Functional distinctiveness represent the dissimilarity of any one species in terms of their traits relative to all the other species in the community (Violle et al. 2017). Finally, we investigated potential signs of homogenization across the transition zone by estimating the pair-wise dissimilarity between the North and South region for each year using the full set of species and trait-based β-indices above. All indices were represented by the average values and 95% confidence intervals across the random permutations.

Results

The Northern and Southern islands showed pronounced temporal variations in species and functional (trait) richness (Fig. 2). We did not observe clear long-term trends in the Northern region (species richness: $p = 0.49$, $r^2 = 0.03$; functional richness: $p = 0.87$, $r^2 < 0.01$). However, species and functional richness in the south showed a slight long-term decline (species richness: $p = 0.02$, $r^2 = 0.38$; functional richness: $p < 0.01$, $r^2 = 0.53$). When comparing the first and last years of the time series, the species richness in the Southern region showed a pronounced decline by 50.5%. Our results demonstrate that both species and functional richness are higher in the Northern (warmer) areas compared to the Southern (colder) areas. Although the trends are different when comparing regions individually, the inter-annual variation between them are correlated and follow the same pattern (Fig. S4). In terms of species evenness, we did not observe linear trends for any region (north region: $p = 0.78$, $r^2 < 0.01$; south region: $p = 0.08$, $r^2 = 0.25$). However, the northern region showed a declining trend for functional evenness ($p = 0.04$, $r^2 = 0.29$). The same was not observed in the south (functional evenness: $p = 0.71$, $r^2 = 0.01$).

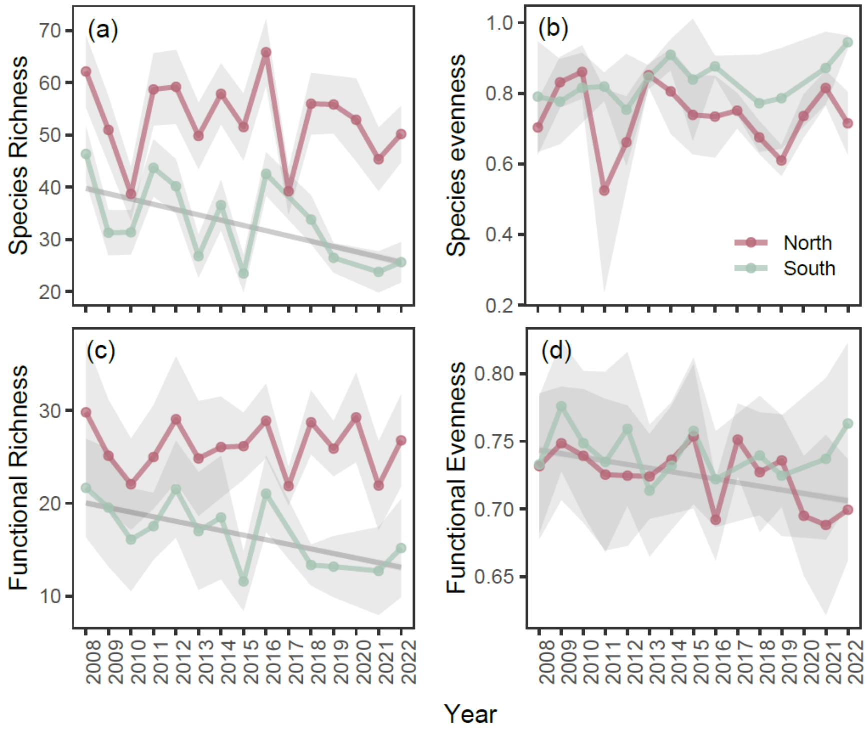

Figure 8. Temporal taxonomic (a) and functional (c) richness trends and taxonomic (b) and functional (d) evenness in Northern (purple) and Southern (green) region. Solid lines and shaded areas represent the mean and 95% CI for each metric, while the grey lines show significant linear trends (derived from linear regressions with year as a predictor).

Taxonomic temporal β-diversity had a higher turnover between years than functional turnover, especially for the Southern region (Fig. 3). These differences were more pronounced for both metrics weighted by abundances compared to presence/absence. Although the Northern and Southern regions showed differences in local species and functional richness (Fig.2), the mean (or initial) level of turnover was similar (amounting to ~0.5). Furthermore, we demonstrate that while the Northern area shows a slight positive trend (especially for presence/absence data: $p = 0.02$, $r^2 = 0.38$), the Southern region demonstrates a pronounced increase in turnover over time, especially in terms of abundance-based taxonomic β-diversity ($p < 0.01$, $r^2 = 0.65$, Table. S2).

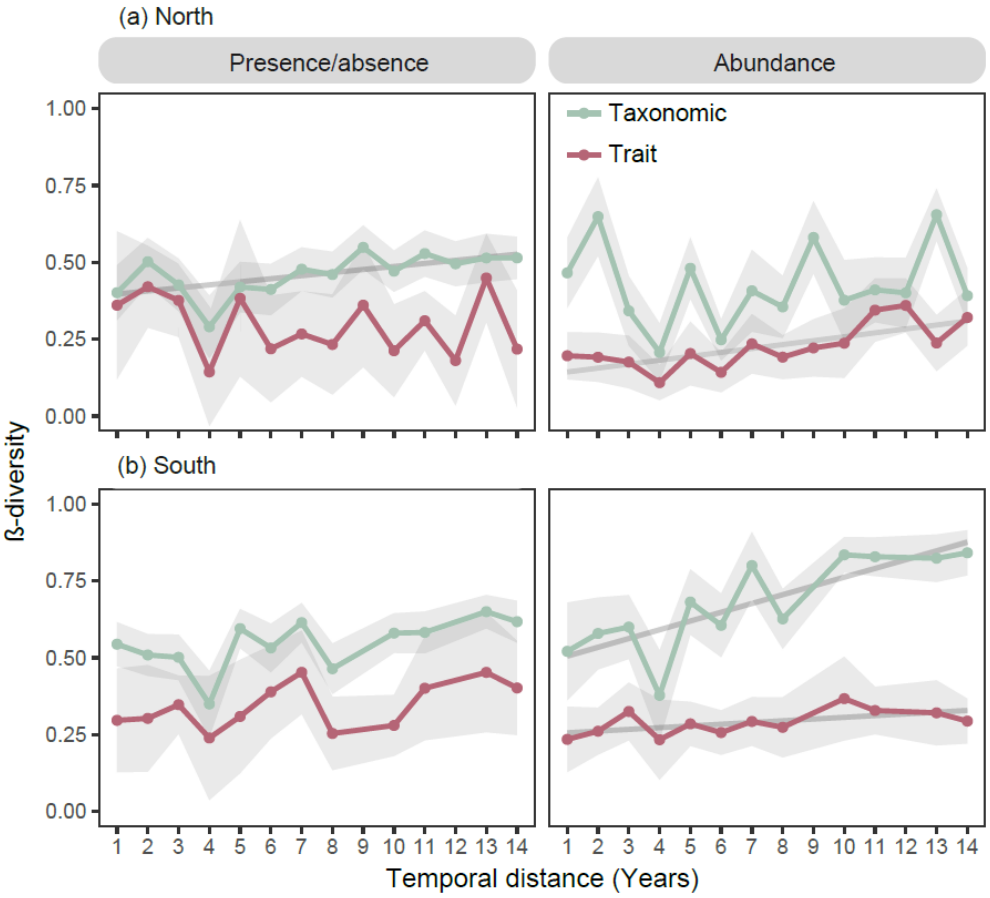

Figure 9. Taxonomic and functional β-diversity turnover observed over time in North (a) and South (b) regions relative to the starting year. Solid lines and shaded areas represent the mean and 95% CIs for each metric when using presence/absence data or weighted by abundances. The grey lines show significant temporal trends (derived from linear regressions with year distance as a predictor).

When looking at the compositional differences between the first and the last year in more detail, our results from SIMPER demonstrate that 20 species contribute to at least 70% of the variation in abundance in the Northern region, while only eight species contribute to the variance in the South (Fig. 4). We found that species contributing most to the β-diversity (dissimilarity) are predominately species with the lowest distinctiveness values (generalists), especially in the south (Fig. 4, blue colors) and whose abundances are decreasing over time (Fig. S5 and S6).

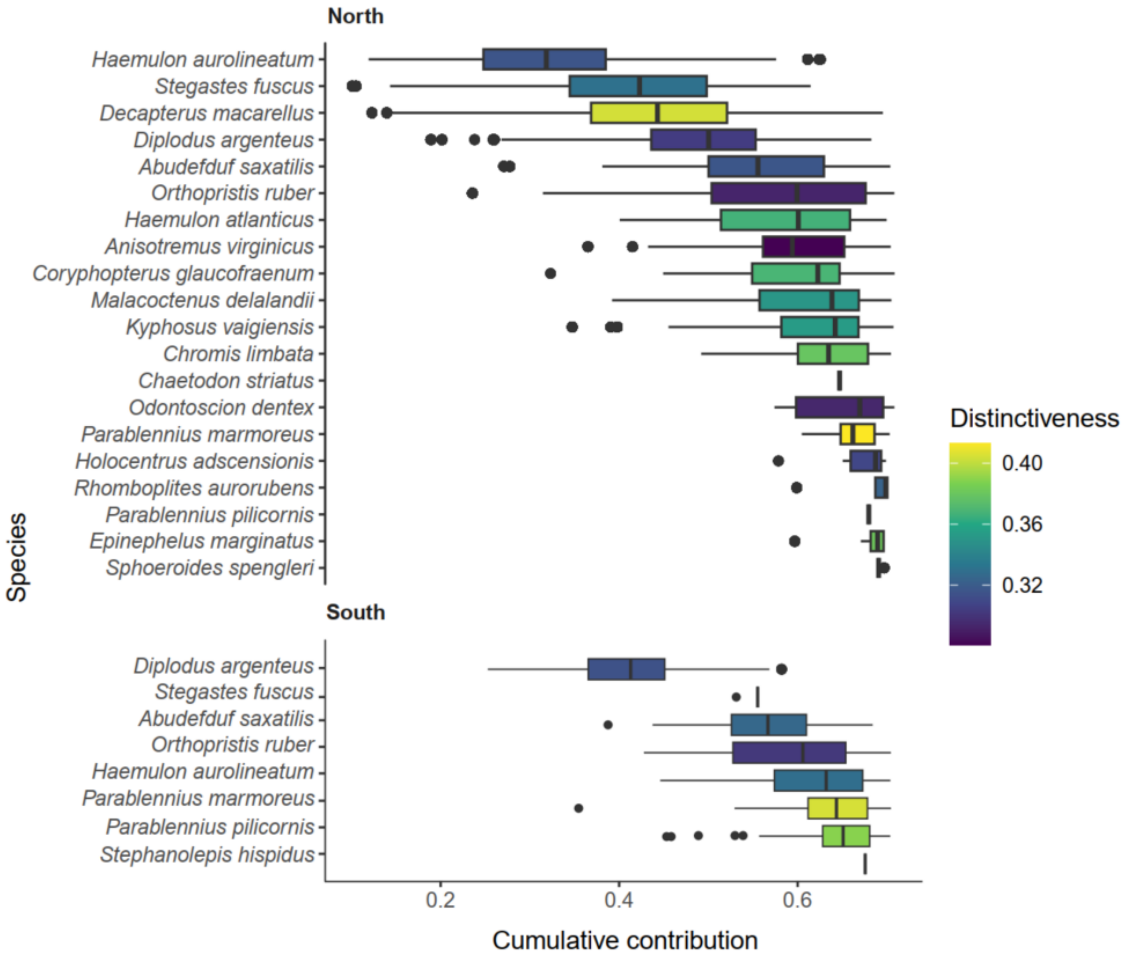

Figure 10. Fish species contributing most to the cumulative dissimilarity (threshold value selected: 70%) between the first (2008) and last year (2022) in the Northern and Southern regions. The boxplots are based on values obtained from each of the 99 permutations. The color gradient illustrates the respective value of species trait distinctiveness (i.e., representing the degree to which the species are generally considered as having a common set of traits (low distinctiveness) or a rare set of traits (high distinctiveness) in comparison to all species in each community).

Finally, our pairwise comparison between the Northern and Southern region show on average more similar trait composition (i.e., lower beta diversity) compared to taxonomic composition (Fig. 5). This is especially evident if also accounting for abundances, where the average taxonomic and trait beta-diversity across all years amount to about 0.70 (SD = 0.13) and 0.30 (SD = 0.05), respectively. In terms of temporal changes, there is moderate inter-annual variability, yet no clear linear trend in the different metrics (taxonomic presence/absence: p = 0.12; $r^2 = 0.20$; trait abundance: $p = 0.72$; $r^2 = 0.01$), with the notable exception of trait turnover using presence/absence data (p = 0.05; r^2 = 0.29) and abundance weighted taxonomic beta-diversity, that increased markedly throughout the time period ($p = 0.02$; $r^2 = 0.38$).

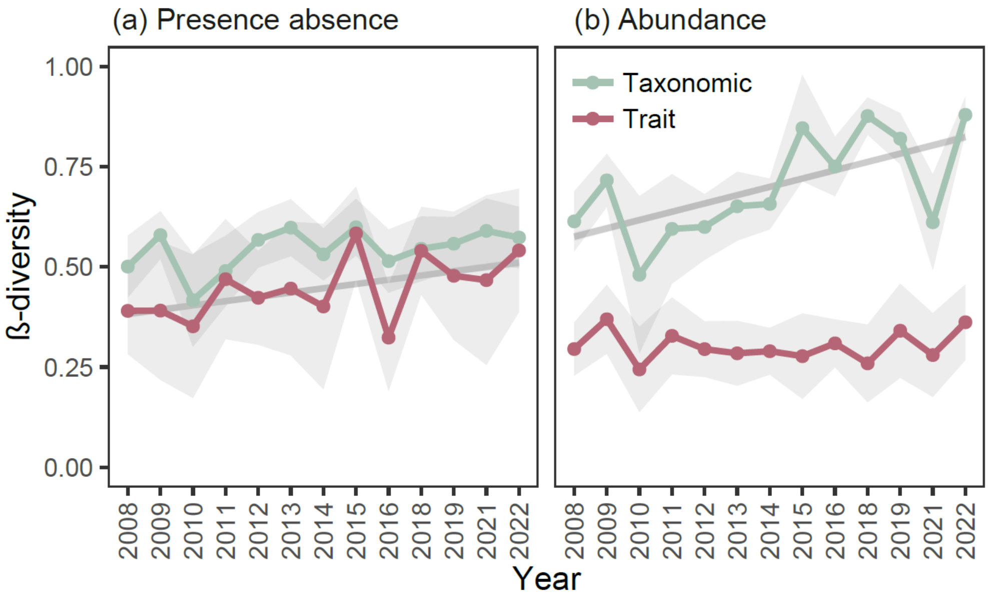

Figure 11. Time series of annual pair-wise taxonomic- and functional β-diversity across the transition zone, reflecting the dissimilarity in species and trait composition between the northern and southern regions over time. Solid lines and shaded areas represent the mean and 95% CIs for each metric when using presence/absence data (a) or weighted by abundances (b), respectively. The grey lines show significant temporal trends (derived from linear regressions with year as a predictor).

Discussion

Global warming is generally expected to cause a loss of species in warmer, tropical areas, while colder, temperate areas will instead gain species from the more diverse pool of tropical taxa moving poleward (Poloczanska et al. 2016, Sommer et al. 2017). Our results contrast this general pattern, with the Southern (colder) region instead experiencing a marked decrease in taxonomic and functional richness, while in the Northern (warmer) region richness remain largely stable. Although it is well known that the current biodiversity crisis and loss is global in scope (Bongaarts 2019), different and rapid changes are more likely to be observed at more local scales (Garcia et al. 2018). Our study conforms to such findings demonstrating pronounced local differences in diversity trends across the Southwestern Atlantic transition zone, despite the general warming trend throughout the region.

Furthermore, we observed that while taxonomic composition may change over time, the trait composition is in general more conserved. This is particularly true in the south where the species composition in each consecutive year became more different compared to the starting year, whereas the turnover in trait composition was less pronounced. This may imply that the increasing taxonomic turnover in the south is primarily driven by the disappearance of species, rather than by species replacement. This is supported by the observation that species richness in this region is declining markedly. Higher turnover is often more evident in local species pools which are characterized by generally low richness, because overall composition is more sensitive to the disappearance of single species compared to speciose communities (Legendre 2014). Thus, the lower overall number of species, combined with declining richness trend can explain the different compositional changes in the south compared to the more species rich northern region. Interestingly, the patterns are even more pronounced when accounting for abundances, indicating that not only changes in distribution and occurrences, but also in terms of number of individuals is affecting community composition and turnover. The increased dissimilarity in taxonomic composition, but unvarying dissimilarity in trait composition in the south can largely be explained by the low trait uniqueness of the species that contribute most to the cumulative change in composition from the first to the last year of the time series. These include some of the most frequently observed families in the southwestern Atlantic, including Gobiidae, Haemulidae, Labridae, Serranidae, Lutjanidae, and Pomacentridae (Moura & Sazima 2000, Floeter & Gasparini 2000, Bender et al. 2013). In terms of their traits, these species can broadly be described as common reef species (referred here as "generalists") as they share combinations of traits with some or most of the regional species pool (i.e., mostly mobile invertebrate feeders, diurnal, territorial, benthopelagic associated, small group formers and pelagic spawners). Although these species share common traits, they are generally highly abundant (Pinheiro et al. 2018) and provide several common functions in the reefs (Siqueira et al. 2020), including secondary production and nutrient excretion (Brandl et al. 2019). Hence, as their abundances fluctuates and declines over time, it may lead to variations in terms of biomass accumulation and the availability of dissolved nutrients through excretion (Brandl et al. 2019).

Despite the general expectation of increased homogenization caused by warming, our results show no directional change towards increased similarity in composition between the northern and southern region over time. This contrasts previous results found for different latitudes in other marine provinces (Magurran et al. 2015). Instead, the areas tend to become more different, especially when considering species composition weighted by abundances. Since the overall richness and composition in the north display no, or only a marginal directional change throughout the period, the increased dissimilarity between areas is primarily caused by changes occurring in the south. Notably, it indicates that species previously shared between both areas (i.e., contributing to compositional similarity) are becoming less abundant, and may even disappear locally in the south. However, as mentioned in the previous section these declining species primarily constitute common and "generalist" species sharing rather similar traits with the rest of the community (i.e., low distinctiveness). This in turn explains why the trait turnover between areas is rather consistent and unchanged throughout the time period.

Global warming has emerged as a main driver of species range shifts and community reorganization worldwide (Pinsky et al. 2013, Pradervand et al. 2014, Magurran et al. 2015). Increasing temperatures has also been shown to impact the trait composition of marine fish communities, at both larger- and regional scales (Frainer et al. 2017, Beukhof et al. 2019b, Pecuchet et al. 2020, McLean et al. 2021), including the Southwestern Atlantic transition zone (Silva et al. 2023). Consequently, warming may potentially explain some of the observed changes in diversity and composition also in our study. Notably, the correlated inter-annual variability in species richness in both regions (Fig. S4) suggest the presence of a similar underlying driver acting across regions. However, if responding similarly to warming, both regions would also show corresponding trends in diversity; yet only the southern region show marked trends in both α and β-diversity. Hence, it is likely that the reef fish communities are responding differently, or to other aspects of temperature variations, beyond simply the increase in mean SST. For instance, there is evidences suggesting that the southwestern Atlantic oceanic circulation is not only warming, but intensifying in the past decade (Sánchez et al. 2015, Franco et al. 2020), and that the thermal tolerance of fish in this region is being influenced by temperature (Silva et al. 2023). As observed in the study of Perez & Sant'Ana (2022), Brazil's Current dynamics intensification is affecting species composition and biomass of warm- and cold-affinity species. In our study, we found a higher degree of temperature seasonality, especially in the south (Fig. S7). It is plausible that the increasing difference between the minimum and maximum SST in the south may serve to constrain not only cold-adapted species limited by the warmer summers, but also more warm-affinity species (from the north) limited by the consistently cooler winters. Whether such environmental filtering may explain the observed changes in richness and composition is unclear and merit further research to better understand the underlying mechanisms and responses of reef fish communities to climate change.

It is also known that climate change potentially acts in synergy with other stressors, including human disturbance and over-exploitation (Jackson 2008, Figueroa-Pico et al. 2021). More specifically, fishing activity have been shown to modify community structure (Froese & Kesner-Reyes 2002, Young et al. 2014), thereby increasing the sensitivity of fish communities to climate variability (Jackson 2008). Interestingly, the region demonstrating temporal turnover in species composition correspond to the southernmost islands that are located outside an MPA and therefore exposed to fishing. Since the turnover is primarily evident if accounting for changes in abundances fishing may contribute to some of the observed changes in the overall β-diversity. However, among the species targeted by the local fishery, only one (*Epinephelus marginatus*) is experiencing a decline in abundance (Fig. S6). This indicates that the beta-diversity patterns observed in this study could potentially be influenced indirectly by fishing activities, but we acknowledge that the species are likely being impacted by several other factors, including the influence of temperature, ocean circulation, and their specific thermal tolerances. Hence, further research is needed to understand the potential cumulative impacts of fishing and climate change acting on the diversity and composition of reef fish communities in the area and beyond.

Our findings highlight the importance of considering multiple metrics of taxonomic and trait α and β-diversity, while accounting for both presence-absence and abundances, to better understand changes in diversity and its potential impacts on structure and functioning of systems. Although single metrics of α-diversity (typically species richness) can reveal spatial and temporal changes, it cannot alone capture important changes in the underlying composition and evenness of assemblages (Bello et al. 2008, Sommer et al. 2017, Waldock et al. 2019; Richardson et al. 2018). This limits our understanding on the potential implications for ecosystem functioning. Our study comparing multiple aspects of diversity of reef fish communities demonstrates that while pronounced differences exists in terms of species richness and composition, trait turnover is considerably weaker, or even unchanged within and between areas. This highlights a high degree of trait redundancy in these communities and support the idea that the Southwestern Atlantic communities are able to maintain a range of ecological processes due to few functional entities (i.e., unique combinations of functional traits) performing similar functions (Mouillot et al. 2014). A higher trait redundancy may in turn increase the resilience of communities to change (Flensborg et al. 2023). However, rare and specialist species are likely to support vulnerable functions in reef ecosystems due to their unique functional roles (Mouillot et al. 2013, McLean et al. 2019). Hence, the replacement of specialists by generalists species resulting from homogenization could result in ecological functions not perfectly performed as expected by more specialist species (Quimbayo et al. 2018). Therefore, studies exploring links between diversity, composition and ecosystem functions are key to a more holistic view of the effects of community changes on ecosystems (Duffy et al. 2016, Maureaud et al. 2020). In that regard, predictive models, for instance based on joint-species distribution models or trait-based food-web models (Ovaskainen et al. 2017, Jetz et al. 2019, Maureaud et al. 2020, van Denderen et al. 2021) could help to better characterize past, present and future changes in reef fish community composition and its potential impacts on ecosystem structure and functioning.

In summary, we observed a loss of taxonomic and trait richness in the southern (colder) islands of the Southwestern Atlantic transition zone, while no directional trend was observed in the Northern (warmer) region. Furthermore, we found no compositional changes in terms of traits, but demonstrate pronounced turnover in taxonomic composition in the south, at least if accounting for species abundances. Taken together, our study shows no evidence of a directional change towards increased homogenization across the transition zone, despite the general warming trend. On the contrary, our study shows increased differences in taxonomic composition, but high trait redundancy over time throughout the area. We therefore highlight the importance to consider the maintenance of the trait structure of communities in addition to species composition in order to anticipate how communities might respond to disturbances (McLean et al. 2019). Finally, future studies in transition zones could consider the specific responses of communities exposed to climate change and other drivers of biodiversity loss, such as habitat diversity, to compare with the findings obtained here.

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Supplementary material

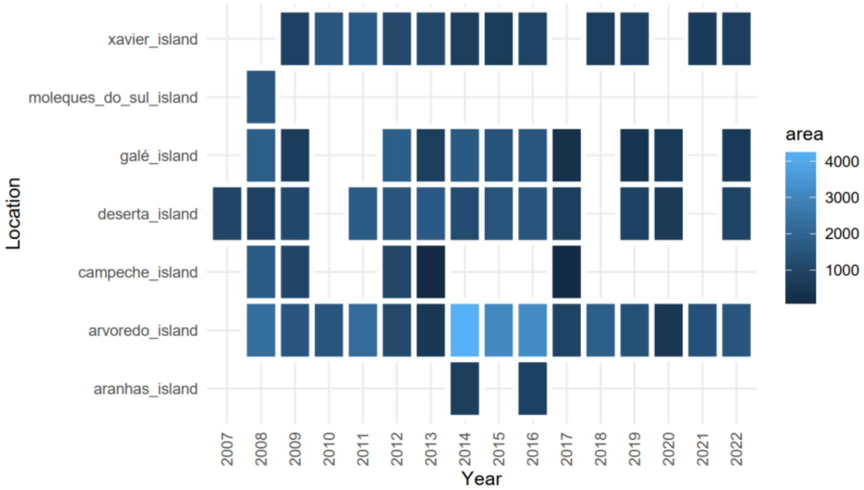

Figure S5. Community data available for each year and island sampled. The color gradient represents the sampling effort in square meters. The gaps in the figure represent the absence of sampling.

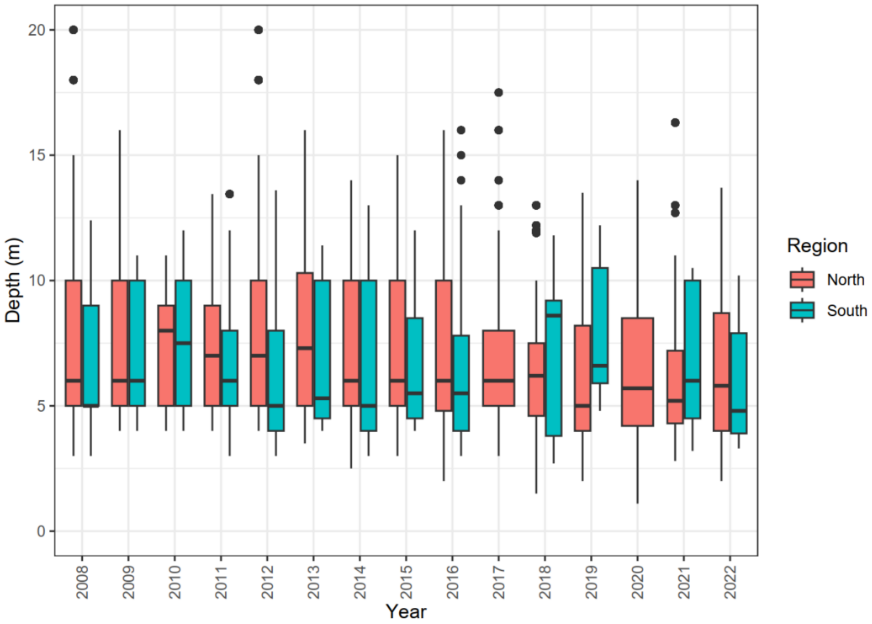

Figure S6. Depth distribution of Underwater Visual Census (UVCs) observed over time. Red color represents all UVCs performed in the North region and blue color represents all UVCs performed in the South region. Boxplots shown medians (black line), upper and lower quartiles, and 95% confidence intervals.

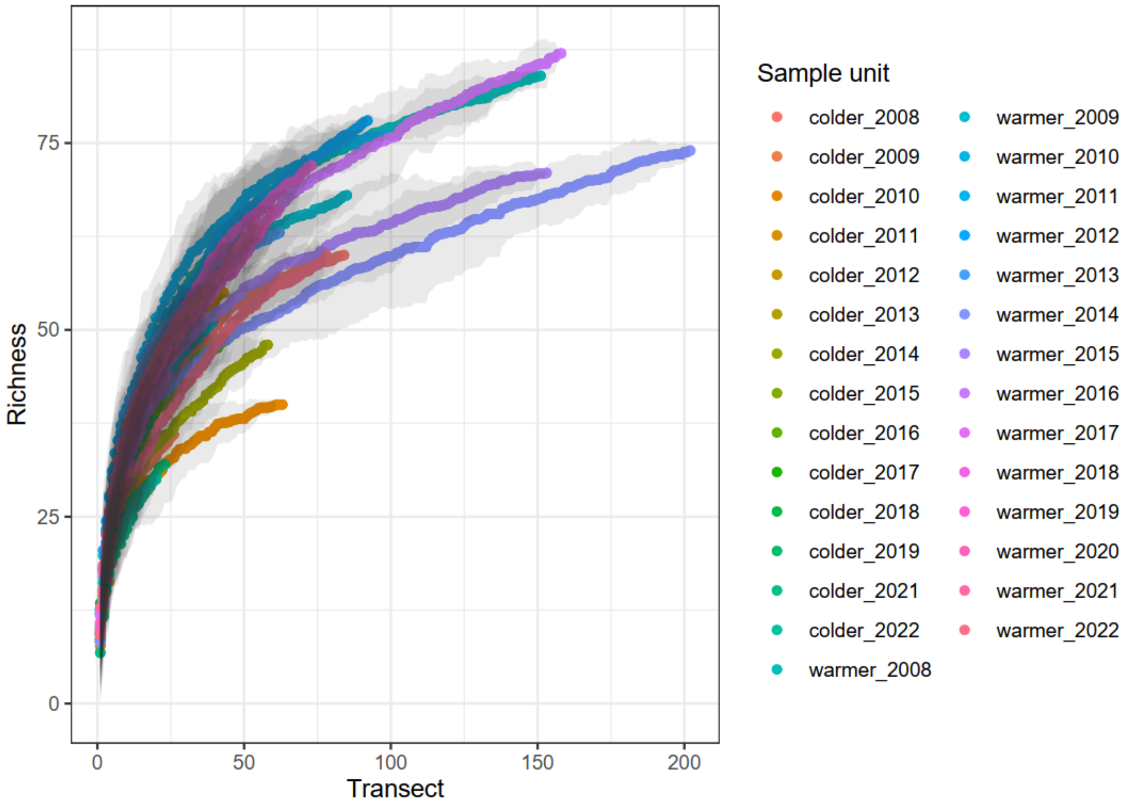

Figure S7. Sampling effort heterogeneity between regions and years (i.e., number of Underwater Visual Census – UVC in each sampling unit) as shown by species accumulation curves, where species richness is a function of the number of UVCs within sample units.

Table S2. Table derived from Species Accumulation Curves (SAC) showing: Sample unit = region and year where samples were made (warmer – north, colder - south); n.census = number of Underwater Visual Census (UVC) done per sample unit; n.census.min = minimal number of UVC done per sample unit; keep = if the sample unit should be kept in the analysis considering species richness sampled; sr = species richness; chao = extrapolated species richness using Chao equation; limit0.8/ limit0.75/ limit0.65 = percentage richness of 80%, 75%, and 65% respectively reached if using n.census.min in the analysis; aympt = mean value of the coefficients from the species accumulation model.

Sample unit	n.census	n.census.min	keep	sr	chao	limit0.8	limit0.75	limit0.65	asympt
colder_2008	84	24	YES	60	74	53	40	25	68.03719194
colder_2009	26	15	YES	36	52	26	20	13	44.45773385
colder_2010	63	15	YES	40	43	28	21	13	43.32159398
colder_2011	43	19	YES	55	102	28	21	13	61.31346198
colder_2012	40	20	YES	48	62	39	29	18	58.0096504
colder_2013	12	11	YES	30	36	NA	11	7	38.28968758
colder_2014	58	19	YES	48	73	39	29	18	52.60022614
colder_2015	18	10	YES	29	38	12	9	6	33.31592054
colder_2016	45	21	YES	49	53	45	34	21	59.95544172
colder_2017	3	6	NO	20	21	NA	NA	2	27.32901545
colder_2018	19	16	YES	38	44	NA	19	12	49.64139334
colder_2019	23	11	YES	32	80	15	12	7	35.99363183
colder_2021	16	11	YES	28	47	NA	13	8	34.34560156
colder_2022	20	12	YES	30	40	19	14	9	35.67445824
warmer_2008	151	33	YES	84	97	77	57	35	91.51169001
warmer_2009	85	24	YES	68	75	39	29	18	73.56695892
warmer_2010	39	17	YES	51	86	24	18	12	56.03168348
warmer_2011	99	28	YES	76	83	51	38	24	84.87196847
warmer_2012	92	29	YES	78	111	55	42	26	85.20613279
warmer_2013	62	22	YES	63	67	34	26	16	69.59557396
warmer_2014	202	29	YES	74	94	86	65	40	75.9307288
warmer_2015	153	27	YES	71	83	58	44	27	74.20678313
warmer_2016	158	35	YES	87	111	89	67	42	94.00781686
warmer_2017	24	18	YES	44	57	NA	23	14	56.01153771
warmer_2018	73	31	YES	72	116	66	50	31	85.25758943
warmer_2019	61	27	YES	66	143	59	44	28	77.03199797
warmer_2020	54	25	YES	64	129	47	35	22	73.28418385
warmer_2021	36	19	YES	55	72	28	21	13	62.68354531
warmer_2022	78	26	YES	60	82	69	52	32	70.06578451

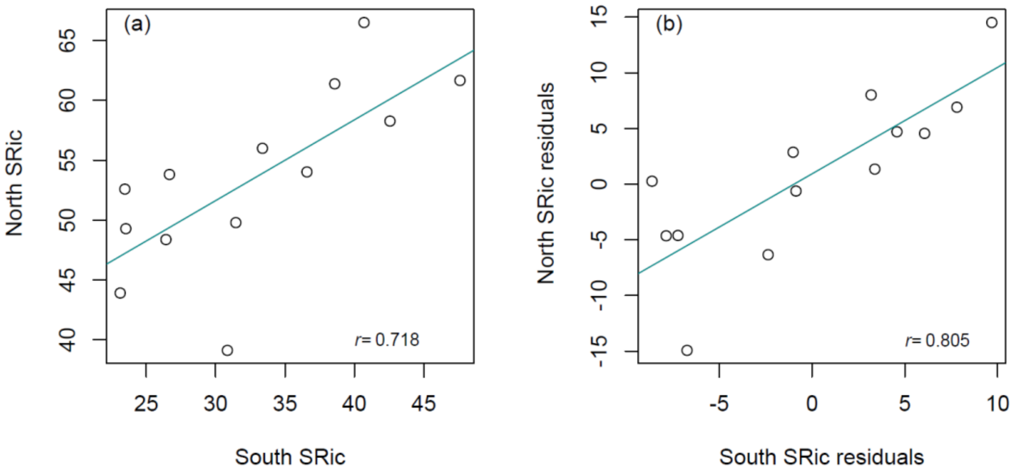

Figure S8. Correlation between north and south species richness per year using the time series with temporal trends (a); and without temporal trends (b). For the latter case were used residuals from the linear regressions between species richness and year. The green line shows the general trend derived from linear regressions and the r values in the bottom right represents the Pearson correlation.

Table S3. Linear regression analysis results for the temporal trends of the β- diversity metrics (taxonomic and trait/functional) weighted and non-weighted by abundances for North and South regions of the southwestern Atlantic. The abbreviation Est. represents the estimated coefficients of regression. Standard error (SE) was estimated for each parametric coefficient. The p-value represents the significance of the results and significant values ($p < 0.05$) are highlighted in bold.

Model	Est.	SE	t val.	p	r^2
North					
Presence/absence					
Taxonomic temp. distance	0.01	<0.01	2.72	**0.02**	0.38
Trait temp. distance	<0.01	<0.01	-0.88	0.39	0.06
Abundance					
Taxonomic temp. distance	<0.01	<0.01	0.36	0.73	0.01
Trait temp. distance	0.01	<0.01	3.75	**<0.01**	0.54
South					
Presence/absence					
Taxonomic temp. distance	0.01	<0.01	2.13	0.06	0.31
Trait temp. distance	0.01	<0.01	1.92	0.08	0.62
Abundance					
Taxonomic temp. distance	0.03	0.01	4.40	**<0.01**	0.65
Trait temp. distance	<0.01	<0.01	2.31	**0.04**	0.34

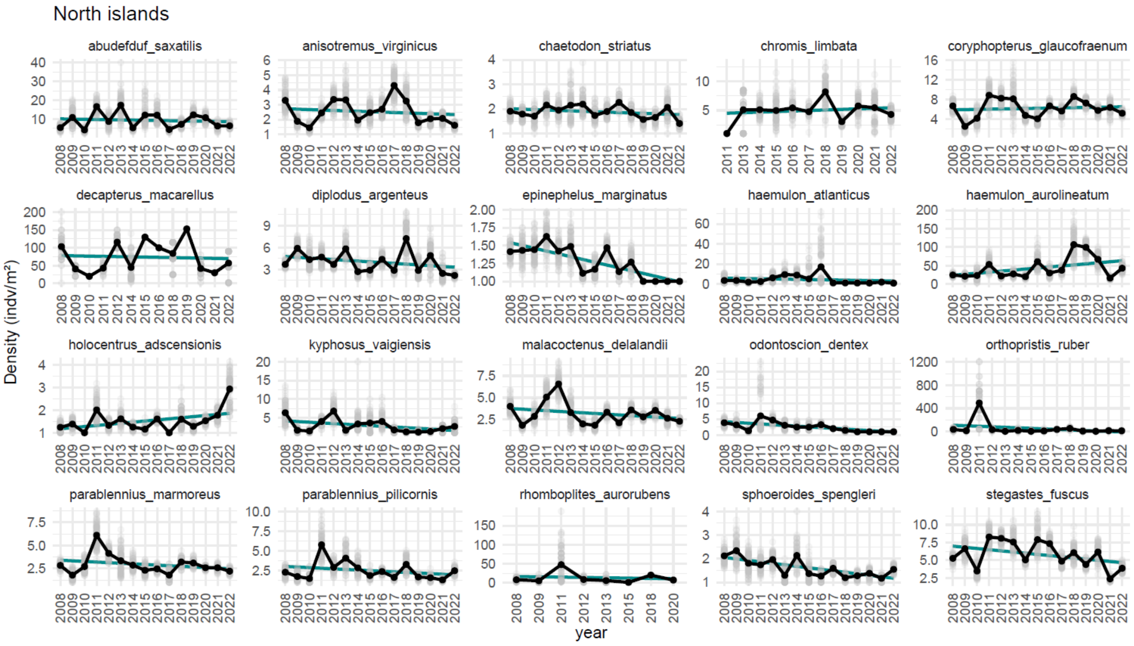

Figure S9. Time series of density (individuals/m^2) of the species contributing to at least 70% of the variation in abundance in the Northern region. Note that for some years there is no data available. The gray dots represent the range of 99 density values calculated from the computed random communities. The black dots represent the mean density value for each year per specie. The green line shows the general temporal trend derived from linear regressions with year as a predictor.

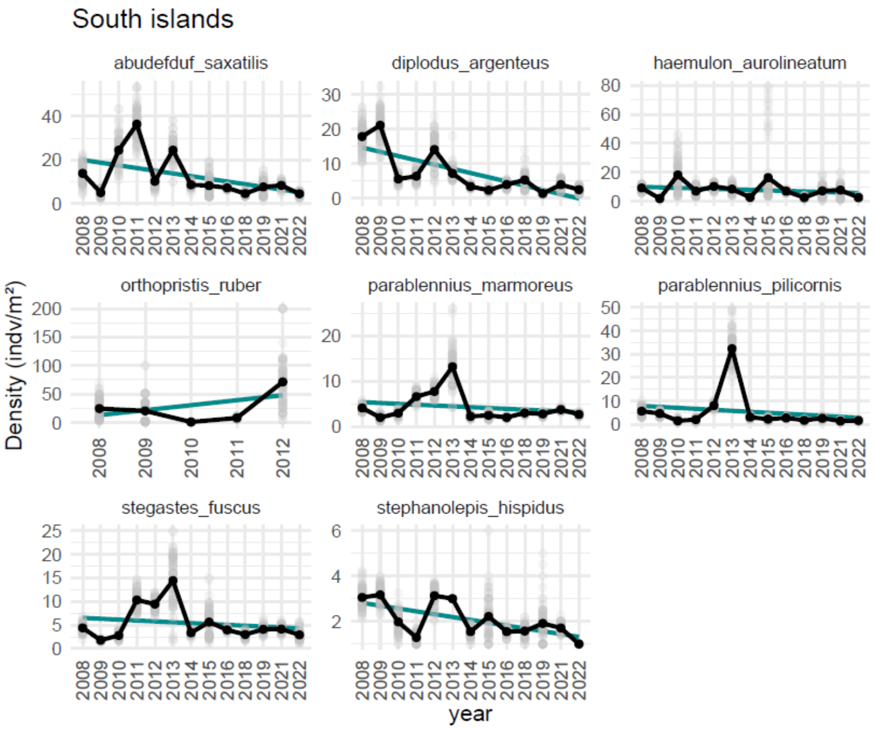

Figure S10. Time series of density (individuals/m^2) of the species contributing to at least 70% of the variation in abundance in the Southern region. Note that for some years there is no data available. The gray dots represent the range of 99 density values calculated from the computed random communities. The black dots represent the mean density value for each year per specie. The green line shows the general temporal trend derived from linear regressions with year as a predictor.

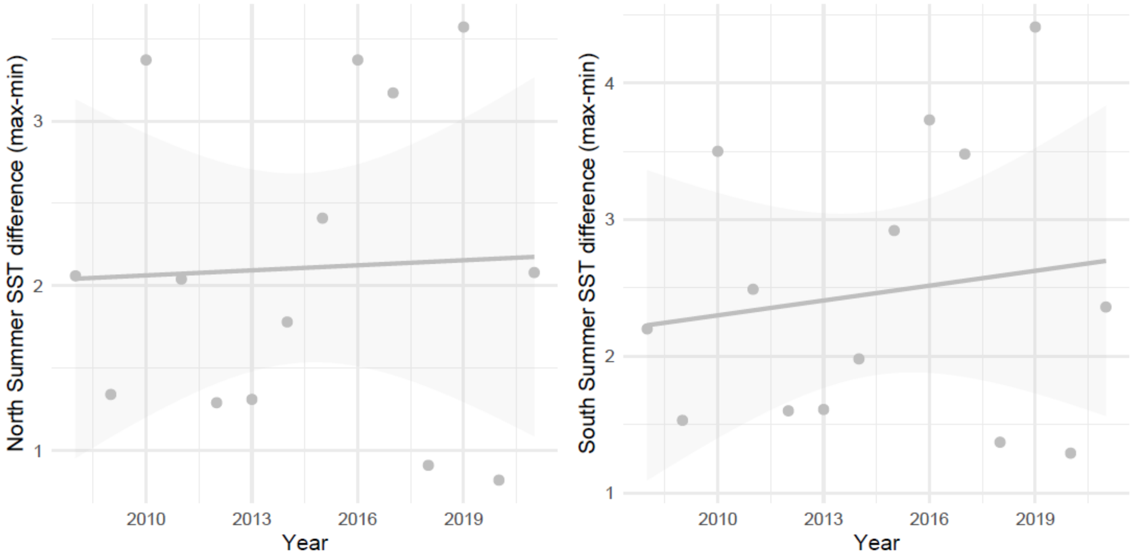

Figure S11. Scatter plot of the difference between maximum and minimum sea surface temperature (SST) for North and South regions over time. The gray line and shadow area represent the trend from linear regressions.

North and South regions over time. The gray line and shadow area represent the trend from linear regressions.

CAPÍTULO III

Warming induced changes in reef fish community traits in the Southwestern Atlantic transition zone

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Warming induced changes in reef fish community traits in the Southwestern Atlantic transition zone

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Keywords: *Reef-fish, fish abundance, Community Weighted Mean, community thermal index, climate change, rocky reef, trait reorganization*

Abstract

Marine communities are subject to alterations in environmental conditions, due to both natural variability and climate change. For instance, the rapid increase in sea surface temperature (SST) can modify spatial distribution patterns and abundances of reef fishes and therefore alter the overall diversity, structure, and functioning of these communities. Trait-based approaches may accurately detect community responses to such environmental changes because species traits would reflect resource and habitat requirements. Here we investigated temporal variability in reef fish trait composition and thermal affinity and assessed whether shifts are linked to recent ocean warming. We combined species traits related to feeding, growth, and survival with abundance data on reef fish from underwater visual census in seven islands of the Southwestern Atlantic subtropical transition zone. All islands exhibited gradual trait reorganization from fish assemblages dominated by large-size species at the beginning of the time period to small, cryptobenthic species towards the end. The temporal changes in Community Weighted Mean traits and community thermal index were related to SST, indicating a numerical response of species to climatic variations. Tropical species are slowly becoming more abundant over time and temperate species are becoming less abundant, reflecting an initial change in fish composition in this transition zone. These results have ecological implications leading communities to a faster turnover, lower food-chain complexity, as well as higher vulnerability to change. We highlight the importance of integrating traits and abundance time series data for a holistic understanding of reef dynamics and community responses to environmental variation, including global warming.

Introduction

Natural climate changes regularly occur in space and over time (Pinsky et al. 2020). However, due to increasing anthropogenic pressures involving carbon emissions and excessive resource use, human-induced changes have become more severe and frequent, threatening the health and integrity of our ecosystems (Rockström et al. 2009, IPCC 2018, Holbrook et al. 2020). Evidence in marine environments includes a rapid increase in sea surface temperatures (SST), causing mass coral bleaching events (Sully et al. 2019) and reorganization of community structure (Stuart-Smith et al. 2017). Other negative impacts on marine organisms include increased metabolic stress, variation in growth and reproductive rates, as well as a decrease in calcification capacity (Harley et al. 2006, Brierley & Kingsford 2009, Barneche et al. 2018).

Reef fishes are key constituents of rocky and coral reefs given their contribution in several ecosystem functions (e.g., nutrient cycling and biomass production) and are an important source of food and livelihood for human societies worldwide (Moberg & Folke 1999, Villéger et al. 2017, Hicks et al. 2019). Ecology and conservation studies have focused primarily on describing patterns and changes in reef fish species richness, abundance, and biomass (Connolly et al. 2005, Floeter et al. 2007, Villéger et al. 2010). However, the use of trait-based approaches as proxies for functional structure to answer long-term and pressing ecological questions, such as how biodiversity varies along environmental gradients, or what the consequences of species loss are for ecological processes, has increased exponentially only in the last two decades (Mouillot et al. 2014).

Species traits can provide an essential tool to uncover and generalize biodiversity organization, allowing predictions of species and community effects on ecosystem functions and services (Mouillot et al. 2014). Moreover, trait-based ecology allows understanding of how aspects of history, ecology, and environment influence marine organisms at different spatiotemporal scales (Yeager et al. 2017). For instance, warmer seasons influence the functional composition of fish by selecting species with traits adapted for these conditions (Mouillot et al. 2013). Traits such as low generation time, rapid sexual maturity, and wide dispersal ability are correlated with warmer temperatures and tend to be more dominant under these circumstances (Pecuchet et al. 2017, McLean et al. 2018, Beukhof et al. 2019b). In this sense, temporal trait-based approaches may accurately detect how assemblages respond to environmental changes, considering that variations in species abundance promote trait turnover over time (Beukhof et al. 2019a, Pecuchet et al. 2020).

Over time, trait-based reorganizations in communities have implications for the functioning of ecosystems (Pecuchet et al. 2020). For instance, studies in the Indo-Pacific showed that warmer temperatures increase macroalgae consumption by abundant herbivorous fish affecting local productivity and nursery habitats (Bates et al. 2014, Hyndes et al. 2016, Vergés et al. 2016). However, despite the relevance of understanding how fish communities' traits vary over time, few studies have shown temporal variations (Anderson et al. 2020). Additionally, there are few studies exploring climate change projections and their effects on reef fish of the Atlantic Ocean (Inagaki et al. 2020). Therefore, considering the progressive increase in frequency and intensity of marine heatwaves in the Southwestern Atlantic in the last decade (Brauko et al. 2020), there is a need for characterizing community composition not only in terms of species richness and abundances, but also trait composition in response to these events.

Here, we use long-term survey data of reef fish assemblages sampled in seven islands along an environmental transition zone in the Southwestern Atlantic to evaluate potential changes and variability in species traits composition over time using Community Weighted Means (CWM), and multivariate statistics. This area has been particularly impacted by global warming during the past decades and the intensification of the subtropical anticyclonic gyre, whereby the Brazil Current brings warm waters southwards (Franco et al. 2020). We also investigate potential changes in the thermal affinity dynamic using the community thermal index (CTI) and model the patterns and changes to assess whether they can be explained by recent warming. Since studies in the North Atlantic have shown that climatic oscillations drive modifications in functional structure (McLean et al. 2018, 2019a), we assess whether variations in species abundance over the years can influence the trait composition in our study area. Thus, based on previous regional and global assessments of fish community responses to warming (Antão et al. 2020, McLean et al. 2021, Galvan et al. 2022), we hypothesized that tropical species are expanding their distribution range due to an increase in SST, whereas ranges of temperate species are contracting. This response is expected to occur in the present study area due to its location inside a transition zone, revealing a different pattern compared to other regions where temperate communities demonstrate wide distributional shifts (Fossheim et al. 2015). We also expect that warm-affinity traits would increase in their relative dominance in response to higher temperatures, while cold-affinity traits should decrease in dominance in the assemblages. In summary, our work aimed to investigate the temporal effects of warming on fish communities using CWM and CTI values as proxies for species range shifts in order to detect possible expansions and/or contractions in their distributions.

Materials & methods

Study area

The temporal variation in trait composition of reef fish assemblages was assessed at seven islands located in the subtropical-warm temperate transition zone of the Southwestern Atlantic (Fig. 1). By applying Ward Clustering to species composition and abundance (see Fig. S1 for more detail), the islands can be divided into a Northern (Galé, Arvoredo and Deserta), and Southern regions (Aranhas, Xavier, Campeche and Moleques do Sul). Three of these islands are located inside of the Marine Protected Area (MPA) Arvoredo Marine Biological Reserve (i.e., Arvoredo: 27°29’ S and 48°36’ W, Deserta: 27º27’ S and 48º33’ W, Galé: 27º18’ S and 48º41’ W), and four are located outside the MPA: Aranhas Islands (27°48’ S and 48°36’ W), Moleques do Sul (27°51’S and 48°26’ W), Campeche (27°42’ S and 48°27’ W) and Xavier Island (27°36’ S and 48°23’ W). Furthermore, the northern islands showed generally higher temperatures, varying from 17.3 – 28.9°C (mean summer SST), whereas the southernmost islands experienced cooler conditions, varying from 15.6 – 26.8 °C (mean summer SST) (Faria-Junior & Lindner 2019). The rocky reefs in all islands were mainly covered by algal turfs, erect macroalgae and zoanthids without clear separation of benthic habitats along depth range gradient (Aued et al. 2018). Due to their position between subtropical and temperate biogeographical zones, all islands were exposed by the same regional variation in temperature dynamics, which plays an important role in communities due to its change in short temporal scales (Beger et al. 2014). This temperature variation supports the overlap of tropical and subtropical reef fish fauna observed in the area (Ebeling & Hixon 1991, Anderson et al. 2015).

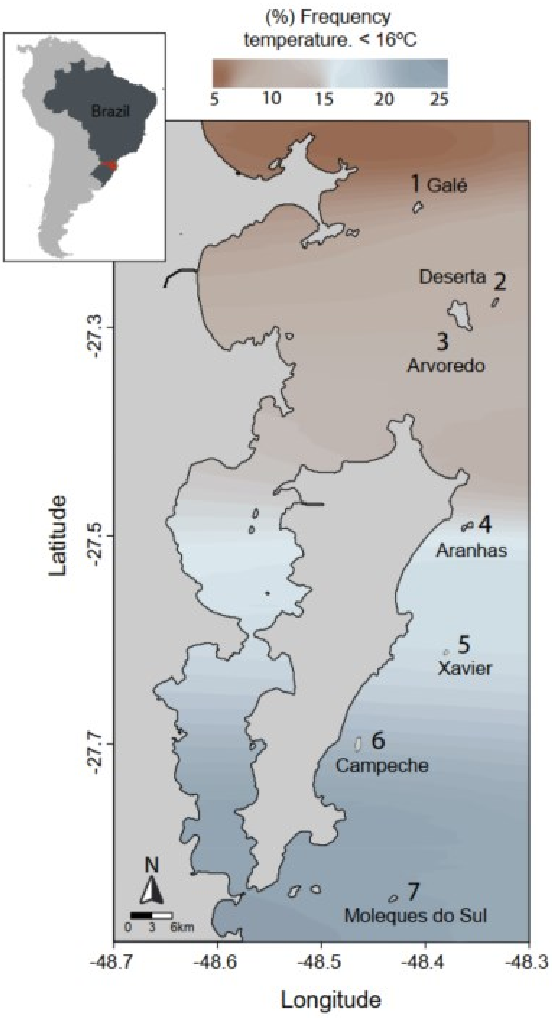


Figure 12. Map of sampled islands. Numbers indicate Galé Island (1), Deserta Island (2), Arvoredo Island (3), Aranhas Island (4), Xavier Island (5), Campeche Island (6), and Moleques do Sul Island (7). The color range represent the frequency of temperature below 16 ºC during the austral winter in Santa Catarina Coast.

Fish sampling

Reef fish assemblages were sampled during the summer seasons through 1,306 underwater visual censuses (UVCs) made while scuba diving carried out between 2008 and 2020. In each UVC, the diver starts the process at the first encounter using a tape measure and visually identifies, counts, and size-estimates (total length to the nearest centimeter) all actinopterygian fish species along belt transects (2 x 20 m, 95% of them at a 1.5 - 18 m depth interval). While unwinding the tape, the diver collects data of non-cryptic species (>10 cm) in the water column and while retracting the tape, follows the same procedure for bottom-associated and cryptic species (<10 cm) (Morais et al. 2017).

Fish traits

In order to represent the general ecology of species, all species observed in the UVCs were classified according to 16 traits representing their morphological, physiological or behavioral adaptations and characteristics involved in the key processes of feeding/resource acquisition, reproduction/growth, and survival/predator avoidance aspects (Table 1). The classification and selection of traits builds on previous trait-based descriptions of marine organisms (Litchman & Klausmeier 2008, Litchman et al. 2013), adopted in recent studies on marine fish community structure and changes (e.g., Dencker et al. 2017; Pecuchet et al. 2017; Beukhof et al. 2019a, b). These traits were obtained from (Quimbayo et al. 2021).

Table 4. Traits compiled from Quimbayo et al. (2021). All the trait information provided was compiled through a review of published checklists, online repositories, local reports, books, and monographs. For some traits, a combination of sources was used to obtain information for all species.

Trait	**Definition and categories**	**Category**	**Levels**	**Class**	**Reference**
Ativity	Period of the day that species feed and breed	Categoric	Day, night or both	Feeding/resource acquisition	(Robertson & Allen 2016, Robertson & Van-Tassell 2019, Froese & Pauly 2021)
Caudal fin	Shape of caudal fin	Categoric	Forked, lanceolated, pointed, rounded, and truncated		(Froese & Pauly 2021)
Depth range	Difference between the maximum and minimum depth reported for the species	Numeric	-		(Robertson & Allen 2016, Robertson & Van-Tassell 2019, Froese & Pauly 2021)
Diet	Main items consumed by species (categorical)	Categoric	Herbivore-detritivore (feed epilithic algal matrix), macroalgal (feed macroalgae >1cm high or seagrass), sessile invertebrates (feed corals, sponges and ascidians), mobile invertebrates (feed crustaceans, annelids, echinoderms and mollusks), planktonic (feed zooplankton, coelenterates, detrital aggregates, etc.), omnivore (feed animal material and plant and/or detrital material) or piscivore (feed fishes and cephalopods)		(Robertson & Allen 2016, Robertson & Van-Tassell 2019, Froese & Pauly 2021)
Geographic range distribution	Estimation from the number of grid cell (5º x 5º) where a species has been recorded	Numeric	-		(Parravicini et al. 2014)

Level water	Position in water column	Categoric	Bottom (staying at the bottom all the time, low (live slightly above the bottom, occasionally rest on the bottom) or high (several meters above the bottom)		(Robertson & Allen 2016, Robertson & Van-Tassell 2019, Froese & Pauly 2021)
Mouth position	Anatomic jaw position	Categoric	Superior (lower jaw protruding upwards), terminal (upper and lower jaws equal in length), subterminal (upper jaw protruding downwards), inferior (mouth in ventral position), tubular (enlargement of mouth cavity) or elongated (long snout due to the increase in the bones premaxillary, maxillary and dental)		(Froese & Pauly 2021)
Trophic level	Position in the food web based on diet composition and mean trophic level of food items (reported in FishBase)	Numeric	-		(Froese & Pauly 2021)
PLD	Pelagic larval duration	Discrete	-	Reproduction/ growth	(Luiz et al. 2013)
Maximum body size	Maximum total length of species observed in the census	Numeric	-		(Robertson & Allen 2016, Robertson & Van-Tassell 2019, Froese & Pauly 2021)
Spawning	The way that species deposit eggs in water	Categoric	Attach to objects, demersal (deposit directly on the substrate), live (birth without external larval stage), oral (parental care when female or male keep the eggs in their mouth) or pelagic		(Froese & Pauly 2021)
STI	Specie temperature index: average and maximum temperature estimated from temperature reported in each island where species occur	Numeric	-		(Quimbayo et al. 2021)
Aspect ratio caudal fin	An indicative value of species activity calculated from the squared height of caudal fin (h) divided by its surface (s) area (h^2/s) (reported in FishBase)	Numeric	-	Survival/ predator avoidance	(Froese & Pauly 2021)
Body shape	Morphological specialization for swimming	Categoric	Box shaped (globular as in Diodontidae), compressed (flattened laterally),		(Froese & Pauly 2021)

			depressed (flattened dorsoventrally), eel-like (elongated, snake-like shape and locomotion), elongated (long in relation to length) or fusiform (spindle shap, most hydrodynamic form)	
Group size	Gregariousness behavior	Categoric	Solitary, pairing, small groups (3-20 individuals), medium groups (20-50 individuals) or large groups (>50 individuals)	(Froese & Pauly 2021)
Mobility	Area of activity	Categoric	Sedentary, territorial, mobile or very mobile	(Froese & Pauly 2021)

Environmental data

To test relationships and effects of warming on trait composition across years, we included two abiotic variables representing local and global scale drivers. As a local driver, we used sea surface temperature (SST) of each island sampled while El Niño/Southern Oscillation (ENSO) was used as a global driver. SST, which has the potential to impact the dynamic of communities due to direct influence on fish distribution, metabolism and/or growth (Morais & Bellwood 2018), was compiled for winter and summer seasons. Mean SST values per summer and winter season per year were extracted from multi-scale ultra-high resolution sea surface temperature analysis (Chin et al. 2017) which presents daily SST estimated on a global 0.01° × 0.01° grid available in the NOAA repository (https://coastwatch.pfeg.noaa.gov/erddap/index.html). We obtained the Monthly Multivariate ENSO index from NOAA's Earth System Research Laboratory (esrl.noaa.gov/psd/enso/mei) and calculated mean values per summer and winter seasons to include in the analysis. ENSO values are a combination of different variables related to sea level pressure, temperature, wind, and radiation over the Tropical Pacific basin calculated for 12 overlapping bi-monthly seasons (Wolter & Timlin 1993, Kobayashi et al. 2015).

Data analysis

Given that sampling effort was not uniform across years and in each island (Fig. S2), sample size was standardized using a rarefaction technique (Magurran & McGill 2011). We first identified the smallest sampled area (120 m^2) for each island and year, and then fixed this number for all other years as the minimal sampled area, and randomly sub-sampled individual transects until the minimal sampled area was reached. This method has been used to compare fish assemblages from oceanic islands (Quimbayo et al. 2019). As multiple combinations of transects could be used to compose the minimal sampled area, samples for any given combination of year and island were bootstrapped 1,000 times to produce distributions of species composition and abundance along the study area (Fig.S3-9). In each permutation, we conducted the analysis to explore community trait variation and at the end of the bootstrap, where the mean values were used as input for the subsequent analysis.

Following bootstrapping we conducted a Multiple Factor Analysis - MFA (Abdi & Valentin 2007) to identify temporal trait dynamics in the seven islands of the transition zone. This multivariate analysis takes into account the structure of data in groups (Abdi & Valentin 2007), which in our study correspond to three classes of traits (feeding/resource acquisition, reproduction/growth, and survival/predator avoidance). The data division balances the contribution of each group of traits in the total variation and allows quantifying the contribution of the most important ones. For each year, temporal trait dynamics were evaluated through Community Weighted Mean (CWM) (Lavorel et al. 2008), as trait values weighted by $\log_e(x + 1)$ abundance of species to meet the assumption of equal variances in statistical analysis. Since samples were bootstrapped, we used the mean CWM values of all traits within classes obtained from reef fish composition in each island and year as input for the MFA analysis. This serves to illustrate community trait variation through time along the transitional zone but may not reflect the full range of variation in traits within individual islands. The results displaying temporal trait changes per year were summarized by assessing the loadings on the first and second dimension of the MFA. For modeling, we used only values of the first dimension since they account for the most part of the total variability. To test the sensitivity of results to the inclusion, or exclusion of species targeted by local fishermen, we repeated the analysis while excluding all species classified as being under heavy fishing pressure (e.g., species targeted by multiple gear types or fishing methods across a wide range of coastline) according to (Floeter et al. 2006). One mean value per region per year was utilized in the analysis to address potential fishing effects in large and high trophic level species over time.

To quantify warming signals, we estimated the CTI for each year based on the average thermal affinity of the community. A thermal distribution was constructed for all 147 fish species recorded, using occurrence records from available checklists of distribution (Quimbayo et al. 2021) combined with mean SST from the Bio-ORACLE data set (Assis et al. 2017). Based on the corresponding temperature reported in each locality where species were present, a temperature distribution was obtained for each species. We used the midpoint of distribution as a measure of the central thermal tendency for each species, or thermal affinity. The midpoint was chosen to be less sensitive to the distribution across the temperature range of species (Stuart-Smith et al. 2015). The CTI was calculated from the average of thermal midpoint values for species recorded by year in each island, weighted by their log ($x + 1$) abundance. This measure is considered a useful proxy for detecting responses to climate change, since it reflects immediate turnover under extreme temperatures (Burrows et al. 2019). To better visualize trajectories in CTI, we compared these values with SST in both inside and outside MPA which can be grouped, respectively, into northernmost and southernmost islands. Moreover, this separation also corresponds to warmest and coldest regions and allows us to compare different community responses to temperature.

To examine potential collinearity among the predictors used in the models, we used Pearson's correlation, considering a correlation coefficient $r <\pm 0.7$ as a cut-off value (Fig.S10), since values below this threshold are unlikely to involve multicollinearity in models (Dormann et al. 2013). We tested for the effect of SST and ENSO in summer and winter seasons, locality (i.e., the seven islands) and survey (i.e., inside/outside MPA) on the CWM trait and CTI values per year using generalized additive models (GAM) with Gaussian distribution. This distribution was chosen considering the nature of the data (continuous values from negative to positive sign) and that the residuals are normally distributed (Zuur et al. 2009). The degrees of freedom of the spline smoother function (s) were further constrained to three knots ($k = 3$) to allow for potential non-linearities, but also restrict flexibility and risk of overfitting. We performed a set of models testing for survey (inside or outside MPA) as specific slopes of SST and ENSO in summer and winter separately, and using islands as fixed factors to account for any geographical (i.e., latitudinal) differences between sites, not represented by variation in temperature. Then, we performed a model selection approach using Akaike Information criterion 'AIC' (Burnham & Anderson 2002). The significance of predictors in the final model was evaluated using *p values* ≤ 0.05, and to ensure model assumptions were satisfied we verified the normal distribution of residuals (Fig. S11-S14). All statistical analysis were done in R 4.0.2 (R Core Team 2020), using the libraries FactoMineR (Lê et al. 2008, Husson et al. 2013), mgcv (Wood 2017), FD (Laliberté et al. 2015), and car (Fox & Weisberg 2019).

Results

Temporal patterns of trait composition

Our results showed that 30.1% of the total variability in CWM traits for whole community weighted by abundance was explained by the first dimension (Dim 1, Fig. S15). This dimension displays a gradual temporal change in trait composition from positive to negative values from 2008 to 2020, with rather low inter-annual variability (Fig. 2a). The feeding, reproduction, and survival traits each contribute to around 30% of the explained variance, indicating that all broad trait groups have the same importance on Dim 1 (Fig. 2a). At the start of the time period the fish assemblages are characterized by high weighted abundance of large and mobile species, as reflected by the positive loadings of these traits on Dim 1 (Fig. 2b). In the first years the traits fusiform, mobile, pelagic spawners, large body size, forked caudal fin and low-level water habitat were dominating, hence highlighting the presence of predator species in the beginning of the time series. For instance, species belonging to highest trophic levels such as the grouper *Epinephelus marginatus* were frequent at the beginning of the time series, but not represented in the last few years (Fig. S16). In contrast, the community trait composition in the latest years was primarily composed of species with traits such as elongated body, sedentary, demersal spawners and bottom-associated, as reflected by the negative loadings. This reflects an increase in the abundance of small and cryptic species, such as *Parablennius pilicornis* and *P. marmoreus*, which are relatively more abundant in recent years (Fig. S16). The average body size in the first years ranged from 5 to 32 cm, whereas throughout the remaining years it ranged from 1 to 26 cm. Dimension 1 also shows fluctuations in the abundance of the tropical affinity species *Priacanthus arenatus* and the exotic cooler water species *Chromis limbata*.

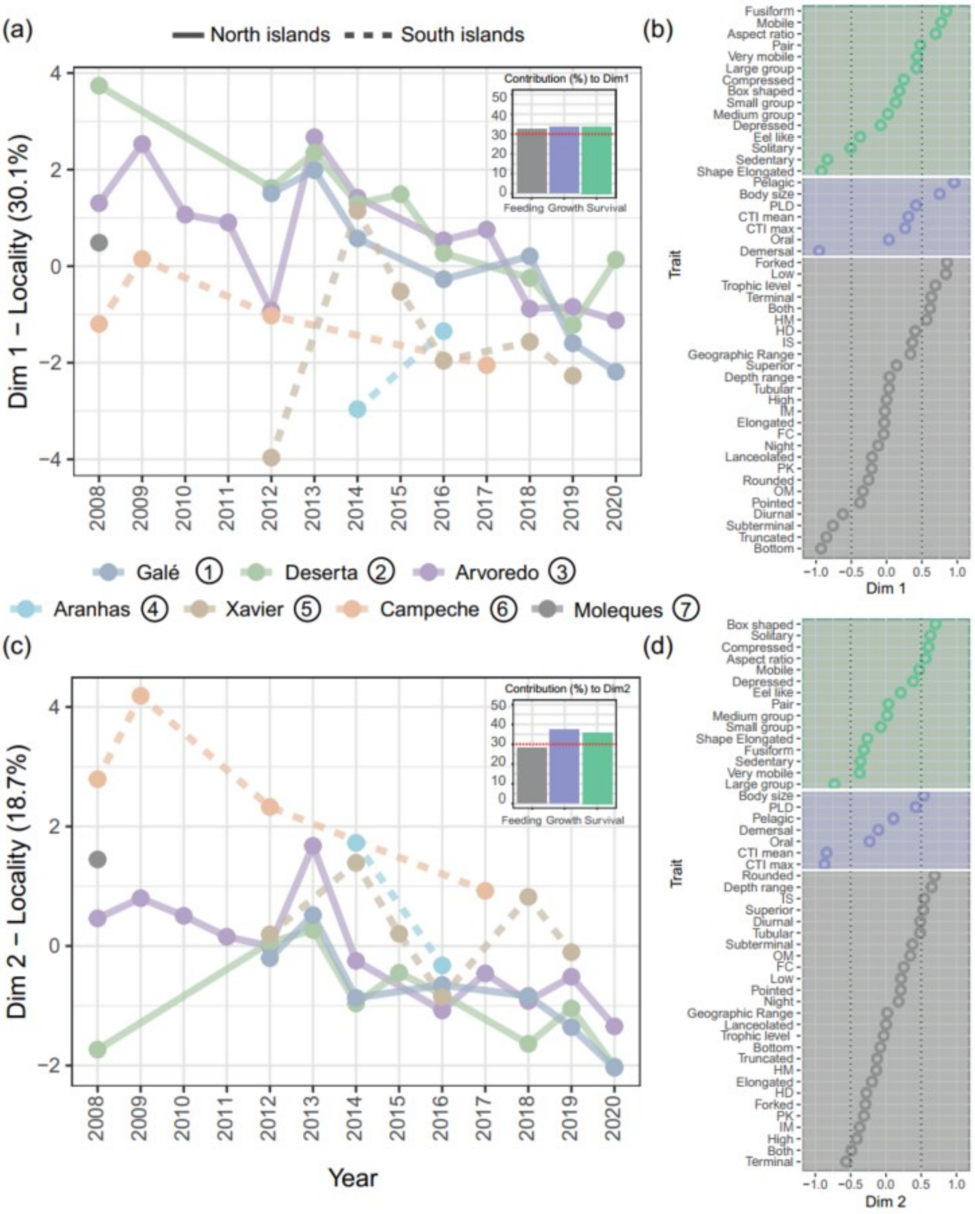


Figure 13. Temporal variation in the reef fish traits (CWM) weighted by abundances in several islands of Santa Catarina - Brazilian province ordered by the latitudinal gradient (Galé, Deserta, Arvoredo, Aranhas, Xavier, Campeche, and Moleques) obtained from Multiple Factor Analysis (MFA). After bootstrapping, mean CWM values were used as input to conduct the MFA resulting in one single value per island per year. Time Time-series of the Dimension 1 (a) and Dimension 2 (c) of CWM traits variability and the contribution of each group of traits to the dynamic. CWM traits loadings displayed for Dim 1 (b) and Dim 2 (d). The groups of traits are represented by colors: gray (feeding), violet (growth) and green (survival). We include the black dotted line to clarify loadings values higher and lower than 0.5. Trait loadings > 0.5 were considered as the most important for the temporal trends.

The second dimension (Dim 2) accounts for 19.7% of the total variability in CWM traits weighted by abundance but does not display a clear and consistent decreasing trend across islands (Fig. 2c). Growth traits explain a large part of the CWM trait variability (37.1%), followed by survival (35.2%) and feeding traits (27.7%). This dimension mainly captures the variation in the proportion of box shaped, large body size, and rounded caudal fin individuals in the early years (Fig. 2d). These traits refer to species such as *Stephanolepis hispidus,* which was more prevalent in early years (Fig. S16). On the other hand, species forming large groups, having low thermal affinity (i.e., low values of CTI) and with terminal mouths were most abundant in recent years. These traits correspond to cryptic species, such as *Malacoctenus delalandii* and *Coryphopterus glaucofraenum*, which became more abundant in recent years, as well as *Chaetodipterus faber*, a specie often found to form schools (Fig. S16).

The temporal trends for reef fish trait communities excluding fishing target species were similar to those found when considering the entire community. The dimensions of MFA revealed a negative trend associated to the predominance of large and high trophic level traits in the beginning of the time series, while cryptobenthic traits were most abundant in the later years (Fig. S17).

Temporal patterns of the Community Thermal Index (CTI)

We observed an increase in abundance of warm affinity species over time reflected by the higher CTI values (Fig. 3) whilst some tropical species also showed increasing trends in abundance (Fig. S18). The trend is even more pronounced for southern islands, revealing a spatial response of fish assemblage in thermal affinity. This trend was related to the corresponding shifts in environmental temperature for both outside MPA (Southernmost) and inside MPA (Northernmost) islands and broadly follow patterns in SSTs of the Southwestern Atlantic transition zone. Particularly for islands outside MPA, the observed CTI values were slightly below the SST, compared to islands inside MPA. The CTI trends considering the community without fishing target species also were like those trends observed for all fish community (Fig. S19).

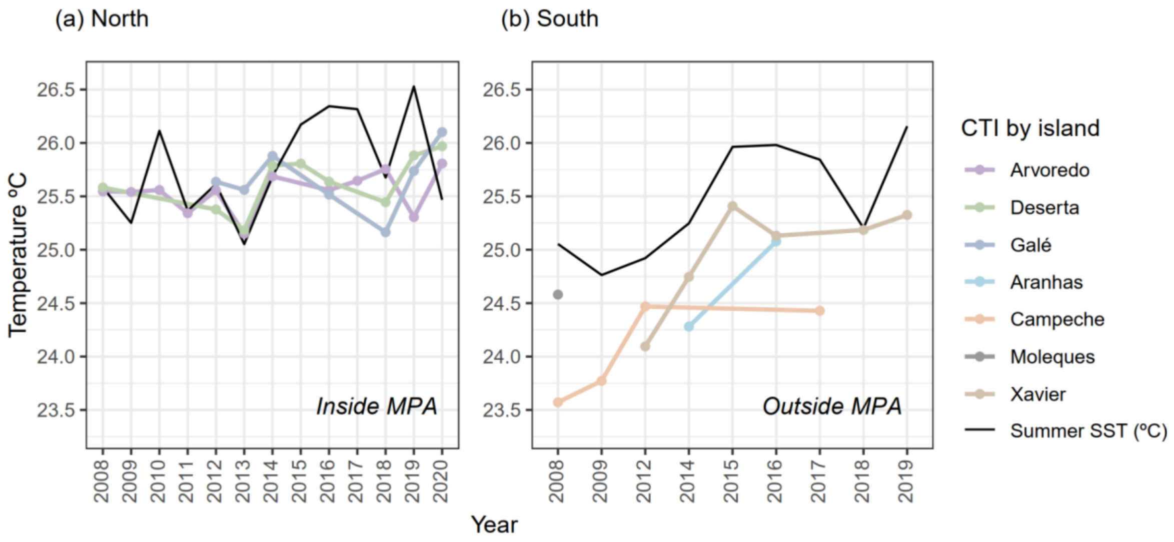


Figure 14. Sea Surface Temperature (SST) at North (a) and South (b) region of Santa Catarina transition zone from 2008 to 2020, and associated Community Thermal Index (CTI) trends for reef fishes weighted by abundance. North and South regions are equivalent to Inside and outside Marine Protected Area (MPA), respectively. CTI represents the mean of the Species Temperature Index for all species recorded in a survey weighed by their abundances and is presented here as the mean across all surveys in each year. SST represents the mean of sea surface temperature summer to each survey date.

Environmental effects on CWM and CTI dynamic

The overall trait dynamic represented by Dim 1 of the MFA for the whole community was negatively related to summer SST without specific slopes (inside/outside MPA) in the model ($p = 0.012$, Fig. 4). The final GAM selected by AIC explained 35% of the total variance (Table 2). Furthermore, the islands (i.e., fixed factor) inside MPA (Arvoredo, Deserta, and Galé; Table 3) had significantly higher intercepts. This result indicates differences between regions not only in terms of taxonomic composition, as previously mentioned, but also in terms of trait composition. In terms of CTI, the final GAM explained 68% of the variability (Table 2), where the increasing trend in CTI over time was positively related to winter SST (Fig. 5a) but showed a significant slope only inside MPA (Northernmost islands, $p < 0.01$). Furthermore, the model demonstrated a significant effect of island where inside MPA (Arvoredo, Deserta, and Galé) showed higher intercepts, indicating a higher mean CTI compared to islands outside MPA

Southern islands; Table 3). These results were not obtained while analyzing islands separately in regressions (Table S1).

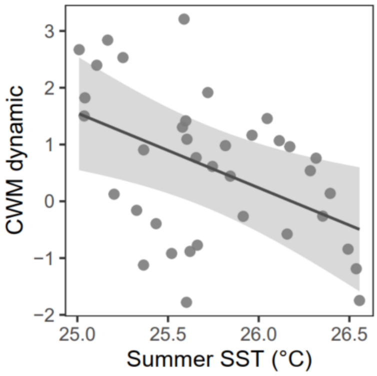


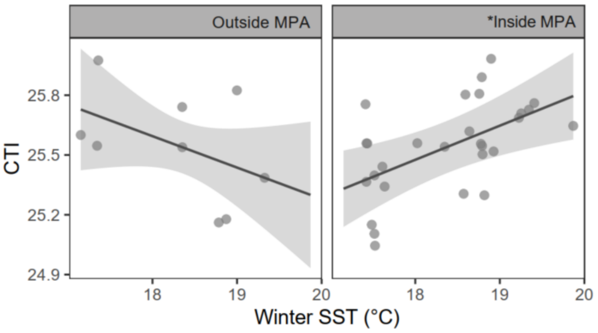
Figure 15. Generalized Additive Model (GAM) smooth plot showing the partial effects of summer Sea Surface Temperature (SST) on the Community Weighted Mean (CWM) dynamic for the whole community and filtering fishing target species. The trends for both datasets were the same. Ribbons in gray indicate 95% confidence intervals and the dots represent the partial residuals of the model.

Table 5. Model selection using AIC criteria of Generalized Additive Models for Community Weighted Mean (CWM) traits and Community Thermal Index (CTI) values considering the whole community dataset and filtering fishing target species. The islands were considered as a fixed factor and the survey (inside/outside Marine Protected Area - MPA) as specific slopes for Sea Surface Temperature (SST) and El Niño/Southern Oscillation (ENSO) values for winter and summer seasons. Results are presented for the best models in Table 3. All the combinations tested with their corresponding degrees of freedom (df) and coefficient of determination adjusted (r^2 adj) are shown.

Response Variable	**Model**	**AIC**	**df**	**r^2 adj**
CWM traits (whole community)	s(summer SST) + Survey + Island	132.59	9	0.35
	s(summer SST, by = Survey) + Island	134.37	10	0.33
	s(summer ENSO) + Survey + Island	138.31	9	0.24
	s(winter ENSO) + Survey + Island	139.88	10	0.21
	s(winter SST) + Survey + Island	140.38	9	0.19
	s(summer ENSO, by = Survey) + Island	140.75	9	0.23
	s(winter ENSO, by = Survey) + Island	141.82	10	0.18
	s(winter SST, by = Survey) + Island	142.35	10	0.17
CWM traits (without fishing target species)	s(summer SST) + Survey + Island	129.73	9	0.41
	s(summer SST, by = Survey) + Island	130.99	10	0.40
	s(summer ENSO) + Survey + Island	136.93	9	0.28
	s(winter ENSO) + Survey + Island	137.98	10	0.24
	s(winter SST) + Survey + Island	138.89	9	0.23
	s(summer ENSO, by = Survey) + Island	139.45	9	0.28

	s(winter ENSO, by = Survey) + Island	140.15	10	0.23
	s(winter SST, by = Survey) + Island	141.32	10	0.21
CTI (whole community)	s(winter SST, by = Survey) + Island	6.19	10	0.68
	s(summer SST) + Survey + Island	7.29	11	0.67
	s(summer SST, by = Survey) + Island	7.72	10	0.68
	s(winter SST) + Survey + Island	11.77	9	0.62
	s(summer ENSO) + Survey + Island	12.30	10	0.61
	s(summer ENSO, by = Survey) + Island	13.27	9	0.63
	s(winter ENSO) + Survey + Island	14.98	9	0.59
	s(winter ENSO, by = Survey) + Island	15.45	11	0.60
CTI (without fishing target species)	s(summer SST, by = Survey) + Island	2.10	11	0.74
	s(summer SST) + Survey + Island	2.27	10	0.74
	s(winter SST, by = Survey) + Island	2.85	10	0.73
	s(summer ENSO, by = Survey) + Island	6.65	10	0.71
	s(winter SST) + Survey + Island	7.04	9	0.70
	s(summer ENSO) + Survey + Island	8.95	9	0.68
	s(winter ENSO, by = Survey) + Island	9.26	11	0.69
	s(winter ENSO) + Survey + Island	9.31	9	0.68

(a) Whole community



(b) Without fishing target species

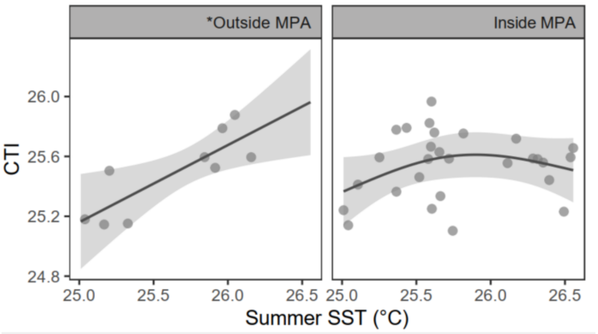


Figure 16. Generalized Additive Models (GAMs) smooth plots showing the partial effects of Sea Surface Temperature (SST) on the Community Weighted Mean (CTI) dynamic for the whole community (a) and filtering fishing target species (b) in islands inside and outside Marine Protected Area (MPA) of the Southwestern Atlantic transition zone. For CTI models, survey inside MPA as specific slope was significant when analyzed the whole community and survey outside community was significant while excluding fishing target species (represented by * mark). Ribbons in gray indicate 95% confidence intervals and the dots represent the partial residuals of the model.

Table 6. Effects of islands and abiotic predictors on the Community Weighted Mean values (CWM) and Community thermal index (CTI) for the whole community and the community without fishing target species based on Generalized Additive Models with Gaussian distribution selected by AIC. The islands were considered as a fixed factor and the survey (inside/outside Marine Protected Area - MPA) as specific slopes for Sea Surface Temperature (SST) and El Niño/Southern Oscillation (ENSO) values. SE = Standard Error were estimated for each parametric coefficient. Edf (estimated degrees of freedom) and Df (degrees of freedom) represent the complexity of the smooth term in the model. The *p* value represents the significance of results in relation to the null hypothesis and ns = non significative in the model.

	Whole community								**Without fishing target species**							
Predictors	**CWM**				**CTI**				**CWM**				**CTI**			
	Estimate	**SE**	***t* value**	***p* value**	**Estimate**	**SE**	***t* value**	***p* value**	**Estimate**	**SE**	***t* value**	***p* value**	**Estimate**	**SE**	***t* value**	***p* value**
Aranhas	-2.21	0.90	-2.43	**0.02**	24.64	0.16	148.74	**<0.01**	-2.43	0.87	-2.79	**<0.01**	24.72	0.15	160.58	**<0.01**
Arvoredo	0.67	0.39	1.69	0.10	0.89	0.17	5.02	**<0.01**	0.81	0.37	2.13	**0.04**	0.81	0.16	4.91	**<0.01**
Campeche	0.30	1.57	0.19	0.84	-0.06	0.31	-0.19	0.84	0.25	1.51	0.16	0.86	-0.59	0.26	-2.20	**0.03**
Deserta	1.19	0.42	2.83	**<0.01**	0.97	0.18	5.34	**<0.01**	1.26	0.40	3.01	**<0.01**	0.95	0.17	5.64	**<0.01**
Galé	0.26	0.45	0.57	0.56	1.01	0.18	5.42	**<0.01**	0.21	0.43	0.50	0.61	0.93	0.17	5.36	**<0.01**
Moleques do Sul	1.78	1.60	1.11	0.27	-0.06	0.28	-0.21	0.82	1.87	0.54	1.21	0.23	0.15	0.29	0.51	0.61
Xavier	0.11	1.07	1.03	0.30	0.48	0.19	2.49	**0.01**	1.43	1.03	1.39	0.17	0.47	0.18	2.59	**0.01**
Smooth term	**Edf**	**Df**	**F**	***p* value**	**Edf**	**Df**	**F**	***p* value**	**Edf**	**Df**	**F**	***p* value**	**Edf**	**Df**	**F**	***p* value**
Summer SST	1	1	7.18	**0.01**	ns				1	1	8.85	**<0.01**	**Inside MPA**			
													1.73	1.92	1.32	0.23
													Outside MPA			
													1	1	6.28	**0.01**
Winter SST	ns				**Inside MPA**				ns				ns			
					1	1	8.42	**<0.01**								
					Outside MPA											
					1	1	1.84	0.18								
Summer ENSO	ns				ns				ns				ns			
Winter ENSO	ns				ns				ns				ns			

The trait dynamic for the community filtering fishing target species was also negatively related to summer SST ($p < 0.01$, Table 3). However, the CTI model showed a positive relation to summer SST only on islands outside MPA ($p = 0.01$ for Aranhas, Xavier, Campeche, and Moleques do Sul islands, Fig. 5b). We did not observe any effect of ENSO for any model.

Discussion

Our study is the first assessment in the Southwestern Atlantic transition zone that investigated the temporal variation in trait composition of reef fish assemblages. Our results showed that all islands broadly followed the same general pattern of change over time. The trait composition changed substantially, reflecting variations in species abundances. Additionally, we found signs of warmer thermal affinity in response to rising temperatures supporting our hypothesis that tropical species are expanding their range distribution in response to an increase in SST. These patterns reveal a new perspective for temporal changes in the southwestern transition zone since previous studies did not find any relationship between global predictors (e.g., El Niño and La Niña) and species-specific data (Anderson et al. 2020).

The trait changes observed during the 13 years period indicate recent, large-scale reorganizations of fish assemblages in this area in response to ocean warming. The traits showing the largest changes were the same for all islands and reflect a general decrease in larger-sized predator species, (e.g., groupers) and an increase in smaller, bottom-dwelling species (i.e., cryptobenthic fish), even after removing the fishing target species from the dataset. Changes in the trait composition can be related to a shift in the dominance of different life-history strategies (Pecuchet et al. 2017, Beukhof et al. 2019b), notably a general increase in species with rapid growth and short generation time, which favor a faster population increase in response to temperature variations (McLean et al. 2018, Brandl et al. 2020). The increase in smaller and opportunistic species in the communities over time would lead to faster turnover by introducing novel trophic interactions and modifying mortality and competition rates (Cantor et al. 2018). Body size is considered one of the most influential traits in behavior and demographic characteristics (such as diet, dispersal, metabolic rate, and mortality rates; Luiz et al. 2013, Barneche et al. 2019), consequently influencing nutrient transport, trophic regulation, and community composition (Tavares et al. 2019). In this sense, food webs can be affected by species variations reducing their stability and robustness due to the depletion of large size and highly connected species (Navia et al. 2016). In healthy and protected ecosystems, the high energy transfer efficiency is maintained in part by a high production of lower trophic levels which is converted into production at the upper trophic levels reflected by their higher abundance and biomass (Seguin et al. 2022). Conversely, fish communities in the southwestern Atlantic could be experiencing a higher turnover associated with the positive temperature response of small and lower trophic level species with fast growth, suggesting disruption of the ideal trophic structure. Thus, it is important to recognize the implications of trait reorganization on the structure and functioning of ecosystems, since these temporal changes could result in higher community variability and vulnerability to environmental changes.

A pronounced decline in the values of CWM was revealed for all islands. Although our results demonstrated changes in reef fish abundances, with an overall increase of cryptic species, this does not necessarily reflect a decrease in the abundance of large-sized species (Fig. S18). Furthermore, many large-sized and high trophic level species could be growing and increasing in total length over years, especially in the Northern islands (Arvoredo, Galé and Deserta located within the Arvoredo Marine Protected Area (MPA). It is known that effective MPAs promote larger species and optimize marine biodiversity conservation (Edgar et al. 2014). Therefore, the large individuals present in early 2008 could still be present and growing in size and biomass in later years, even if the actual abundances are unchanged, as shown in another study at the same MPA (Anderson et al. 2020). Taken together, our results indicate that the temporal trait changes observed across the transition zone are primarily due to numerical responses of species abundance to warming, while potential changes in fishing pressure may have played a minor, or more local role on the overall trait dynamic. This can be supported by the same trends found in the analysis excluding fishing target species from the dataset. Nevertheless, we stress the need for further studies investigating the unique and cumulative impact of fishing and other anthropogenic stressors, including climate change and habitat loss on the trait composition of reef fish communities worldwide (Pecuchet et al. 2020, Pinsky et al. 2020).

The abundance-driven changes in traits observed in our study underpin community reorganization with increasing temperatures. This change was evident also in trends of CTI weighted by abundances using the whole dataset and filtering fishing target species, which showed reef fish assemblages to be responsive to temperature. For islands located in both the Northern and Southern part of this transition zone, CTI followed the increasing trends of SST, suggesting CTI to be a good indicator of community changes associated with temperature variations (Day et al. 2018). Underlying the changes in CTI is an increase in abundance of tropical species over time, while temperate species were becoming less abundant (Fig. S11). This is in line with findings from previous studies in transition zones (Vergés et al. 2014, Horta e Costa et al. 2014), to a lesser extent, however. For instance, in the tropical-temperate reefs of Australia, the range extension of tropical herbivorous fishes (tropicalization) shifts the community to an alternate kelp-free state, threatening the stability of these ecosystem (Vergés et al. 2016). We could not assume the same response for the Southwestern Atlantic reefs since the benthic structure is mainly composed of turf algae (Aued et al. 2018), which does not support the same functional richness as in other marine regions where corals are dominant (Mouillot et al. 2014). On the other hand, we may foresee a potential increase in the demographic connectivity of tropical species in future years due to their ability to acclimate to ocean warming (Lima et al. 2021). As an example, observations of tropical parrotfishes such as *Sparisoma* spp. and *Scarus trispinosus* are becoming more frequent in Santa Catarina over the last three years (Floeter, pers. comm). In the future, this increase in abundance may trigger a gradual process of tropicalization. Interestingly, our results indicate that the fish communities have more tropical affinity than expected, because the maximum values of CTI are close to the maximum SST values, especially in northern islands. Therefore, the species composition in this area is mostly constituted of species with tropical affinity. However, species inhabiting transition zones are less tropical and more temperate due to the wider thermal tolerance allowing them to withstand temperatures higher than their optimal (Rummer & Munday 2017). This may imply that the communities in our study area have lower thermal vulnerability and are potentially more resilient to climate disturbances because of their wide thermal tolerance. Considering that the CTI values were below SST outside MPA (South islands), we could expect a negative impact of extreme minimum temperatures, due to the individual's inability to maintain homeostasis during colder periods (Feary et al. 2014).

Our results suggest that warmer temperatures can profoundly alter trait composition in reef fish communities. Warmer SST in the summers were related to an increase in cryptobenthic fish traits, such as elongated body, demersal spawning and a bottom-dwelling habitat association. These findings agree with previous studies showing fish trait changes with increasing temperatures (McLean et al. 2018, 2019b, Beukhof et al. 2019a). Temperature-driven changes in fish populations may occur through a range of physiological and/or behavioral responses (avoiding unsuitable habitats), changes in the balance between mortality, growth and reproduction during thermal stress, and changes in productivity and/or trophic interactions (Rijnsdorp et al. 2009). During summer the SST in the Southwestern Atlantic shelf is generally warmer near the coast due to seasonal stratification, averaging 25.5 °C, while the winter average SST is lower (18.2 °C - present study, see methods) and vertically more homogeneous as a consequence of weak currents (Matano et al. 2010). Thus, the mechanism behind our observed pattern could be explained by the metabolic theory, which states that warm waters accelerate growth and reproduction of short-living small species, whereas cold waters favor the dominance of large and slow-growing species (Pecuchet et al. 2017, Beukhof et al. 2019b).

The increase in the thermal average of communities driven by warming, as illustrated by higher CTIs, suggests a strong indication of the sensitivity of ocean communities in response to climate changes (Burrows et al. 2019). CTI for the whole community inside MPA shows a positive response to winter SST, reflecting the tolerance and maintenance of species to higher temperatures reached in winter (±20ºC). In other words, maximum winter temperatures are within the range of temperatures encountered in summer, which are tolerated by the community. When fishing target species are removed from the dataset, summer SST becomes the driver of CTI and the trend remains positive. This highlights that species other than fishing targets are responding to the increase in temperature. However, our sampled area is located in a transition zone and is affected by Southern winds during winter, which transport nutrients and contribute to decrease sea temperatures (Lopes et al. 2006, Bordin et al. 2019). This suggest that in the Southern hemisphere, the impact of warming in fish communities could be less intense due to the buffering action of cold-water currents (Inagaki et al. 2020). Studies using mark-recapture techniques could be helpful to verify whether tropical-species can tolerate winter conditions and remain in the region over consecutive summer seasons, which would confirm a tropicalization trend. Additionally, temperature also plays an important role in the vertical structure and distribution of marine organisms through stratification (Rijnsdorp et al. 2009). Comparing aspects of physiology such as the optimum temperature for aerobic performance among fish populations also provides a tool to test whether species are adapting to their thermal environment (Rummer & Munday 2017). In this sense, further studies examining temporal trends of ecological traits could be improved by taking into account the effects of water column stratification on the depth distribution of fish species, in addition to horizontal changes in distributions (range expansion) and physiological tolerance to warming. Considering the unknown effects of the increased frequency of marine heatwaves in the Southwestern Atlantic (Rodrigues et al. 2019, Brauko et al. 2020), more integrative studies are needed to identify reorganizing patterns in fish community structure and their links to environmental changes.

Overall, out results have important implications, demonstrating that communities respond to environmental changes altering species abundances and reorganizing trait composition according to external factors. This study present new evidences about the increase in frequency of warm-affinity species to temperature, although less intense than the tropicalization processes observed in other marine provinces located at the same latitude and in north hemisphere (Vergés et al. 2014, 2019). Therefore, tropicalization should be evaluated not only considering shifts in abundance of species, but also variations in terms of species traits, which can present a different response to the environment temperature.

Caveats

Although Aranhas and Moleques islands have few years of data, the inclusion of these southernmost islands increases sample size and variability and highlights the differences between regions. Furthermore, our standardization method based on resampling the minimal sampled area, which is equivalent to a sample-based rarefaction procedure for species richness (Gotelli & Colwell 2001), was fully developed to cope with such limitations while incorporating most of the dataset rather than excluding UVCs and/or islands. Although we did not specifically account for the potential effects of MPA performance in our study, it has been shown to play a role in determining species and trait composition (Hackradt et al. 2014, Karlovic et al. 2021). However, since we obtained similar results for both inside and outside MPAs when repeating all analyses while excluding fishing target species, we deem these effects to be of less direct importance. This implies that the observed trait responses likely result primarily from variations in SST rather than other factors, including fishing. Nevertheless, we stress the need for information and data regarding MPA enforcement and performance to assess potential fishing impacts on fish community composition in the area. Lastly, habitat quality/composition would also play an important role filtering species and trait dominance in the system (Aued et al. 2018). Regardless of lack of data, we acknowledge that species pool metrics may be influenced by habitat and further studies including this variable would certainly be useful in understanding trait dynamics over time. Thus, despite the limitations due to the lack of fishing effort data, MPA performance, and quality composition to include in the present analysis, we provided interesting results and insights for the ecology of reef fish in Southwestern Atlantic. Our findings open an avenue for further studies to investigate potential impacts of these aspects on trait composition of reef fish communities.

Conclusions

The gradual trait reorganization observed in the Southwestern Atlantic subtropical-warm temperate transition zone has potential implications for the reef ecosystem functioning. The trophic dynamics, for instance, could be affected if the abundance of smaller and r-selected species changes over time, leading to variations in prey consumption of large piscivorous species (McLean et al. 2019a). The assemblage, which was composed by large fish in the beginning of the time series, became dominated by small cryptobenthic species in recent years. These can produce large amount of consumable biomass and larvae that dominate near-reef ichthyoplankton (Brandl et al. 2019). This shift may directly impact the energy transfer in reef habitats and provide insights for future studies on the underlying mechanisms of reef ecosystem functioning and its changes in space and time. Overall, the trait reorganization can lead to changes in the food web structure, ecosystem functioning, and community vulnerability. Notably, the increase in smaller, opportunistic species may lead to faster turnover, lower food-chain complexity, as well as higher vulnerability to change.

Our study shows the influence of warming on community trait structure, indicating possible responses of reef fish assemblages to ongoing climate changes. Considering the progressive increase in SST (Frölicher et al. 2018), marine heatwaves (Brauko et al. 2020), and that some responses to disturbances are only detected by a functional-trait view (Mouillot et al. 2013), our approach could help to reach a holistic understanding of reef fish dynamics under environmental variations in the Southwestern Atlantic.

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Supplementary material

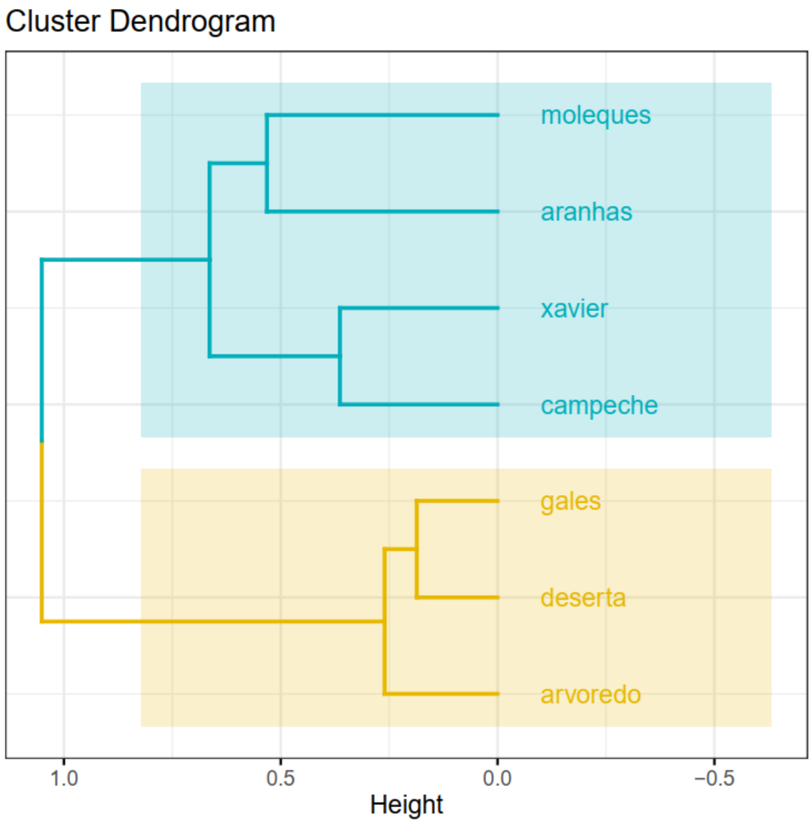

Figure S12. Classification of seven islands from southwestern Atlantic through hierarchical cluster analysis using the Bray-Curtis similarity index as a distance measure and Ward group method for cluster formation. The rectangles represent the northernmost (blue) and southernmost (yellow) islands that correspond to north and south regions.

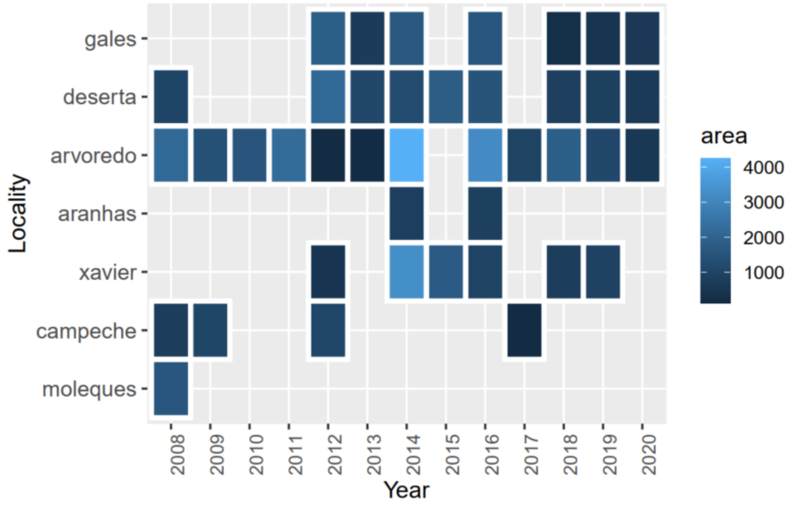

Figure S13. Community data available for each year and island sampled. The color gradient represents sampling effort in square meters. The absence of data is due to the absence of sampling.

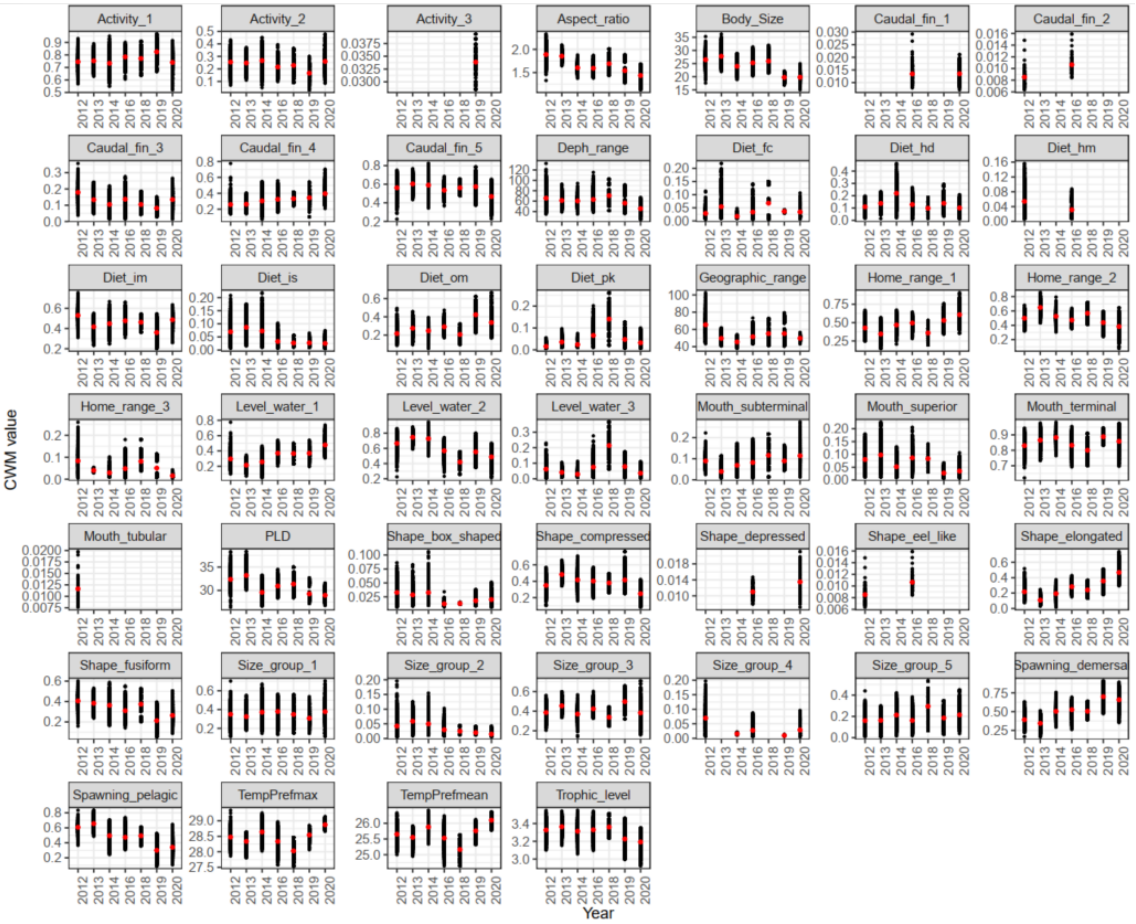

Figure S14. Time-series of the community weighted mean (CWM) traits of fish in **Galé Island**. Note that for some years there is no data available. The black dots represent the range of 1000 CWM traits values calculated from the computed random communities. The red dots represent the mean CWM trait value for each year, and are the value used as input in the multiple factor analysis (MFA).

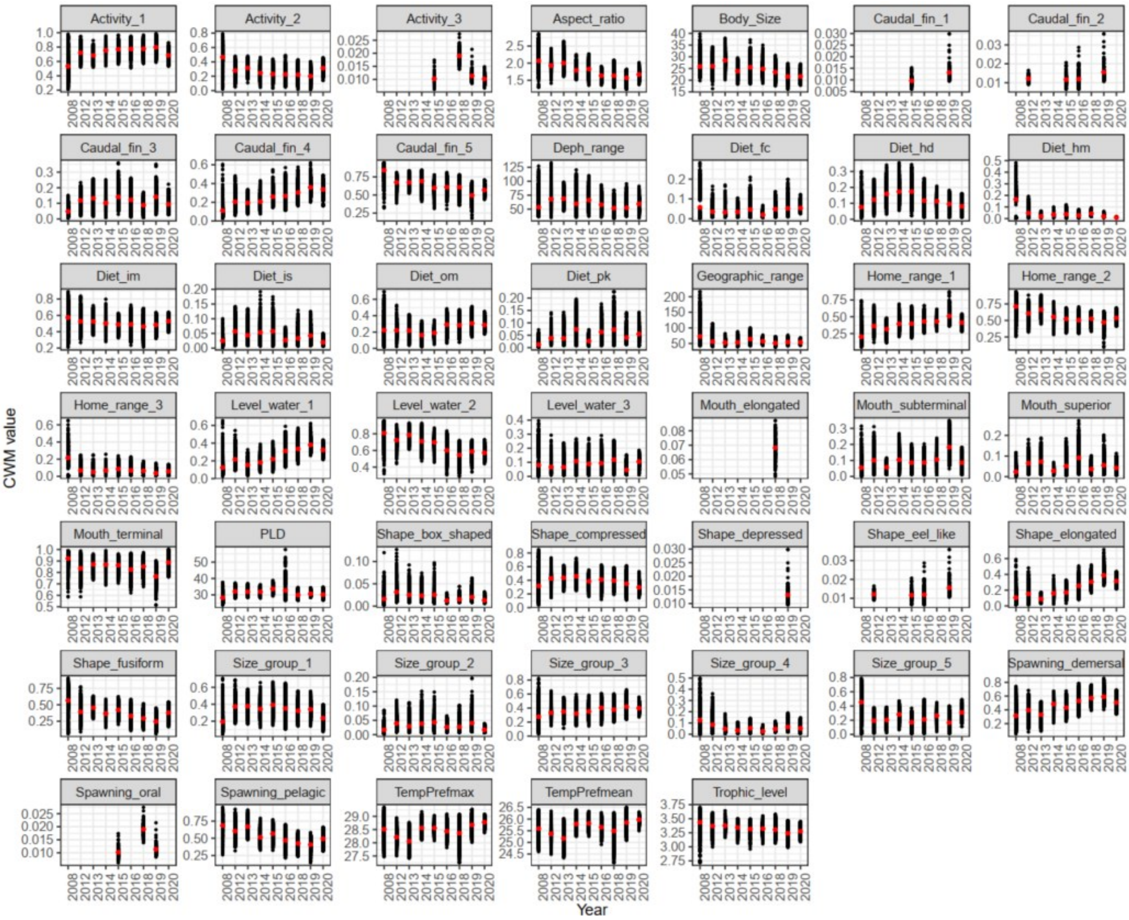

Figure S15. Time-series of the community weighted mean (CWM) traits of fish in **Deserta Island**. Note that for some years there is no data available. The black dots represent the range of 1000 CWM traits values calculated from the computed random communities. The red dots represent the mean CWM trait value for each year, and are the value used as input in the multiple factor analysis (MFA).

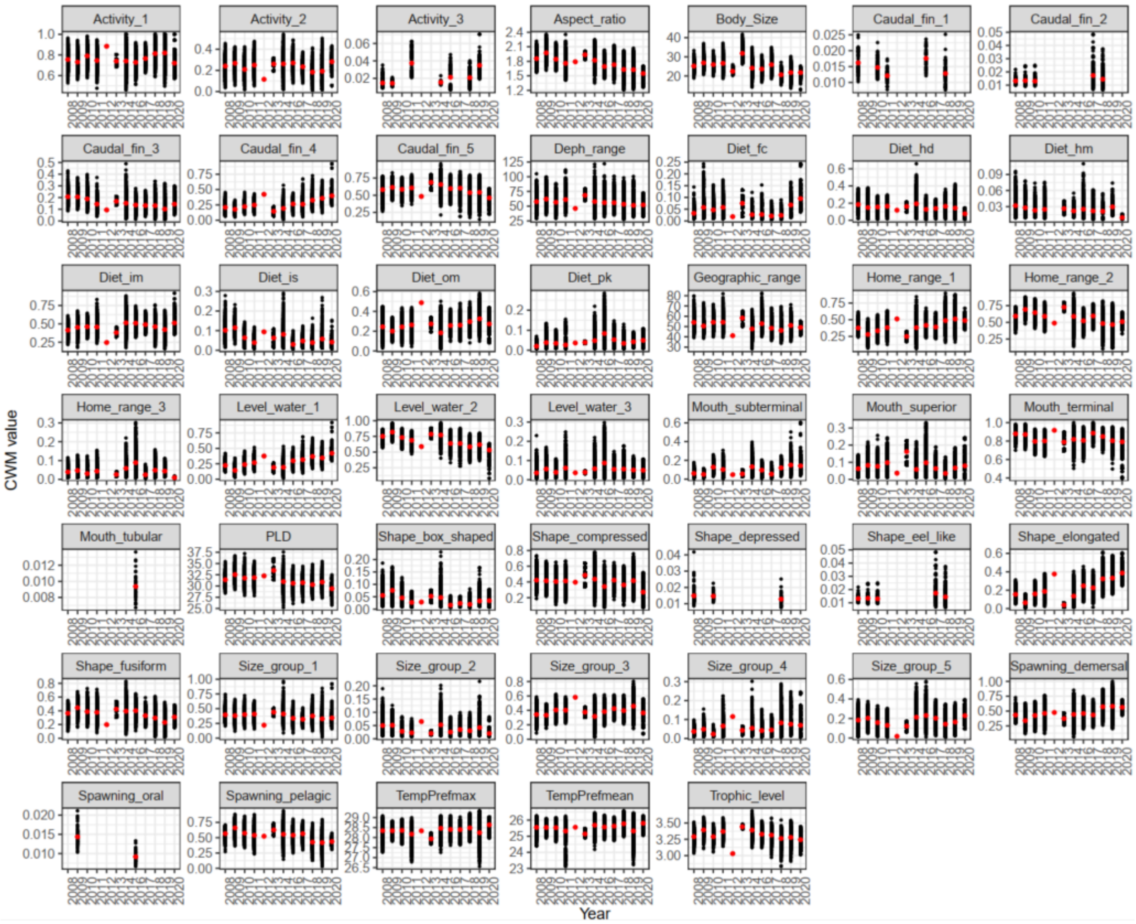

Figure S16. Time-series of the community weighted mean (CWM) traits of fish in **Arvoredo Island**. Note that for some years there is no data available. The black dots represent the range of 1000 CWM traits values calculated from the computed random communities. The red dots represent the mean CWM trait value for each year, and are the value used as input in the multiple factor analysis (MFA).

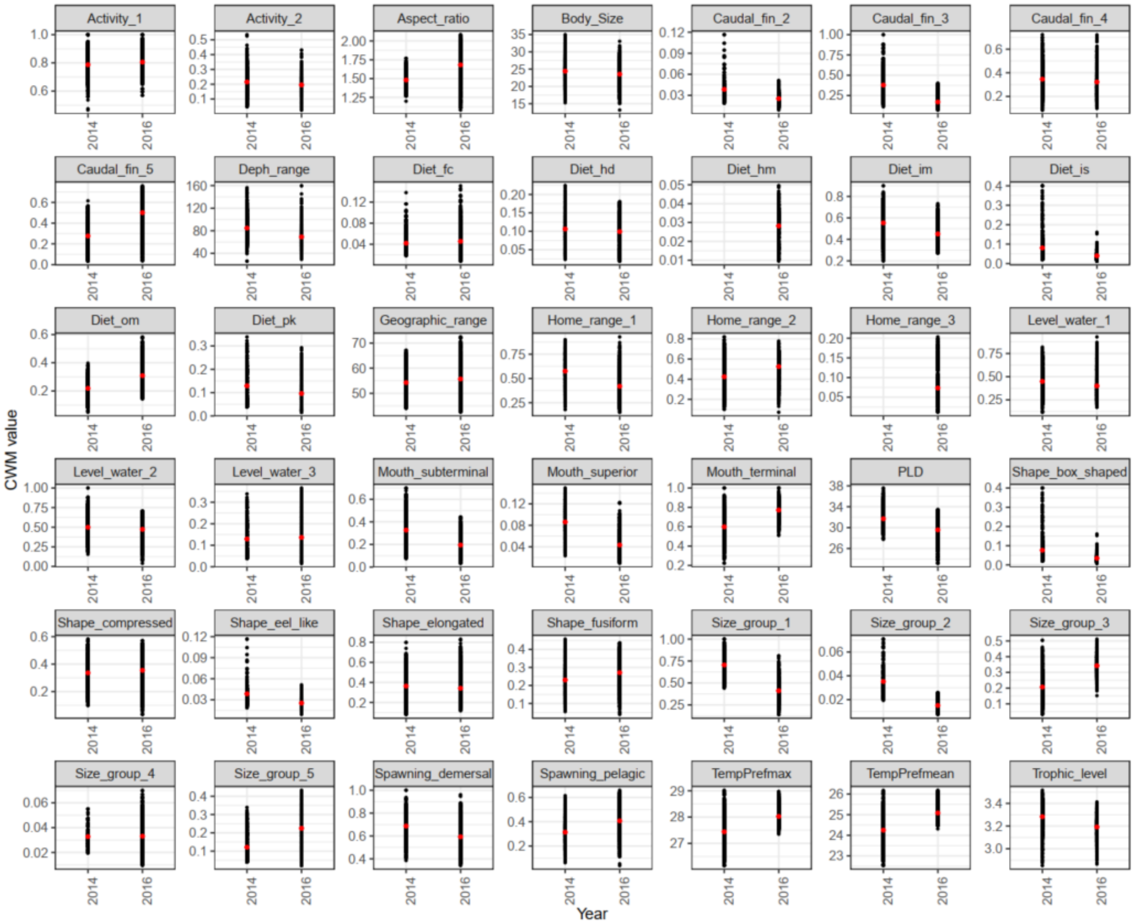

Figure S17. Time-series of the community weighted mean (CWM) traits of fish in **Aranhas Island**. Note that for some years there is no data available. The black dots represent the range of 1000 CWM traits values calculated from the computed random communities. The red dots represent the mean CWM trait value for each year, and are the value used as input in the multiple factor analysis (MFA).

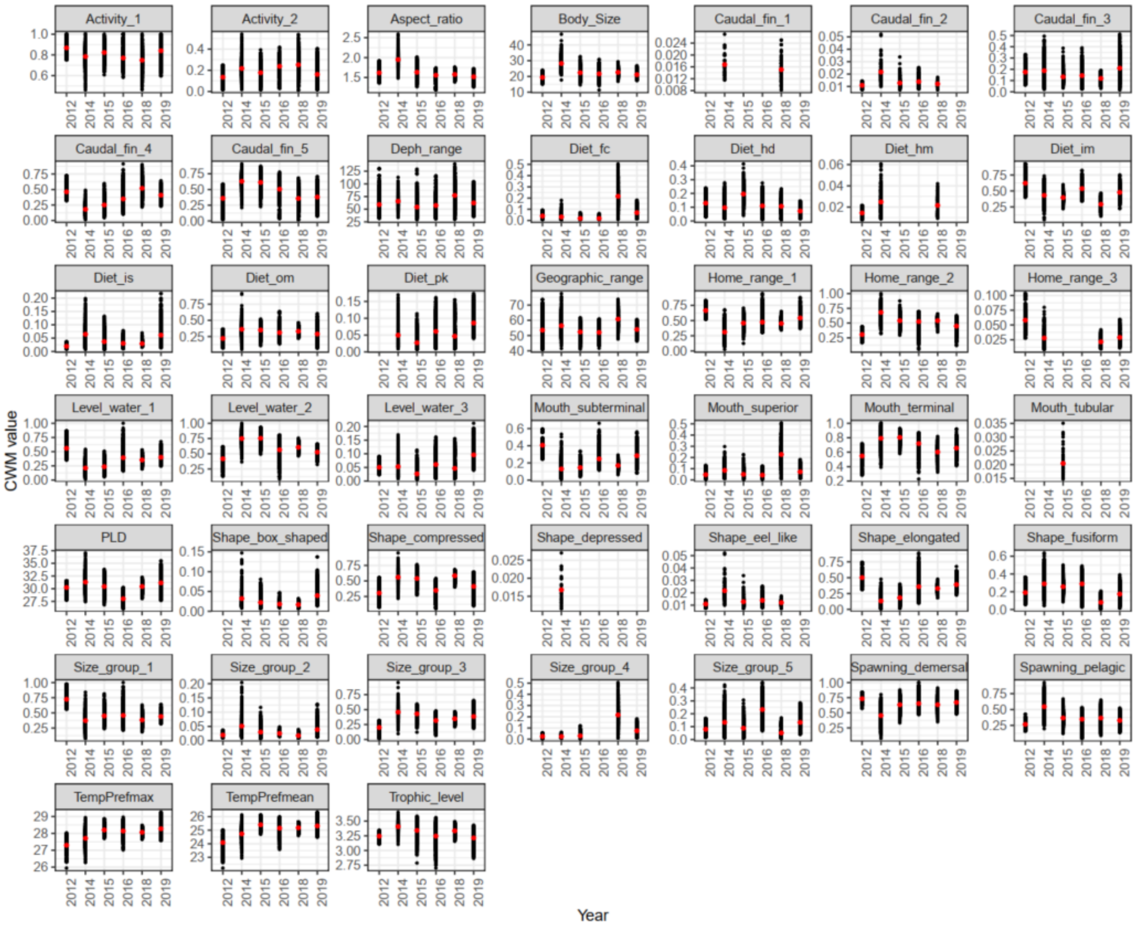

Figure S18. Time-series of the community weighted mean (CWM) traits of fish in **Xavier Island**. Note that for some years there is no data available. The black dots represent the range of 1000 CWM traits values calculated from the computed random communities. The red dots represent the mean CWM trait value for each year, and are the value used as input in the multiple factor analysis (MFA).

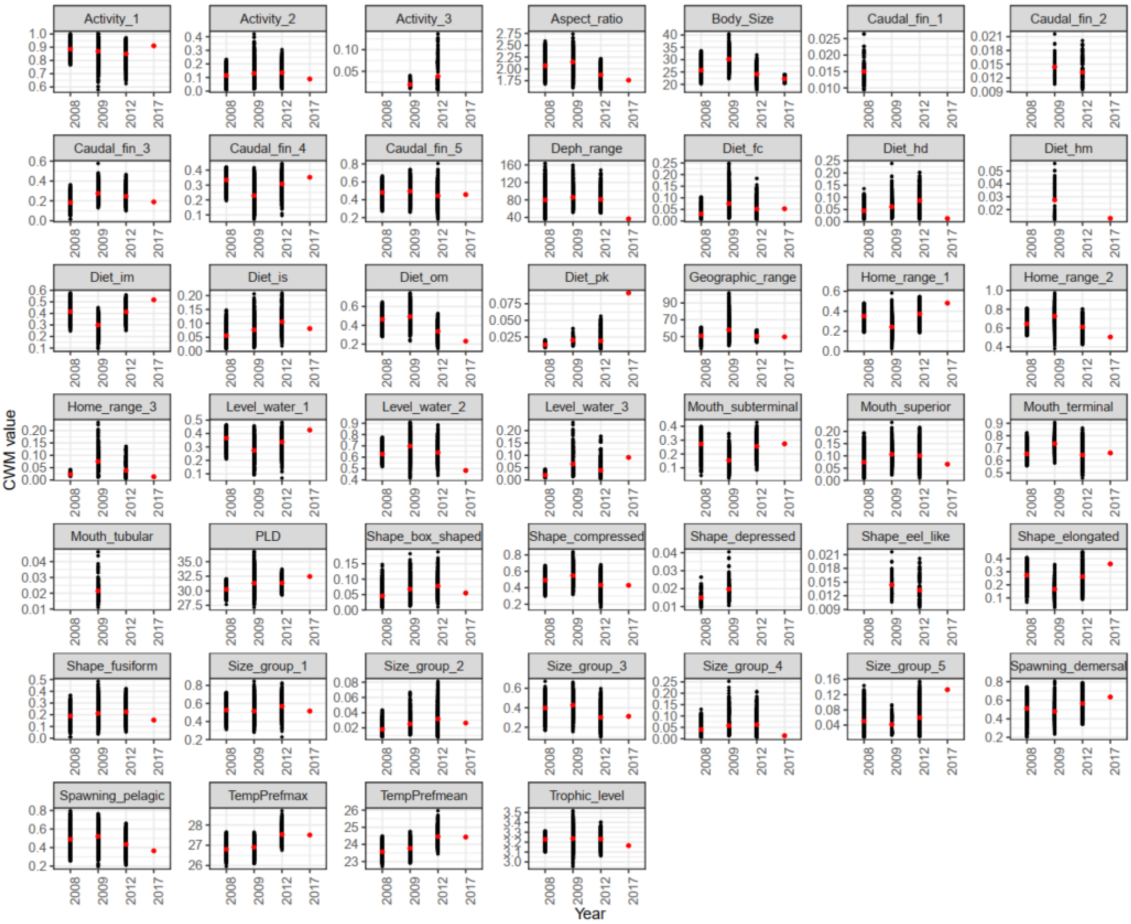

Figure S19. Time-series of the community weighted mean (CWM) traits of fish in **Campeche Island**. Note that for some years there is no data available. The black dots represent the range of 1000 CWM traits values calculated from the computed random communities. The red dots represent the mean CWM trait value for each year, and are the value used as input in the multiple factor analysis (MFA).

Figure S20. Time-series of the community weighted mean (CWM) traits of fish in **Moleques do Sul Island**. Note that for some years there is no data available. The black dots represent the range of 1000 CWM traits values calculated from the computed random communities. The red dots represent the mean CWM trait value for each year, and are the value used as input in the multiple factor analysis (MFA).

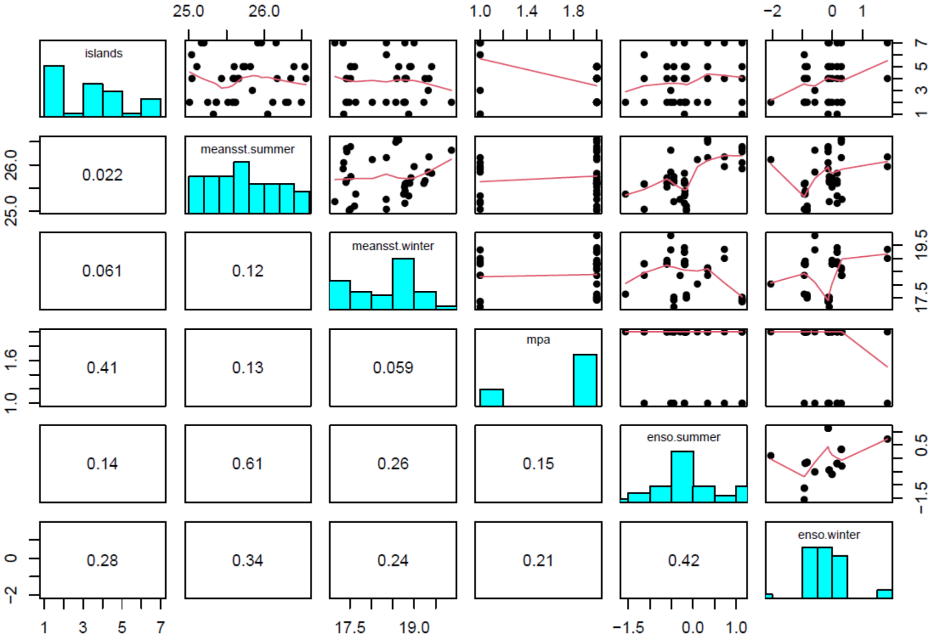

Figure S21. Pearson’s correlation among all environmental and geographical predictors considered in the models. Correlations r < ± 0.7 are considered as a cut-off to define collinearity among variables in GAMs (see Material and Methods, main text). Seven islands sampled (islands), Mean SST in summer season (meansst.summer), Mean SST in winter season (meansst.winter), Protection level – inside or outside Marine Protected Area (mpa), El Niño/Southern Oscillation (ENSO) in summer season (enso.summer), El Niño/Southern Oscillation (ENSO) in winter season (enso.winter).

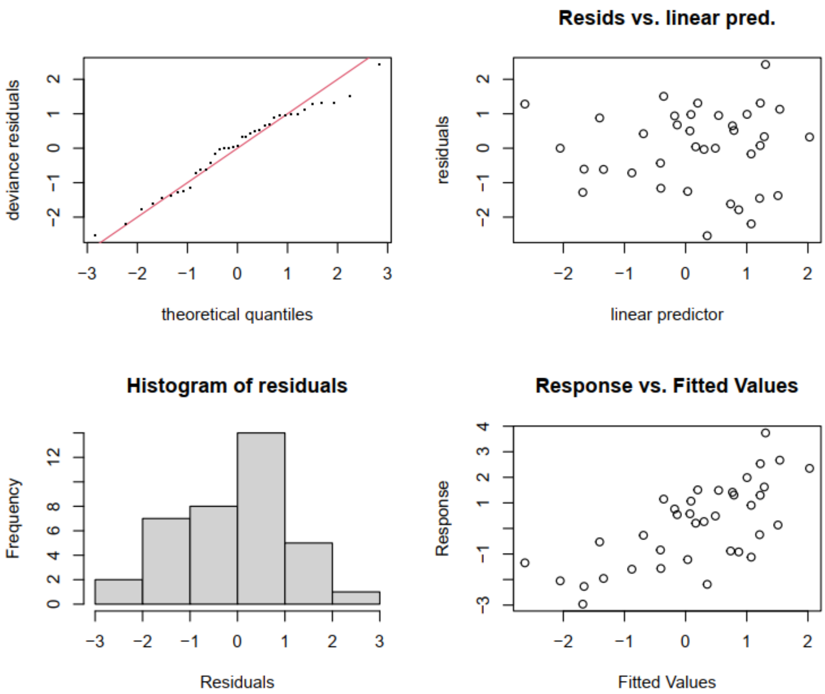

Figure S22. Validation of the generalized additive models for CWM trait dynamic (weighted by abundance) through residuals distributions.

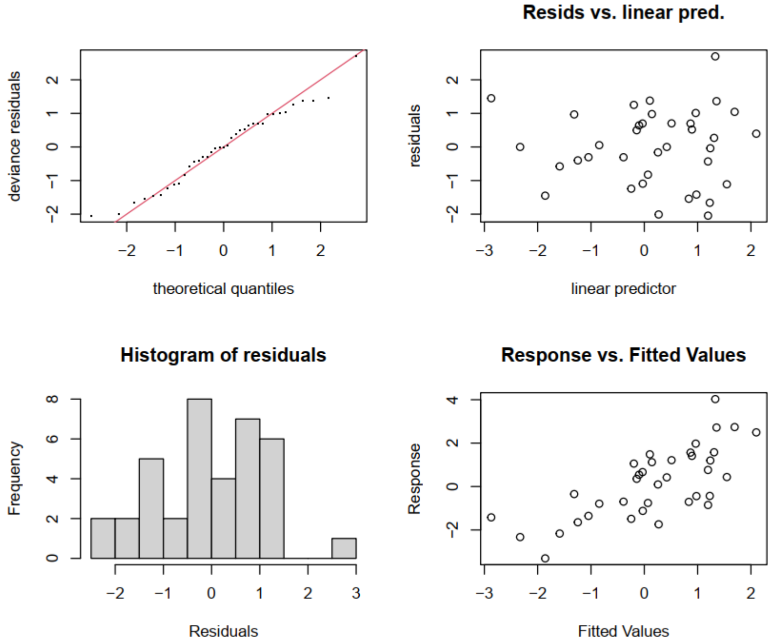

Figure S23. Validation of the generalized additive models for CWM trait dynamic (weighted by abundance) without fishing target species in the dataset.

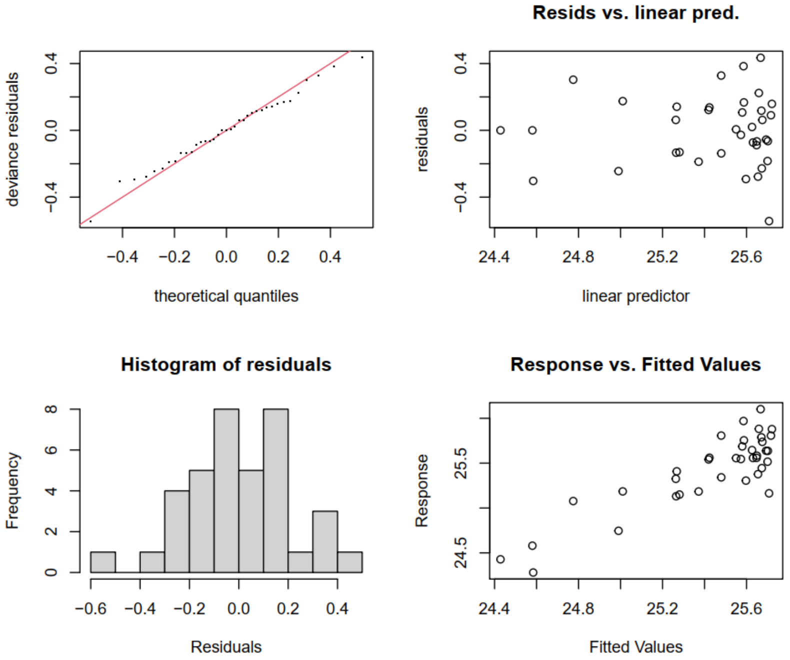

Figure S24. Validation of the generalized additive models for CTI values through residuals distributions.

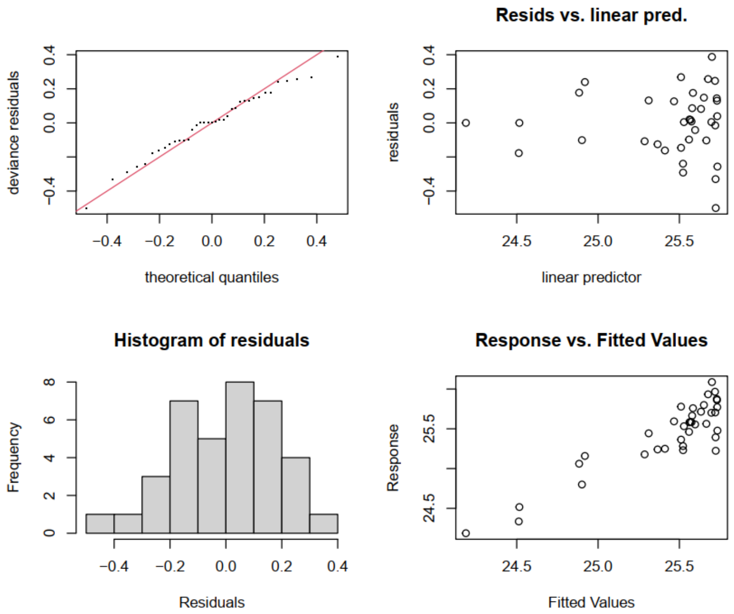

Figure S25. Validation of the generalized additive models for CTI values without fishing target species data through residuals distributions.

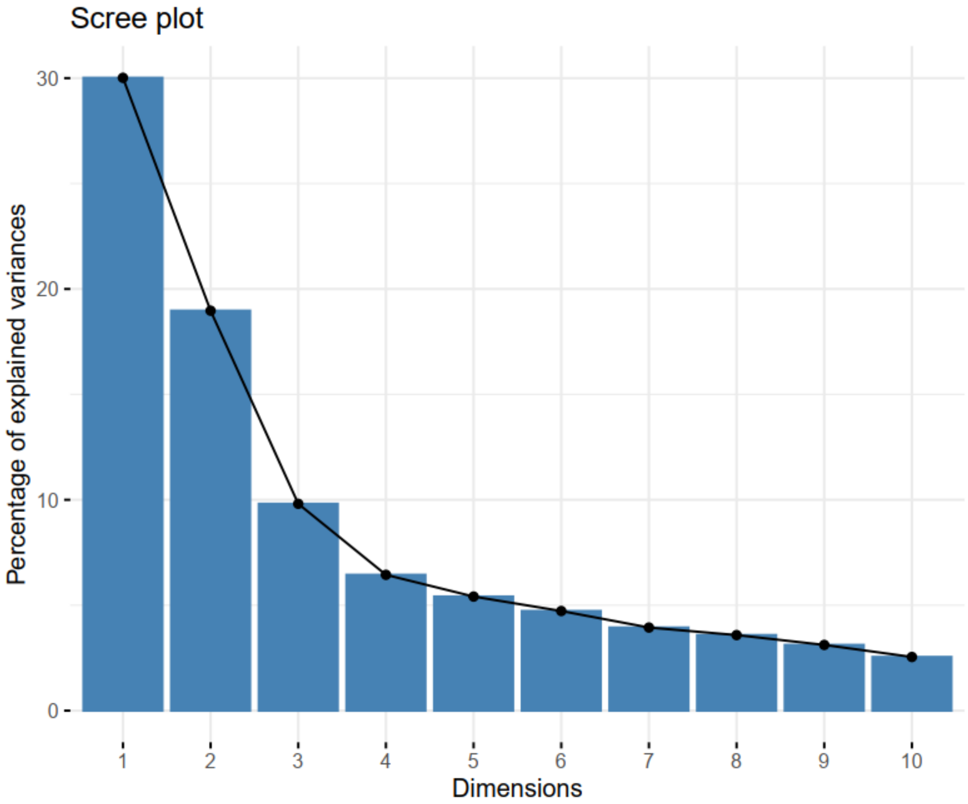

Figure S26. Visualization of the eigenvalues showing the percentage of variances (r^2) explained by each principal component of the MFA analysis considering whole community dataset.

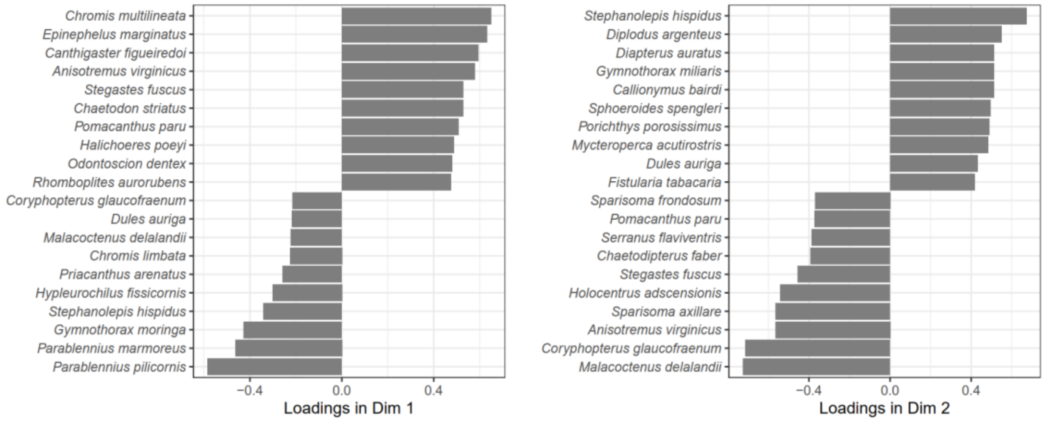

Figure S27. Highest and lowest Loadings of the reef fish species weighted by abundances (considering whole community dataset) along the first (a) and second (b) dimensions obtained from a multiple factor analysis (MFA) for the studied area. Species abundance data were included in the analysis as an additional group of variables and therefore did not impact the MFA results.

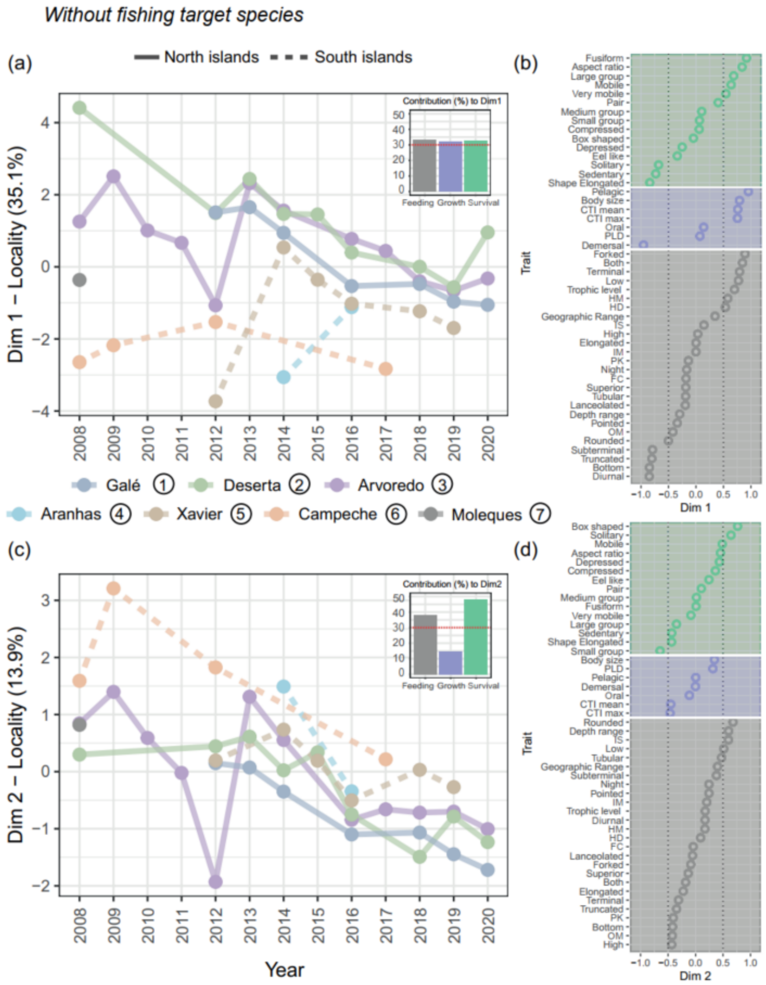

Figure S28. Temporal variation in the reef fish traits (CWM) weighted by abundances filtering fishing target species from the dataset in several islands of Santa Catarina - Brazilian province (Aranhas, Arvoredo, Campeche, Deserta, Galé, Moleques do Sul, and Xavier). The results were obtained from Multiple Factor Analysis (MFA). After bootstrapping, mean CWM values were used as input to conduct the MFA resulting in one single value per island per year. Time Time-series of the Dimension 1 (a) and Dimension 2 (c) of CWM traits variability and the contribution of each group of traits to the dynamic. CWM traits loadings displayed for Dim 1 (b) and Dim 2 (d). The groups of traits are represented by colors: gray (feeding), violet (growth), and green (survival). We include the black dotted line to clarify loadings values higher and lower than 0.5. Trait loadings > 0.5 were considered the most important for the temporal trends.

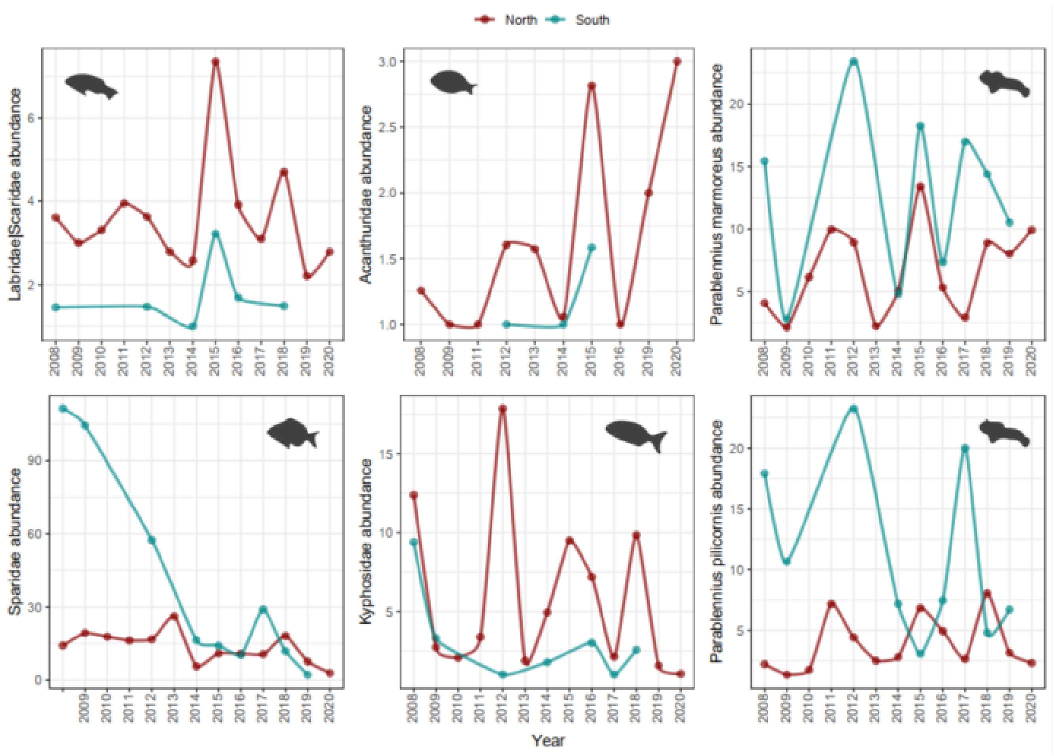

Figure S29. Temporal abundance of key families and species of reef fish inside (north) and outside (south) MPA islands of Santa Catarina - Brazilian province. To better visualize trajectories in species abundances, we grouped the values of the far north (Galé, Arvoredo and Deserta) and the southernmost locations (Aranhas, Xavier, Campeche and Moleques do Sul). Warm affinity: Labridae/Scaridae (a), Acanthuridae (b) and *Parablennius marmoreus* (c). Cold affinity: Sparidae (d) Kyphosidae (e) and *Parablennius pilicornis* (f).

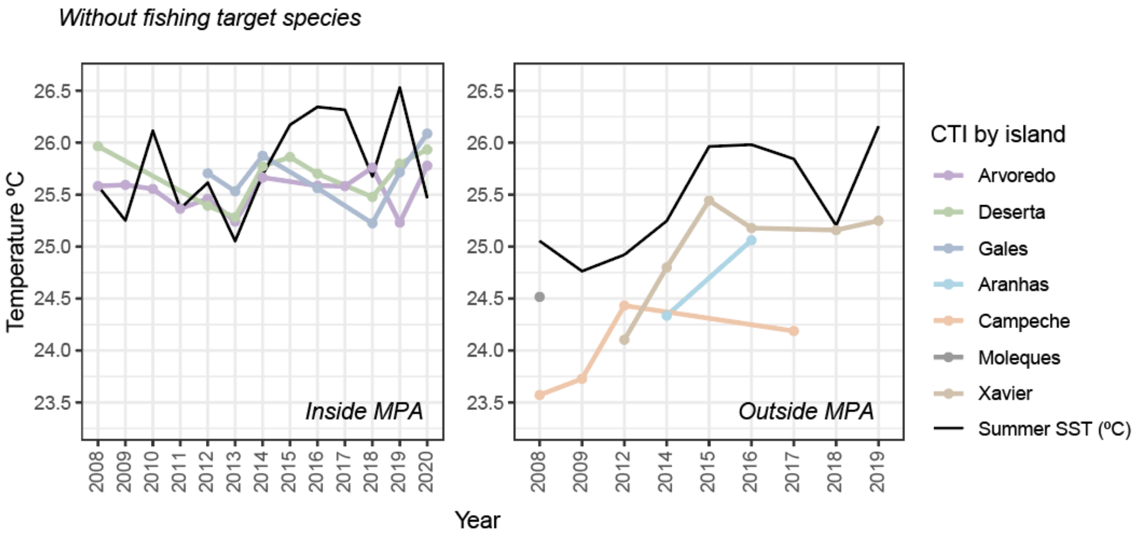

Figure S30. Sea surface temperature (SST) at islands located inside Marine Protected Area – MPA (North, left panel) and outside MPA (South, right panel) in Santa Catarina transition zone from 2008 to 2020. The associated Community Thermal Index (CTI) trends for reef fishes weighted by abundance were calculated using the dataset filtering fishing target species. CTI represents the mean of the Species Temperature Index for all species recorded in a survey weighed by their abundances and is presented here as the mean across all surveys in each year. SST represents the mean of sea surface temperature summer to each survey date.

Table S4. Pearson correlation coefficients between north and south islands isolated and combined.

Islands	*Pearson correlation*
Galé	0.008
Deserta	0.412
Arvoredo	-0.048
All north islands	0.156
Aranhas	1
Xavier	0.759
Campeche	0.219
Moleques	-
All south islands	0.679

CONCLUSÃO GERAL

Os resultados desta tese demonstram a importância da integração de métricas clássicas de estrutura de comunidades com abordagens funcionais para o entendimento da dinâmica das comunidades no espaço e tempo. Ressaltamos a separação das comunidades de peixes recifais da zona de transição do Atlântico Sudoeste em dois principais grupos: de espécies adaptadas a temperaturas quentes ao norte e espécies adaptadas a temperaturas frias ao sul. Temporalmente, também foi possível perceber dinâmicas distintas para as duas regiões em termos taxonômicos e funcionais. Tais variações ocorreram de maneira gradual, o que ressalta a resposta diferencial das comunidades (MIZEREK *et al.*, 2021; SOMMER *et al.*, 2017) quando comparadas à outras zonas de transição que experienciam mudanças de fase abruptas (HYNDES *et al.*, 2016; SMITH *et al.*, 2021)

Espacialmente, as comunidades de peixes recifais de Santa Catarina são estruturadas de acordo com suas amplitudes de tolerância térmica, ou seja, as variações de temperatura suportadas (Capítulo I). O comumente estabelecido padrão de distribuição de abundâncias (MCGILL *et al.*, 2007) também foi encontrado, onde poucas espécies contribuem para altos valores de densidade e frequência de ocorrência média por unidade amostral e muitas espécies aparecem raramente e em poucos indivíduos. As características tróficas das espécies também revelam associações com os aspectos oceanográficos da região, por exemplo, a alta abundância de planctívoros em ilhas mais ao norte compostas por águas mais claras e com maior abundância de fito e zooplâncton (LOPES *et al.*, 2006).

Ao longo do tempo, apesar do aumento da temperatura superficial do mar, não foram encontradas evidências de homogeneização das comunidades ao norte e ao sul (Capítulo II), como predito pela literatura (MAGURRAN *et al.*, 2015). Os resultados revelam maiores diferenças na composição taxonômica do que funcional, principalmente na região sul, composta por ilhas expostas à menores temperaturas e aos impactos da pesca. Isso ressalta a redundância funcional encontrada nas ilhas ao sul, suportando a ideia de que poucas espécies são capazes de manter funções ecológicas básicas nos ecossistemas apesar do número de espécies (MOUILLOT *et al.*, 2014). Além, da não-homogeneização, as espécies que mais contribuem para a variação temporal em termos taxonômicos são aquelas com combinações comuns de atributos, representando espécies recorrentes nos recifes e que contribuem com funções chave de produção secundária e excreção de nutrientes.

Quando avaliadas individualmente, as comunidades de peixes de cada uma das ilhas exibiram reorganização em termos dos atributos ao longo do tempo, a qual foi influenciada pela temperatura superficial do mar (Capítulo III). Tal modificação apresenta potenciais implicações para o funcionamento dos recifes, pois as comunidades que tinham alta importância de espécies grandes e de alto nível trófico no início da série passaram a ser compostas por alta dominância de espécies pequenas e crípticas em anos recentes. Ao longo do tempo, tal substituição pode potencialmente gerar variações nas redes tróficas considerando a contribuição de espécies crípticas na produção de biomassa consumível nos recifes (BRANDL *et al.*, 2019). Adicionalmente, outro atributo com marcante variação ao longo do tempo foi o relacionado à tolerância térmica (*Community Thermal Index* - *CTI*). Isso demonstra que as comunidades de peixes na zona de transição do Atlântico estão seguindo variações na temperatura superficial do mar, o que pode implicar variações futuras de distribuição geográfica em virtude das mudanças climáticas.

Finalmente, esta tese contribui para um entendimento mais holístico das comunidades de peixes recifais em zonas de transição considerando a dinâmica espacial e temporal dentro de um contexto de variações de temperatura. Estes resultados também fornecem base e perspectivas de estudos futuros englobando diferentes aspectos ambientais, bem como funções ecossistêmicas na dinâmica espacial e temporal das comunidades. Considerando as previsões futuras de aquecimento dos oceanos (BRAUKO *et al.*, 2020; FRÖLICHER; FISCHER; GRUBER, 2018; IPCC, 2018), esta abordagem pode contribuir na previsão de como as comunidades responderão às variações climáticas futuras. Conhecer a dinâmica das comunidades no espaço e no tempo através de séries temporais permite o entendimento de quais atributos são mais afetados pelas variações do clima atual, provendo informações base para modelos complexos de estimativas de distribuição, como por exemplo, Modelos Hierárquicos de Comunidades de Espécies (do inglês: *Hierarchical Modelling of Species Communities* - HMSC).

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APÊNDICE A – TimeFISH: Long-term assessment of reef fish assemblages in a transition zone in the Southwestern Atlantic.

Base de dados referente aos censos visuais coletados nas ilhas de Santa Catarina e utilizados nesta tese, publicados na revista *Ecology*.

METADATA

CLASS 1. DATA SET DESCRIPTORS

A. Data set identity: *TimeFISH: Long-term assessment of reef fish assemblages in a transition zone in the Southwestern Atlantic.*

B. Data set identification code:

- TimeFISH_census_data.csv
- TimeFISH_taxonomic_information.csv
- TimeFISH_location_information.csv

C. Data set description

1. Originators: Juan P. Quimbayo[1], Lucas T. Nunes[2], Fernanda C. Silva[2], Antônio B. Anderson[3], Diego R. Barneche[4,5], Angela M. Canterle[2], Isadora Cord[2], Andrea Dalben[6], Débora S. Ferrari[2], Luisa Fontoura[7], Thiago M.J. Fiuza[8], Ana M.R. Liedke[2], Guilherme O. Longo[9], Renato A. Morais[10], Alexandre C. Siqueira[11], Sergio Ricardo Floeter[2]

[1] Center for Marine Biology, University of São Paulo, São Sebastião, Brazil.

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[3] Federal University of Espírito Santo, Vitória, Brazil.

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[5] Oceans Institute, The University of Western Australia, Crawley, Australia.

[6] Biosonar institution, Florianopolis, Brazil.

[7] School of Natural Sciences, Macquarie University Sydney, New South Wales, Australia.

[8] Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Australia.

[9] Marine Ecology Laboratory, Department of Oceanography and Limnology, Federal University Rio Grande do Norte, Brazil.

[10] CRIOBE École Pratique des Hautes Études, Université Paris Sciences et Lettres, France.

[11] Research Hub for Coral Reef Ecosystem Functions, College of Science and Engineering, James Cook University, Townsville, Australia.

2. Abstract: The TimeFish database provides the first public time-series dataset on reef fish assemblages in the Southwestern Atlantic (SWA), comprising 15 years of data (2007-2022) based on standardized Underwater Visual Censuses (UVCs). The rocky reefs covered by our dataset are influenced by pronounced seasonal cycles of ocean temperatures with warm tropical waters from the Brazil Current in the summer (~27°C) and colder waters from the La Plata River Plume discharge and upwelling from the South Atlantic Central Water in the winter (~18°C). These oceanographic conditions characterize this area as the southernmost tropical-subtropical climatic transition zone in the Atlantic Ocean. As a result, reef fish assemblages comprise both tropical and subtropical species. All records included in TimeFish were collected using UVCs, a non-destructive method that allows the estimation of fish species richness,

abundance, and body size distributions. UVCs were performed through 40 m^2 belt transects by scuba diving in nine locations along the southern Brazilian coast (25°S – 29°S). Four of these locations lie within the boundaries of the no-entry Arvoredo Marine Biological Reserve, where fishing and recreational activities are forbidden, and the remaining locations are unprotected from these activities. During each belt transect, a diver swam at a constant depth above and parallel to the reef, identifying fish species, counting the number of individuals, and estimating the total body length (Lt in cm) of all detected individuals. All fish individuals in the water column (up to 2 m above the substratum) and at the bottom were targeted. A total of 202,965 individuals belonging to 163 reef fish species and 53 families were recorded across 1,857 UVCs. All survey campaigns were funded by either public or mixed capital (private-public) sources, including seven grants from the Brazilian federal and Santa Catarina state government. Part of the data have already been used in multiple MSc and PhD theses and scientific articles. TimeFISH represents an important contribution for future studies aiming to examine temporal and spatial variations of reef fish assemblages in transition zones. No copyright restrictions apply to the use of this data set, other than citing this publication.

D. Keywords: Abundance, fish body size, fish richness, rocky reefs, temporal series.

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description

1. Identity: *TimeFISH*: Long-term assessment of reef fish assemblages in a transition zone in the Southwestern Atlantic.

2. Originators: Juan P. Quimbayo, Lucas T. Nunes, Fernanda C. Silva, Antônio B. Anderson, Diego R. Barneche, Angela M. Canterle, Isadora Cord, Andrea Dalben, Débora S. Ferrari, Luisa Fontoura, Thiago M.J. Fiuza, Ana M.R. Liedke, Guilherme O. Longo, Renato A. Morais, Alexandre C. Siqueira, Sergio Ricardo Floeter.

3. Period of study: Underwater visual censuses started in 2007 and were performed in all austral summers since. The data collection is still ongoing and presented here until the 2022 campaign.

4. Objectives: (1) To record reef fish species richness, abundance, and body size in nine locations over time in the southern transition zone in the Southwestern Atlantic Ocean. (2) To provide an open dataset supporting future investigations of temporal trends in reef fish assemblages in transition zones.

5. Abstract: Same as above

6. Sources of funding:

- Projeto Ilhas do Sul. PI: Sergio R. Floeter (Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq: 475367/2006-5).
- MCT-Jovens Pesquisadores. PI: Sergio R. Floeter (Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq: 571295/2008-8).
- Rede Nacional de Pesquisa em Biodiversidade Marinha (SISBIOTA-Mar). PI: Sergio R. Floeter (Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq: 563276/2010-0).
- Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina. PI: Sergio R. Floeter (FAPESC: 6308/2011-8).
- Project MAArE – Monitoramento Ambiental da Reserva Biológica Marinha do Arvoredo e Entorno. PI: Barbara Segal (PETROBRAS).
- Projeto Biodiversidade Marinha do Estado de Santa Catarina. PI: Alberto Lindner (FAPESP 4302/2010-8)
- Programa de monitoramento de ambientes recifais na Reserva Biológica Marinha do Arvoredo. Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

B. Specific subproject description

1. Site description

Data assembled in the TimeFISH database were collected in nine locations on the coast of Santa Catarina State (Figure 1). This area represents approximately 7% of the Brazilian coast (Diehl and Horn Filho 1996). The region is under the influence of two main marine water systems: the Brazil current, which carries warm tropical waters from the north, and the La Plata River plume discharge, which transports cold waters from the south. Additionally, the waters beyond the coast are influenced by the South Atlantic Central Water, also a cold-water system. Due to these specific oceanographic conditions, this region is recognized as a transition zone (i.e., where both tropical and temperate species distributions overlap and changes in sea surface temperature are most pronounced, Ferro and Morrone 2014). The southernmost limit of distribution of tropical reef fish fauna in the Southwester Atlantic is located along the coast of Santa Catarina State (Anderson et al. 2015, 2020, Pinheiro et al. 2018). Four sampled locations are situated within the limits of the No-entry Arvoredo Marine Biological Reserve, whereas the remaining locations lie in unprotected areas (Figure 1). The Arvoredo Marine Biological Reserve was established in 1990, and encompasses an area of 17,800 ha, characterizing the only nearshore no-take and no-entry Brazilian MPA (Magris et al. 2020). It comprises three islands: Arvoredo (-27.17 | -48.36), Deserta (-27.16 | -48.19), and Galé Island (-27.10 | -48.24; Figure 1). Part of Arvoredo Islands is located within the MPA (-27.17 | -48.36), and other part outside the MPA (-27.28 | -48.37). The surveyed locations outside of the marine reserve include one continental location in Porto Belo (-27.7 | -48.31), and four in coastal islands, Aranhas (-27.29 | -48.21), Campeche (-27.41| -48.27), Moleques do Sul (-27.50 | -48.25) and Xavier Island (-27.36 | -48.23; Figure 1).

The benthic communities include a diverse assemblage of algal turfs, macroalgae and zoanthids that are common across the sampled locations (Horta et al. 2008, Pascelli et al. 2013, Aued et al. 2018). At Galé Island, we also find free-living colonies of *Madracis decactis* that occur in sandy substratum (Capel et al. 2012). One location in the northern part of Arvoredo Island (inside MPA) contain a relatively extensive rhodolith bed occurs (Horta et al. 2008, Pascelli et al. 2013). The most recent and comprehensive local fish species checklist published for the Santa Catarina State reported 278 reef fish species belonging to 170 genera and 74 families (Anderson et al. 2015). Approximately 8.3% of these species are classified as threatened by the International Union for Conservation of Nature (IUCN), comprising mostly top predators and large Brazilian endemic herbivores (Anderson et al. 2015).

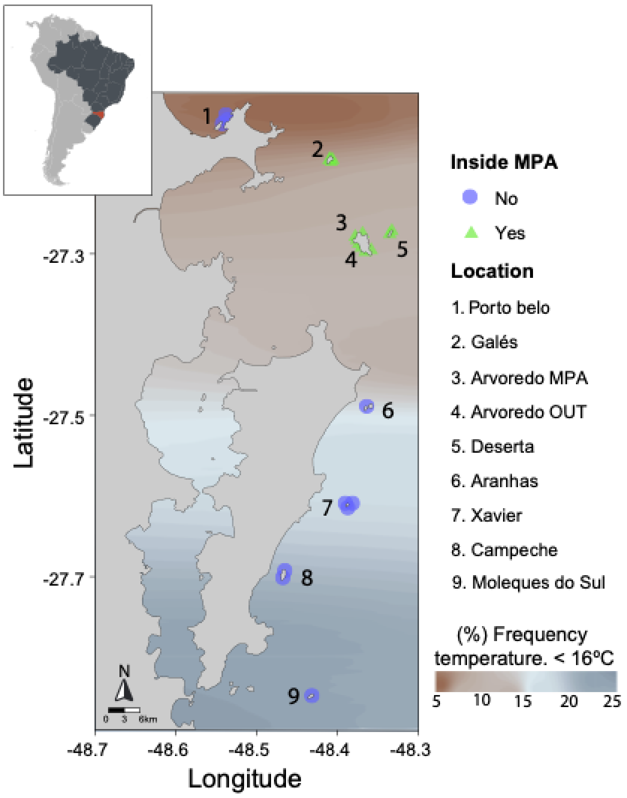

Figure 1. Geographical position of the nine locations sampled over 15 years in the Southwestern Atlantic. Sea surface temperature data were extracted from Faria-Junior and Lindner (2019).

2. Experimental or sampling design

Underwater visual censuses

Reef fish assemblages were sampled using Underwater Visual Censuses (UVCs), a non-destructive technique that provides estimates of species richness, abundance, and body size with minimal habitat impacts (Brock 1954, Kulbicki 1998). During the UVCs (20 X 2m = 40m²), all fish species observed in the water column and at or near the bottom were identified, counted, and had their individual body size estimated. To perform such activity, a diver first swam horizontally and parallel to the rocky shore while simultaneously laying out a 20 m measuring tape and writing down all information assessed from the species observed in the water column. Then, the diver swam back retrieving the measuring tape and writing down information on all detected species associated with the benthos. Such technique has been repeatedly and successfully used along the Brazilian coastal and oceanic reefs (Floeter et al. 2007, Krajewski and Floeter 2011, Pinheiro et al. 2011, Longo et al. 2014, 2015, Luiz et al. 2015, Morais et al. 2017, Quimbayo et al. 2019), in other regions in the Atlantic Ocean (Maia et al. 2018, Freitas et al. 2019), and for regional or global assessments of reef fish assemblages (Barneche et al. 2019, Inagaki et al. 2020, Quimbayo et al. 2021a). A total of 1,857 UVCs were performed throughout the last 15 years across the nine locations sampled in Santa Catarina (Figure 2).

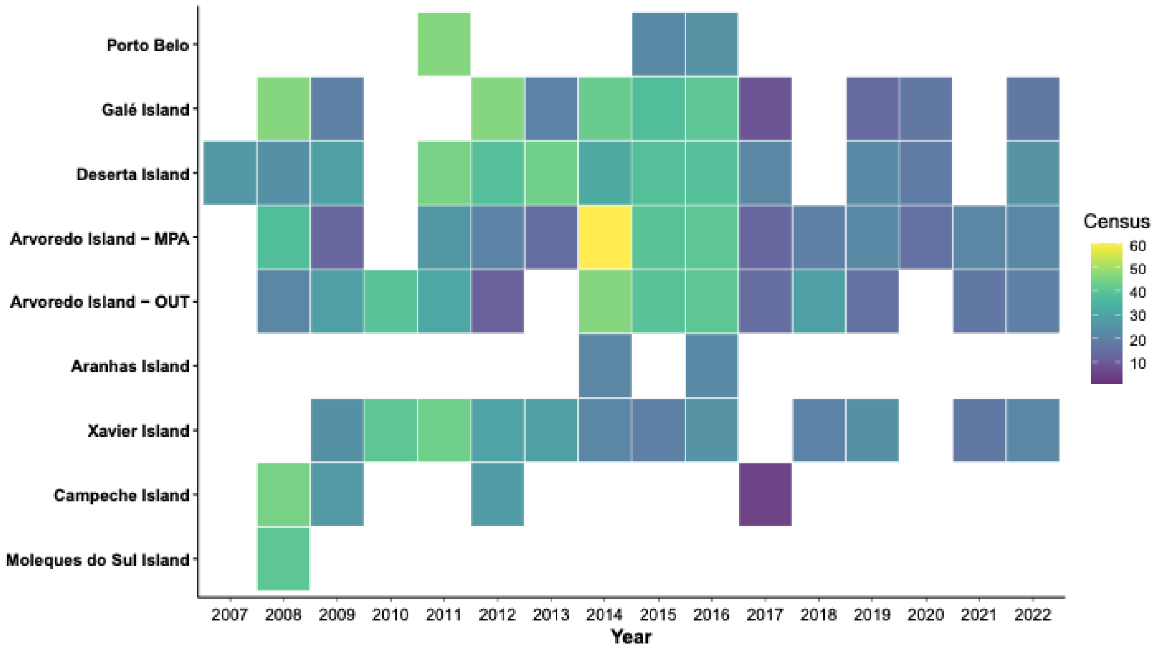

Figure 2. Number of underwater visual censuses performed over 15 years in nine locations in the Southwestern Atlantic. The warmer colors depict a higher sampling effort. This uneven sampling effort is associated with the lack of consistent funding to sample all locations over time.

A total of 202,965 individuals from 163 reef fish species were recorded across all surveys included in the TimeFISH database. This set of species represents 58% of the reef fish fauna reported for the whole Santa Catarina state (Anderson et al. 2015). Parts of the dataset have supported over 20 international and national publications or reports, highlighting the importance of evaluating temporal and spatial patterns of reef fish in transition zones. As an example, the detection and assessment of the population density patterns of the invasive *Chromis limbata* in the study area emphasizes the benefits of such long-term monitoring programs (Anderson et al. 2017, 2020).

3. Research methods

Taxonomic and systematics

The taxonomic classification followed the Eschmeyer's Catalog of Fishes (Fricke et al. 2020).

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

1. Latest update: 2022

2. Latest archive data: 2022

3. Metadata status: Metadata are complete

4. Data verification: All data were reviewed according to CLASS V section B and checked for any input errors.

B. Accessibility

1. Storage location and medium: All data and metadata are stored with this publication in the journal *Ecology*.

2. Contact persons:

- Juan Pablo Quimbayo, Center for Marine Biology, University of São Paulo, São Sebastião, Brazil. Email: quimbayo.j.p@gmail.com
- Sergio Ricardo Floeter, Marine Macroecology and Biogeography Laboratory, Federal University of Santa Catarina, Florianópolis, Brazil. Email: sergio.floeter@ufsc.br

3. Copyright or propriety restrictions: There are no copyright or proprietary restrictions for research or teaching proposes.

4. Proprietary restrictions: None.

5. Citation: This paper.

CLASS IV. DATA STRUCTURAL DESCRIPTORS

A. Data set files

1. Identity

- TimeFISH_census_data.csv
- TimeFISH_taxonomic_information.csv
- TimeFISH_location_information.csv

2. Size

- TimeFISH_census_data: [27,377 rows + header, 5 columns; (1.3MB)]
- TimeFISH_taxonomic_information: [163 rows + header, 9 columns; (14KB)]
- TimeFISH_location_information: [1,958 rows + header, 23 columns; (363KB)]

3. Format and storage: Digital data file in *.csv

4. Header information: See column description in section B.

5. Alphanumeric information: Mixed.

B. Variable information

Each row of the data files represents a unique value, i.e., one species observed in one location and one year (Table 1).

Table 1. List of column names found in TimeFISH

Variable name	Variable definition	Nature	Units	Variable name
Province	Marine biogeographic province defined by Spalding et al. (2007)	Categorical (nominal)		Province

State	Brazilian political federation unit	Categorical (nominal)		State
Location	Marine location where the belt transects were performed	Categorical (nominal)		Location
Site	Sites where the belt transects were performed (smallest-scale unit within the location)	Categorical (nominal)		Site
Thermal_category	Classification of locations according to the water thermal regime, estimated from the mean summer sea surface temperature (warm locations are those with a mean temperature higher than 24°C, and cool locations are those with a mean temperature lower than 24°C)	Categorical (nominal)		Thermal_category
No_take_zone	Whether or not inside a No-take area	Categorical (nominal)		No_take_zone
Longitude	Longitude for the sampling site in decimals (Western: -180 to 0, Eastern: 0 to 180)	Continuous	Degrees	Longitude
Latitude	Latitude for the sampling position in decimals (Southern: -90 to 0, Northern: 0 to 90)	Continuous	Degrees	Latitude
ntransect	Number tag of the belt	Discrete		ntransect

	transect in the year sampled			
transect_id	Transect identification following the combination: year + ntransect	Categorical (nominal)		transect_id
Observer	Observer name	Categorical (nominal)		Observer
Sampling_method	Sampling method used (UVC)	Categorical (nominal)		Sampling_method
Sampling_area_m2	Transect area of 20x2 (40m^2)	Continuous	Square meters	Sampling_area_m2
Day	The day when sampling occurred	Discrete		Day
Month	The month when sampling occurred	Discrete		Month
Year	The year when sampling occurred	Discrete		Year
Sampling_season	Season during which the sampling occurred. We considered the climatic classification of the southern hemisphere	Categorical (nominal)		Sampling_season
Depth	Depth at which the belt transect was performed. Expressed in meters	Continuous	Meter	Depth
Temperature	Water temperature recorded from dive computer, for each belt transect	Continuous	Degrees Celsius	Temperature
Complexity	Substratum complexity visually estimated in each belt transect in three levels (Figure 3): 1=low complexity (Flat large	Discrete		Complexity

	boulders with very few crevices, which have low coverage and diversity of benthic organisms); 2=medium complexity (Rounded large boulders with some crevices and high coverage and diversity of benthic organisms); 3=high complexity (A mix of large and small boulders with many crevices and holes associated with high coverage and diversity of benthic organisms).			
Visibility	The horizontal visibility estimated in each belt transect and expressed in meters	Continuous		Visibility
Start_time	Exact starting time of the belt transect	Continuous	Hour	Start_time
End_time	Exact finishing time of the belt transect	Continuous	Hour	End_time
Biotop	Biotope on the reef where the belt transect was performed. Slope (all rock reef that contain boulders, crevices, holds and benthic communities associate), rhodolith	Categorical (nominal)		Biotop

	(bottom cover 100% rhodolite), interface (intercept between rocky reef and sand bottom), and sand (bottom cover more than 80% sand)		
Trophic_group_1	Trophic group based on diet data available in the literature (see Quimbayo et al. 2021b) Levels: hd = herbivore detritivore hm = macroalgivore im = mobile invertebrate feeder is = sessile invertebrate feeder pk = planktivore om = omnivore fc = fish & cephalopods	Categorical (nominal)	Trophic_group_1
Trophic_group_2	Trophic group based on local diet analyses Levels: herb_detri = herbivore detritivore macroalgivore = herbivore macroalgivore minv = mobile invertebrate feeder sinv = sessile invertebrate feeder plank = planktivore mcar = macrocarnivore	Categorical (nominal)	Trophic_group_2

	(fish and Brachyura) omni = omnivore			
Family	Family name following the Eschmeyer’s Catalog of Fishes	Categorical (nominal)		Family
Genus	Genus name following the Eschmeyer’s Catalog of Fishes	Categorical (nominal)		Genus
Species	Species name following the Eschmeyer’s Catalog of Fishes	Categorical (nominal)		Species
Fishbase_code	Species code following the FishBase database	Discrete		Fishbase_code
Species_code	Code defined by the combination of the first three letters from the genus column and the three letters from the species column	Categorical (nominal)		Species_code
Total length	Visually estimated fish total length	Continuous	Centimeters	Total length
Abundance	Absolute number of individuals	Discrete		Abundance
a	Length-weight coefficient: Weight = a x Length^b	Continuous	Grams/ Centimeters^b	a
b	Length-weight coefficient: Weight = a x Length^b	Continuous		b

Missing value code: NA

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data acquisition: See details in the section Class II, more specifically the Data Collection.

B. Quality assurance/quality control procedures: The name of all fish species observed in the UVCs over 15 years, were reviewed and updated according to the Eschmeyer's Catalog of Fishes (Fricke et al. 2020). The fish trophic groups and species-specific length-weight conversion coefficients were extracted from Quimbayo et al. (2021b).

C. Computer programs and data processing algorithms

Data processing was performed in the R environment version 4.0.2 (R Core Team 2020) using the packages "dplyr" (Wickham et al. 2022), "ggplot2" (Wickham 2016), and "tidyr" (Wickham and Girlich 2022).

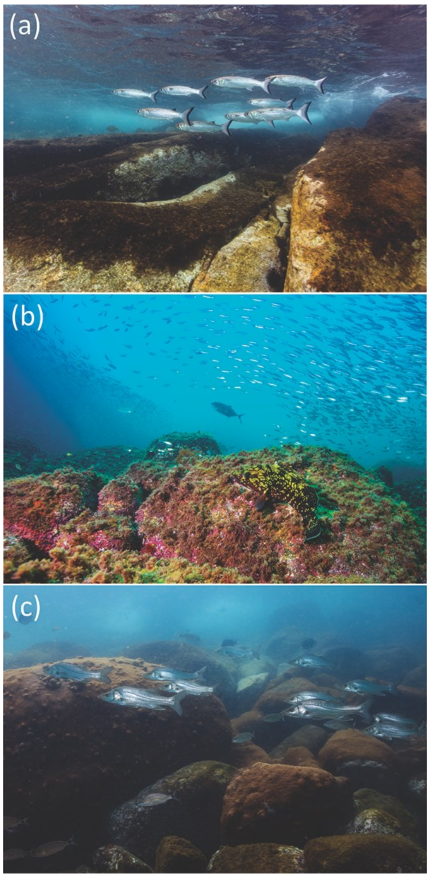

Figure 3. Types of substratum complexity estimated in each belt transect. a) Low complexity = 1 (Flat large boulders with very few crevices, which have low coverage and diversity of benthic organisms); b) medium complexity = 2 (Rounded large boulders with some crevices and high coverage and diversity of benthic organisms); and c) high complexity = 3 (A mix of large and small boulders with many crevices and holes associated with high coverage and diversity of benthic organisms). Images: J.P. Krajewski.

Acknowledgments

We thank all public and private national institutions for their financial support over these 15 years (Conselho Nacional de Desenvolvimento Científico e Tecnológico CNPq, Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina FAPESC, PETROBRAS, and Instituto Chico Mendes de Conservação da Biodiversidade ICMBio). We also thank all past and present members from the Laboratório de Biogeografia e Macroecologia

Marinha at Universidade Federal de Santa Catarina for assistance with data collections. Special thanks to the ICMBio staff for field support, permits, and valuable information over the years, especially Hellen J. F. Rocha, Dan J. Pretto, Adriana C. Fonseca, Leandro Z. da Silva, and Ricardo C. Vieira. We also acknowledge Bertuol, Água Viva (specially Fabricio R. Rodrigues), Parcel, Cultura SubAquatica, Acquanauta, and Sea Divers diving centers for logistic support over the years. J.P.Q. received a post-doctoral fellowship from FAPESP (2018/21380-0 and 2021/09279-4). G.O.L. and S.R.F. are grateful to their research productivity scholarship provided by the Brazilian National Council for Scientific and Technological Development (CNPq 310517/2019-2 and 307340/2019-8 respectively). A.B.A. post-doctoral fellowship is funded by Biodiversa+, WaterJPI, and Europe Union.

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APÊNDICE B – Life-history traits, geographical range and conservation aspects of reef fishes from the Atlantic and Eastern Pacific

Base de dados referente aos atributos de história de vida coletados para as espécies de peixes recifais do Atlântico e Pacífico Tropical utilizados nesta tese, publicados na revista *Ecology.*

Life-history traits, geographical range and conservation aspects of reef fishes from the Atlantic and Eastern Pacific

Short title: *Reef fish data from isolated realms*

Juan Pablo Quimbayo[1*], Fernanda Carolina da Silva[2], Thiago Costa Mendes[3], Débora Silva Ferrari[2], Samara Leopoldino Danielski[2], Mariana Gomes Bender[4] Valeriano Parravicini[5], Michel Kulbicki[6], Sergio Ricardo Floeter[2]

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Abstract

Reef fish represent one of the most diverse vertebrate groups on Earth, with over 7000 species distributed around the globe. This richness is not evenly distributed around the globe. The Atlantic (AT) and the Eastern Pacific (EP) are considered the most isolated realms and encompass 30% of the global species richness. These areas have been isolated from the marine biodiversity hotspot in the Indo-Pacific by several barriers, such as the Tethyan closure and the distance between the EP and the western Pacific. Despite their comparatively lower species richness, these realms host unique fish assemblages characterized by a remarkable proportion of regional endemics and species with large body size. Here, we present the largest database of life-history traits, biogeographical and conservation aspects presently available for the reef fish fauna of the AT and the EP realms. The database includes 21 traits distributed into behavioral (home range, diel activity, group size, level in the water column, three measures of preferred temperature), morphological (maximum body size, size class, body shape, aspect ratio, caudal fin, mouth position) and ecological (trophic level, diet, spawning strategy, depth of occurrence, two allometric constants, pelagic larval duration and life span), as well as biogeographical (geographic range index, range extension, and species distribution in 20 marine provinces), and conservation aspects (IUCN status, vulnerability and global market price). We compiled these data through a careful review of 101 local checklists published between 1982 and 2019, online repositories, local reports, books, and monographs on specific families or genera. We limited our database to localities situated between latitude 51ºN and 45ºS that harbor coral and/or rocky reefs habitats. Our database covers 2,152 species belonging to 144 families and 646 reef fish genera distributed in two marine realms (1,330 in the AT, 754 in the EP, and 68 in both realms) and 20 marine provinces. This unique integrated database of reef fish for the AT and EP offers the opportunity to explore novel ecological and evolutionary questions at different spatial and temporal scales.

Keywords: Taxonomic richness, behavioral traits, morphological traits, ecological traits, biogeographical information, threatened species, fish price, species distribution, checklist, Atlantic, Eastern Pacific.

METADATA

CLASS I. DATA SET DESCRIPTORS

A. Data set identity: Life-history traits, geographical range and conservation aspects of reef fishes from the Atlantic and Eastern Pacific

B. Data set identification code:

- Fish_aspects_EasternPacific_Atlantic_Realms.csv

C. Data set description

1. Originators: Juan Pablo Quimbayo[1*], Fernanda Carolina da Silva[2], Thiago Costa Mendes[3], Débora Silva Ferrari[2], Samara Leopoldino Danielski[2], Mariana Gomes Bender[4] Valeriano Parravicini[5], Michel Kulbicki[6], Sergio Ricardo Floeter[2]

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2. Abstract: Reef fish represent one of the most diverse vertebrate groups on Earth, with over 7000 species distributed around the globe. This richness is not evenly distributed around the globe. The Atlantic (AT) and the Eastern Pacific (EP) are considered the most isolated realms and encompass 30% of the global species richness. These areas have been isolated from the marine biodiversity hotspot in the Indo-Pacific by several barriers, such as the Tethyan closure and the distance between the EP and the western Pacific. Despite their comparatively lower species richness, these realms host unique fish assemblages characterized by a remarkable proportion of regional endemics and species with large body size. Here, we present the largest database of life-history traits, biogeographical and conservation aspects presently available for the reef fish fauna of the AT and the EP realms. The database includes 21 traits distributed into behavioral (home range, diel activity, group size, level in the water column, three measures of preferred temperature), morphological (maximum body size, size class, body shape, aspect ratio, caudal fin, mouth position) and ecological (trophic level, diet,

spawning strategy, depth of occurrence, two allometric constants, pelagic larval duration and life span), as well as biogeographical (geographic range index, range extension, and species distribution in 20 marine provinces), and conservation aspects (IUCN status, vulnerability and global market price). We compiled these data through a careful review of 101 local checklists published between 1982 and 2019, online repositories, local reports, books, and monographs on specific families or genera. We limited our database to localities situated between latitude 51ºN and 45ºS that harbor coral and/or rocky reefs habitats. Our database covers 2,152 species belonging to 144 families and 646 reef fish genera distributed in two marine realms (1,330 in the AT, 754 in the EP, and 68 in both realms) and 20 marine provinces. This unique integrated database of reef fish for the AT and EP offers the opportunity to explore novel ecological and evolutionary questions at different spatial and temporal scales.

3. Keywords: Taxonomic richness, behavioral traits, morphological traits, ecological traits, biogeographical information, threatened species, fish price, species distribution, checklist, Atlantic, Eastern Pacific.

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description

1. Identity: Life-history traits, geographical range and conservation aspects of reef fishes from the Atlantic and Eastern Pacific

2. Originators: Juan Pablo Quimbayo[1*], Thiago Costa Mendes[2], Mariana Gomes Bender[3] Valeriano Parravicini[4], Michel Kulbicki[5], Sergio Ricardo Floeter[6]

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3. Period of study: Data of source publications range from 1982 to 2019.

4. Objectives: (1) Compile the occurrences of all extant reef fish species in the tropical and subtropical reefs of the Atlantic and Eastern Pacific realms (b) identify behavioral, morphological and ecological traits, as well as biogeographical and conservation aspects of reef fish from the Atlantic and Eastern Pacific.

5. Abstract: Same as above

6. Source: Foundation for Research on Biodiversity – France | São Paulo Research Foundation (FAPESP 2018/21380-0) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 563276/2010-0)

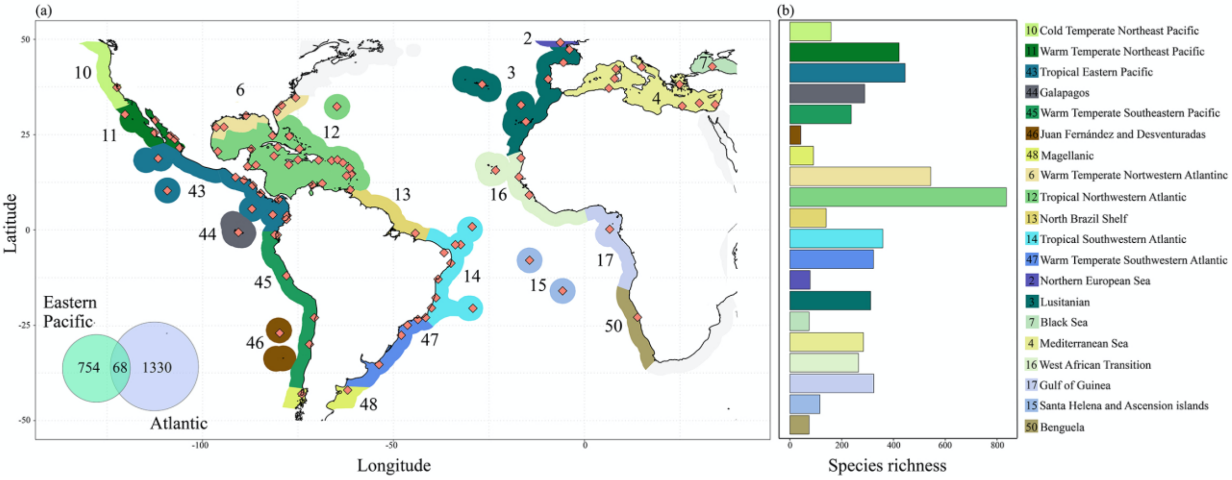
B. Specific subproject description

1. Sites description

Our research comprises 101 localities from the Atlantic and Eastern Pacific marine realms (Kulbicki et al. 2013) located between latitude 51ºN and 45ºS (Figure 1a). The Atlantic is considered the second most isolated marine realm due to three main biogeographic barriers: the emerged Rea Sea land bridge *c.* 12-18 Myr which separated its fish fauna from the Indian realm (Floeter et al. 2008, Belmaker et al. 2013); the closure of the Isthmus of Panama *c.* 3Myr which disconnected the Atlantic from the Eastern Pacific; and the cold Benguela Current which has largely prevented the colonization of Atlantic reefs by species arriving from the Indian realm for at least 2 Myr (Floeter et al. 2008). The Eastern Pacific (EP) is recognized as the most isolated marine realm due to an approximately 5000-km-wide expanse of deep open ocean that separates Clipperton Island, the westernmost locality in that region from the nearest Central Pacific islands. This stretch of deep ocean is known as the Eastern Pacific Barrier "EPB" (Robertson and Cramer 2009). Moreover, the closure of the Isthmus of Panama *c.* 3 Myr, isolated the EP from the Caribbean provinces (Coates and Stallard 2013). Finally, the EP is strongly influenced by two cold currents (the California current in the north and Humboldt current in the south) that split the tropical and subtropical fish fauna found in this realm (Robertson and Cramer 2009). The localities distributed in these two realms encompass 20 marine provinces (six in the Eastern Pacific and fourteen in the Atlantic; Figure 1a), which were defined by Spalding et al. (2007) as larger areas that have distinct biotas consistent across evolutionary time periods.

We found 2,152 reef fish belonging to 144 families and 646 genera distributed heterogeneously in these 20 marine provinces (Figure 1b). The species richness observed in the different marine provinces ranges from 42 to 836 species (mean ± SD: 270 ± 194), the Tropical Northwestern Atlantic province being the richest, whereas the Juan Fernández and Desventuradas Islands, the poorest (Figure 1b). More species occur in the Atlantic realm than in the Eastern Pacific (1,330 *vs* 754 exclusive species, respectively), whereas only 68 occur in both realms (Figure 1a).

Figure 1. Geographical distribution of 101 localities considered in this study (a). Each color on the map represents a marine province according to Spalding et al. (2007). (b) Comparison of species richness distribution across 20 marine provinces. (c) Total species richness found in each marine realm defined according to Kulbicki et al. (2013).



2. Experimental or sampling design

Data collection period

We compiled checklists for 101 localities from articles found online through search tools (Web of Science, Scopus and Google Scholar), online repositories (Robertson and Allen 2016, Robertson and Van-Tassell 2019, Fricke et al. 2020, Froese and Pauly 2020), local reports, books, and monographs on specific families or genera. We used combinations of the following search terms, in English, Portuguese, French, and Spanish: fish assemblages, fish checklists, new record, reef fish community, reef fish geographical distribution, biogeographic patterns of reef fish, Eastern Pacific and Atlantic. We did not consider Elamosbranchii because species in this group have different biological traits and evolutionary histories when compared to bony fish (see for more details Kulbicki et al. 2013). We limited our search to localities situated between latitude 51ºN and 45ºS with coral and/or rocky reefs habitats. Life-history traits were compiled from the GASPAR (General Approach to Species-Abundance Relationships) research group databases (Halpern and Floeter 2008, Luiz et al. 2013, Kulbicki et al. 2013, Parravicini et al. 2013, Mouillot et al. 2014, Alzate et al. 2019), books and online repositories (Robertson and Allen 2016, Robertson and Van-Tassell 2019, Froese and Pauly 2020).

3. Research methods

Taxonomy and systematics

The taxonomic classification follows the hierarchical system proposed by Linnaeus. All fish names compiled from checklists, online repositories, local reports and monographs were verified according to Eschmeyer's Catalog of Fishes (Fricke et al. 2020).

CLASS III. DATA SET STATUS AND ACESSIBILITY

A. Status

1. Latest update: 2020

2. Latest archive data: 2020

3. Metadata status: Metadata are complete

4. Data verification: All data was reviewed according to CLASS V section B and checked for any input errors.

B. Accessibility

1. Storage location and medium: All data and metadata are stored with this publication in *Ecology* journal.

2. Contact person: Juan Pablo Quimbayo, Center for Marine Biology, University of São Paulo, Brazil. E-mail: quimbayo_jp@gmail.com

3. Copyright or proprietary restrictions: There are no copyright or proprietary restrictions for research or teaching purposes.

4. Proprietary restrictions: None.

a. Citation: This paper

CLASS IV. DATA STRUCTURAL DESCRIPTORS

A. Data set file

1. Identity: Fish_aspects_EasternPacific_Atlantic_Realms.csv

2. Size: header + 2,152 rows and 58 columns (622 KB)

3. Format and storage: Digital data file is comma-delimited text files (*.csv)

4. Header information: See column description in section B.

5. Alphanumeric information: Mixed

B. Variable information

Each row in the database represents one species and columns show information on taxonomy classification, behavioral, morphological and ecological traits, biogeography and conservation information (Table 2; Figure 2).

Table 1. Column names (n=58), variable definition, variable nature and variable units for the database. These columns contain information on behavioral, morphological and ecological traits, as well as biogeographical, and conservation aspects relative to 2,152 reef fish species from the Eastern and Atlantic realms. The realms were defined according to Kulbicki et al. (2013).

Variable Name	Variable definition	Nature	Units
fb_code	This code is an identifier assigned to each species according to FishBase (Froese and Pauly 2020)		
Class	Taxonomic class		
Order	Taxonomic order		

Family	Taxonomic family	
Genus	Taxonomic genus	
Species	Taxonomic specific epithet	
Name	Scientific Name (Genus and specific epithet)	
Home_range	Area of activity: • Sedentary or Territorial species (sed): species staying in a restricted area (less than a few 100 m^2) for extended periods (at least a month). • Mobile species (mob): species staying in area of more than 100 m^2 or traveling among different reef areas. • Very mobile (vmob): species which frequently change reefs or travel daily large distances over the same reef.	Categorical (ordinal)
Diel_activity	Period of the day that species feed and breed: • day: diurnal species - species active essentially during day time hours. • night: nocturnal species – species mainly active during the night. • both: species active during both night and day.	Categorical (nominal)
Size_group	Gregariousness behavior: • solitary (sol): species usually living alone. • pairing (pair): species usually seen in pair. • small groups (smallg): species living in small groups (3 to 20 individuals on average). • medium groups (medg): species living in groups of 21-50 individuals on average. • large groups (largeg): species living in large groups or schools (> 50 individuals on average).	Categorical (ordinal)
Level_water	Position in water column: • bottom: species staying on the bottom at all the times.	Categorical (ordinal)

	• low: species that live slightly above the bottom but occasionally rest on the bottom. • high: species spending most of their active time high above the bottom (several meters).		
Preferred_temperature	Average temperature at which the species occurs. This data was compiled from the temperature values reported in each locality. [Mean=TempPref_mean, Minimum=TempPref_min, and Maximum=TempPref_max]	Continuous	Degrees Celsius
Body_size	Maximum total length of species.	Continuous	Centimeters
Size_class	Maximum total length of species divided into ordered categories • s1: 0 - 7 cm • s2: 7.1 - 15 cm • s3: 15.1 - 30 cm • s4: 30.1 - 50 cm • s5: 50.1 - 80 cm • s6: > 80 cm	Categorical (ordinal)	Centimeters
Body_shape	Morphological specialization for swimming. • box_shaped: globular form, such as in Diodontidae. • compressed: body flattened laterally. • depressed: body flattened dorsoventrally. • eel_like: body elongated, but with snake-like shape and locomotion. • elongated: long in relation to length. • fusiform: body spindle-shaped, the most hydrodynamic form.	Categorical (nominal)	
Aspect_ratio	An indicative value of species activity calculated from the squared height of caudal fin (h) divided by its surface (s) area (h^2/s).	Continuous	Nondimensional
Nphoto	Number of photos on which the calculus of aspect ratio metric was based.	Discrete	Nondimensional
Caudal_fin	Shape of caudal fin: • forked: caudal fin with a deeply concave or excavated hind margin.	Categorical (nominal)	

	• lanceolated: spear shaped caudal fin. • pointed: when the dorsal and anal fins are joined to the caudal. • rounded: caudal fin with only one lobe and concave margin. • truncated: caudal fin with only one lobe and straight margin. • heterocercal: asymmetric fin.		
Mouth_position	Anatomic jaw position: • superior: lower jaw is protruding upwards. • terminal: the upper and lower jaws are equal in length. • subterminal: upper jaw is protruding downwards. • inferior: mouth located in ventral position. • tubular: enlargement of mouth cavity. • elongated: long snout due to the increase in the bones premaxillary, maxillary and dental.	Categorical (nominal)	
Trophic_level	Position in the food web based on diet composition and mean trophic level of food items	Continuous	Nondimensional
Diet	Main items consumed by species: • herbivore-detritivore (hd): feeds predominantly on the epilithic algal matrix (EAM). • macroalgal feeder (hm): feeds predominantly on macroalgae (>1cm high) or seagrass. • sessile invertebrates (is): feeds predominantly on sessile benthic invertebrates including corals, sponges and ascidians. • mobile benthic invertebrates (im): feeds predominantly on mobile benthic invertebrates including crustaceans, annelids, echinoderms and mollusks. • planktonic (pk): feeds predominantly on invertebrate material in the water column including zooplankton,	Categorical (nominal)	

	coelenterates, detrital aggregates, etc. • omnivore (om): feeds on a range of organisms and includes a large proportion of animal material and plant and/or detrital material. • piscivore (fc): feeds predominantly on fishes but may also include cephalopods.		
Spawning	The way that species deposit eggs in water: • attach: attach their eggs to objects. • demersal: deposit their eggs directly on the substrate such as rocks. • live: species birth without external larval stage. • oral: parental care when female or male keep the eggs in their mouth until complete development. • pelagic: eggs free in the column water	Categorical (nominal)	
Depth_min	Minimal depth reported for the species.	Continuous	Meters
Depth_max	Maximal depth reported for the species.	Continuous	Meters
Depth_range	Difference between the maximum and minimum depth reported for the species	Continuous	Meters
Allometric_a	Constant allometric coefficient estimated from the relationship between size and weight	Discrete	
Allometric_b	Constant allometric coefficient estimated from the relationship between size and weight	Discrete	
PLD	Pelagic larval duration.	Discrete	Days
PLD_level	Taxonomic level at which the information was compiled • family • genus • species	Categorical (nominal)	
Life_span	Maximum age expected according to growth curves reported in the FishBase	Discrete	Years

Geographic_range_index	Estimation from the number of grid cell (5º x 5º) where a species has been recorded	Discrete	Nondimensional
Range_extension	Classification on the geographical origin of species: • invasive: exotic species that causes harm. • lessepsian: migratory species from the Red Sea to the Mediterranean. • native: species from Atlantic or Eastern Pacific. • transatlantic: species with restricted distribution in one part of the Atlantic but were recently reported in other localities. • transpacific: species native from Pacific but were recently reported in Atlantic.	Categorical (nominal)	
Provinces	Presence or absence in provinces distributed on 20 columns named province_number (binary). These provinces were defined by Spalding et al. (2007)	Binary	0/1
IUCN_status	Conservation status of species • NE: Not evaluated • DD: Data deficient • LC: Least concerned • NT: Near threatened • VU: Vulnerable • EN: Endangered • CR: Critically endangered		
Vulnerability	Continuous values ranging from 0 to100, provided by FishBase and based on fish life-history traits.	Continuous	Nondimensional
Price_category	Price value based on ex-vessel price for the species. • unknow • low • medium • high • very high	Categorical (ordinal)	

Missing value code: NA

Figure 2. Schematic representation of some the behavioral (blue rectangles), morphological (dark yellow rectangles), and ecological traits (green rectangles), as well as biogeographical (purple rectangles), and conservation aspects (red rectangles) included in the database. From left to right schematic figures represent: (1) Home range (very mobile/mobile/sedentary); (2) Diel activity (day/both/nigh); (3) Size group (solitary/par/small

group/medium group/large group); (4) Level in the water (bottom/low/high); (5) Preferred temperature (minimal/mean/maximum); (6) Body size (cm); (7) Body shape (box shape/compressed/depressed/eel like/elongated/fusiform); (8) Aspect ratio (h^2/s); (9) Caudal fin (forked/lanceolated/pointed/rounded/truncated/ heterocercal); (10) Mouth position (superior/terminal/subterminal/inferior/tubular/elongated); (11) Trophic level; (12) Diet (herbivore-detritivore/macroalgal feeder/sessile invertebrate feeders/mobile invertebrate feeders/planktivores/omnivores/piscivores); (13) Spawning (attach/demersal/live/oral/pelagic); (14) Range extension (invasive/lessepsian/native/ transatlantic); (15) Marine provinces; (16) IUCN status (NE: not evaluated/DD: data deficient/LC: least concern/NT: near threatened/VU: vulnerable/EN: endangered/ CR: critically endangered); (17) Price category according to FishBase (unknow/low/medium/high).

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data acquisition: See details in the section Class II, more specifically the Data collection. **B. Quality assurance/quality control procedures:** External fish experts reviewed all species records. Besides all the species names were update according to Eschmeyer's Catalog of Fishes (Fricke et al. 2020).

C. Computer programs and data processing algorithms

This procedure was performed in R environment ver. 3.2.4 (R Core Team 2018) using plyr (Wickham 2011), reshape (Wickham 2007), ggplot2 (Wickham 2016), rgeos (Bivand et al. 2019b), rgdal (Bivand et al. 2019a), rfishbase (Boettiger et al. 2012), sp (Pebesma and Bivand 2005) packages.

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APÊNDICE C – The COVID-19 pandemic has altered illegal fishing activities inside and outside a marine protected area

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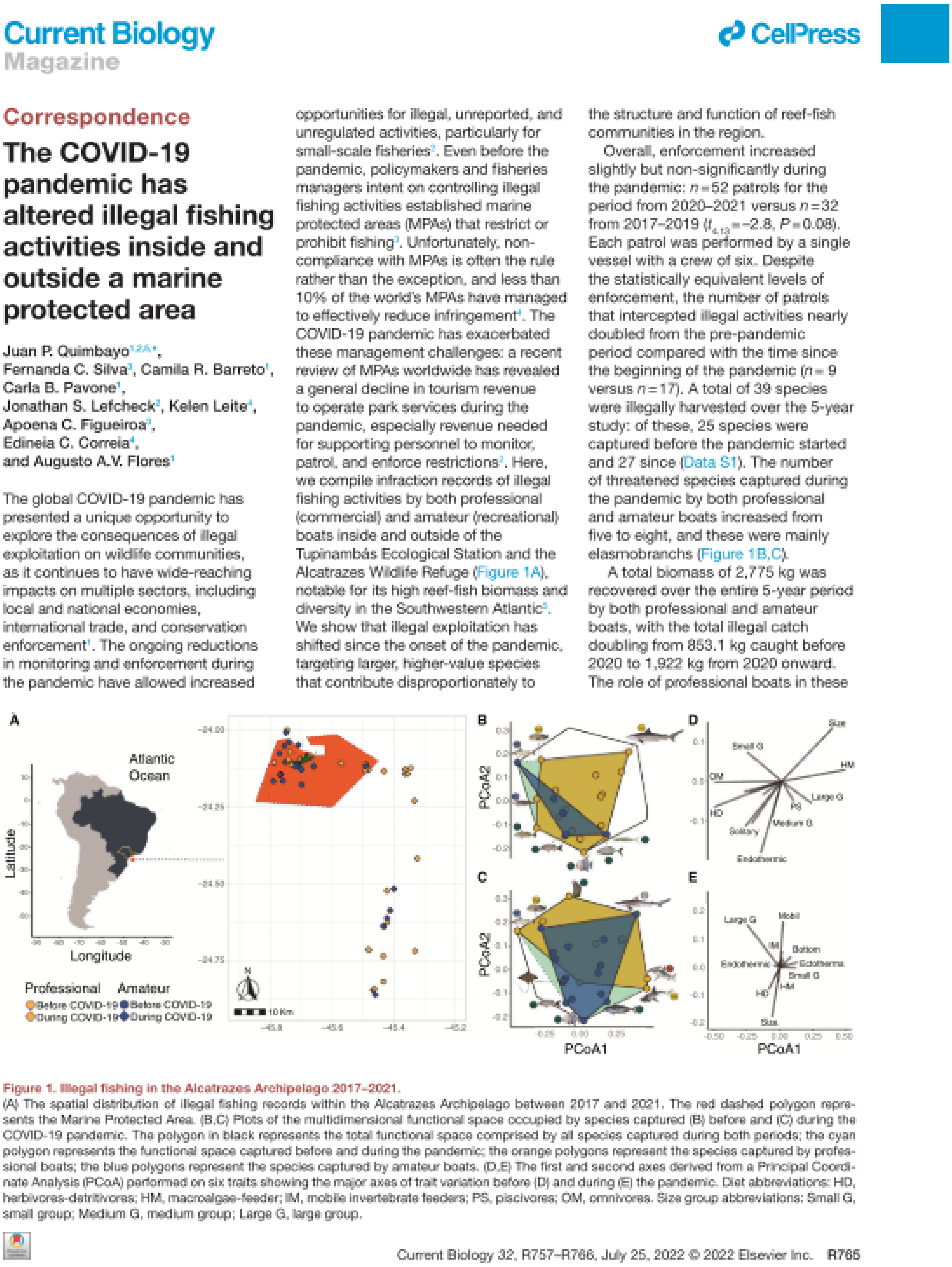

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The COVID-19 pandemic has altered illegal fishing activities inside and outside a marine protected area

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The global COVID-19 pandemic has presented a unique opportunity to explore the consequences of illegal exploitation on wildlife communities, as it continues to have wide-reaching impacts on multiple sectors, including local and national economies, international trade, and conservation enforcement[1]. The ongoing reductions in monitoring and enforcement during the pandemic have allowed increased opportunities for illegal, unreported, and unregulated activities, particularly for small-scale fisheries[2]. Even before the pandemic, policymakers and fisheries managers intent on controlling illegal fishing activities established marine protected areas (MPAs) that restrict or prohibit fishing[3]. Unfortunately, non-compliance with MPAs is often the rule rather than the exception, and less than 10% of the world's MPAs have managed to effectively reduce infringement[4]. The COVID-19 pandemic has exacerbated these management challenges: a recent review of MPAs worldwide has revealed a general decline in tourism revenue to operate park services during the pandemic, especially revenue needed for supporting personnel to monitor, patrol, and enforce restrictions[2]. Here, we compile infraction records of illegal fishing activities by both professional (commercial) and amateur (recreational) boats inside and outside of the Tupinambás Ecological Station and the Alcatrazes Wildlife Refuge (Figure 1A), notable for its high reef-fish biomass and diversity in the Southwestern Atlantic[5]. We show that illegal exploitation has shifted since the onset of the pandemic, targeting larger, higher-value species that contribute disproportionately to the structure and function of reef-fish communities in the region.

Overall, enforcement increased slightly but non-significantly during the pandemic: $n = 52$ patrols for the period from 2020–2021 versus $n = 32$ from 2017–2019 ($t_{4.13} = -2.8$, $P = 0.08$). Each patrol was performed by a single vessel with a crew of six. Despite the statistically equivalent levels of enforcement, the number of patrols that intercepted illegal activities nearly doubled from the pre-pandemic period compared with the time since the beginning of the pandemic ($n = 9$ versus $n = 17$). A total of 39 species were illegally harvested over the 5-year study: of these, 25 species were captured before the pandemic started and 27 since (Data S1). The number of threatened species captured during the pandemic by both professional and amateur boats increased from five to eight, and these were mainly elasmobranchs (Figure 1B,C).

A total biomass of 2,775 kg was recovered over the entire 5-year period by both professional and amateur boats, with the total illegal catch doubling from 853.1 kg caught before 2020 to 1,922 kg from 2020 onward. The role of professional boats in these

Figure 1. Illegal fishing in the Alcatrazes Archipelago 2017–2021.

(A) The spatial distribution of illegal fishing records within the Alcatrazes Archipelago between 2017 and 2021. The red dashed polygon represents the Marine Protected Area. (B,C) Plots of the multidimensional functional space occupied by species captured (B) before and (C) during the COVID-19 pandemic. The polygon in black represents the total functional space comprised by all species captured during both periods; the cyan polygon represents the functional space captured before and during the pandemic; the orange polygons represent the species captured by professional boats; the blue polygons represent the species captured by amateur boats. (D,E) The first and second axes derived from a Principal Coordinate Analysis (PCoA) performed on six traits showing the major axes of trait variation before (D) and during (E) the pandemic. Diet abbreviations: HD, herbivores-detritivores; HM, macroalgae-feeder; IM, mobile invertebrate feeders; PS, piscivores; OM, omnivores. Size group abbreviations: Small G, small group; Medium G, medium group; Large G, large group.

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APÊNDICE D – Integrated ecosystem assessment around islands of the tropical South Mid-Atlantic Ridge

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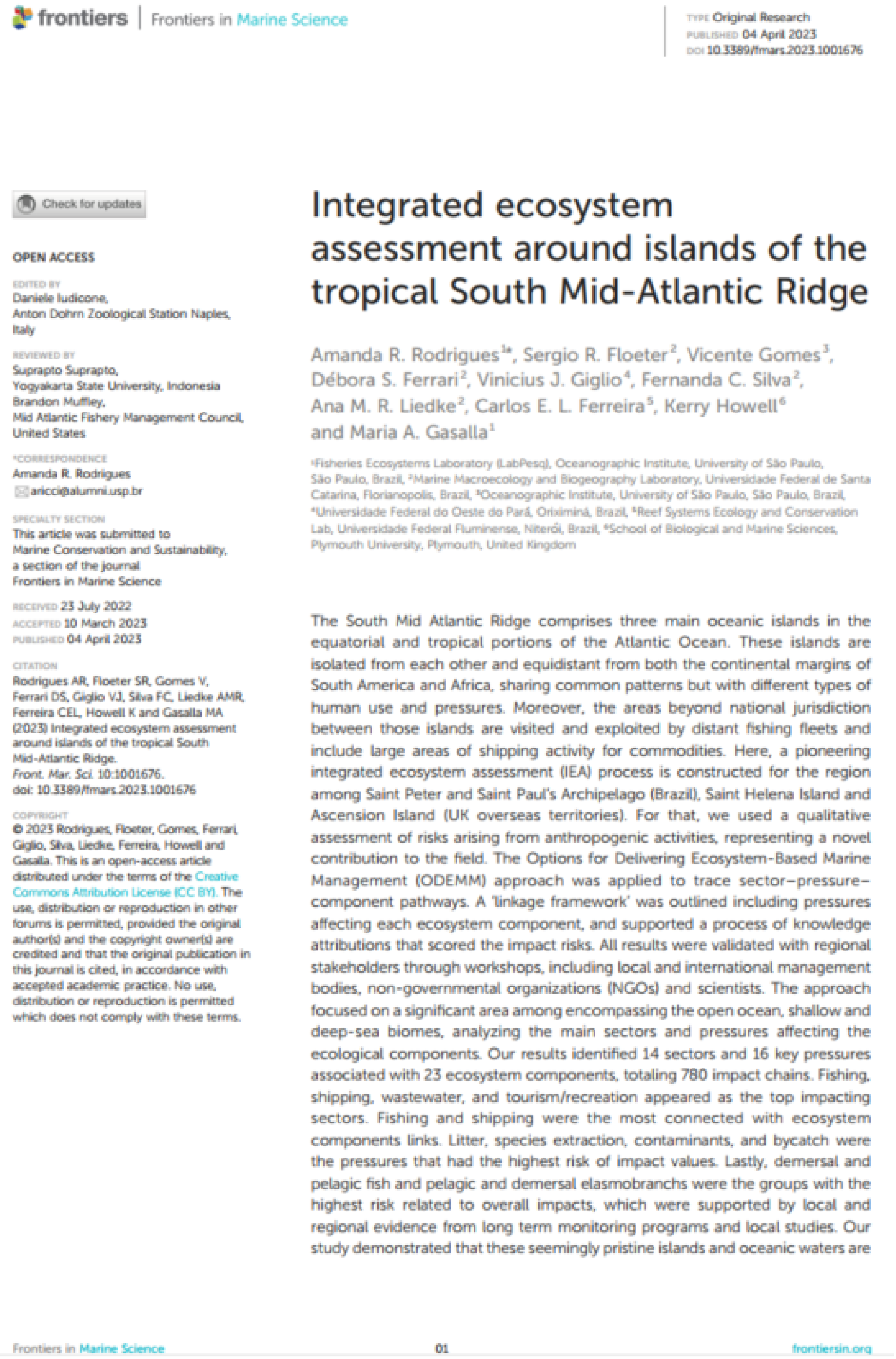

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Integrated ecosystem assessment around islands of the tropical South Mid-Atlantic Ridge

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The South Mid Atlantic Ridge comprises three main oceanic islands in the equatorial and tropical portions of the Atlantic Ocean. These islands are isolated from each other and equidistant from both the continental margins of South America and Africa, sharing common patterns but with different types of human use and pressures. Moreover, the areas beyond national jurisdiction between those islands are visited and exploited by distant fishing fleets and include large areas of shipping activity for commodities. Here, a pioneering integrated ecosystem assessment (IEA) process is constructed for the region among Saint Peter and Saint Paul's Archipelago (Brazil), Saint Helena Island and Ascension Island (UK overseas territories). For that, we used a qualitative assessment of risks arising from anthropogenic activities, representing a novel contribution to the field. The Options for Delivering Ecosystem-Based Marine Management (ODEMM) approach was applied to trace sector–pressure–component pathways. A 'linkage framework' was outlined including pressures affecting each ecosystem component, and supported a process of knowledge attributions that scored the impact risks. All results were validated with regional stakeholders through workshops, including local and international management bodies, non-governmental organizations (NGOs) and scientists. The approach focused on a significant area among encompassing the open ocean, shallow and deep-sea biomes, analyzing the main sectors and pressures affecting the ecological components. Our results identified 14 sectors and 16 key pressures associated with 23 ecosystem components, totaling 780 impact chains. Fishing, shipping, wastewater, and tourism/recreation appeared as the top impacting sectors. Fishing and shipping were the most connected with ecosystem components links. Litter, species extraction, contaminants, and bycatch were the pressures that had the highest risk of impact values. Lastly, demersal and pelagic fish and pelagic and demersal elasmobranchs were the groups with the highest risk related to overall impacts, which were supported by local and regional evidence from long term monitoring programs and local studies. Our study demonstrated that these seemingly pristine islands and oceanic waters are