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Ecologia e conservação das comunidades recifais de ilhas oceânicas do Atlântico Sul

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Ecologia e conservação das comunidades recifais de ilhas oceânicas do Atlântico Sul

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Débora Ferrari da Silva

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A todas as formas de vida marinha, e a todos aqueles que, fascinados pelo oceano, encontram nele uma fonte inesgotável de paz e inspiração.

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“Feliz aquele que transfere o que sabe e aprende o que ensina”
(Cora Coralina)

RESUMO

A organização das comunidades biológicas ao longo de escalas espaço-temporais é uma das principais questões que norteiam as teorias ecológicas. Essa organização depende de processos ecológicos mediados por fatores bióticos e abióticos. Sob a influência desses processos e de fatores antrópicos, a distribuição e abundância das espécies podem variar em diferentes escalas espaciais. Compreender como a interação desses processos molda o ecossistema recifal é essencial para criar estratégias de conservação, principalmente em locais isolados e pouco estudados como as ilhas oceânicas. Sendo assim, essa tese de doutorado teve como objetivo investigar como a sinergia entre diferentes processos ecológicos, fatores ambientais e atividades humanas moldam a estrutura das comunidades recifais de ilhas oceânicas do Atlântico. Para isso, a tese de doutorado foi dividida em três capítulos. O primeiro capítulo buscou compreender como as características do habitat e as espécies hiperdominantes influenciam a pressão alimentar de peixes recifais sobre o bentos em ilhas oceânicas do Atlântico Sul. O principal resultado revelou que espécies hiperdominantes realizam forrageio em diversos habitats, indicando uma notável plasticidade alimentar. Como consequência, essas espécies são responsáveis por moldar os padrões encontrados, destacando-as como espécies-chave para o equilíbrio ecológico nesses recifes. O segundo capítulo buscou investigar a influência da temperatura da superfície do mar (SST) e de outros fatores ambientais e históricos na estrutura das assembleias de peixes recifais. O resultado principal evidenciou que as variações mensais na SST tiveram influência na estrutura da assembleis de peixes recifais devido às limitações fisiológicas das espécies. Além disso, o nicho térmico das espécies seguiu o padrão conhecido com maiores amplitudes térmicas em direção às regiões mais frias. Por fim, o terceiro capítulo utilizou a abordagem de sistemas socioecológicos para realizar uma avaliação integrada do ecossistema recifal da ilha de Santa Helena, na Dorsal Meso-Atlântica. Foi observado que as águas residuais, a pesca e o transporte marítimo são os principais setores contribuindo para pressões como resíduos e contaminantes, afetando principalmente os peixes demersais, aves marinhas e mamíferos marinhos. Esta tese evidenciou que a estrutura e a sustentação das comunidades recifais em áreas isoladas são influenciadas por uma combinação de fatores naturais, tais como interações tróficas e temperatura, além de fatores antrópicos, como a poluição marinha. Além disso, destaca os principais grupos e espécies chaves, bem como os determinados setores e pressões antrópicas que requerem atenção nas estratégias de conservação para uma gestão eficaz do ecossistema recifal das ilhas oceânicas do Atlântico.

Palavras-chave: Peixes recifais; Hiperdominância; Interação alimentar; Estrutura de comunidades; Tolerância térmica; Impactos antrópicos.

ABSTRACT

The organization of biological communities across spatial and temporal scales is one of the central issues guiding ecological theories. This organization depends on ecological processes mediated by biotic and abiotic factors. Under the influence of these processes and anthropogenic factors, the distribution and abundance of species can vary at different spatial scales. Understanding how the interplay of these processes shapes the reef ecosystem is essential for developing effective conservation strategies, especially in isolated and understudied locations such as oceanic islands. Therefore, this thesis aimed to investigate how the synergy between different ecological processes, environmental factors, and human activities shapes the structure of reef communities in Atlantic oceanic islands. To achieve this, the thesis was divided into three chapters. The first chapter aimed to understand how habitat characteristics and hyperdominant species influence the feeding pressure of reef fish on benthic organisms in oceanic islands of the South Atlantic. The main result revealed that hyperdominant species forage in various habitats, indicating a remarkable feeding plasticity. Consequently, these species play a pivotal role in shaping the observed patterns, highlighting their significance as key species for maintaining ecological balance in these reefs. The second chapter investigated the influence of sea surface temperature (SST) and other environmental and historical factors on the structure of reef fish assemblages. The main finding was that monthly variations in SST influence the structure of reef fish assemblages due to physiological limitations of species. Additionally, the thermal niche of species followed the known pattern of higher thermal amplitudes towards cooler regions. Finally, the third chapter employed a socio-ecological systems approach to conduct an integrated assessment of the reef ecosystem of Saint Helena Island in the Mid-Atlantic Ridge. It was observed that wastewater, fishing, and shipping are the main sectors contributing to pressures such as litter and contaminants, affecting primarily demersal fish, seabirds, and marine mammals. This thesis revealed that the structure and sustenance of reef communities in isolated areas are influenced by a combination of natural factors, such as trophic interactions and temperature, as well as anthropogenic factors, such as marine pollution. Additionally, it highlights key groups and species, as well as specific sectors and anthropogenic pressures that require attention in conservation strategies for effective management of the reef ecosystem in Atlantic oceanic islands.

Keywords: Reef Fish; Hyperdominance; Trophic Interaction; Community Structure; Thermal Tolerance; Anthropogenic Impacts

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INTRODUÇÃO GERAL

Estruturação de comunidades biológicas

A estruturação das comunidades biológicas ao longo de escalas espaço-temporais está entre as principais questões que norteiam as teorias ecológicas (BEGON et al., 2006). A estrutura de comunidades é moldada por uma sucessão de processos que resultam na coexistência das espécies (MITTELBACH, 2012). Estas são influenciadas tanto por processos evolutivos, nos quais a origem e evolução das espécies depende da dinâmica entre os processos de dispersão, especiação e extinção (MACARTHUR; WILSON, 1967; WHITTAKER et al., 2017), quanto por processos ecológicos em diferentes escalas espaciais (ex. regional, local), que ocorrem através de fatores abióticos (ex. área, isolamento, temperatura) e bióticos (ex. interações biológicas) (OVASKAINEN et al., 2017), influenciando a distribuição e abundância das espécies em nível local (STACHOWICZ, 2001; WILSON et al., 2007). Sendo assim, a sinergia desses processos evolutivos e ecológicos promove a distribuição e abundância das comunidades em diferentes escalas espaciais (OVASKAINEN et al., 2017). A temperatura destaca-se como um fator primário na distribuição e estabelecimento das espécies (TITTENSOR et al., 2010). Essa influência é atribuída à processos fisiológicos e ecológicos, bem como à capacidade de adaptação das espécies (STUART-SMITH et al., 2017). As interações biológicas incluem processos como a predação, competição e mutualismo, e podem ocorrer desde micro-habitats até quilômetros quadrados. Essas interações têm papel estruturador em um ecossistema, podendo influenciar espécies dentro de uma pequena teia trófica ou comunidades inteiras (ESTES et al., 2011), atenuando a dominância de uma espécie específica e promovendo a diversidade ecológica geral. No entanto, a dominância desproporcional de algumas espécies, i.e., hiperdominância, é amplamente encontrada tanto em ambientes terrestres (RODRIGUES et al., 2019) quanto marinhos (DIETZEL et al., 2021). Em situações de hiperdominância de algumas poucas espécies dentro de uma comunidade, isso resulta em uma influência desproporcional na estrutura e no funcionamento de um ecossistema (DE SOUZA et al. 2022).

Avaliar a estrutura das comunidades é crucial para compreender a complexidade e a dinâmica de um ecossistema. Nos estudos ecológicos, diferentes métricas são utilizadas para fornecer informações acerca da organização das comunidades. A riqueza e diversidade de espécies são indicadores fundamentais, as quais podem ser avaliadas com métricas como a diversidade alfa, que contabiliza a diversidade de espécies em um único local (MAGURRAN, 2021), ou através da diversidade beta, que avalia a variação na composição de espécies entre diferentes locais (BASELGA, 2010). A estrutura trófica, por sua vez, analisa as relações alimentares, com métricas como a dieta e a taxa alimentar (KENT; SHERRY, 2020), que refletem a distribuição de organismos em diferentes níveis tróficos, oferecendo diferentes percepções sobre a estabilidade e complexidade da teia trófica (GERKING, 1994). Além disso, é possível avaliar a estrutura de tamanho, que examina a distribuição de tamanhos corporais ou biomassa na comunidade. Em conjunto, essas e outras métricas oferecem uma visão abrangente da organização e funcionamento das comunidades biológicas, contribuindo para a compreensão dos processos ecológicos que moldam esses sistemas.

Ecossistemas recifais

O sistema recifal está entre os mais produtivos e diversos ecossistemas marinhos, sendo composto de ambientes que fornecem abrigo, alimentação e locais de reprodução para milhares de espécies (CONNELL, 1978). Dentre as espécies que constituem esse sistema, os organismos bentônicos—como algas e corais—promovem tridimensionalidade aos recifes, além de possuírem uma especial ligação com a ictiofauna, formando habitats e fornecendo alimentos para os peixes recifais (BELLWOOD et al., 2004). Os peixes recifais constituem o grupo mais diverso neste sistema e são os principais consumidores, desempenhando importante papel nas redes tróficas (BRANDL et al., 2019). Devido à vasta diversidade de dieta e comportamentos, os peixes recifais compõem diferentes grupos tróficos, e a pressão alimentar que eles exercem sobre a comunidade bentônica é um importante processo para a estrutura e funcionamento do ecossistema recifal (LONGO et al., 2014), bem como são responsáveis por processos chaves dentro desse ecossistema (BONALDO et al., 2014). Por exemplo, a herbivoria tem papel crítico na estrutura das comunidades bentônicas, sendo os peixes herbívoros responsáveis por controlar possíveis mudanças de fase no sistema recifal—de ambientes dominados por corais, para ambientes cobertos por macroalgas (HUGHES et al., 2007).

Além das características tróficas dos peixes (i.e., dieta), as características morfológicas também influenciam a performance dessas espécies no ecossistema (MOUILLOT et al., 2014). A combinação do conjunto de características biológicas das espécies forma uma entidade funcional e em nível de comunidade, várias espécies podem se encaixar na mesma entidade funcional, i.e., realizam a mesma função, levando a uma redundância funcional. Por outro lado, algumas poucas espécies pertencem a grupos funcionais específicos, levando a alta vulnerabilidade funcional (MOUILLOT et al., 2014). No caso das ilhas oceânicas, quanto mais isoladas e com menor riqueza taxonômica, maior é a vulnerabilidade funcional (Ferrari et al., 2023).

Através das características das espécies e das funções ecossistêmicas desempenhadas por elas, os ambientes provêm bens e serviços ecossistêmicos para a população humana, como a proteína advinda dos pescados e atividades de turismo (MOBERG; FOLKE, 1999). Entretanto, nas últimas décadas houve uma intensa ocupação humana em torno das zonas costeiras, levando à sedimentação, poluição e superexploração dos recursos marinhos (HALPERN et al., 2015; HINRICHSEN, 1999).

Avaliação integrada do ecossistema

A sinergia dos distúrbios naturais e antrópicos vem alterando os recifes e levando à perda de espécies e, por consequência, à perda das funções ecossistêmicas (MOBERG; FOLKE, 1999). Dentre os recursos amplamente explorados, podemos citar a atividade pesqueira, sendo essa também grande responsável pela captura de espécies chaves—responsáveis pelo equilíbrio dinâmico do ecossistema—, como os grandes carnívoros (BENDER et al., 2014). Apesar de ainda existir um senso de separação entre o sistema marinho e a população humana, a maioria dos sistemas recifais estão intrinsicamente correlacionados dentro de um sistema sócio-ecológico (CINNER et al., 2009). Dessa forma, uma melhor compreensão das ligações entre as ações antrópicas e as pressões que elas causam no ecossistema recifal é o primeiro passo para identificar os impactos e propor possibilidades de gestão e manejo.

A dinâmica entre os setores antrópicos e as pressões que eles criam formam uma complexa rede de interações que pode afetar os habitats e espécies recifais, gerando riscos para o ecossistema (HALPERN et al., 2009). Dessa forma, para que haja uma gestão eficaz das atividades humanas no ambiente marinho, se faz necessário uma avaliação com bases ecossistêmicas (KNIGHTS et al., 2013). Definindo o ecossistema como uma entidade única, composta por diferentes partes interagindo dinamicamente (CURTIN; PRELLEZO, 2010), é intrínseco que avaliações integradas do ecossistema tenham pilares ecológicos. Tal abordagem ressalta a importância de estudos ecológicos de base, avaliando padrões e processos das comunidades biológicas, e fornecendo informações necessárias para subsidiar avaliações e gestão com suporte ecossistêmico.

A avaliação integrada do ecossistema (Integrated Ecosystem Assessment - IEA) desenvolvida pelo NOAA (National Oceanic and Atmospheric Administration; LEVIN et al., 2008) é uma abordagem que integra grande parte dos componentes de um ecossistema, incluindo as necessidades e atividades humanas (LEVIN et al., 2009; MONACO et al., 2021). Através do IEA é possível envolver cientistas e gestores no processo de elaboração da avaliação e da tomada de decisão. O IEA é constituído por algumas etapas, sendo o primeiro passo definir o sistema a ser avaliado e os objetivos; após, deve-se selecionar os indicadores e iniciar a análise de risco; por fim, é avaliado as estratégias de gestão do ecossistema escolhido (MONACO et al., 2021). Recentemente, o projeto ODEMM (Options for Delivering Ecosystem-Based Marine Management; ROBINSON et al., 2014) foi desenvolvido para acessar as diferentes etapas do IEA, tendo as estruturas e ferramentas necessárias que auxiliam na avaliação do ecossistema. Tais estruturas são baseadas nas ligações entre setores, pressões e componentes ecológicos, permitindo identificar as relações e as cadeias de impactos entre as atividades humanas e os componentes ecológicos (KNIGHTS et al., 2013). Mediante esse método é possível gerar uma avaliação do risco ecológico do sistema, o qual avalia a probabilidade e as consequências de uma ou mais cadeias de impacto ocorrerem. Através desse conhecimento, é possível analisar como a gestão efetiva de determinados setores ou pressões pode reduzir o impacto no ecossistema.

Estudos que abordam a avaliação integrada do ecossistema são, geralmente, realizados em sistemas com alta interferência antrópica e em grandes áreas (e.g. PEDRESCHI et al., 2019; FLETCHER et al., 2014). Contudo, apesar da grande necessidade de investigações nas áreas com alta probabilidade de impacto, também é de extrema importância compreender os riscos nos ecossistemas que ainda são pouco afetados pela ação antrópica, como é o caso das ilhas oceânicas. Essas ilhas são consideradas sistemas únicos para estudar os mecanismos ecológicos que atuam em escalas locais e evolutivas (ROMINGER et al., 2016). Além disso, o funcionamento ecológico dessas ilhas, incluindo taxas de colonização e endemismo, difere dos modelos observados em outros ecossistemas (FERREIRA et al., 2021).

Ilhas oceânicas

As ilhas oceânicas não apresentam conexão geológica com o continente já que estão fora da plataforma continental e distantes da linha costeira dos continentes, dessa forma, geralmente apresentam baixa riqueza de espécies e um alto grau de endemismo (WHITTAKER;

FERNANDEZ-PALACIOS, 2007; HACHICH et al., 2015; 2020). A dinâmica ecológica dessas ilhas é altamente distinta do observado em outros ecossistemas (FERREIRA et al., 2021). O isolamento elevado e a distinta dispersão, colonização, especiação e extinção de espécies observadas em ilhas oceânicas proporcionam valiosas perspectivas para hipóteses biogeográficas e montagem de comunidades (HACHICH et al., 2020). Tanto as ilhas oceânicas brasileiras quanto as ilhas do Atlântico central diferem quanto às suas características, como distância da costa, grau de hidrodinamismo, produtividade primária, temperatura da água e composição de espécies (FLOETER et al., 2001; GHERARDI; BOSENSE, 2001; PEREIRA-FILHO et al., 2011). As quatro ilhas oceânicas brasileiras (Arquipélago de São Pedro e São Paulo – ASPSP, Atol das Rocas, Fernando de Noronha e a Ilha da Trindade) compartilham a maior parte das suas espécies com a costa Ocidental do Oceano Atlântico, sendo um subconjunto das províncias do Caribe e Brasil (BRIGGS, 1995). Ademais, o ASPSP também compartilha espécies com a província das ilhas do Atlântico central, Ascension e Santa Helena. Essas ilhas possuem elevada semelhança faunística entre elas, e compartilham muitas espécies endêmicas, assim como possuem espécies provenientes tanto com o Atlântico ocidental quanto do oriental (KULBICKI et al., 2013).

Ilhas oceânicas, em geral, são consideradas altamente vulneráveis em relação à funcionalidade das espécies de peixes (FERRARI et al., 2023). No entanto, as ilhas oceânicas do Atlântico apresentam uma vulnerabilidade ainda maior devido à combinação do isolamento com a baixíssima riqueza de espécies (FERRARI et al., 2023). Diante desse cenário, torna-se essencial estudar essas ilhas para uma compreensão mais aprofundada das comunidades recifais, especialmente aquelas que são vulneráveis, hiperdominantes e isoladas. Ademais, entre as ilhas oceânicas do Atlântico, a Ilha de Santa Helena se destaca tanto pelo considerável número de habitantes quanto pela extensão de sua área emersa. Portanto, torna-se crucial estudar os possíveis impactos humanos e suas interações com os componentes recifais.

Estrutura e objetivos da tese de doutorado

Uma tese de doutorado é geralmente definida como um trabalho original que proporciona uma contribuição única e substancial, oferecendo uma nova perspectiva do conhecimento em uma área específica de estudo. A partir desse conceito, a presente tese de doutorado visou contribuir no preenchimento de lacunas do conhecimento acerca dos processos ecológicos e dos impactos humanos que moldam a estrutura das comunidades recifais das ilhas oceânicas do Atlântico Sul, tendo como principal pergunta norteadora da tese: Como diferentes processos ecológicos, fatores ambientais e ações humanas interferem na estrutura das comunidades recifais de ilhas oceânicas?

Hipotetiza-se que a composição das comunidades recifais nas ilhas oceânicas seja moldada por um subconjunto de espécies continentais, as quais exibem características adaptativas favoráveis à dispersão de longa distância, em decorrência do isolamento característico dessas ilhas. Além disso, postula-se que o estabelecimento e o subsequente aumento da abundância e biomassa dessas espécies sejam influenciados pelo nicho térmico, alinhando-se com as variações térmicas específicas de cada ilha. Adicionalmente, hipotetiza-se que o padrão de hiperdominância de algumas espécies resulta do grau de plasticidade alimentar e do comportamento generalista desses organismos. Por fim, postula-se que as práticas de pesca e alterações na qualidade da água representem potenciais riscos de impacto no ecossistema recifal, resultantes do aumento da população humana residente e do turismo.

Para responder a principal questão, a tese será dividida em três capítulos através de diferentes abordagens (veja Figura 1), escalonando de comunidades para ecossistema, somando-se os impactos antrópicos. Ademais, a presente tese de doutorado está vinculada ao projeto Mission Atlantic (missionatlantic.eu), financiado pela União Europeia, que visa mapear e avaliar o estado atual e futuro dos ecossistemas marinhos do Atlântico. Essa tese concentrou-se nas ilhas oceânicas do Atlantico Sul, sendo que o primeiro capítulo abrangeu as ilhas oceânicas brasileiras e a Ilha de Ascension. O segundo capítulo explorou um dos estudos de caso do Projeto Mission Atlantic; As Ilhas da Dorsal Meso-Atlântica, que compreende o Arquipélago de São Pedro e São Paulo, a Ilha de Ascension e a Ilha de Santa Helena. A escolha para o terceiro capítulo ter sido focado na Ilha de Santa Helena decorreu do apoio fornecido pelo Projeto Mission Atlantic para a realização de um workshop presencial com os gestores da Ilha de Santa Helena. Além disso, esse suporte viabilizou a coleta de dados biológicos, que compôs parte do segundo capítulo. Desta maneira, esta tese inseriu o sistema recifal da Ilha de Santa Helena no contexto de abordagens baseadas em ecossistemas, conectando-o à escala do Oceano Atlântico e contribuindo para o objetivo geral do projeto Mission Atlantic de realizar uma avaliação integrada do ecossistema em todo o Oceano Atlântico.

Chapter 1. Hyperdominance and habitat composition drive reef fish foraging at Atlantic oceanic islands.

O objetivo deste estudo foi investigar a relação entre os habitats, a hiperdominância de espécies, e a pressão alimentar de peixes recifais em cinco ilhas oceânicas do Atlântico Sul. Especificamente, buscou-se compreender como as espécies hiperdominantes e as características do habitat influenciam os padrões de pressão alimentar. A hipótese formulada sugere que espécies dominantes de peixes apresentam maior grau de plasticidade alimentar, comportando-se como generalistas, sem preferências específicas de habitat para a alimentação. Consequentemente, tais espécies hiperdominantes exercem pressão alimentar mais intensa.

Chapter 2. Thermal tolerance as a driver of reef fish community structure at the isolated tropical Mid-Atlantic Ridge Islands

Esse capítulo buscou investigar a influência da temperatura da superfície do mar (SST) e de outros fatores, como isolamento, área e idade, na estrutura das assembleias de peixes recifais no Arquipélago de São Pedro e São Paulo, Ilha da Ascensão e Ilha de Santa Helena. A hipótese sustenta que variações mensais na SST teriam impacto na abundância das espécies devido às limitações fisiológicas. Além disso, espera-se que a tolerância térmica do nicho das espécies seja maior em Santa Helena, a ilha com maior variação térmica mensal, alinhando-se ao padrão conhecido de um aumento na amplitude térmica em direção às regiões mais frias.

Chapter 3. Assessing potential human impacts and risks on the Saint Helena reef system, a South Mid-Atlantic Ridge Island

O estudo buscou realizar uma avaliação integrada do ecossistema recifal da Ilha de Santa Helena. Especificamente, buscou-se: 1) Estabelecer cadeias de ligação examinando as interações entre setores, pressões e componentes ecológicos; 2) Pontuar as cadeias de acordo com níveis de frequência, intensidade e espacialidade em que ocorrem; 3) Realizar uma avaliação dos principais riscos identificados para o ecossistema recifal de Santa Helena. A hipótese formulada sugere que, com o aumento do número de habitantes e turistas, os setores da pesca e embarcações exerceriam as principais pressões, como o lixo marinho, afetando as espécies de peixes e mamíferos marinhos.

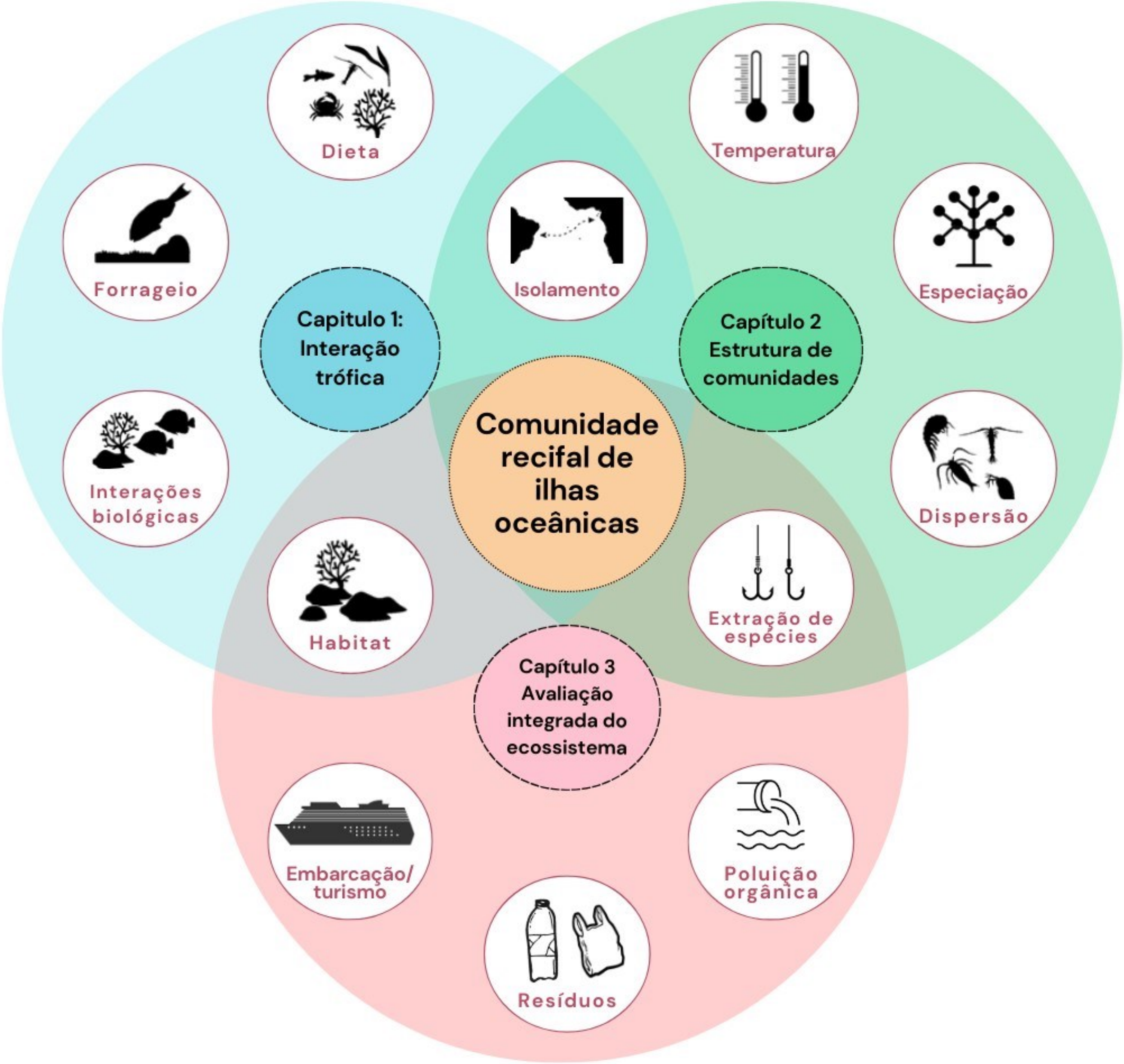

Figura 1. Conceitos chaves representando e interligando os três artigos científicos desenvolvidos nesta tese.

A presente tese de doutorado desempenha um papel importante ao explorar os processos ecológicos, fatores ambientais e ações humanas que afetam as comunidades recifais de ilhas oceânicas. Cada capítulo fornece uma investigação aprofundada sobre alguns desses aspectos, contribuindo não apenas com novas informações sobre esses ecossistemas, mas também com uma compreensão mais ampla de como podem vir a responder às mudanças ambientais e às ações humanas. A relevância dessa pesquisa vai além do preenchimento de lacunas no conhecimento existente, oferecendo novas perspectivas para políticas de conservação e gestão eficazes. Em resumo, a tese representa uma peça significativa no quebra-cabeça do entendimento ecológico, com implicações práticas importantes para a conservação do ecossistema recifal das ilhas oceânicas do Atlântico.

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CAPÍTULO I

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Hyperdominance and habitat composition drive reef fish foraging at Atlantic oceanic islands

Débora S. Ferrari, Lucas T. Nunes, Thiago C. Mendes, Carlos Eduardo L. Ferreira, Sergio R. Floeter. (2024) Hyperdominance and habitat composition drive reef fish foraging at Atlantic oceanic islands. *Marine Ecology Progress Series*, 726, 1-15

Abstract

Spatial and temporal patterns of benthic community structure play a crucial role in shaping reef habitats and have a direct impact on fish foraging dynamics, alongside density-dependent effects on the whole community. At isolated oceanic islands, the relatively low fish species richness often leads to the hyperdominance of a few species and a general reduced trophic redundancy. However, the influence of benthic habitat features and hyperdominant species on foraging selection at oceanic islands has been largely overlooked. We used remote underwater videos (RUVs) to investigate whether reef fishes consistently forage on specific habitats across 5 different oceanic islands in the Atlantic Ocean, especially focusing on the importance of the role of hyperdominant species. We analysed 295 RUVs, within 2 m² areas (3–15 m deep), totalling 49 h of video. Photoquadrats were utilised to gauge benthic group coverage in the same habitats. Our results revealed 5 prevalent habitats and 6 fish trophic groups interacting with reef benthos. The intensity of feeding pressure varied across islands, depending on the diversity of habitats. Herbivores and omnivores exhibited the highest feeding pressure, with omnivores foraging on crustose coralline algae and macroalgae habitats, while herbivores primarily fed on habitats dominated by the epilithic algal matrix. Hyperdominant species forage in multiple habitats, indicating a comparatively high degree of dietary plasticity. Our findings also demonstrated that fish feeding pressure is influenced by both habitat features and fish biomass. Therefore, our study can provide valuable insights for prioritising the management of key species in isolated oceanic reefs.

Keywords: Hyperdominance · Dietary plasticity · Benthic habitats · Remote underwater videos · Oceanic island · South Atlantic

1. INTRODUCTION

Trophic interactions are fundamental processes of ecosystem function (van der Putten et al. 2004, Estes et al. 2011, Lefcheck et al. 2019). These interactions are crucial to maintaining an efficient transfer of energy and nutrients along the food chain. Trophic interactions also contribute to increasing biodiversity, preventing one species from dominating an ecosystem, and making it possible for a greater variety of species to coexist (Paine 1980, McCauley et al. 2015). Interactions within the food web are intrinsically related to species' functional roles, with some species playing disproportionately important roles. Herbivorous fishes that help regulate algal biomass and maintain ecosystem balance (Bellwood et al. 2019) are among those key groups. These fish are considered to be critical in estimating ecosystem functions and prioritising conservation efforts (Lefcheck et al. 2019, Schiettekatte et al. 2022).

Niche diversity facilitates the partitioning of resources among species and regulates population sizes through predation and herbivory, effectively mitigating the dominance of any particular species and fostering overall ecological diversity (Estes et al. 2011). However, disproportionate dominance in abundance or biomass by a few species is well-known in both terrestrial (ter Steege et al. 2013, Fauset et al. 2015, Rodrigues et al. 2019) and coral reef communities (Dietzel et al. 2021). In ecological studies, the term 'hyperdominance' has been employed to describe this differential high abundance or biomass of organisms within a community (Lohbeck et al. 2016, Tebbett et al. 2023). In the marine environment, Dietzel et al. (2021) reported that of 318 species examined in the Indo-Pacific coral fauna, only 17 hyperdominant species accounted for half of the total community abundance. These species have a disproportionate influence on the structure and functioning of shallow coral reef ecosystems across the Indo-Pacific.

Hyperdominant species typically exhibit characteristics that confer a competitive advantage over other species, such as rapid growth, efficient resource use, resistance against environmental disturbances and enhanced dispersal abilities (Dietzel et al. 2021, De Souza et al. 2022). As a result, hyperdominant species outcompete and surpass other species, leading to their increased abundance and biomass within the community (de Souza et al. 2022). Since trophic interactions are highly correlated to either species abundance or biomass (Elmhagen & Rushton 2007, Longo et al. 2014, Nunes et al. 2020), hyperdominant species can monopolise these trophic functions, facilitated by characteristics such as a more generalist diet and habitat use. These characteristics are especially prevalent within groups at lower trophic levels

(Kavanagh & Olney 2006, Mendes et al. 2019), while they facilitate the establishment of populations in remote locations, such as oceanic islands (Hachich et al. 2020, Ferrari et al. 2023). However, our current understanding of the potential impact of hyperdominance on trophic interactions and energy flow in bottom-up processes, particularly in highly diverse systems like reefs, remains insufficient and requires large-scale comparisons.

Reefs represent one of the Earth's most diverse ecosystems, harbouring hundreds of thousands of species that depend on them to live and thrive (Reaka-Kudla 1997). This remarkable diversity is shaped by global factors, such as distance from diversity centres (Hughes et al. 2002), regional processes (e.g. connectivity; Jones et al. 2009) and local biological interactions (e.g. Canterle et al. 2020), which influence patterns of community structure. Among these processes, habitat diversity plays a recognisable role in shaping 3-dimensional structural complexity while favouring environmental heterogeneity, therefore influencing local species diversity and abundance (Graham & Nash 2013, Bracewell et al. 2018), as well as fish foraging dynamics (Hay 1991, Canterle et al. 2020, Nunes et al. 2020). Habitats on reef systems can be delimited according to physical biotopes (e.g. slope, interface) or benthic composition, such as calcareous algae, epilithic algal matrix (EAM), macroalgae and sessile invertebrates (Aued et al. 2018, Canterle et al. 2020). These benthic components will influence ecological interactions by either modifying structural complexity or food availability and, therefore, consumer selectivity (Michel et al. 2020). The EAM substrate, for example, has a well-known trophic importance on reef systems for herbivory (Wilson et al. 2003, Lefcheck et al. 2019) and invertivory (Kramer et al. 2013). This substrate can be defined as a matrix containing a diversity of algae, microorganisms, detritus and associated invertebrates (Wilson et al. 2003, Kramer et al. 2012), while it has been estimated to be the bulk of reef substrate coverage elsewhere (Tebbett et al. 2023). The association of organisms with the EAM substrate fosters a diverse array of food sources (e.g. Kramer et al. 2013), hence we can expect a greater diversity of consumers (species and trophic groups) foraging in this habitat compared to other more homogeneous habitats on reefs, such as sand and sponges (Canterle et al. 2020). In fact, the foraging performed by reef fishes on EAM habitat, such as herbivory and detritivory, is recognised as an essential process to reef resilience (Wilson et al. 2003, Bellwood et al. 2004, Hughes et al. 2007, Longo et al. 2019). In the South Atlantic Ocean, the EAM is also one of the most dominant habitats within coastal and oceanic reefs (Figueiredo et al. 2008, Aued et al. 2018).

Oceanic islands are unique systems for studying evolutionary and ecological processes (Rominger et al. 2016). They are located outside the continental shelf and generally have low species richness and high endemism (Whittaker & Fernández-Palacios 2007, Hachich et al. 2015, 2020, Ferrari et al. 2023). Reef fish biomass on oceanic islands is usually higher than on coastal reefs, as they are less affected by human activities. Oceanic islands have suffered comparatively less from anthropogenic influence (Morais et al. 2017); however, they are not entirely protected from impacts, especially considering the influx of anthropogenic pollutants, such as oil spills and plastics (Alava et al. 2023). The process of trophic dominance and unique trophic roles can be better understood with critical support to manage ecosystem functions. Nevertheless, in low-diversity locations, such as oceanic islands, the extent to which fishes select or may depend on specific habitats, such as the EAM, to forage remains poorly studied.

In this study, our main objective was to investigate the relationship between reef habitats, species hyperdominance and fish feeding pressure on oceanic is lands. To achieve this, we first defined distinct reef habitats based on the dominant benthic components present. Subsequently, we examined how these habitat characteristics and the hyperdominant species influenced fish foraging. Our study aimed to address the following research questions: (1) Do fish trophic groups exhibit similar feeding pressure intensity and habitat preferences across different oceanic islands? We hypothesised that the feeding pressure would vary among trophic groups, based on their abundance and composition. However, we expected habitats dominated by the EAM to be highly selected by all trophic groups across the islands. (2) How do hyperdominant species and habitat features influence patterns of feeding pressure? Our hypothesis was that dominant fish species would display a higher degree of dietary plasticity and behave as generalists, lacking specific habitat preferences for foraging. Consequently, we anticipated that these hyperdominant species would exert a greater feeding pressure. By addressing these questions, we aim to gain a better understanding of the complex interplay between fish trophic groups, hyperdominant species, habitat characteristics and feeding pressure near oceanic islands.

2. MATERIALS AND METHODS

2.1. Study area

We sampled the 4 Brazilian oceanic islands: St Peter and St Paul’s Archipelago (SPSPA; 0° 55’ 1.39” N, 29° 20’ 44.14” W), approximately 1010 km away from the mainland; Fernando de Noronha Archipelago (3° 51’ 9” S, 32° 25’ 14” W), ~360 km from the mainland; Rocas Atoll (3° 51’ 49” S, 33° 48’ 41” W), ~230 km from the mainland; and Trindade Island (20° 29’ 48” S, 29° 19’ 54” W), located 1160 km away from the mainland; we also sampled Ascension Island (7° 56’ 26” S, 14° 22’ 25” W), a British Overseas Territory located in the South Mid-Atlantic Ridge around 1600 km from the western coast of Africa (Fig. 1). The shallow reefs of Fernando de Noronha, Ascension and Trindade Island are mainly formed by volcanic rock, while Rocas Atoll is formed by coralline algae and vermetid gastropods (Gherardi & Bosence 2001). SPSPA is composed of rocks from exhumations of the upper mantle (Maia et al. 2016). These oceanic islands also present similarities, such as low species richness, high endemism and more oligotrophic waters compared to coastal locations (Quimbayo et al. 2019). Among these islands, Fernando de Noronha presents the highest reef fish richness with 118 species, followed by Trindade Island with 105 species, Rocas Atoll with 102 species and Ascension Island with 91 species. In contrast, SPSPA has the lowest species richness among these islands, with only 58 reef fish species recorded to date (Ferrari et al. 2023). All islands have marine protected areas (MPAs) with different protection levels. SPSPA and Trindade Island have 2 categories of protected areas each, a larger part being Environmental Protected Areas (EPAs) where use is allowed (CAT V-IUCN), and a small no-take area (CAT III-IUCN) (Giglio et al. 2018). Fernando de Noronha is also within an EPA (CAT V-IUCN) and a no-take National Marine Park (CAT II-IUCN). Rocas Atoll is the most protected of them, being a no-entry marine reserve (CAT Ia-IUCN). The entire 445 000 km2 marine zone of Ascension Island has been designated as an MPA, which prohibits large-scale commercial fishing and seabed mining.

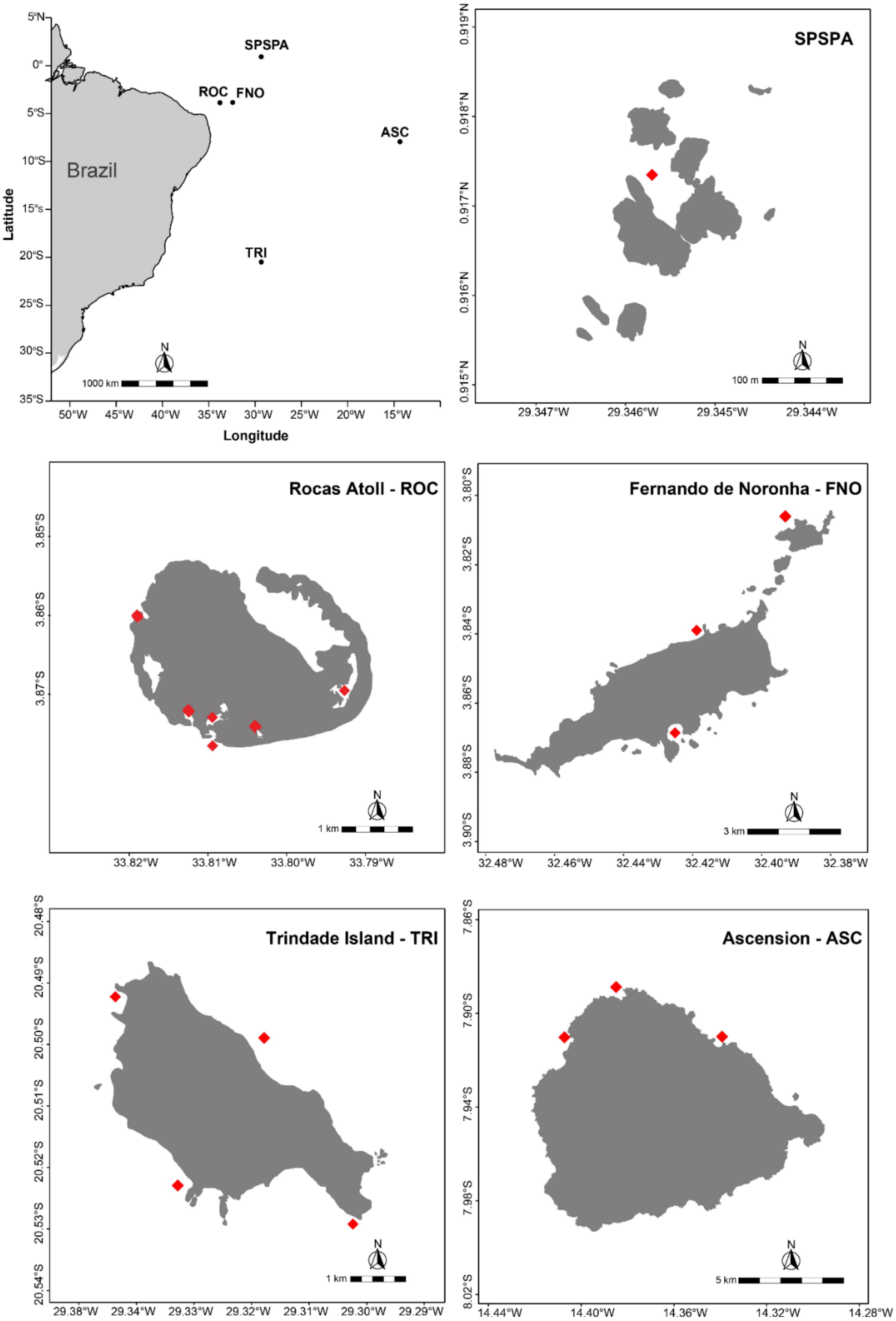

Fig. 1. Geographical location of sampled oceanic islands on the Atlantic Ocean. SPSPA: St Peter and St Paul's Archipelago; FNO: Fernando de Noronha; ROC: Rocas Atoll; ASC: Ascension Island; TRI: Trindade Island. Red diamonds represent the sampled sites.

2.2. Sampling and laboratory procedures

On each island, we recorded remote underwater videos (RUVs) to quantify feeding pressure of fishes on the benthic community (following Longo et al. 2014). Sampling was conducted during the daytime (between 09:00 and 15:00 h) in the consolidated substrate of shallow reefs (between 3 and 15 m deep). Sampling was conducted at different locations within each island based on accessibility factors such as wave and current conditions, while also adhering to a specific depth pattern. Subsequent data analyses involved comparisons within individual sites on each island, revealing no notable distinctions of significance. Videos were recorded with a digital camera (GoPro Hero #3 model) focused on a 2 m2 reef area, previously demarcated with a measuring tape. Each area was recorded for 15 min, with the central 10 min of each video used for analysis (i.e. discarding the first and last 2 min and 30 s of each recording). A minimum separation of 3 m between plot areas was applied to avoid overlapping. For each video, we identified all individual fishes that exhibited foraging (i.e. biting the substrate) inside the focal area. We emphasize that the RUV method filters species that feed in the benthos, excluding other groups such as planktivores and carnivores. For each individual, we counted the number of bites, estimated its total length (TL) and assigned it to a trophic group (Ferreira et al. 2004, Longo et al. 2014). The individual TL was used to calculate its biomass, which was obtained from length–weight relationships retrieved from the literature (Quimbayo et al. 2021). To determine the individual feeding pressure (FP), we combined the number of bites and biomass of each individual through the equation FP = (bites × biomass) / (2 m2 × 10 min). For each video (i.e. sample), we obtained the feeding pressure for each trophic group, by summing the feeding pressure of all individuals within the same species and trophic group based on literature (Ferreira et al. 2004, Longo et al. 2014). Within the designated area of 2 m2, the photoquadrat method was employed after the RUVs to estimate the percentage cover of each benthic group on the substrate. Five photos (25 × 25 cm) were taken inside each RUVs' area. In the laboratory, the proportion of coverage for each benthic group was estimated using PhotoQuad software (Trygonis & Sini 2012). In each photo, 50 points were randomly distributed, and the organism below each point was identified to the lowest possible taxonomic level. When it was unfeasible to identify an organism to the lowest taxonomic level, we categorized it into a functional group based on Aued et al. (2018). The percentage cover of each group is equivalent to the total number of points overlying that group divided by the total points analysed in the photoquadrat. We then calculated a mean occurrence for benthic substrates in each video by dividing the sum of each benthic substrate by the total number of photos per video (i.e. 5 photos). For Brazilian oceanic islands, we used published data on species abundance and individual TL from visual censuses recorded in the literature (i.e. Cordeiro et al. 2021), and for Ascension Island, we performed visual censuses. This method consists of a linear transect of 40 m2 (20 × 2 m), carried out close to the RUV area, in which a diver constantly swims, counting the number and estimating the TL of each fish (Morais et al. 2017). The TL was also used to calculate the corresponding biomass of fish obtained from length–weight relationships from the literature (Quimbayo et al. 2021). The species that collectively accounted for at least 50% of the biomass were considered hyperdominant species. RUVs, photoquadrats and visual census techniques were performed concomitantly during sampling by different divers. The specific sampling dates for each location were as follows: Fernando de Noronha in October 2011, Rocas Atoll in February 2012, Trindade Island in July 2012, SPSPA in November 2013 and Ascension Island in August 2015.

2.3. Statistical analysis

We first used the benthic composition data, obtained from the photoquadrats, to group each video plot into a specific habitat according to the prevalence of a benthic component within the 2 m2 video area. For this, we performed a cluster analysis for each oceanic island, by using Euclidean distance and the UPGMA clustering method. We then ‘cut’ the dendrogram resulting from the clusters into 5 groups based on a 50% distance height (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m726p001_supp.pdf). We also performed a principal coordinate analysis (PCoA) followed by a permutational multivariate analysis of variance (PERMANOVA) to validate our habitat clustering (Fig. S2). Descriptive analyses were employed to illustrate the percentage cover of benthic substrate on each island (Fig. S3). Additionally, a stacked plot was generated to visually represent the relative proportions of benthic composition and feeding pressure on each oceanic island, and feeding pressure across the habitats. Furthermore, a barplot was constructed to display the mean biomass of reef fish species on each sampled oceanic island. A scatterplot was generated to visually represent the relationship between relative biomass and relative feeding pressure on each oceanic island. Additionally, another scatterplot was created to illustrate the relationship among the mean biomass, mean feeding pressure and number of habitats. Due to the different total number of samples among habitats, we randomly sorted out 30 samples as a minimum sample effort for each habitat and calculated the average frequency for the benthic substrates and feeding pressure of fish trophic groups. For this, the feeding pressure matrix (response variable) was transformed to a proportion. We then repeated this procedure 1000 times for each habitat, resulting in a matrix of 4000 observations (i.e. 1000 for each habitat). The habitat dominated by zoanthids was not used due to the limited number of available samples, of which there were only 3 (Fig. S2). To understand the influence of benthic composition on fish feeding pressure, we performed a canonical correlation analysis, with a subsequent ANOVA of the canonical axes. To examine how species' feeding pressure is influenced by fish biomass, trophic group and the number of feeding habitats used (i.e. as a proxy indicating a generalist and plastic feeding habit), we fitted a general linear model (GLM) with a Gaussian distribution. All analyses were performed using the 'clustsig' (Whitaker & Christman 2014), 'dplyr' (Wickham et al. 2021), 'vegan' (Oksanen et al. 2020), 'ggdendro' (Vries & Ripley 2020), 'ggplot2' (Wickham 2016), 'ISLR' (James et al. 2021) and 'tidyr' (Wickham 2021) packages of R software (R Core Team 2021).

3. RESULTS

We recorded 42 videos (210 photoquadrats) in SPSPA; 43 videos (215 photoquadrats) in Fernando de Noronha; 83 videos (415 photoquadrats) in Rocas Atoll; 84 videos (420 photoquadrats) in Trindade Island; and 42 videos (210 photoquadrats) in Ascension Island. Through our photoquadrats, we found 9 benthic cover categories (Fig. 2A; Fig. S3): EAM, (defined here as a matrix formed by a group of low height and heterogeneous algae), macroalgae (discrete patches of algae, but not limited to a specific size or height, generally functionally similar to EAM in terms of aggregating detritus), crustose coralline algae (CCA), cyanobacteria, coral, zoanthids, filter/suspension feeders, other invertebrates and sand/rubble. EAM was the dominant group in Rocas Atoll (mean cover = 55%), Fernando de Noronha (52%) and Ascension (46%). Macroalgae had a high cover on Trindade Island (40%) and SPSPA (36%). CCA cover was higher on Trindade Island (29%) and Ascension (19%). The cover of all invertebrates was low, below 5%, in all islands, with the exception of zoanthids (Palythoa caribaeorum) in SPSPA (8%) (Fig. 2A; Fig. S3).

By clustering the videoplots using these benthic components, we obtained 5 major habitats: 'dominated by EAM' (129 plots), 'dominated by CCA' (38 plots), 'dominated by macroalgae' (87 plots) and 'dominated by sand' (37 plots), which were recorded on all islands; and 'dominated by zoanthids' (3 plots), which was only observed in SPSPA (Figs. S2 & S3). A total of 6 fish trophic groups were observed feeding on the habitats at all oceanic islands (Fig.

2B). Omnivores (OMNI) were the dominant group in terms of feeding pressure in SPSPA (87%), Ascension (58%) and Trindade (78%), whereas herbivores/detritivores (HERD) were the most important group in Fernando de Noronha (85%) and Rocas Atoll (68%). Territorial herbivores (THER), macroalgivores (MALG), mobile invertebrate feeders (MINV) and sessile invertebrate feeders (SINV) were the groups with the lowest values of feeding pressure at all of the islands (Fig. 2B).

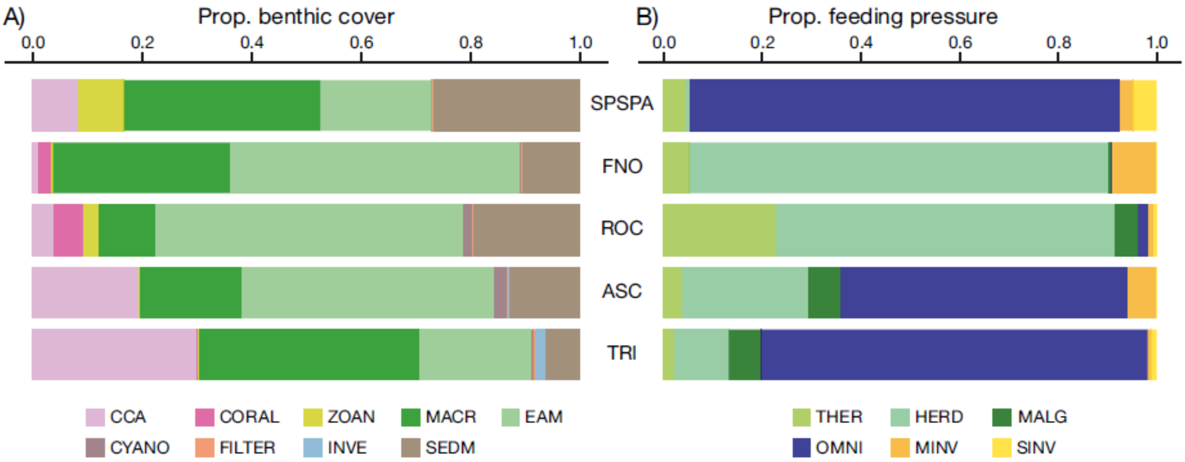

Fig. 2. (A) Relative proportion of benthic cover and (B) fish feeding pressure on 5 oceanic islands (abbreviations as in Fig. 1). Colours represent different benthic components and fish trophic groups. CCA: crustose coralline algae; CYANO: Cyanobacteria; CORAL: scleractinian coral; FILTER: suspension/filter feeders; ZOAN: zoanthids; INVE: other invertebrates; MACR: macroalgae; SEDM: sediment composed mostly of sand; EAM: epilithic algae matrix; THER: territorial herbivores; OMNI: omnivores; HERD: herbivores–detritivores; MINV: mobile invertebrate feeders; MALG: macroalgivores; SINV: sessile invertebrate feeders.

The predominant habitat foraged by all trophic groups in SPSPA was the habitat dominated by macroalgae (Fig. 3). In Fernando de Noronha, all trophic groups foraged almost exclusively in the habitat dominated by EAM. In Rocas Atoll, there was a difference in the habitat use among trophic groups, but habitats dominated by sand and EAM were the predominant habitats explored by fishes (Fig. 3). The habitat dominated by CCA was highly foraged by omnivores in Ascension and by macroalgivores and sessile invertebrate feeders in Trindade Island (Fig. 3).

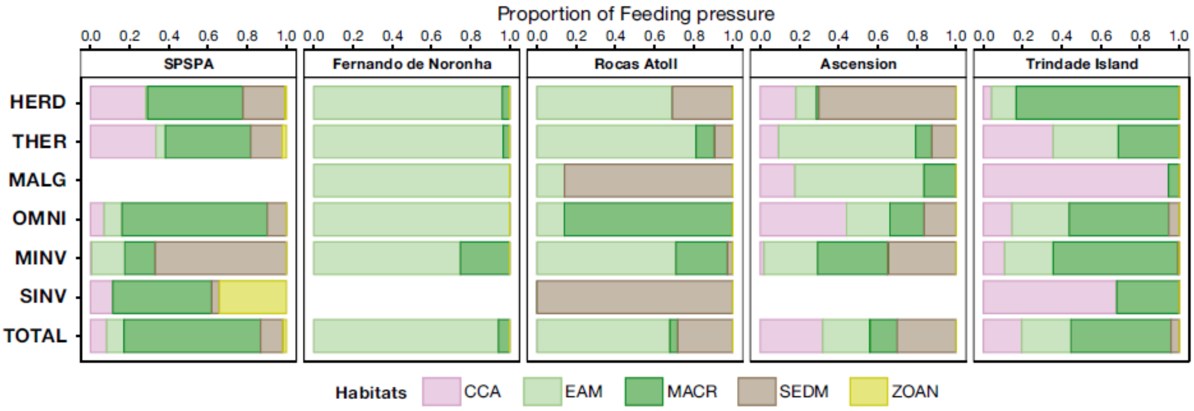

Fig. 3. Relative proportion of feeding pressure performed by different fish trophic groups on the 5 habitats. Colours represent different habitats. Abbreviations as in Figs. 1 & 2

Benthic habitats explained approximately 81% of the observed fish feeding pressure patterns (Fig. 4). In general, the proximity of all fish trophic groups to the centroid of canonical correlation analysis indicated a correlation between their feeding pressure pattern and the different habitats. Notably, specific patterns emerged, such as macroalgivores and omnivores being more closely associated with habitats dominated by CCA, territorial herbivores exhibiting associations with habitats dominated by EAM, and mobile invertebrate feeders associated with habitats dominated by sand and macroalgae.

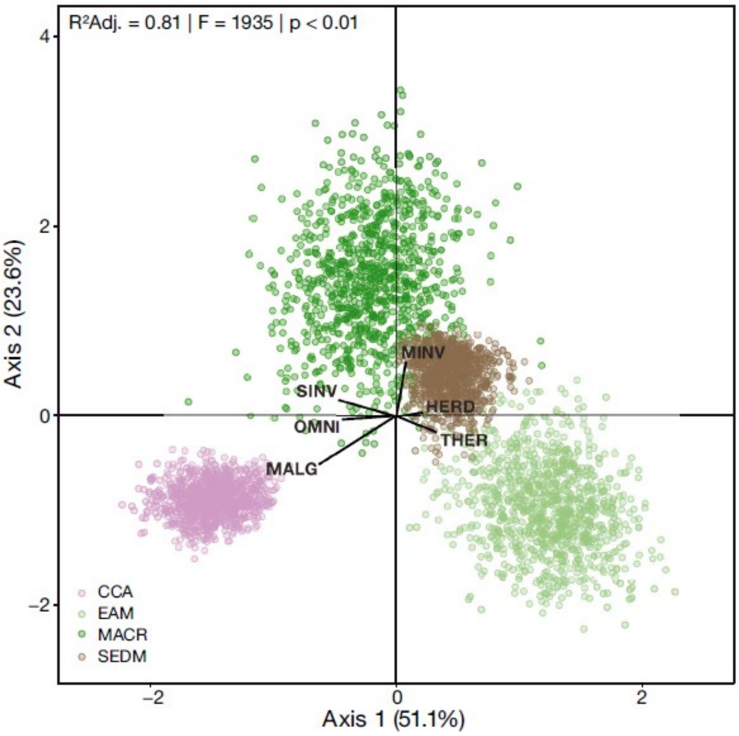

Fig. 4. Canonical correlation analysis (CCoA) between the benthic-dominated habitats and the feeding pressure of fishes in all 5 islands. Colours indicate habitats. Abbreviations as in Fig. 2

There was a positive correlation between feeding pressure and fish biomass (Table S1, Figs. S4 & S5), particularly within the herbivore and omnivore groups (Fig. 5A). However, we found no significant effect of trophic group or the number of habitats used on the feeding pressure. Omnivores and territorial herbivores generally accounted for higher biomass and interacted with more habitats. In terms of biomass, the omnivore group was mainly composed of the species *Melichthys niger*, which interacted with up to 4 different habitats. The herbivore–detritivore group was mainly composed of 2 species from the genus Acanthurus (Fig. 5A). A hyperdominance of omnivores was observed in Rocas, SPSPA and Trindade in terms of relative biomass and feeding pressure, while herbivores–detritivores were predominant in Rocas Atoll (Fig. 5B). In terms of the hyperdominance of reef fish, our observations revealed that the black triggerfish *M. niger*, an omnivore, exhibited the highest biomass among all species in SPSPA, Trindade Island and Ascension, accounting for 85.2, 61.5 and 85.5% of the total fish biomass at each island, respectively (Fig. 6). These islands exhibit lower species richness as well as a greater distance from the coast. Conversely, in Rocas Atoll and Fernando de Noronha, where there is higher species richness and closer proximity to the mainland, 2 herbivorous–detritivorous species displayed the highest biomass, but neither can be considered hyperdominant; in Rocas Atoll, the surgeonfish *Acanthurus chirurgus* corresponded to 43.2% of the total fish biomass, whereas in Fernando de Noronha, the biomass of the parrotfish *Sparisoma amplum* represented 22.6% of the total (Fig. 6).

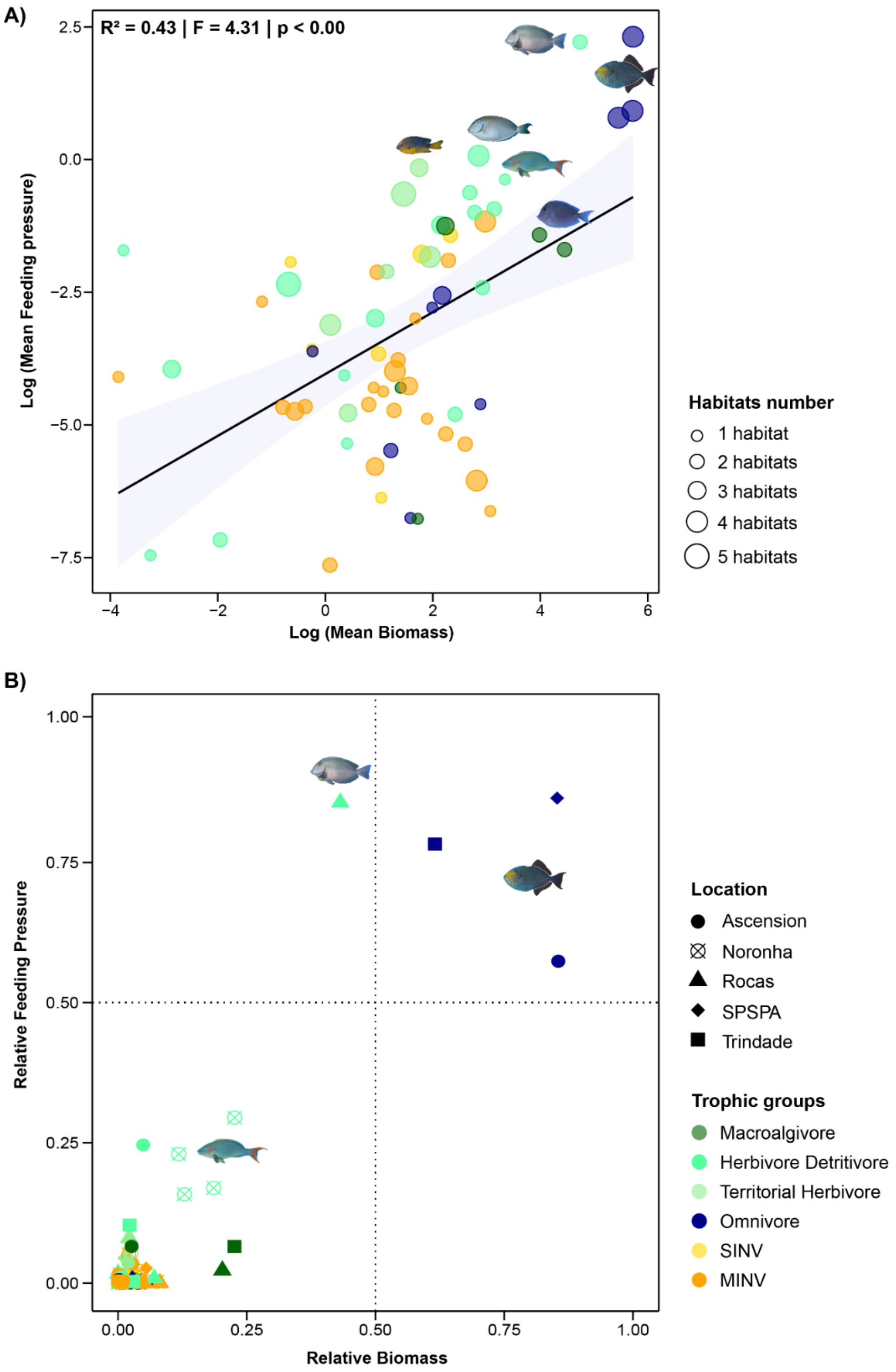

Fig. 5. Relationship between (A) mean biomass and mean feeding pressure and (B) relative biomass and relative feeding pressure of reef fish species which forage in the benthos at all sampled oceanic islands. Each symbol indicates a species within a specific trophic group. In (A), sizes indicate the number of habitats; in (B), shapes indicate each island sampled, and in (A) and (B), colours indicate functional groups. Fish images represent the species with the highest biomass within each trophic group. SINV: sessile invertebrate feeders; MINV: mobile invertebrate feeders.

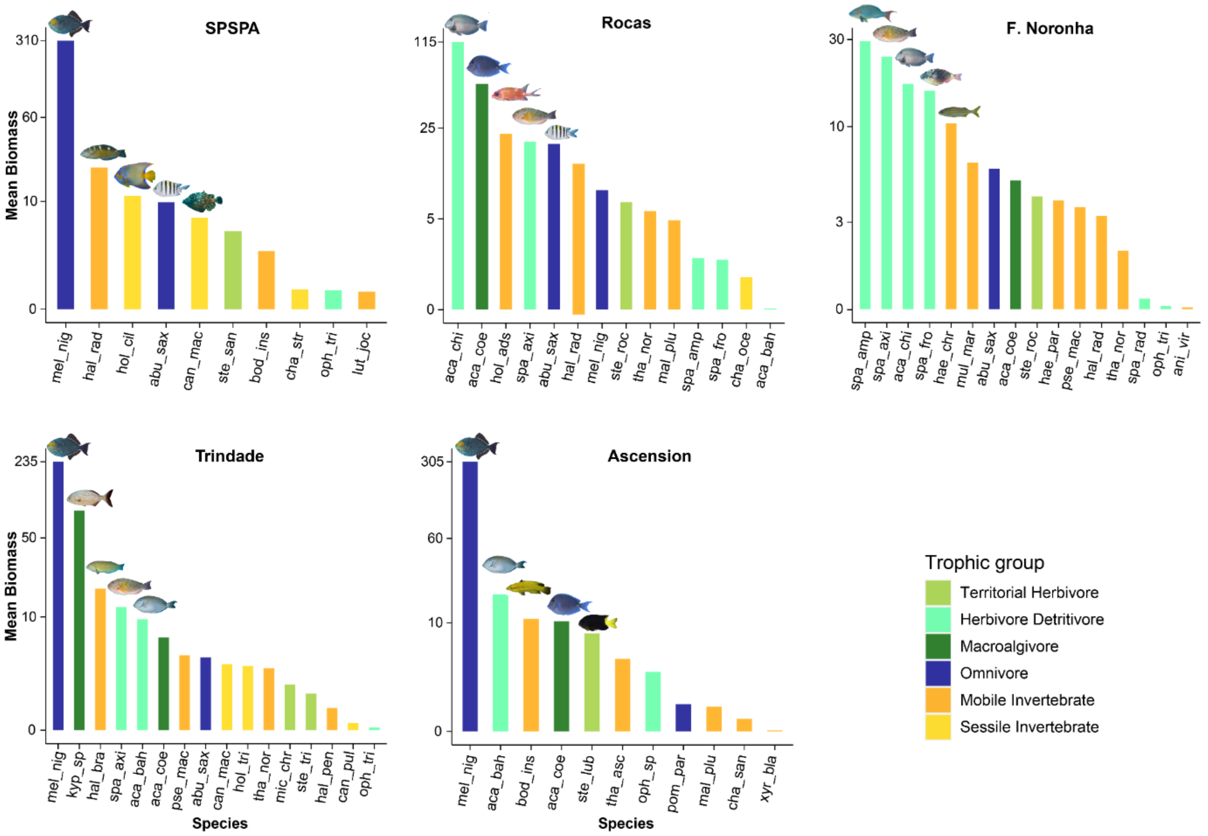

Fig. 6. Mean biomass (g m–2) of reef fish species which forage in the benthos at each sampled oceanic island. SPSPA: St Peter and St Paul's Archipelago. The y-axis scale is log10 transformed for better visualisation of data dispersion (note different scales among islands). Colours represent fish trophic groups. abu_sax: *Abudefduf saxatilis*; aca_bah: *Acanthurus bahianus*; aca_chi: *Acanthurus chirurgus*; ani_vir: *Anisotremus virginicus*; bod_ins: *Bodianus insularis*; can_mac: *Cantherhines macrocerus*; can_pul: *Cantherhines pullus*; cha_oce: *Chaetodon ocellatus*; cha_san: *Chaetodon sanctaehelenae*; cha_str: *Chaetodon striatus*; hae_chr: *Haemulon chrysargyreum*; hae_par: *Haemulon parra*; hal_bra: *Halichoeres brasiliensis*; hal_pen: *Halichoeres penrosei*; hal_rad: *Halichoeres radiatus*; hal_cil: *Holacanthus ciliaris*; hol_tri: *Holacanthus tricolor*; hol_ads: *Holocentrus adscensionis*; kyp_sp: *Kyphosus* spp.; lut_joc: *Lutjanus jocu*; mal_plu: *Malacanthus plumieri*; mel_nig: *Melichthys niger*; mic_chr: *Microspathodon chrysurus*; mul_mar: *Mulloidichthys martinicus*; oph_sp: *Ophioblennius* spp.; oph_tri: *Ophioblennius trinitatis*; pom_par: *Pomacanthus paru*; pse_mac: *Pseudupeneus maculatus*; spa_amp: *Sparisoma amplum*; spa_axi: *Sparisoma axillare*; spa_fro: *Sparisoma frondosum*; ste_lub: *Stegastes lubbocki*; ste_roc: *Stegastes rocasensis*; ste_san: *Stegastes sanctipauli*; ste_tri: *Stegastes trindadensis*; tha_asc: *Thalassoma ascensionis*; tha_nor: *Thalassoma noronhanum*; xyr_bla: *Xyrichtys blanchardi.*

4. DISCUSSION

Our research focused on investigating trophic interactions in shallow reef substrates dominated by EAM, calcareous algae and macroalgae, which are representative habitat types of reef systems throughout the globe (Aued et al. 2018, Tebbett et al. 2023). We sampled 5 Atlantic oceanic islands with lower fish species richness compared to coastal reefs (Morais et al. 2017). The highest intensity of trophic interactions between fishes and benthic organisms was attributed to hyperdominant generalist species, which were feeding on items such as crustose coralline algae, macroalgae, detritus and others. They displayed foraging behaviour across various habitats, with feeding pressure intensity varying among islands, influenced by fish composition and habitat heterogeneity (Canterle et al. 2020). These empirical findings substantiate our hypothesis that hyperdominant species exhibit successful foraging strategies across diverse habitats, underscoring the significance of habitat diversity (Nunes et al. 2020, Canterle et al. 2020), trophic characteristics (Ferreira & Gonçalves 2006) and biomass (Longo et al. 2014) in shaping the feeding behaviour of reef fish in the Atlantic oceanic islands. Additionally, our findings indicate a distinction in terms of habitat use between different trophic groups. Our study provides valuable insights into the intricate trophic dynamics of reef fishes in insular ecosystems, emphasizing the importance of habitat diversity within these unique systems.

The hyperdominance (i.e. >50% of the total biomass) of black triggerfish *Melichthys niger* in SPSPA, Trindade and Ascension, along with its generalist feeding behaviour, has resulted in a foraging pattern that encompasses a wide range of habitats and exerts high feeding pressure, particularly on macroalgae and CCA. This generalist feeding behaviour enables *M. niger* to effectively exploit vacant ecological niches on oceanic islands (Kavanagh & Olney 2006, Mendes et al. 2019) and allows this single species to dominate the feeding pressure exerted by fish on the benthos in these 3 islands. For instance, in SPSPA, the generalist behaviour and plasticity of this species, in combination with the absence of abundant herbivorous–detritivorous fish (Luiz et al. 2015, Morais et al. 2017), allows *M. niger* to assume the herbivory function within this archipelago (Mendes et al. 2019). Although *M. niger* is not exclusively herbivorous, our findings align with the typical trend of increased herbivory intensity observed in tropical regions. Herbivory is known to intensify towards tropical regions due to factors such as metabolic rates, algal palatability and species diversity involved in these functional roles (Longo et al. 2014, 2019). Although *M. niger* forms large shoals and exhibits high abundance at oceanic islands worldwide (Lubbock 1980, Lubbock & Edwards 1981, Kavanagh & Olney 2006), this species is not always hyperdominant, and the reasons for this are not completely understood. For instance, in the Caribbean, *M. niger* is one of the most important species to consume the macroalgae from the genus *Galaxaura* in feeding assays (Tebbett et al. 2020). The lack of hyperdominance of *M. niger* in the Caribbean is likely a result of the high regional species richness, since the herbivory function is shared among several species. Similarly, in the open pools of Rocas Atoll, *M. niger* appeared among the 4 most important fish species foraging over reef substrates (Longo et al. 2015), but it did not exhibit hyperdominance either, since herbivorous surgeonfishes (*Acanthurus chirurgus* and *A. coeruleus*) and parrotfishes (*Sparisoma amplum* and *S. axillare*) are abundant. In fact, *M. niger* is found both in Rocas Atoll and Fernando de Noronha, but never reaches hyperdominance (Krajewski & Floeter 2011, Longo et al. 2015, Morais et al. 2017). Our study provides further evidence of the remarkable plasticity and adaptability of *M. niger* to different local conditions. Across the 3 islands where it exhibited hyperdominance, this species utilised 4 (out of 5) distinct habitats to forage. These findings support the concept that a single species can play a disproportionately significant functional role on island reefs. Investigating the drivers of such differences is crucial for a deeper understanding of reef functioning in these unique ecosystems.

Fernando de Noronha and Rocas Atoll are 2 islands connected by the same seamount chain and are closest to the coast (Fig. 1). Feeding interactions in these islands were predominantly driven by herbivores–detritivores. Fernando de Noronha stands out as nearest to the mainland and the largest in terms of area, consequently displaying a higher species richness, in line with the principles of island biogeography (Whittaker & Fernández-Palacios 2007). Regions with higher species richness, specifically those that interact with the benthos, might be influencing the consistent pattern of feeding pressure among species, thereby not favouring the dominance of a specific species in Fernando de Noronha. While Rocas Atoll is indeed the closest to the coast, its reef area is relatively small, and a single species, the surgeonfish A. chirurgus, was responsible for the majority of the total feeding pressure. Although it encompasses 43.2% of the total biomass, it is not considered hyperdominant. On the other hand, in Fernando de Noronha, the parrotfishes *S. amplum, S. frondosum* and *S. axillare* alongside *A. chirurgus* exhibited similar relative biomasses and feeding pressure, with no dominance pattern. *Sparisoma* spp. are generally considered scrapers/browsers (Ferreira & Gonçalves 2006, Bonaldo et al. 2014), but they also play a functional role in removing EAM or endolithic primary producers (Clements & Choat 2018). The lack of dominance in Fernando de Noronha and the fact that the 3 parrotfish species forage in similar habitats suggests that some level of competition can take place.

Despite these differences, herbivorous–detritivorous surgeonfishes and parrotfishes usually attain higher biomass and feeding pressure on tropical reefs (Longo et al. 2014, 2015, 2019, Tebbett et al. 2020, Pessarrodona et al. 2022). In a uniquely large latitudinal gradient study in the Western Atlantic, Longo et al. (2019) indicated that fish–benthos interactions in shallow tropical reefs were primarily driven by herbivorous fishes (scrapers) such as surgeonfishes and parrotfishes. In contrast, subtropical reefs in both hemispheres were dominated by omnivorous sparids. However, the dominance exhibited by sparids of the genus Diplodus did not meet the criteria for hyperdominance. It appears that hyperdominance of single species (like *M. niger*) in the Atlantic oceanic islands is limited to the most isolated ones with tropical characteristics (temperature above 24°C) (Kavanagh & Olney 2006), but also those with low species richness, as seen in the case of SPSPA and Ascension Island.

The richer Indo-Pacific parrotfish fauna exhibit niche partitioning by feeding on endolithic and epilithic micro-photoautotrophs on a much smaller scale than what we observed here (Nicholson & Clements 2023). Unfortunately, we know almost nothing about the nutritional targets of the Atlantic parrotfishes (but see Mendes et al. 2018, Cardozo-Ferreira et al. 2023). This highlights the importance of understanding the nutritional properties of food and food processing modes to fully understand trophodynamics on reefs. Surgeonfishes in the Atlantic are typically scrapers, feeding on various substrates dominated by EAM, macroalgae or other delicate primary producers, ingesting algae, detritus and some animal material (Ferreira & Gonçalves 2006, Mendes et al. 2018, Cardozo- Ferreira et al. 2023). On the other hand, *A. coeruleus* is the single acanthurid that browses on EAM in the Atlantic Ocean (Ferreira & Gonçalves 2006). Interestingly, in Rocas Atoll, sediment and detritus represent a large proportion of the diet of *A. chirurgus*, while *A. coeruleus* ingested mainly red corticated algae, especially *Digenea simplex* (Longo et al. 2015). This suggests a higher feeding plasticity of *A. chirurgus* that feeds on EAM and sandy habitats, while *A. coeruleus* feeds more predominantly on EAM and macroalgae.

As our study shows, the EAM is the most common habitat in 3 of the 5 islands and has a high tolerance under different environmental conditions and pressures. This fast-growing matrix has a great capacity to compete for space, which allows its large distribution (Littler & Littler 1980, Airoldi 1998). It is composed of algae, detritus and small invertebrates, thereby enhancing its nutritional value and significance within the food chain (Wilson et al. 2003).

Notably, organic detritus derived from the EAM often contains higher concentrations of protein amino acids compared to filamentous algae (Crossman et al. 2001). However, the relative importance of each food item within the EAM for the nutrition of herbivores in the Atlantic fish fauna is yet to be determined (Mendes et al. 2018).

Territorial herbivores forage on the EAM on local scales while also opportunistically capturing plankton, depending on species and resource availability (Ferreira et al. 1998, Ceccarelli 2007). The rates of interaction between territorial herbivores and benthic communities were found to be consistent across the studied oceanic islands, aligning with the values reported for tropical and subtropical reefs along the Brazilian coast and the Caribbean (Longo et al. 2019). Mobile invertebrate fish feeders (MINV) included labrids, haemulids, holocentrids and mullids. Haemulids (*Haemulon* spp.) never contributed to the majority of feeding pressures, but they were more abundant in less isolated islands, while labrids appeared secondarily in more isolated ones (i.e. *Bodianus* spp. and *Halichoeres* spp.). All MINV were very plastic in terms of their foraging substrate associations, exploring EAM, macroalgae and sand flats searching for a diverse set of nutritious cryptic invertebrates. This behaviour was influenced by the availability of corresponding substrates on each island (Lucena et al. 2022).

In addition to diet and food plasticity, foraging selection patterns on a specific island can be influenced by biogeographical factors (e.g. dispersal ability of species). On those very isolated islands, feeding pressure patterns are typically driven by a few dominant species. However, it is important to note that the composition of these dominant species can vary across different locations. While hyperdominant species are typically characterised by their wide geographic range (Dietzel et al. 2021), a subset of these species can be among the rarest within specific regions of their distribution, indicating that their dominance in terms of trophic interactions does not necessarily extend throughout their entire geographic range (Schiettekatte et al. 2022). These factors play a crucial role, especially in insular systems, where their influence is particularly pronounced. By accounting for such factors, we can achieve a more precise understanding of the feeding ecology and species interactions in different ecosystems.

The advent of remote video technology has transformed our ability to study animal behaviour and its role in natural ecosystems (McQuillen & Brewer 2000, Tanedo & Hollmen 2020). In the marine environment, video cameras have significantly enhanced our understanding of species and processes across various habitats, from the deep-sea to shallow waters (Longo et al. 2015, Prat-Varela et al. 2023). Standardised remote video methods have revealed global patterns and trends (Fontoura et al. 2020, Simpfendorfer et al. 2023). In the field of reef ecology, remote cameras have been commonly used to assess herbivore feeding selectivity (e.g. Mantyka & Bellwood 2007, Longo et al. 2015, Mendes et al. 2015) and herbivory rates through algae assays (e.g. Fox & Bellwood 2008, Hoey & Bellwood 2011, Martin et al. 2018), while only a few studies have examined feeding interactions with the benthos involving entire fish communities (Longo et al. 2014, 2015, 2019, Canterle et al. 2020, Pessarrodona et al. 2022). It is important to highlight that the use of cameras provides a good view of patterns and processes occurring on reefs but fails to provide details on how species partition their resources, for instance. Here we categorized feeding substrate on broad categories based on the dominant group of organisms (e.g. EAM, macroalgae). However, species may partition their resources on a much finer scale (e.g. different species feeding on the EAM may target different food resources, Purcell & Bellwood 1993, Mendes et al. 2018) and by taking only video into account, we may lose definition to infer food partitioning among species. While this certainly does not discredit the use of RUVs while studying reef ecology, we suggest that using multiple methods jointly will improve our understanding of how reefs function.

Understanding trophic interactions, particularly between fish and the benthic environment, is crucial in reef ecology for understanding natural, short- and long-term changes. It also helps us to assess the impact of human activities and climate change on energy transfer within the ecosystem (Brandl et al. 2019). The reef substrate plays a significant role in accumulating primary production (Hay 1991, Tebbett et al. 2020), with fish comprising the majority of vertebrate biomass in tropical and subtropical reefs (Sale 1991). In order to enhance our understanding, future studies about how food resources are partitioned among reef dwellers in the face of human and natural disturbances are imperative and strongly encouraged.

5. CONCLUSIONS

Our study demonstrates that fish feeding pressure is influenced by both habitat features and fish biomass. Specifically, we detected that each trophic group is dominated by only 1 or 2 species in terms of biomass, which aligns with previous findings by Cowburn et al. (2021). Despite the comparatively lower species richness observed on oceanic islands in comparison to coastal environments, the underlying patterns and processes that shape biodiversity are similar. Our study holds important implications for the conservation and management of marine biodiversity, highlighting the necessity of considering both habitat heterogeneity and species dominance in conservation planning. Furthermore, as the study areas comprise various types of

MPAs, a recommended approach would involve giving special attention to species that play crucial functional roles in maintaining habitat diversity. This is primarily due to the significant isolation of these islands, which hinders the introduction of new species that could potentially replace functionally important species, like herbivorous fish. Future management and conservation targets should prioritise a controlled management strategy for the fisheries targeting these key species.

Data availability. Data and codes supporting this research are available on Zenodo (https://zenodo.org/records/10190848).

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SUPPLEMENTARY MATERIAL

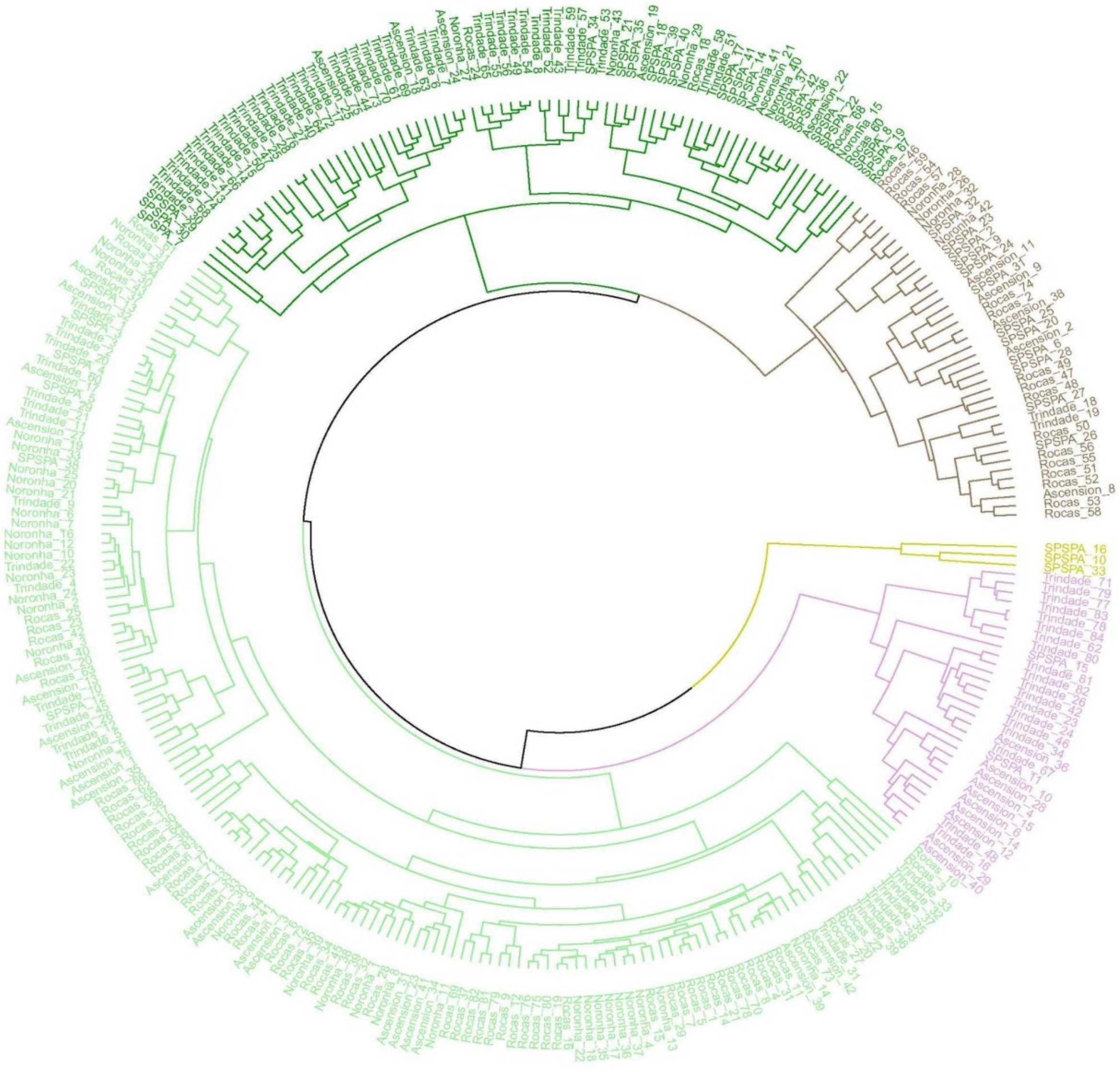

Fig. S1. Clustering analysis of habitats group following Euclidean distance (UPGMA clustering method). The dendrogram shows the results of hierarchical clustering, with benthic substrate clustered into five groups based on a 50% distance height. Dendrogram branches are coloured according to benthic habitat. Pink - Crustose Coralline Algae; Light green - Epilithic algae matrix; Dark green - Macroalgae; Brown - Sand; Yellow – Zoanthid.

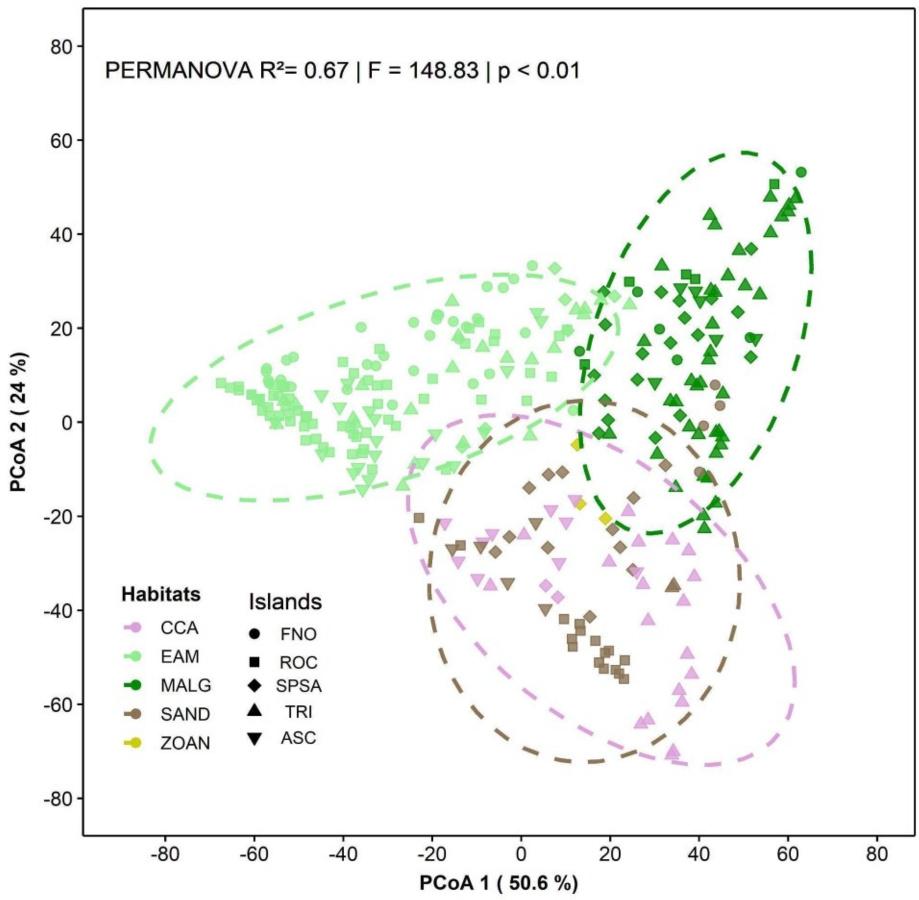

Fig. S2. Principal coordinate analysis (PCoA) showing the ordination of samples according to the benthic habitats. Geometric shapes indicate samples on each oceanic island, and colours indicate habitats. Ellipses indicate a 95% confidence interval.

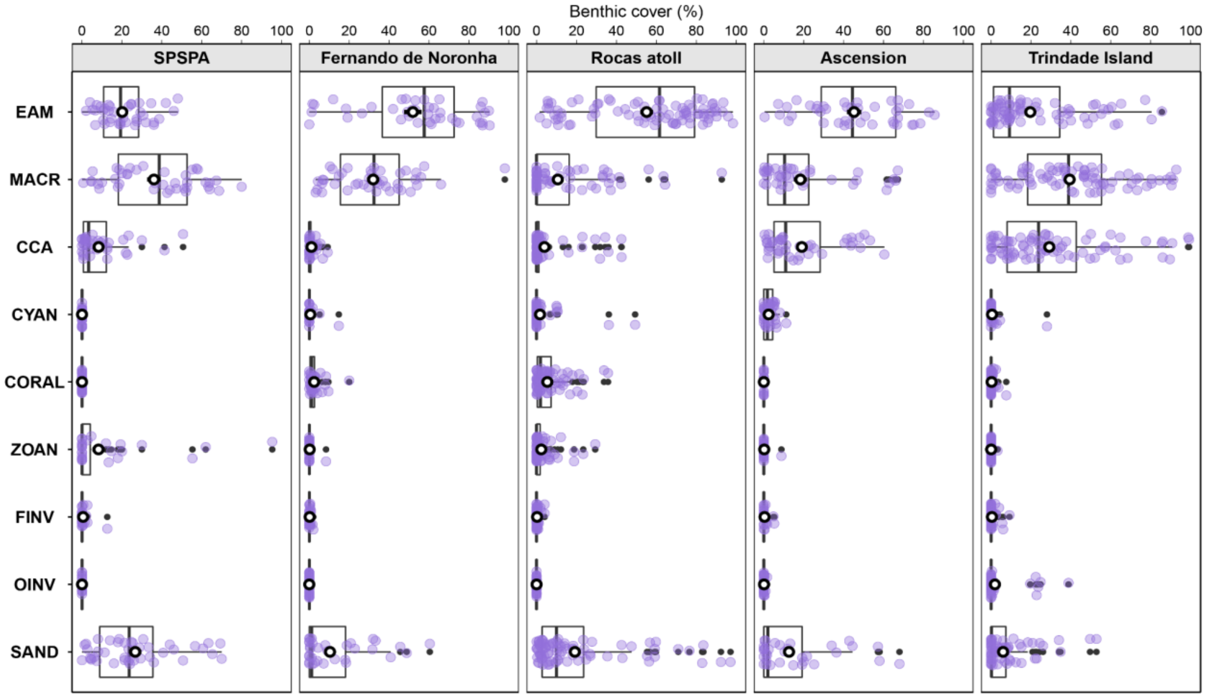

Fig. S3. Boxplot and scatter plot showing the cover of nine benthic substrates found on the oceanic island. EAM - Epilithic Algal Matrix, MACR - Macroalgae, CCA - Crustose Coralline Algae, CYAN - Cyanobacteria, ZOAN - Zoanthid, FINV - Filter/suspension feeders, OINV - Other invertebrates. Each purple circle represents a RUV and the cover (%) of a benthic component in that RUV. White circles and black lines indicate the mean and standard error, respectively. SPSPA (St Peter and St Paul's Archipelago).

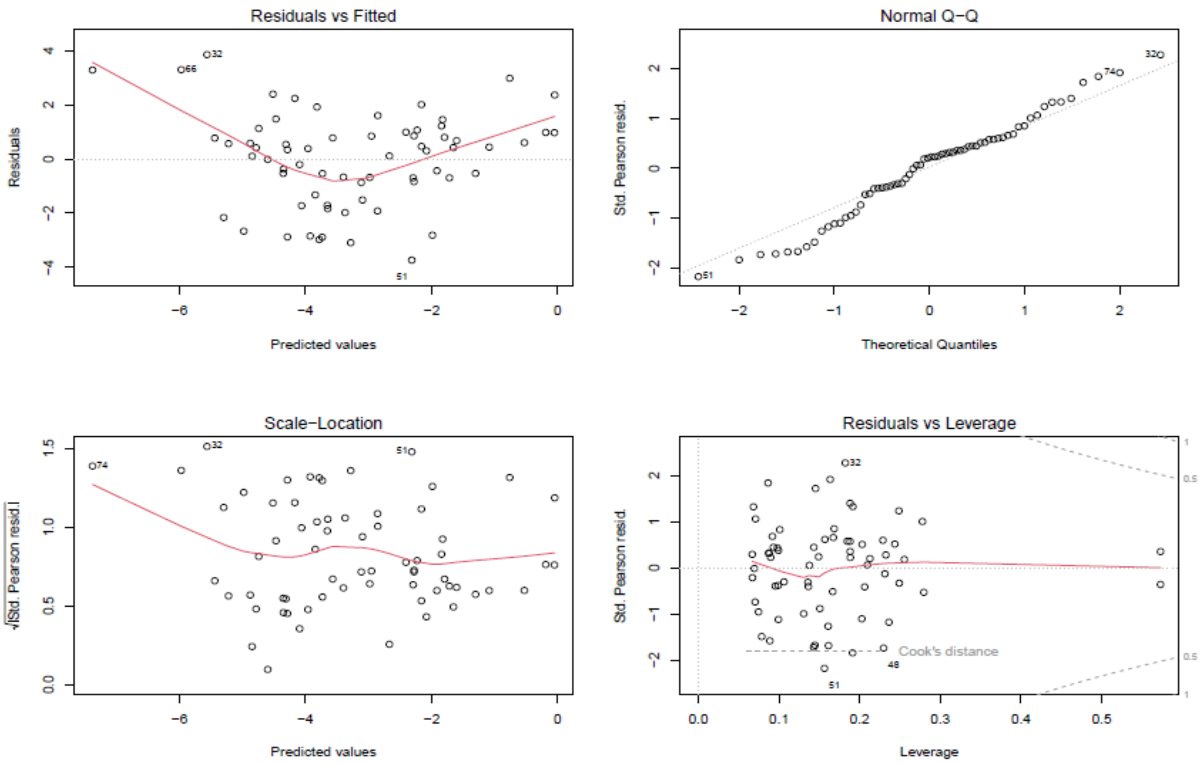

Fig. S4. Validation of the General Linear Model (GLM).

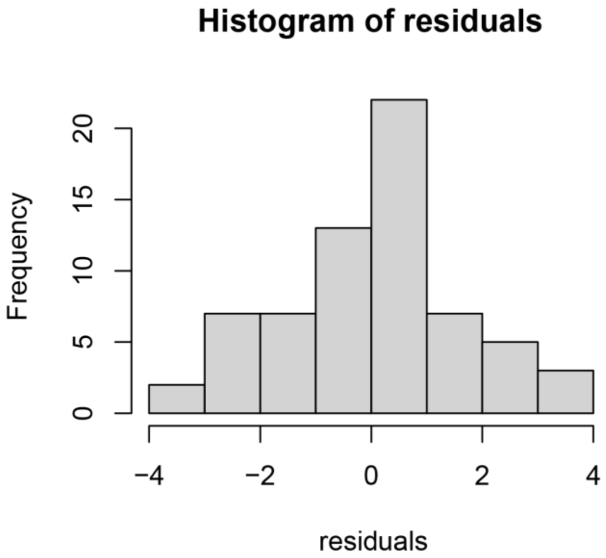

Fig. S5. Residual histogram.

Table S1 Summary General Linear Model (GLM). Relationships of mean biomass of reef fish, habitats and fish trophic group.

Coefficients:	**estimate**	**std. Error**	**t value**	**pr(>|t|)**
(intercept)	**-3.5843**	**0.5837**	**-6.141**	**9.52e-08 *****
Log(mean_biomass)	**0.5265**	**0.1460**	**3.606**	**0.000672 *****
Habitats 2	0.3266	0.6235	0.524	0.602449
Habitats 3	0.8018	0.7230	1.109	0.272235
Habitats 4	1.5539	0.8859	1.754	0.084991
Habitats 5	2.0289	1.4688	1.381	0.172755
Macroalgivore	-1.2464	0.9983	-1.249	0.217126
Mobile invertebrate	**-1.7659**	**0.6046**	**-2.921**	**0.005056 ****
Omnivore	-1.0312	0.8487	-1.215	0.229548
Sessil invertebrate	-0.2455	0.8961	-0.274	0.785129
Territorial herbivore	-0.2977	0.9403	-0.317	0.752753

CAPÍTULO II

(Publicado em Marine Environmental Research)

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Thermal tolerance as a driver of reef fish community structure at the isolated tropical Mid-Atlantic Ridge Islands

Débora S. Ferrari, Lucas T. Nunes, Kirsty L. Jones, Carlos E. L. Ferreira., Sergio R. Floeter (2024). Thermal tolerance as a driver of reef fish community structure at the isolated tropical Mid-Atlantic Ridge Islands. *Marine Environmental Research.*

Abstract

Reef fish communities are shaped by historical and ecological factors, including abiotic and biotic mechanisms at different spatial scales, determining species composition, abundance and biomass. The oceanic islands in the Mid-Atlantic Ridge (St. Peter and St. Paul’s Archipelago - SPSPA, Ascension, and St. Helena), exhibiting differences in community structure along a 14-degree latitudinal and a 10°C thermal gradient. We investigate the influence of sea surface temperature, area, age, isolation and phosphate on reef fish community structures. Reef fish trophic structure varies significantly across the islands, with planktivores and herbivore-detritivores showing the highest abundances in SPSPA and Ascension, while less abundant in St. Helena, aligning with the thermal gradient. Variations in reef fish community structures were predominantly influenced by thermal regimes, corroborating the expansion of species' thermal niche breadth at higher latitudes and lower temperatures. This study highlights that in addition to biogeographic factors, temperature is pivotal on shaping oceanic island reef fish community structure.

Keywords: Oceanic island, Thermal niche breadth, Temperature, Trophic structure, Fish Endemism, Reefs.

1. Introduction

The structure of biological communities is influenced by diverse ecological processes occurring at different spatial scales (Ovaskainen et al., 2017). At the local level, the interplay of biotic and abiotic factors fosters the establishment and abundance patterns of species in natural communities. Meanwhile, at the regional scale, dispersal mechanisms and environmental gradients play a crucial role in shaping species distributions and community composition. In the marine ecosystem, most shallow-water organisms, such as fish, algae, corals, and other invertebrates, have a planktotrophic larval stage in their life cycle. This ability to float, feed, or photosynthesize at the water's surface enhances their dispersal through ocean currents. Thus, the dispersal capacity of marine species, which can range from a few meters to hundreds of kilometres, influences the colonisation of new areas (Luiz et al., 2013; 2015). For reef fish, local community structure is shaped by various mechanisms, including habitat availability and complexity (Pinheiro et al., 2011; Canterle et al., 2020; Ferrari et al., 2024), interspecific interactions (Canterle et al., 2020) and environmental drivers like depth, wave exposure and temperature (Krajewski and Floeter, 2011; Maia et al., 2018; Silva et al., 2023). However, for the successful colonisation of isolated areas, fish species engaged in these dispersal processes are commonly those with generalist or opportunistic habits, exhibiting adaptable physiological and behavioural traits that enable them to thrive in diverse environmental conditions (Luiz et al., 2013; Hachich et al., 2020). In isolated areas, reef fish are selected by a unique set of features that allows the colonisation of these systems, resulting in a community composed only of a subset of the mainland species pool (Bender et al., 2017).

Oceanic islands are a good example of isolated areas, being surrounded by the open ocean and lacking any connection to the continental shelf (Dawson, 2015). These unique characteristics contribute to the prevalence of endemic species (Whittaker and Fernandez-Palacios, 2007; Hachich et al., 2015, 2020), although accompanied by relatively low species diversity and functional redundancy (Ferrari et al., 2023). Oceanic islands have been important models for testing Island Biogeography Theory (Hachich et al., 2015; Ávila et al., 2018; Ferrari et al., 2023) and investigating species evolution (Rominger et al., 2016). The high isolation and distinct dynamics of dispersal, colonisation, speciation, and extinction observed in oceanic islands provide valuable insights into biogeographical hypotheses and community assembly (Hachich et al., 2020), especially self-recruitment which plays a significant role in sustaining populations (Robertson, 2001). The self-recruitment phenomena can potentially result from greater isolation and limited connectivity within reef communities on oceanic islands, in contrast to the mainland (Robertson, 2001).

In the Mid-Atlantic Ridge, three oceanic islands (St. Peter and St. Paul's Archipelago, Ascension and St. Helena) harbour a distinctive collection of biota derived from both the Western and Eastern Atlantic regions (Floeter et al., 2008; Wirtz et al., 2017). Particularly, Ascension and St. Helena share many endemic species (Kulbicki et al., 2013), and were previously classified as a single biogeographic province (Kulbicki et al., 2013), however, new analysis suggests that, along with SPSPA, these three islands constitute a distinct marine biogeographic province (Cord et al., unpublished results). Nevertheless, despite their unique marine biodiversity, comprehensive studies on these three Mid-Atlantic Ridge Islands have been limited primarily to species composition, without quantitative information drawn from standardized methods of data collection. In studies of reef fish communities, measures such as species richness, abundance, and biomass are frequently analysed to understand the organization and functioning of these communities. Additionally, beta diversity, particularly in comparative studies, serves as a valuable tool for evaluating the variation in species composition between different locations (Baselga, 2010). Even though there may be similarity in species composition, the structure of the fish community—including aspects like abundance and biomass—may vary due to the influence of abiotic variables and biotic interactions (Day et al., 2018). The main factors influencing the composition of reef fish communities include biogeographic, anthropogenic, and energetic factors, such as temperature (Quimbayo et al. 2019).

Sea surface temperature stands out as one of the main factors influencing the distribution and establishment of species on a spatial scale (Tittensor et al., 2010). This influence is attributed to physiological and ecological processes, as well as the species' adaptation to local temperature regimes (Edgar et al., 2017; Stuart-Smith et al., 2017; Bosch et al., 2021). The thermal tolerance of species refers to the range of temperatures within which a species can thrive, survive, grow, and reproduce (Ern et al., 2023). Each species has its own thermal niche, consisting of ecological requirements and preferences regarding temperature within its habitat (Day et al., 2018). Tropical species generally exhibit narrower thermal niches, possibly because they are acclimated to a more stable temperature regime and have evolved to adapt to a narrower thermal range (Janzen, 1967). In contrast, temperate species have the widest thermal niches, particularly in regions with extreme seasonal temperatures variations (Sunday et al., 2011; Stuart-Smith et al., 2017).

On the three islands of the Mid-Atlantic Ridge, there is a noticeable pattern of decreasing average temperatures from SPSPA towards St. Helena as latitude increases. The sea surface temperature in these islands shows significant monthly fluctuations, with SPSPA ranging from an average of 26°C to 27.8°C, while in St. Helena it ranges from 20.2°C to 24.9°C. These temperature variations act as a selective filter, influencing the establishment and survival of species that are adapted to specific temperature ranges (Pörtner, 2001). Here, we conduct a quantitative assessment of the reef fish communities of St. Peter and St. Paul's Archipelago, Ascension Island, and Saint Helena Island. First, we evaluated the community structures through a detailed analysis of abundance, biomass, size class, richness, and beta diversity across the islands. Second, given the temperature variation among the islands, we investigate in detail the influence of sea surface temperature on reef fish communities. We hypothesised that monthly variations in SST would influence the abundance of species due to physiological limitations. Consequently, we expected the thermal niche breadth of species to be higher in St. Helena, the island with the lowest temperatures and highest seasonal temperature variation, aligning with the observed pattern of an increasing thermal niche towards higher latitudes (Stuart-Smith et al., 2017).

2. Methods

2.1 Study area

We sampled three oceanic islands located on the Mid-Atlantic Ridge (**Fig. 1**): St. Peter and St. Paul's Archipelago (SPSPA, 0°55'1"N | 29°20'44" W), approximately 1010 km away from the Brazilian northeast coast; Ascension Island (7°56'26"S | 14°22'25" W) located ~1600 km from the western coast of Africa; and St. Helena Island (15°57'56"S | 5°42'41" W) ~1900 km from the mainland of Africa. The SPSPA consists primarily of rocks derived from exhumations of the upper mantle (Maia et al., 2016), while Ascension and St. Helena Island are predominantly composed of volcanic rock formations. These islands are topographic parts of the Mid-Atlantic Ridge and exhibit notable similarities, including lower species richness, high endemism, and oligotrophic waters in comparison to coastal regions (Quimbayo et al., 2019). The three islands share 25 fish species, of which three of them are endemic. Ascension and St. Helena have a higher affinity between them as they share more endemic and sister species (Floeter et al., 2008; Brown et al., 2019). Both islands harbour species originating from the Western and Eastern Atlantic (Kulbicki et al., 2013). The three islands are under some level of protection through Marine Protected Areas (MPAs), St. Helena and Ascension are designated as MPA with Sustainable Use (CAT VI- IUCN) (St. Helena Government, 2022; Ascension Island Government, 2021). SPSPA receives two categories of protected areas, a larger part being Environmental Protected Areas (EPA) where use is allowed (CAT V-IUCN), and a small no-take area (CAT III-138 IUCN) (Giglio et al., 2018).

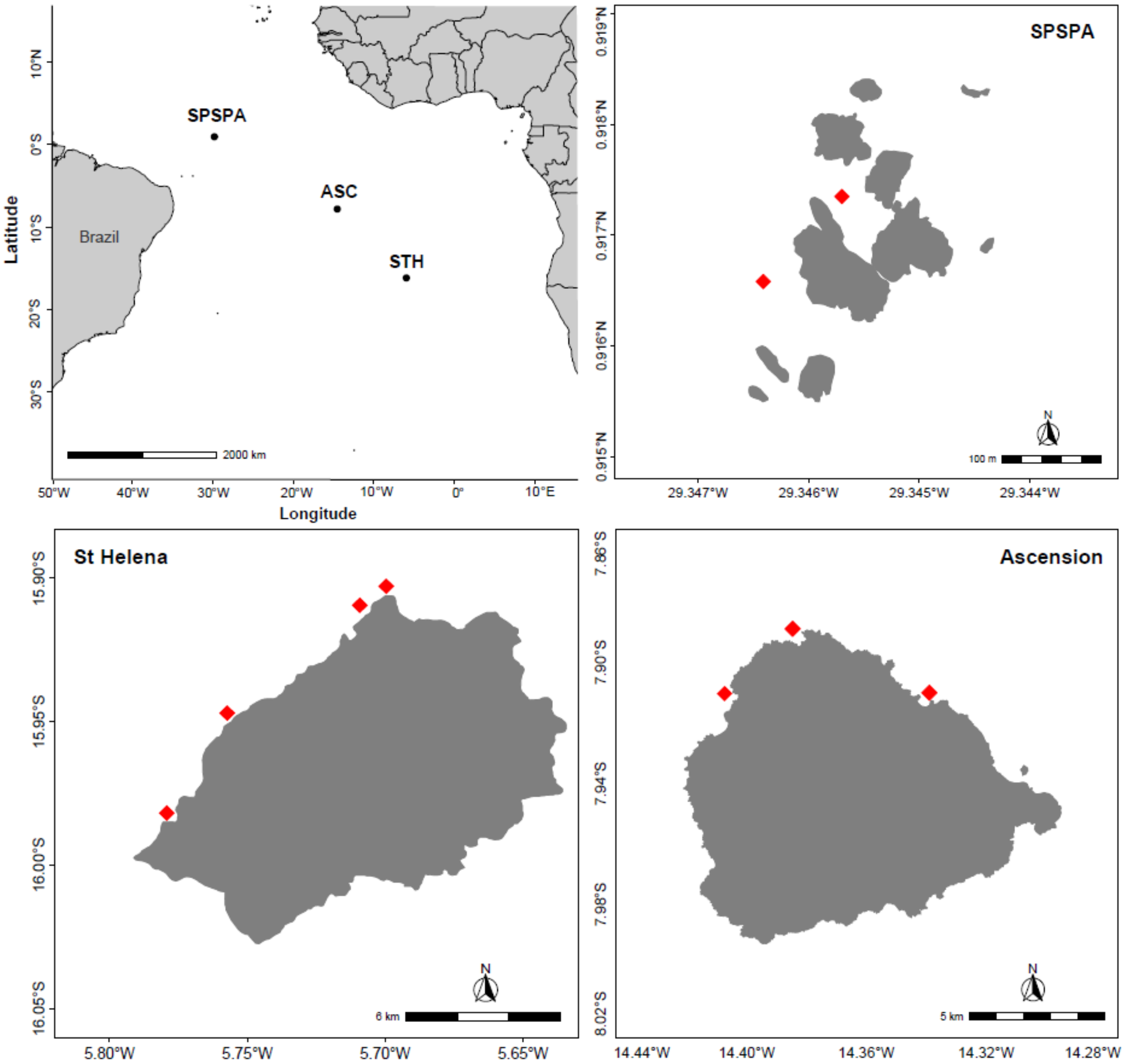

Fig. 1 Geographical location of sampled oceanic islands on the Atlantic Ocean. SPSPA (St Peter and St Paul's Archipelago), ASC (Ascension), STH (St. Helena). Red diamonds represent the sampled sites on each island.

2.2 Data collection

2.2.1 Reef fish communities

Underwater visual surveys (UVS) were employed to sample fish populations within 40m² (20m length × 2m width × 2m height) strip transects during scuba diving excursions. During UVS operations, the diver meticulously unspooled a measuring tape while visually identifying, quantifying, and assessing the total length (LT, cm) of non-cryptic fish specimens exceeding 10 cm in size. Subsequently, while rewinding the tape, identical protocol was followed to document benthic-associated non-cryptic fish species measuring less than 10 cm and cryptic species (Floeter et al., 2007; Krajewski and Floeter, 2011; Morais et al., 2017). Fish size was estimated with varying degrees of precision based on their length: 1 cm precision for fishes with lengths less than 10 cm (LT), 5 cm precision for fishes measuring between 10 and 60 cm, and 10 cm precision for fishes exceeding 60 cm. Estimating fish populations involved the counting of solitary individuals, pairs, or small schools (comprising tens of individuals), while intermediate-sized schools (ranging from tens to hundreds of individuals) were estimated with a precision of 10 individuals. For large schools consisting of many hundreds of individuals, a precision of 50 individuals was applied during the counting process. The range of depths surveyed in Ascension was between 4 metres and 13 metres depending on the site depth. In St. Helena, the shallowest site was 6m, and the deepest site was 18m. In SPSPA, depth varied from 4 metres to 36 metres, with most of the sites between 4-18 metres. There was no statistical difference between depths sampled across islands (Kruskal-Wallis: df = 45, p 0.454). In total, we performed 120 UVSs: 55 in SPSPA, 81 in Ascension, and 65 in St. Helena. All sampling occurred on sites sheltered from the predominant wind and waves on each island. Visual census techniques were performed concomitantly during sampling by different divers. The sampling dates for each location were as follows: SPSPA in October 2018 and 2019, Ascension Island in August 2015 and St. Helena Island in January 2023.

The fish species recorded in the surveys were categorised into distinct trophic groups based on their feeding habits, including macrocarnivores, mobile invertebrate feeders, omnivores, planktivores, herbivores-detritivores, sessile invertebrate feeders, and territorial herbivores (Ferreira et al., 2004; Cowburn et al., 2021; Nunes et al., 2023). To estimate fish biomass, we employed length–weight transformations and allometric conversions using the equation $W = a * LT^{b}$, where the parameters a and b represent constants in the allometric growth equation. In cases where coefficient values were unavailable for a particular species, we substituted coefficients derived from closely related species (congeners).

2.2.2 Biogeographic and environmental data

We incorporated five habitat/island variables to visualise their influence on spatial variation of fish community metrics. The sea surface temperature (SST) of each island was sourced from Rayner et al., (2003), with data extracted from satellite records covering the period from 1870 to 2023. Following this, we computed the mean SST for each year and each month on every island. The age data for St. Peter and St. Paul's Archipelago (SPSPA), Ascension Island, and St. Helena were obtained from Hachich et al., (2015). The isolation from mainland and reef area data were sourced from Ferrari et al., (2023), with an estimate of the area corresponding to the shallow shelf area computed using the Gridded Bathymetric Data GEBCO 30 arc-second grids. Isolation was measured as the distance from each island to the nearest reef area, calculated as the orthodromic distance between both points. The phosphate data for SPSPA and St. Helena were acquired from Cowburn et al., (2021), and for Ascension Island from Mora et al., (2023). See details of data in Table S1.

We also estimate the thermal niche breadth of species. This metric indicates the extent of temperature range that a species can endure, thereby serving as a gauge of its response to fluctuations in temperature (Schuster et al., 2022). To estimate the thermal niche breadth of each species, we gathered data on the maximum and minimum preferred temperatures (i.e. the lower and upper percentiles, specifically the 10th and 90th percentile) within the distribution range of each recorded species. This data was sourced from FishBase (Froese and Pauly 2023) and Aquamaps (Kaschner et al., 2023). For species without recorded values, we used the maximum and minimum sea surface temperature (SST) values from the distribution range.

2.2.3 Data Analysis

We first performed a species accumulation curve to indicate the adequacy of the survey in representing the fish richness at each oceanic island. Species accumulation curves approached an asymptote with 50 samples indicating additional sampling effort yields very few species (Fig. 1S). We then employed descriptive analyses to illustrate reef fish trophic structure. A scatterplot was generated to understand the abundance and biomass patterns of different fish trophic groups per island. A scatterplot was also generated to understand fish abundance and biomass across different size classes. To understand similarities among islands we performed a principal coordinate analysis (PCoA) by using the UVS transects as samples and applying the Bray-Curtis dissimilarity to the abundance data (individuals / m^2). We also performed a permutational multivariate analysis of variance (PERMANOVA) to test for significant differences in the abundance and biomass of species, trophic groups, and size classes among islands. To validate the PERMANOVA results and test for heterogeneity among groups, we used the Betadisper function ($p < 0.05$) along with the ANOVA function for all PERMANOVAs performed. To assess the significance of species on each island, we calculate R^2 and p-values for each species, applying a threshold of $R^2 \geq 0.2$ and p-values ≤ 0.05. A Co-inertia analysis was carried out to visualise the correlation between fish abundance and habitat/island variables. Additionally, we calculated two components of the Beta-diversity: nestedness, i.e. species-poor sites are subsets of those found in more diverse species-rich sites and turnover, i.e. replacement of some species by others, by using a species presence-absence matrix of the three islands and the Jaccard similarity coefficient. To assess whether there were differences in the mean thermal niche breadth of species among the islands, we applied a Kruskal-Wallis test. All analyses and graphics were performed using the "betapart" (Baselga et al. 2020), "tidyr" (Wickham et al. 2021), "vegan" (Oksanen et al. 2020), "ggplot2" (Wickham 2016), "ISLR" (James et al. 2021) and "dplyr" (Wickham 2023) packages of R software (R Core Team 2023).

3. Results

We recorded a total of 30,792 fish individuals belonging to 75 species in the three islands. Only 14 species accounted for 90% of the overall abundance in all islands. Ascension Island exhibited higher species richness in contrast to SPSPA and St. Helena which exhibited a similar pattern of species accumulation **(Fig. 1S)**. The reef fish communities displayed significant variations across the islands. The mean density of individuals per m² recorded in SPSPA was 4.67 ± 0.34 ind/m² (mean ± SE). Ascension held the highest value, with a mean density of 4.80 ± 0.20, whereas St. Helena had the lowest mean 1.91 ± 0.08. The mean density of endemics in SPSPA took third place with 1.28 ± 0.09 ind/m², while Ascension exhibited the highest density at 2.01 ± 0.10, followed by St. Helena with 1.33 ± 0.05 ind/m² (**Table 1**). These endemic densities represented 27% of the total density in SPSPA, 42% in Ascension, and an impressive 70% of the total fish density in St. Helena. The total mean biomass per m² followed a distinct pattern, with Ascension showing the higher biomass (0.86 ± 0.07 g/m²), SPSPA ranking second with 0.38 ± 0.04 g/m², and St. Helena with the lowest value (0.30 ± 0.03 g/m²). However, when considering only the endemic fishes' biomass, a reverse pattern emerged. SPSPA showed the lowest value (0.003 ± 0.001 g/m²), followed by Ascension (0.02 ± 0.001 g/m²), and St. Helena displayed the highest value (0.06 ± 0.004 g/m²) (**Table 1**). In terms of mean species richness, SPSPA recorded 0.25 ± 0.01, with Ascension displaying the highest mean (0.37 ± 0.01), and St. Helena mirroring SPSPA with 0.25 ± 0.01. However, when considering only endemic species richness, SPSPA had the lowest value (0.03 ± 0.001), while Ascension and St. Helena shared the same mean (0.12 ± 0.004) (**Table 1**).

Table 1 Density, biomass and richness of reef fish species recorded during underwater visual census on St. Peter and St. Paul Archipelago (SPSPA), Ascension and St. Helena islands.

	SPSPA	**Ascension**	**St. Helena**
Mean ± SE density (Abundance / m²)	4.67 ± 0.34	4.80 ± 0.20	1.91 ± 0.08
Mean ± SE density of endemics (Abundance / m²)	1.28 ± 0.09	2.01 ± 0.10	1.33 ± 0.05
Mean ± SE biomass (kg / m²)	0.38 ± 0.04	0.86 ± 0.07	0.30 ± 0.03
Mean ± SE biomass of endemics (kg / m²)	0.003 ± 0.001	0.02 ± 0.001	0.06 ± 0.004
Mean ± SE richness (spp / m²)	0.25 ± 0.01	0.37 ± 0.01	0.25 ± 0.01
Mean richness of endemics (spp / m²)	0.03 ± 0.001	0.12 ± 0.004	0.12 ± 0.004
Total richness based on censuses (spp)	32	47	34

3.1 Abundance and biomass of trophic groups

The abundance and biomass of trophic groups displayed significant variations across the islands ($p < 0.001$). Planktivores comprised the most abundant trophic group in SPSPA, ranking second in Ascension and St. Helena (**Fig. 2A**). Among the islands, planktivores exhibited 1.90 ± 0.29 ind/m^2 in SPSPA, then Ascension (1.39 ± 0.16 ind/m^2), and finally St. Helena with 0.54 ± 0.07 ind/m^2 (**Fig. 2A**). Herbivore-detritivores was the most abundant group in Ascension, and ranking second in SPSPA (**Fig. 2A**). SPSPA had an average of 1.31 ± 0.09 ind/m^2, Ascension displayed the highest abundance of them with an average of 1.51 ± 0.07 ind/m^2, and lastly, in St. Helena herbivores accounted for 0.75 ± 0.03 ind/m^2 (**Fig. 2A**). Omnivores exhibited a substantial mean abundance in SPSPA (1.03 ± 0.10 ind/m^2) and Ascension (0.81 ± 0.05 ind/m^2). In St. Helena, omnivores accounted for only a modest abundance of this trophic group (0.08 ± 0.01 ind/m^2) (**Fig. 2A).**

Concerning fish biomass, 20 species contributed to 90% of the total value, with just two of these species, namely Holocentrus adscensionis and Melichthys niger, constituting 58% of the total biomass. SPSPA showed the lowest average of the Mobile Invertebrate Feeder trophic group with only 0.32 ± 0.04 g/m^2, while Ascension displayed the higher average biomass (8.51 ± 1.28 g/m^2), and St. Helena had the second highest value, with an average of 4.52 ± 0.67 g/m^2 (Fig. 2B). A different pattern was observed for the group of macrocarnivores, where St. Helena had the lowest average with only 0.67 ± 0.08 g/m^2, while Ascension had the highest biomass average with 5.85 ± 0.58 g/m^2, followed by SPSPA with an average of 2.20 ± 0.79 g/m^2. The omnivore group also exhibited high biomass. SPSPA had the second highest average of this trophic group with 5.94 ± 0.43 g/m^2, while Ascension once again had the highest average 5.43 ± 0.28 g/m^2. Lastly, St. Helena had the lowest value of 0.08 ± 0.18 g/m^2 (**Fig. 2B**).

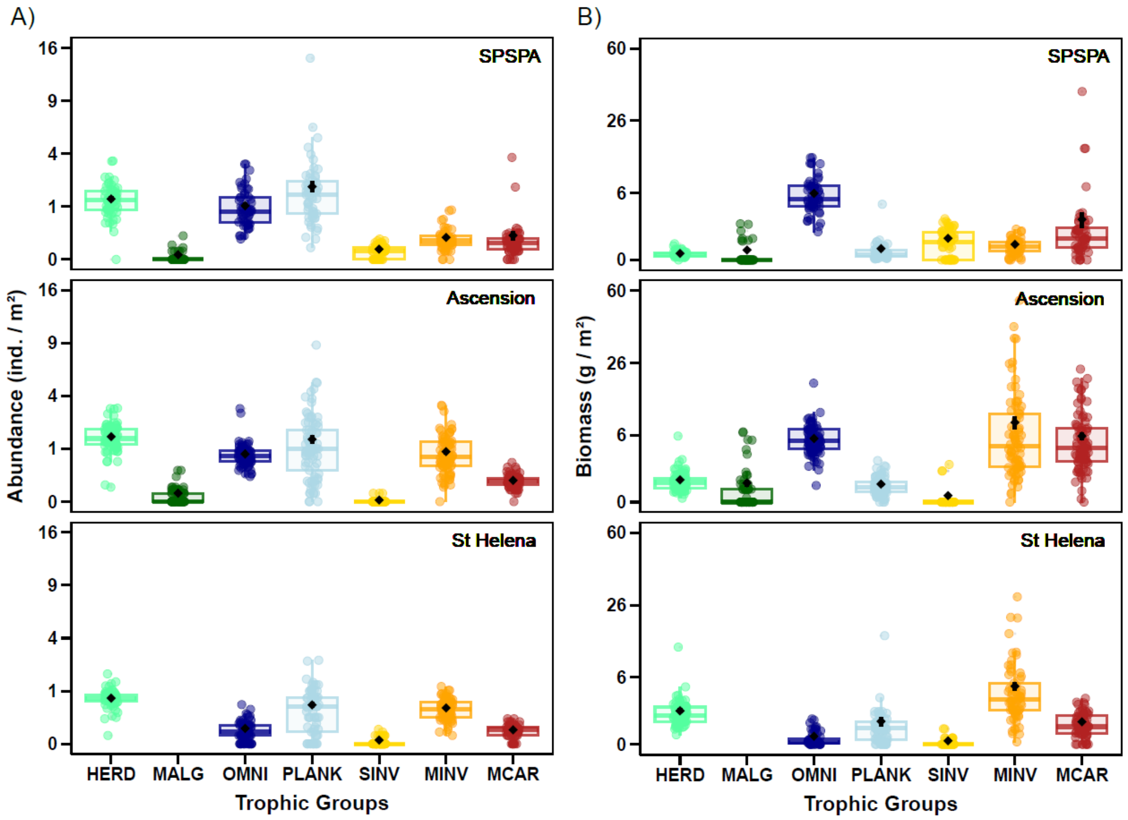

Fig 2. Comparative boxplot and scatterplot showing the A) abundance and B) biomass of reef fish trophic groups on each island. Fish trophic groups: HERD: Herbivore-detritivore; MALG: Macroalgivore; OMNI: Omnivore; PLANK: Planktivore; SINV: Sessile invertebrate feeder; MINV: Mobile invertebrate feeder; MCAR: Macrocarnivore.

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3.2 Body size structure

The abundance and biomass of body size has a significative difference among size class and among islands ($p < 0.001$) **(Fig. 3)**, in SPSPA, the smallest size class (0-7cm) was the most abundant, with an average of 3.19 ± 0.31 ind/m^2. Fishes between 16-30cm come next, with an average of 0.92 ± 0.09 ind/m^2, while larger fishes (>60cm) were the least abundant (0.002 ± 0.00 ind/m^2). In Ascension, fishes measuring 8-15cm had the highest average abundance (2.06 ± 0.13 ind/m^2), followed by the smallest size class (0-7cm) at 1.62 ± 0.18. The largest fishes (>60cm) were the least abundant, with an average of 0.04 ± 0.00. St. Helena follows a similar pattern to Ascension, with fishes measuring 8-15cm having the highest average (0.91 ± 0.06 ind/m^2), followed by the smallest fishes (0-7cm) at 0.48 ± 0.04 (**Fig. 3A**). There was an opposite pattern of biomass among the body size categories, with medium body size (16-30cm) showing higher biomass in SPSPA (300,768 ± 30,892 g/m^2) and in St. Helena (138,800 ± 17,851 g/m^2). Body size of 31-60 cm also displayed high biomass across all islands. SPSPA had the second lowest value with 16,881 ± 12,357 g/m^2, while Ascension held the highest with 100,950 ± 13,346 g/m2, and in St. Helena it was extremely low with 0,633 ± 0,633 g/m^2 (**Fig. 3B**).

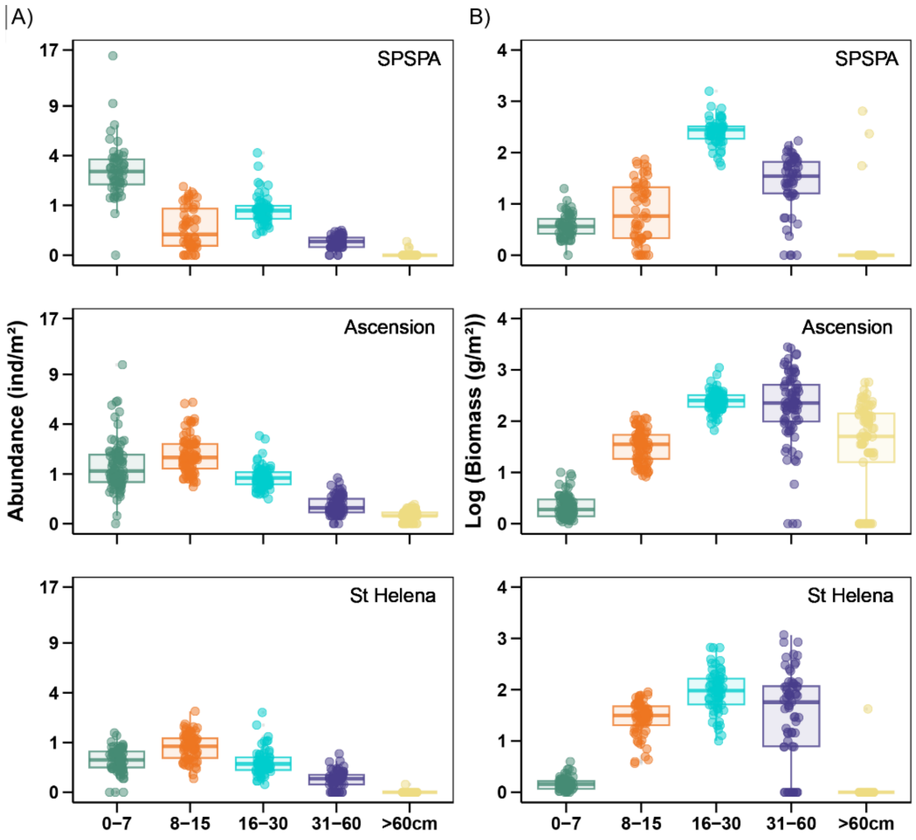

Fig 3. Comparative boxplot and scatterplot showing the abundance and biomass of reef fishes on each island according to body size class.

3.3 Fish communities and environmental correlations

A clustered reef fish structure was observed (**Fig. 4**), indicating dissimilarities among fish communities on the islands (PERMANOVA: $R^2 = 0.61$, $F = 158.1$, $p < 0.001$). Fish abundance and environmental factors showed a positive correlation (**Fig. 4**). For instance, mean sea surface temperatures (SST) correlated with SPSPA and Ascension Island, aligning with their equatorial and tropical characteristics, respectively. Larger reef area and phosphate level were related to the fish assemblage of St. Helena. Age as expected, displayed correlations with the oldest islands, SPSPA and St. Helena (**Fig. 4**).

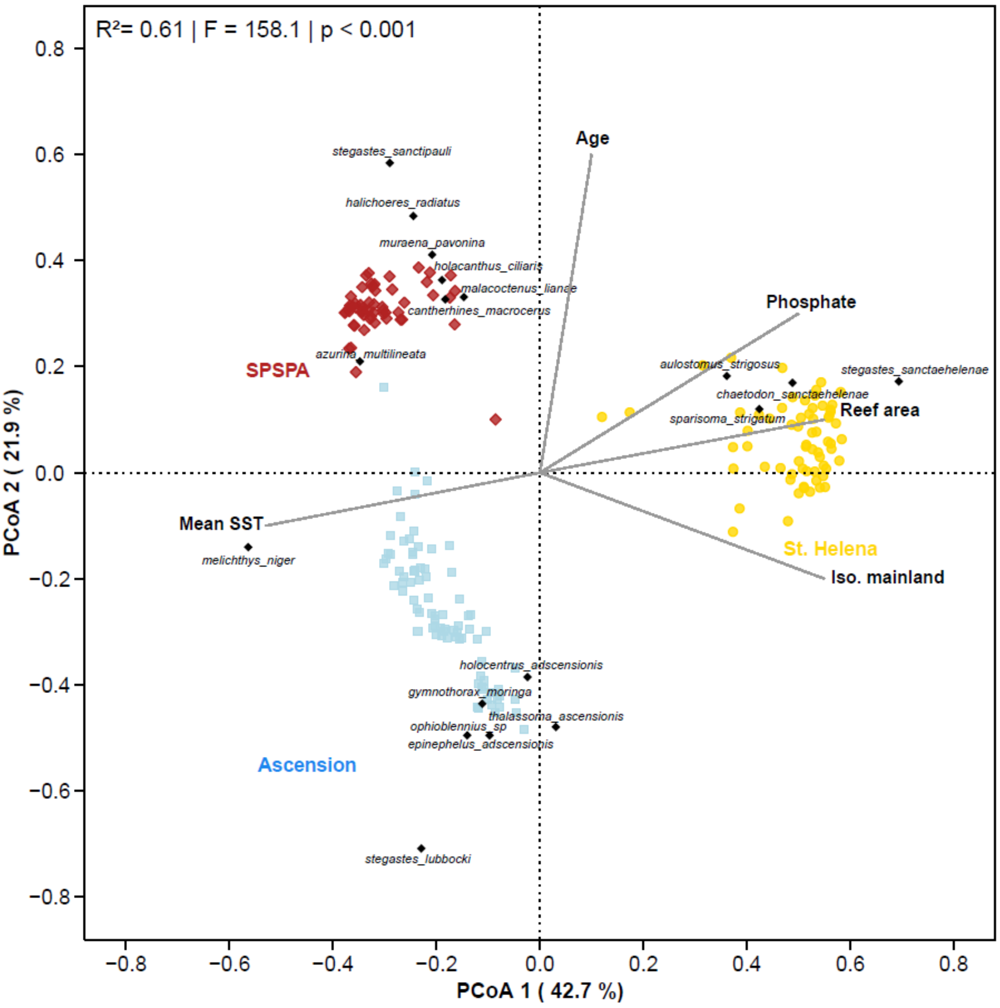

Fig 4. Principal coordinate analysis (PCoA) showing the ordination of samples according to abundance of the fish species. The fish names represent the most significant species on each island (see methods). Geometric shapes and colours indicate censuses on each oceanic island. The black dots indicate the main species found on each island.

The islands exhibited significant dissimilarity, with turnover emerging as the primary driver of beta diversity among the three (**Table 2**). Substantial turnover levels were observed between SPSPA and Ascension, as well as between SPSPA (0.73) and St. Helena (0.82). High species turnover (0.46) was also detected between Ascension and St. Helena. While the nestedness between SPSPA and the other two islands was relatively low, the relationship between Ascension and St. Helena demonstrated a higher value (0.12).

Table 2 Beta-diversity components calculated among the three islands, representing the dissimilarity and variation in species composition and diversity among these locations.

	SPSPA		**Ascension**		**St. Helena**	
	Turnover	Nestedness	Turnover	Nestedness	Turnover	Nestedness
SPSPA	0	1				
Ascension	**0,731**	**0,057**	0	1		
St. Helena	**0,821**	**0,003**	**0,455**	**0,124**	0	1

3.4 Thermal niche

There were marginally significant differences in thermal niche breadth between SPSPA and St. Helena (p-value = 0.056), however, this difference was not observed between Ascension and St. Helena. SPSPA exhibited a lower thermal niche breath average, whereas St. Helena showed a higher average (**Fig. 5A**). In St. Helena, the species with the highest abundance also possess a wider thermal range, such as *Chaetodon sanctaehelenae* and *Stegastes sanctaehelenae* **(Fig. 5A)**. Distinct temperature patterns were evident in the monthly variations across the three islands. St. Helena experiences the highest seasonal variation, with temperatures varying up to 4.9°C between months (**Fig. 5B**). SPSPA had the highest monthly average, reaching a maximum of 27.8°C and a minimum of 26°C. Ascension followed, with a maximum of 27.5°C and a minimum of 24°C. In contrast, St. Helena has a comparatively lower monthly average, ranging between 20.2°C and 24.9°C.

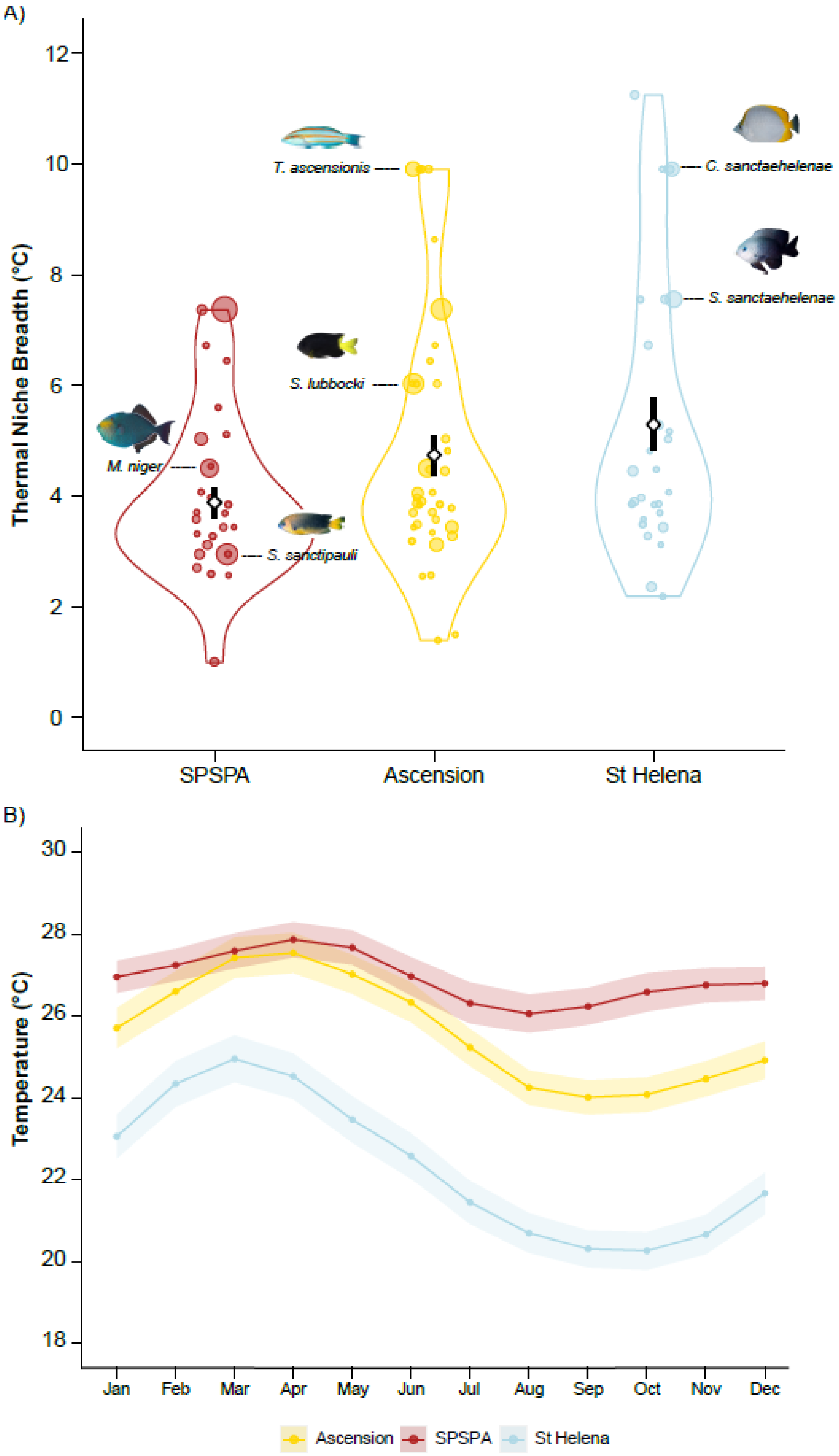

Fig 5. A) Thermal niche breadth of each species. The size of the points corresponds to the abundance of species. Fish figures represent the most abundant species at each island. B) Mean of Sea surface temperature (SST) from 1870 to 2023 of each island. The colours correspond to each island.

4. Discussion

This is the first quantitative assessment of reef fishes that combines data from the three most isolated oceanic islands in the Mid-Atlantic (St. Peter and St. Paul's Archipelago, Ascension Island, and St. Helena), helping to understand patterns of community structure through a 14-degree latitudinal and a 10°C thermal gradient. From the perspective of the entire Atlantic Ocean and its distinct biogeographical provinces, a similarity in species composition is evident among the three islands. However, when populations are compared at the local scale, the structure of reef fish communities varied significantly, displaying distinct patterns between the islands in terms of abundance and biomass of trophic groups, size class of individuals, and beta diversity. The reef fish assemblage patterns are correlated with geological factors such as island area and age, as well as environmental factors such as sea surface temperature. The thermal niche breadth of species was found to be higher on the island with lower temperatures and higher when there is seasonal temperature variation.

The structure of fish communities on reefs is influenced by diverse factors (Floeter et al., 2007; Pinheiro et al., 2011; Canterle et al., 2020), and those typically found on oceanic islands, such as high isolation (Hachich et al., 2015; Quimbayo et al., 2019), can offer valuable insights into community assembly processes. The variation in reef fish communities among the studied islands under different thermal regimes reflects that, in addition to area and isolation, temperature play a crucial role in determining biodiversity distribution (Floeter et al., 2001; Bosch et al., 2021). St. Helena exhibits an interesting pattern, despite its low latitude, large area and high phosphate levels, the influence of the Benguela Current and the South Atlantic Gyre carries cold water towards St. Helena (Brown et al., 2019), resulting in subtropical attributes and lower temperatures (Cowburn et al., 2021). The combination of these factors has resulted in lower biodiversity compared to SPSPA and Ascension. Nevertheless, it stands out for having the highest number of endemic species, attributed to its high isolation (Brown et al., 2019) and old age. Despite being the youngest and second-most isolated of the islands, Ascension displayed the highest diversity, possibly due to the synergy of its large reef area and elevated temperatures compared to St. Helena. Thus, we speculate that age does not seem to be a determining factor, while temperature emerges as a pivotal influence on diversity in these oceanic islands.

The highest temperature found in SPSPA, followed by Ascension, leads to the establishment and reproduction of tropical reef fishes, particularly herbivores and planktivores. There is a consensus that the warmer temperatures found in low latitudes (i.e. tropical regions) influence the richness, abundance, and feeding rate of herbivorous fish (Ferreira et al., 2004; Floeter et al., 2005; Longo et al., 2014, 2019; Nunes et al., 2021). Additionally, the thermal niche breadth of species influences its distribution and establishment, based on physiological adaptation to local temperature regimes (Stuart-Smith et al., 2017). This suggests that species from tropical regions generally have narrower thermal niches. In our study, we observed an interesting pattern among herbivorous species of the genus *Stegastes*, where endemic species on each island exhibit high abundance. The thermal niche breadth of each species varies, with an increasing trend toward islands with lower average temperature (i.e., Ascension and St. Helena). The endemic species *Stegastes sanctipauli* displays a narrow thermal niche breadth in SPSPA. Conversely, in Ascension, the endemic *Stegastes lubbocki* has a broader thermal niche breadth. Finally, in St. Helena, the endemic *Stegastes sanctaehelenae* boasts the widest thermal niche breadth among the genus. Interestingly, the later two species are related to *S. pictus*, while *S. sanctipauli* is related to *S. rocasensis* and *S. fuscus* (McCord et al., 2021). This pattern underscores both the clade-specific nature of thermal niche breadth, which varies following the species evolutionary relationhips, as well as adaptations to local temperature regimes, thereby allowing for greater species abundance. In other words, the variation in thermal limits among species is influenced both by the environment (Stuart-Smith et al., 2017) and their evolutionary relationships (Carbonell and Stoks, 2020). .

The high abundance of planktivorous species in the three islands can be attributed to a combination of ecological and oceanographic factors, as the same pattern resembles that observed on other Atlantic oceanic islands (see Pinheiro et al., 2011, Krajewski and Floeter 2011, Luiz et al., 2015, Maia et al., 2018, Freitas et al., 2019). The oligotrophic waters around these oceanic islands facilitate visually targeting available plankton, thereby supporting the feeding activity of planktivorous fish species (Johansen and Jones, 2013).

Although Ascension and St. Helena share many species (including some shared endemics), there are differences in terms of abundance and biomass. We can observe this pattern within trophic groups, where Ascension shows more than double the abundance in almost all trophic groups, except for sessile invertebrate feeders, although their populations are relatively low on both islands. However, the 12-fold discrepancy in the number of individuals within omnivores on Ascension is partly due to the high abundance of the species *Melichthys niger*, which is very low in abundance in St. Helena. *M. niger* is highly abundant on tropical oceanic islands around the world, with a circumtropical distribution, plastic feeding capabilities and being a successful coloniser (Kavanagh and Olney, 2006). However, there is still no consensus regarding variations in body size and abundance on specific oceanic islands. A hypothesis is that, locations with higher reef fish diversity, especially within the families Balistidae and Monacanthidae, could lead to higher competition and a lower abundance in a local scale (Kavanagh and Olney, 2006). Nevertheless, when we observe the number of species from Balistidae and Monacanthidae families (n=6), as well as species diversity, on St. Helena (Kavanagh and Olney, 2006), it is lower compared to Trindade Island, where there is a high abundance of *M. niger.* This hypothesis does not seem to explain the low abundance of this species on St. Helena. However, given that the thermal tolerance of this species ranges between 24.4 - 28.9°C, with a thermal niche breadth of 4.5°C, we hypothesise that temperature could be the primary limiting factor for the population expansion of this species on St. Helena. While the species thrives in the annual thermal variation of SPSPA and Ascension, it lacks sufficient thermal amplitude to withstand the variations in St. Helena (~20.2 to 24.9 °C), especially during the cold season.

On the other hand, in St. Helena, there is a high abundance of the *Chaetodon sanctaehelenae*, the endemic species of the Central Atlantic, which forms large schools in the water column. We hypothesise that the high trophic plasticity of this species (Nunes et al., 2020), may influence the expansion of its trophic niche. Additionally, its broad thermal niche breadth might enable it to tolerate the high annual thermal variation of St. Helena, consequently leading to this species' establishment and high abundance. Moreover, the reason for their exceptionally high abundance may be their ancestral evolutionary relationship with other species that also use the water column to forage and form aggregations (e.g. *C. miliaris*, *C. dolosus*, *C. sedentarius;* Delrieu-Trottin et al., 2019), as well as tolerate subtropical temperatures (Kuiter, 2002). Similarly, the high niche breadth of the sister species *Thalassoma ascensionis* and *T. sanctaehelenae* could be explained because both species pertain to a group of species related to the Eastern Atlantic (Costagliola et al., 2004), which includes *T. newtoni* from the tropical Gulf of Guinea and *T. pavo* that ranges up to the warm-temperate Mediterranean Sea.

Most endemic species found on oceanic islands worldwide exhibit high abundances (Hobbs et al., 2011). On the three oceanic islands of the Mid-Atlantic Ridge, there is a notable numerical prevalence of endemics, especially on the island of St. Helena, where they constitute an impressive 70% of the total fish density. Interestingly, the abundance of endemic species increases toward islands with a greater degree of isolation (see **Table 2S**) and towards more subtropical conditions that lead to a broader mean thermal niche breadth.

Variation among fish communities also extends to the size of individuals. Although oceanic islands are still considered pristine environments when compared to the mainland, they are not exempt from anthropogenic influence (Alava et al., 2023). This human impact is evident in the absence of the previously observed pattern of large fish individuals (Sandin et al., 2008). All islands have a high abundance of smaller individuals, however, there are variations in biomass patterns. It is noteworthy that on Ascension Island, the high biomass of fish sized between 31-60 cm and above 60 cm is possibly linked to some degree of fishing protection, as this area falls within a marine protected area with sustainable use (Ascension Island Government, 2021), in addition to favourable environmental conditions such as habitat availability. However, even though St. Helena is also situated within a marine protected area with sustainable use (St. Helena Government, 2022), the long-term historical fishing appears to be influencing the low fish biomass of large size. On the other hand, a low biomass of large individuals was already expected in the SPSPA, given its small reef area and limited habitat availability. Furthermore, this archipelago is only partially covered by the marine protected area, as there are still areas where fishing is permitted (Giglio et al., 2018).

Historical and contemporary factors also shape the patterns of beta diversity (Maxwell et al., 2021). Although the three islands share some endemic species suggesting a faunal link between these places (Wirtz et al., 2017; Brown et al., 2019), the high turnover among the studied islands indicates low species connectivity. The greater dissimilarity found for SPSPA can be explained by its stronger affinity with the Brazilian province and Fernando de Noronha Ridge (Floeter et al., 2008). On the other hand, Ascension and St. Helena share trans-Atlantic species and also endemic species (Kulbicki et al., 2013). Despite the similarities between these two islands, there is a higher turnover than nestedness in their species composition. Ascension exhibits a stronger affinity with the Western Atlantic compared to St. Helena, whereas St. Helena shows a similar affinity with both the Western and the Eastern Atlantic (Briggs and Bowen, 2012).

5. Conclusion

Our study shows the variations in the structure of reef fish communities among the three islands of the Mid-Atlantic Ridge. While establishing causal links with environmental variables was not possible through our analysis, our observations revealed correlation patterns. These patterns suggest that a combination of environmental factors, with a particular emphasis on the interplay of sea surface temperatures and the thermal tolerance of species, plays a pivotal role in shaping the reef fish communities of these isolated islands. These trends are noticeable within the prominent trophic groups on each island, as well as in the case of certain dominant species (i.e. *Melichthys niger* and *Chaetodon sanctaehelenae*). Our findings underscore the importance of establishing a baseline understanding, such as quantifying reef fish communities. This information can shed light on various aspects of biodiversity, including abundance and biomass, and proves essential for monitoring community dynamics over time, as well as for detecting early warning signs of ecosystem changes.

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Supplementary material

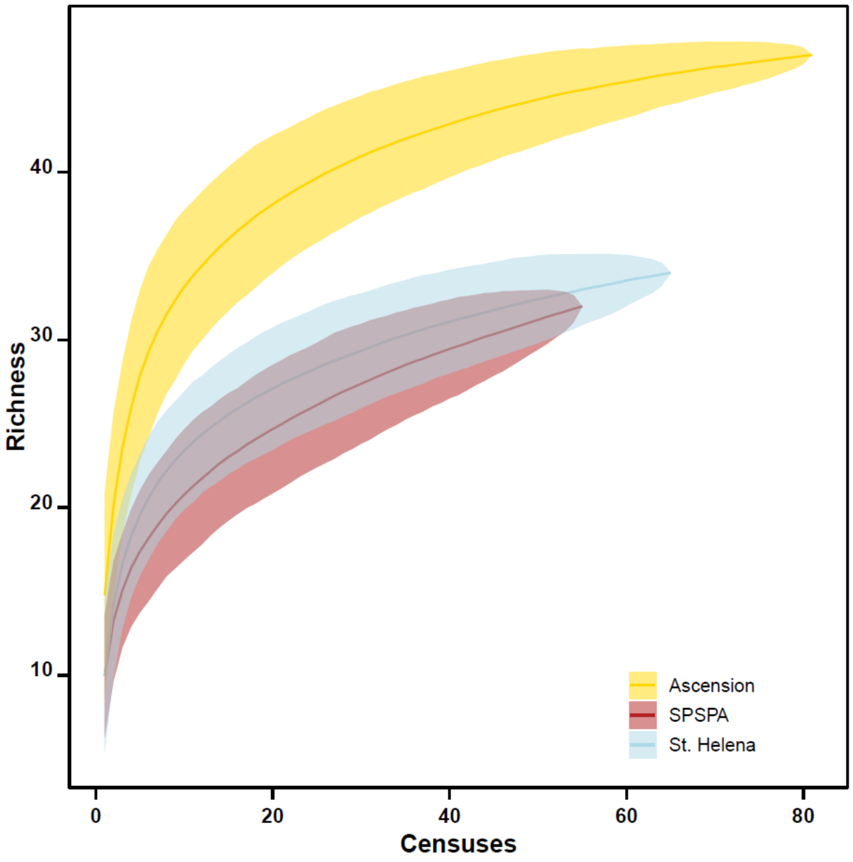

Fig 1S. Species accumulation curves based on sampling effort. The x-axis represents the cumulative number of samples, while the y-axis shows the cumulative number of species.

Table 1S Abiotic data of oceanic islands sampled.

Island	*Area (km²)*	*Age (Ma)*	*SST (annual mean)*	*Mainland isolation (km)*	*Phosphate (annual mean)*
SPSPA	3.5	9	26.9	1010	0.084
Ascension	108.26	1.15	25.6	1658	0.058
St. Helena	264.3	15	22.3	1885	0.236
Source of data	Ferrari et al., 2023	Hachich et al., 2015	Rayner et al., 2003	Ferrari et al. 2023	Cowburn et al., 2021; Mora et al., 2023

Table 2S Frequency of occurrence of endemic (%) reef fish trophic groups recorded during underwater visual census on St. Peter and St. Paul's Archipelago (SPSPA), Ascension and St. Helena islands.

	SPSPA	**Ascension**	**St Helena**
Herbivore-detritivore			
Abundance endemic	95%	97%	86%
Biomass endemic	83%	36%	48%
Richness endemic	59%	73%	71%
Macroalgivore			
Abundance endemic	-	-	-
Biomass endemic	-		-
Richness endemic	-	-	-
Omnivore			
Abundance endemic	-	2.4%	24%
Biomass endemic	-	0.1%	6%
Richness endemic	-	22%	53%
Planktivore			
Abundance endemic	0.7%	2%	75%
Biomass endemic	0.1%	6%	53%
Richness endemic	1.8%	27%	67%
Sessile invertebrate			
Abundance endemic	-	-	15%
Biomass endemic	-	-	3%
Richness endemic	-	-	10%
Mobile invertebrate feeder			
Abundance endemic	2.4%	56%	58%
Biomass endemic	7.2%	4%	9%
Richness endemic	7.5%	53%	49%
Macrocarnivore			
Abundance endemic	-	-	-
Biomass endemic	-	-	-
Richness endemic	-	-	-

CAPÍTULO III

(A ser submetido em Ocean & Coastal Management)

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Assessing potential human impacts and risks on the Saint Helena reef system, a South Mid-Atlantic Ridge Island

Débora S. Ferrari, Amanda R. Rodrigues, Vicente Gomes, Carlos Eduardo L. Ferreira, Elizabeth Clingham, Kirsty Jones, Leeann Henry, Susa Niiranen, Sergio R. Floeter, Maria A. Gasalla (2024). Assessing potential human impacts and risks on the Saint Helena reef system, a South Mid-Atlantic Ridge Island.

Abstract

Saint Helena Island, located on the Mid-Atlantic Ridge, stands as one of the most remote regions in the world. Its isolated location influences the low diversity of reef marine species and contributes to the high rate of endemism in the area. Despite its isolation, the resident human population and tourism is growing, leading to an increase in human activities. Because of the increasing human impacts, studies with an ecosystemic approach become crucial for the effective management of the singular biodiversity found on St. Helena reefs. This study is the first risk assessment of the reef system of St. Helena Island (British Overseas Territory). We used the Options for Delivering Ecosystem-Based Marine Management (ODEMM) methodology for implementing an integrated ecosystem assessment (IEA), focusing on a semi-quantitative assessment identifying sector–pressure–ecological component pathways. Subsequently, these pathways were scored using expert judgment supported by literature and data. The assessment was validated with regional stakeholders through a workshop. Our study identified 12 sectors, 14 pressures and their potential impact on 11 ecosystem components, totalling 463 distinct impact chains. Our findings emphasize that wastewater, fishing, and shipping are the primary sectors generating pressures, such as litter and contaminants. These pressures, in turn, predominantly impact demersal fish, seabirds, and marine mammals. The application of the IEA approach in this study has provided a better understanding of the intricate interactions between human activities and the ecological components of the St. Helena reef system. This study emphasizes the importance of comprehending the primary impacts in these isolated and understudied islands, highlighting the necessity for prioritized management of the key threats to this ecosystem.

Keywords: Integrated Ecosystem, Management, Risk analysis, Impact risk, Oceanic Island.

1. Introduction

Reefs represent the most biodiverse ecosystems in the sea, shaped by biogenic organisms or rocky substrates (Reaka-Kudla, 1997; Withers and Tunnell, 2007). Most reef systems are intrinsically interconnected within a socio-ecological framework, however, there is still a sense of separation between the marine environment and the human population (Cinner et al., 2009). The combined impact of natural and human-induced disturbances has been altering reefs, leading to species loss and ultimately declining ecosystem functions (Moberg and Folke, 1999). Among the extensively exploited resources, fishing activity stands out as a significant contributor to the capture of keystone species—essential for maintaining the ecological balance—such as apex predators (Bender et al., 2014). Therefore, obtaining a better understanding of the links between anthropogenic actions and the pressures they impose on the reef ecosystem is the first step towards identifying impacts and proposing management possibilities.

The interplay between anthropogenic sectors and the pressures creates a complex network of interactions that can affect reef habitats and species, posing risks to the ecosystem (Halpern et al., 2009). Thus, to achieve effective management of human activities in the marine environment, it is necessary to conduct a comprehensive ecosystem-based assessment (Knights et al., 2013). The Integrated Ecosystem Assessment (IEA) is a holistic approach that incorporates a wide range of ecosystem components, including human activities (Levin et al., 2009; Monaco et al., 2021). IEA explores the interdependence of biological and socioeconomic attributes within the ecosystem, providing a comprehensive foundation for evaluating and identifying the most effective management alternatives (Levin et al., 2009). Over the past decade, there has been an increase in studies employing this approach (e.g., Fletcher et al., 2014; Rosellon-Druker et al., 2019; Skein et al., 2022; Polejack et al. 2023). Through IEA, scientists and managers are engaged in the assessment and decision-making processes. This approach focuses on fostering collaboration among scientists, managers, and stakeholders to identify the most effective strategies for achieving their goals. The IEA involves several steps, including defining the target system and establishing objectives. Subsequently, indicators are carefully chosen, and risk analysis is conducted. Ultimately, the management strategies for the selected ecosystem are evaluated (Monaco et al., 2021). Specifically, the framework comprises five steps: scoping, indicator development, risk analysis, management strategy evaluation and ecosystem assessment (Levin et al., 2009; 2014; Samhouri et al., 2014).

Recently, the ODEMM project (Options for Delivering Ecosystem-Based Marine Management; Robinson et al., 2014) has emerged to facilitate the evaluation of various stages within the IEA process. This methodology consists of frameworks and tools to aid in ecosystem assessment. These frameworks are based on the linkages between sectors, pressures, and ecological components, allowing for the identification of relationships and impact chains between human activities and ecological components (Knights et al., 2013). Through this methodology, it is possible to generate an assessment of the ecological risks within the system, which evaluates the probability and consequences of one or more impact chains occurring. This understanding enables an analysis of how effective management of specific sectors or pressures can reduce the impact on the ecosystem. Studies addressing integrated ecosystem assessment and using ODEMM methodology are typically conducted in systems with high anthropogenic interference and in large areas (e.g., Pedreschi et al., 2019; Skein et al., 2022; Scherer et al., 2024). However, this methodology has also been demonstrated to be effective in isolated areas, with less human interference and understudied (e.g. Rodrigues et al., 2023). The ODEMM tool was selected due to its clear and replicable structure, making it suitable for comparative analyses and applicable in data-limited situations (Robinson et al., 2014). Despite the significant need for studies in areas with a high likelihood of impact, it is also crucial to understand the potentially risks in ecosystems that are affected by human action, such as oceanic islands.

Oceanic islands lack geological connection with the mainland as they are situated beyond the continental shelf and far from the coastlines of continents (Dawson, 2015). Consequently, they often exhibit low terrestrial and marine species diversity and a significant prevalence of endemic species (Whittaker and Fernandez-Palacios, 2007; Hachich et al., 2015; 2020). These islands are considered unique systems for studying local and evolutionary ecological mechanisms (Rominger et al., 2016). Moreover, the ecological dynamics of these islands are highly distinct compared to other ecosystem models (Ferreira et al., 2021). Despite their biological significance, integrated assessment approaches are rarely employed in isolated islands, as in the case of the South Mid-Atlantic Ridge Islands, which consist of three oceanic islands: St. Peter and St. Paul Archipelago, Ascension, and St. Helena (Rodrigues et al., 2023).

Fortunately, a recent study conducted by Rodrigues et al. 2023 carried out a risk assessment of the Mid-Atlantic Ridge islands, covering its entire Exclusive Economic Zone (EEZ) and Areas Beyond National Jurisdiction (ABNJ) between these islands. Saint Helena is the most populated and largest one, approximately 3500 km east of Brazil and around 2000 km west of Africa. St. Helena's marine biodiversity exhibits biogeographical affinities with both the western side of the Atlantic and the African coast (Floeter et al., 2008; Kulbicki et al., 2013), and holds a high level of endemism (Hachich et al. 2015). Moreover, it serves as a vital habitat for species undertaking long migratory pathways. Some studies covered St. Helena Island in an integrated approach, such as Rodrigues et al. (2023) and also Mynott et al. (2021), which proposed a standardized approach to risk assessment for sand extraction on Santa Helena island. So far, no study has been carried out integrating and focusing on the reef system of Santa Helena Island. For that, this study represents the first comprehensive integrated approach with the primary aim of conducting a comprehensive risk analysis of the reef ecosystem of St. Helena Island. To achieve that we 1) Establish linkages by examining interactions between sectors, pressures, and ecological components; 2) Evaluate these connections based on their frequency, intensity, and spatial extent; 3) Conduct an assessment of the primary risks identified for the St. Helena reef ecosystem.

This study was conducted within the scope of the Mission Atlantic project, an EU-funded project that will map and assess the present and future status of Atlantic marine ecosystems under the influence of climate change and exploitation. This research represents the initial step in situating the reef system of St. Helena Island within the context of ecosystem-based approaches, connecting it to the larger scale of the Atlantic Ocean and thereby contributing to the overarching goal of conducting an integrated ecosystem assessment throughout the Atlantic Ocean.

2. Methods

2.1. Study area description

St. Helena is an isolated oceanic island (15.96°S | 5.70°W) situated in the South Atlantic, around 930km east of the Mid-Atlantic Ridge, which runs meridionally within the Mid-Atlantic basin. St. Helena is located approximately 3500 km east of Brazil and approximately 2000 km west of Africa. The geographic isolation influences the low diversity of marine species and allows for a high rate of endemism. The marine biodiversity of St. Helena exhibits biogeographical affinities with both the western side of the Atlantic and the African coast (Floeter et al., 2008; Kulbicki et al., 2013). The waters surrounding St. Helena are designated as a Marine Protected Area (MPA) with sustainable use of natural resources (Category VI - IUCN), encompassing the entire Exclusive Economic Zone spanning 448,411km^2. The island of St. Helena covers an approximate area of 122km^2 and is home to a resident population of 4,439 individuals (according to the 2021 census). The study area encompasses the reef system, which includes the shallow depths within a distance of 30 meters along the coastal area of the island.

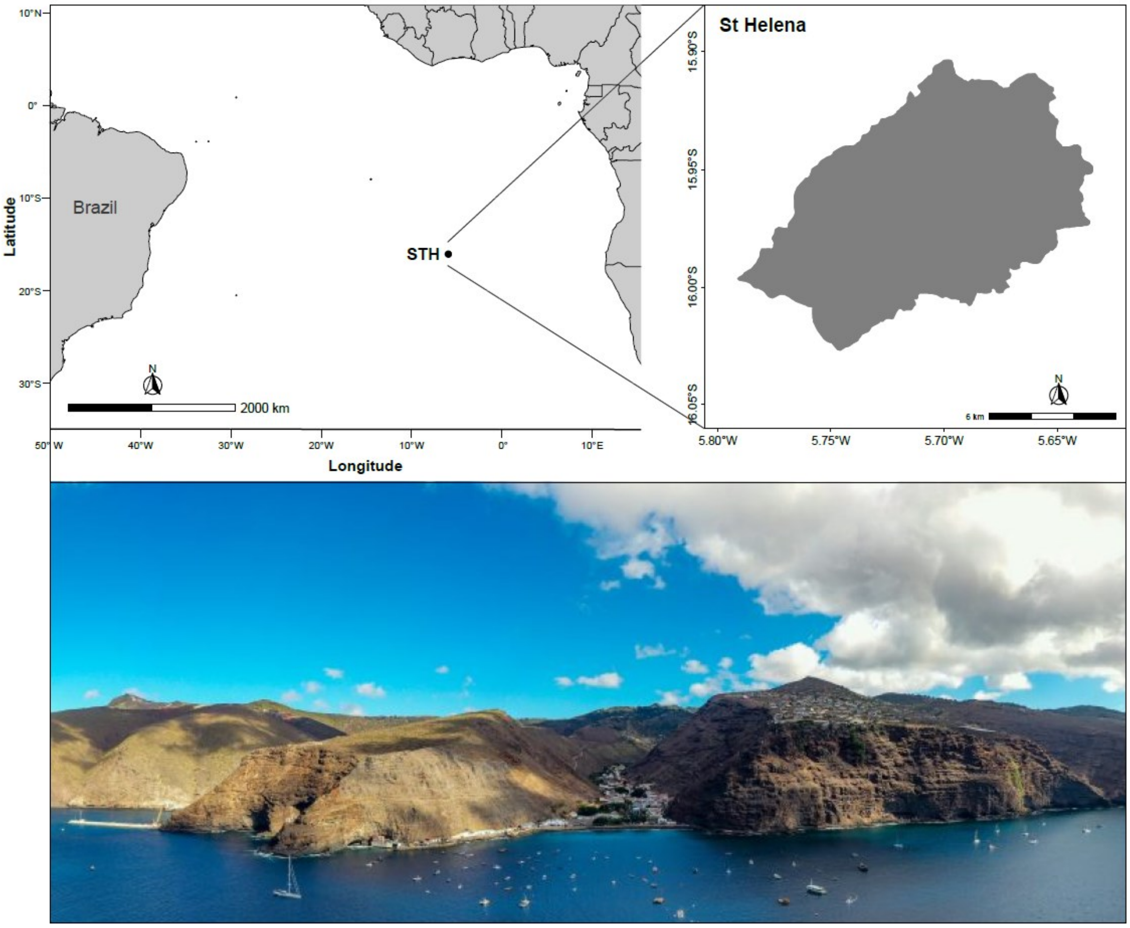

Fig. 1. Map indicating location and photo of St. Helena Island. Photo from St. Helena government

2.2. Data collection

The ecological risk assessment was conducted using the Options for delivering Ecosystem-Based Marine Management (ODEMM) methodology. This methodology facilitates the integrated assessment of the operational ecosystem by providing the framework, tools, and resources required to select and evaluate management options. This establishes connections between the sectors that impact the marine environment, the pressures they generate, and the ecological characteristics that are affected. The methodology employed in this study focuses primarily on the current and direct impacts of the sectors and their pressures on ecological components. We conducted a series of expert opinion meetings to determine the presence or absence of interactions between the assessed variables in our framework. By engaging experts from relevant fields, we ensure a comprehensive perspective, enhancing the depth and accuracy of our analysis. The meeting consisted of nine experts from different scientific institutions, all participants in the Mission Atlantic Project, with diverse disciplinary backgrounds, including marine ecology, fisheries, oceanography, biogeography, and ecotoxicology. This ensured the inclusion of different perspectives.

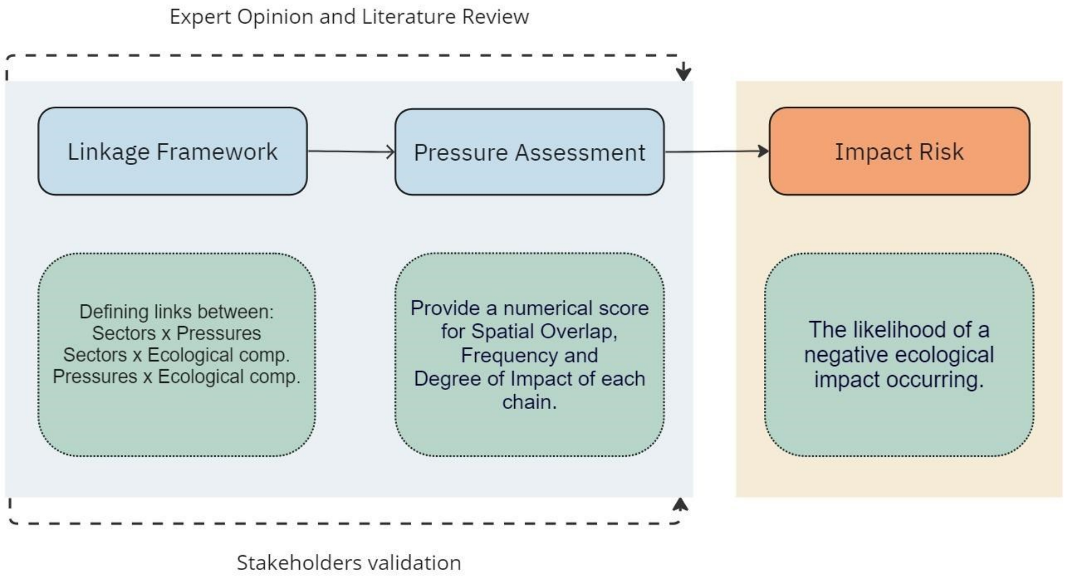

Fig. 2. Framework applied to conduct a risk analysis as part of Integrated Ecosystem Assessment

2.2.1 Linkage Framework, Pressure Assessment and Scoring

The first step, the linkage framework, involves identifying all relevant components of the ecosystem and then describing the connections between individual components to obtain a connected ecosystem structure. Initially, a linkage matrix was created between sectors, pressures, and ecological components. Each linkage corresponds to the potential impact that a sector can generate on an ecological component through a particular pressure. The relevant sectors, pressures, and ecological components identified for the study area are presented in **Table 1**. Definitions for these elements can be found in Table 1S in the supplementary material.

Table 1 Sectors, pressures, and ecological components identified within the study area.

Sectors	Pressures	Ecological Components
Aggregates	Abrasion	Cephalopods
Coastal Infrastructure	Bycatch	Coastal Pelagic
Fishing	Electromagnetic (EMF)	Demersal Elasmobranchs
Harvesting/Collecting	Incidental Loss of species	Demersal Fish
Military	Input of Organic Matter (N&P)	Littoral rock & reef
Navigational Dredging	Introduction of Contaminating	Littoral sediment
Renewable Energy	Invasive species	Seabirds
Research	Litter	Marine Mammals
Shipping	Noise	Reptiles
Telecommunications	Non-living Resources	Shallow rock & reef
Tourism/Recreation	pH changes	Shallow sediment
Waste Water Treatment	Sealing	
	Species Extraction	
	Siltation/Smothering	

After identifying the linkages, a pressure assessment was conducted. This aims to evaluate the probability and consequences of a specific combination (individual link) or an impact chain. Once the linkages were identified, the relative significance of these connections was determined by assigning scores to each linkage chain. This approach weighs each impact chain based on three criteria: spatial extent, occurrence frequency, and degree of impact. These qualitative scores were converted into numerical scoring (according to Pedreschi et al., 2019) and then applied to each category corresponding to these criteria. The list of the values of each respective category is presented in **Table 2**.

Finally, by considering the spatial extent, frequency, and degree of impact, it is possible to obtain the Impact Risk, which represents a measure of the likelihood of a negative ecological impact occurring following the introduction of pressure in a sector. This assessment enables the identification of the most severe impact chain. When the criteria are combined, it produces the 'Impact Risk' score, following the equation:

$$IR = Spatial\ extent\ x\ Frequency\ x\ Degree\ of\ Impact$$

Table 2 Description of criteria used in the scoring phase.

Criteria	Definition	Categories	Score
Spatial extent/ overlap	Spatial overlap between a sector/pressure and an ecological component	Site (>0–5% overlap)	0.03
		Local (5–50%)	0.37
		Widespread (>50%)	1.00
Frequency of occurrence	Timing of the interaction measured in months per year (i.e., between a given sector, pressure, characteristic pathway)	Rare – occurs in one month per year	0.08
		Occasional –occurs in 4 months per year	0.33
		Common – occurs in 8 months per year	0.67
		Persistent – occurs in every month of the year	1.00
Degree of Impact (DoI)	Generic sensitivity of an ecological characteristic to a pressure – regardless of extent or frequency	Low – severe effect not expected	0.01
		Chronic – severe effect likely after multiple occurrences	0.13
		Acute – immediate severe effect	1.00

2.2.2 Bibliographic Review

To validate the impact chains established through the linkage framework and pressure assessment, a thorough literature review was conducted for each identified link. The scientific literature was examined by searching on Google Scholar for a broad range of peer-reviewed and gray literature, including reports, theses, and conference abstracts, using search terms exclusively in English related to each identified chain. Where connections lacked bibliographic support, expert judgment was considered. The assessment process was supported by a comprehensive data search and bibliographic review, with 98 documents scrutinized to establish links and assign scores to the identified linkages.

2.2.3 Stakeholder Validation

Finally, after completing all the mentioned steps, a workshop with stakeholders was conducted to validate the semi-quantitative risk assessment. The workshop took place on St. Helena Island in January 2023, and was attended by a total of 15 participants representing various institutions from St. Helena (i.e. Government marine section, non-governmental organization, elected members, tourism sector, and marine enforcement). The main goal of the workshop was to introduce the Integrated Ecosystem Assessment (IEA) methodology to relevant stakeholders and engage them in in-depth discussions regarding the sectors, pressures, and emerging issues that impact the St. Helena reef system. These issues were identified through scoping activities carried out by experts for the ongoing IEA. Throughout the workshop, a survey was conducted in order to validate the semi-quantitative risk assessment and address emerging issues affecting the St. Helena reef system. The active involvement of stakeholders was crucial to improve our understanding of the current state and to identify any existing gaps.

2.3. Data analyses

The Impact Risk scores were log-transformed to facilitate visual comparisons. The IR ranks were determined by summing and averaging impact risk scores for all impact chains separately by group. Additionally, Proportional Connectance values were calculated to show the connectivity of assessed linkage chains relative to the total number of linkages, irrespective of pathway intensity (not considering the impact risk). The relationships between sectors, ecological components, and pressures (weighted by impact risk) were depicted using network plots (Sankey plots) connecting the interactions. All analyses were carried out in R software (R Core Team 2021) based on the tool developed from the Mission Atlantic project (https://github.com/missionatlantic/MissionAtlantic-RISK-Analysis).

3. Results

A comprehensive risk assessment was carried out to examine the interplay among sectors, pressures, and ecological components. We represented the relationship between them using network plots connecting the interactions, based on spatial extent, frequency, and degree of impact of each linkage chain (Following Pedreschi et al., 2019). In the context of the St. Helena reef system, 12 sectors and 14 pressures were evaluated for their potential impact on 11 ecosystem components. We identified 463 distinct pathways involving various sectors, pressures, and ecosystem components that influenced the ecosystem. The main components of the linkage framework, illustrating the connections and the impact risk score (product of overlap, frequency, and degree of impact) between sectors, pressures, and their impact on the ecosystem components, are shown in **Fig. 3**.

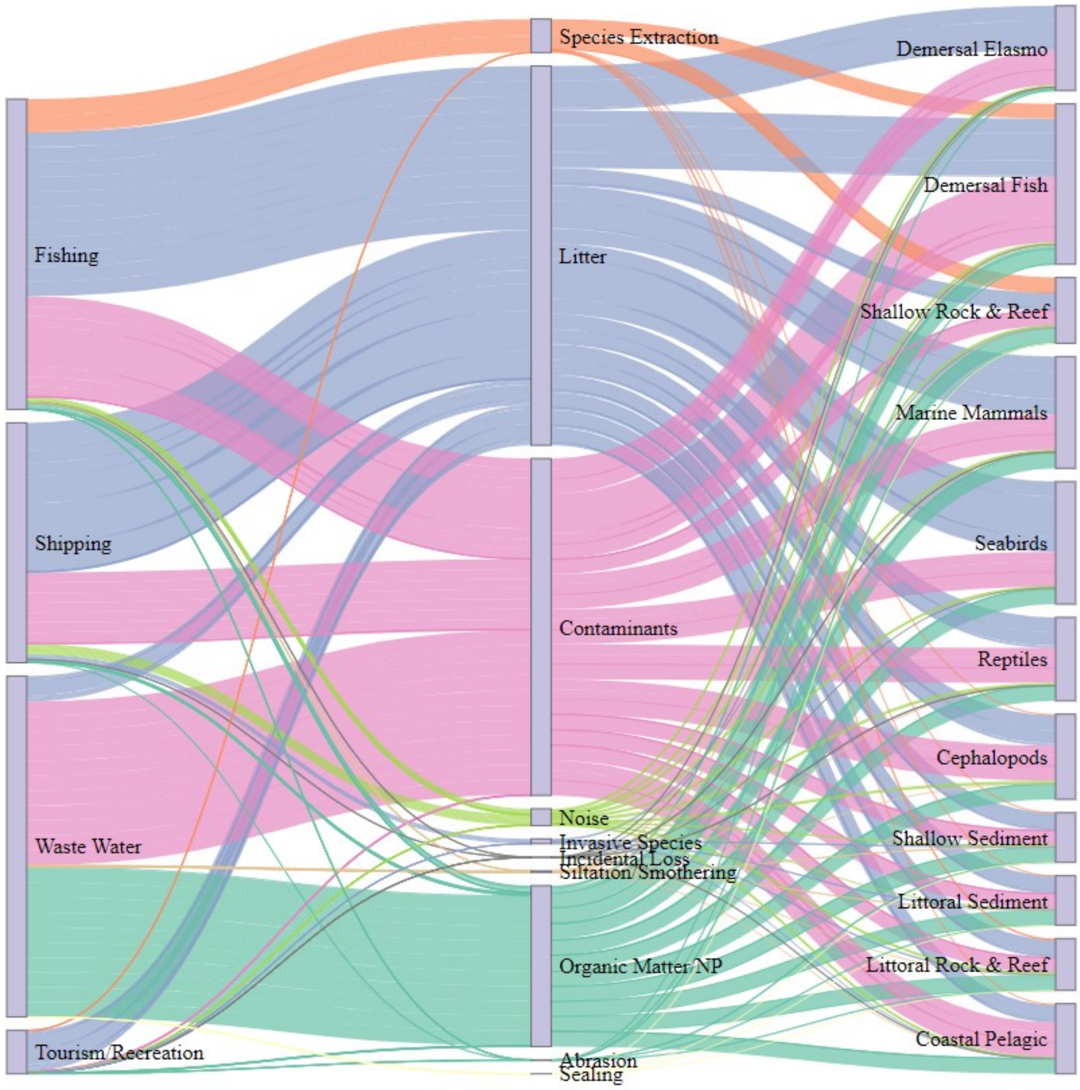

Fig. 3. Sankey diagram of linkages between most important sectors (left), the pressures (middle) and the ecological components (right). The width of lines represents the Impact Risk score (product of overlap, frequency, and degree of impact).

Among the activities undertaken in the study area, the wastewater, fishing and shipping sectors received the highest risk scores (considering the sum and average of impact risks) (**Fig. 3, Table 3**), indicating many widespread and frequent impact chains with severe consequences. While considering the connectance is useful to identify specific characteristics within the linkage chain, it does not reveal too much about impact risk. For example, although the tourism sector is connected with the majority of pressures and ecosystem components (considering the proportion of linkages associated, 14.04 %, **Fig. 4, Table 3**), it had a comparatively lower cumulative risk score (ranking fourth, **Table 3**) due to the generally limited level of impact it has on the environment.

In terms of pressures, it was found that litter has the highest number of connections (86) (**Fig. 4, Table 3**), both with the sectors contributing to this pressure and with the impacted ecosystem components. When considering the sum of impact risk, litter poses the highest risk. However, when considering averaging the impact risks, contaminants emerge as the sector with the highest risk (**Table 3**). The organic matter ranks as the third-highest overall impact risk (when considering the sum and average of impact risks). While the first three ranked pressures exhibited a high level of proportional connectance, the species extraction, in fourth place, showed relatively lower levels of proportional connectance (**Fig. 4, Table 3**).

Concerning the ecosystem components, the Impact Risk scores revealed that demersal fish, seabirds and marine mammals had the highest impact risk, although ranked differently depending on the sum and average of IR (**Fig. 3, Table 3**). Among the habitats, the risk scores were higher for coastal pelagic areas, followed by shallow rock and reef. Conversely, although littoral environments have a high proportional connectance, they showed a relatively lower average impact risk among the pressure impacts (**Fig. 4, Table 3**).

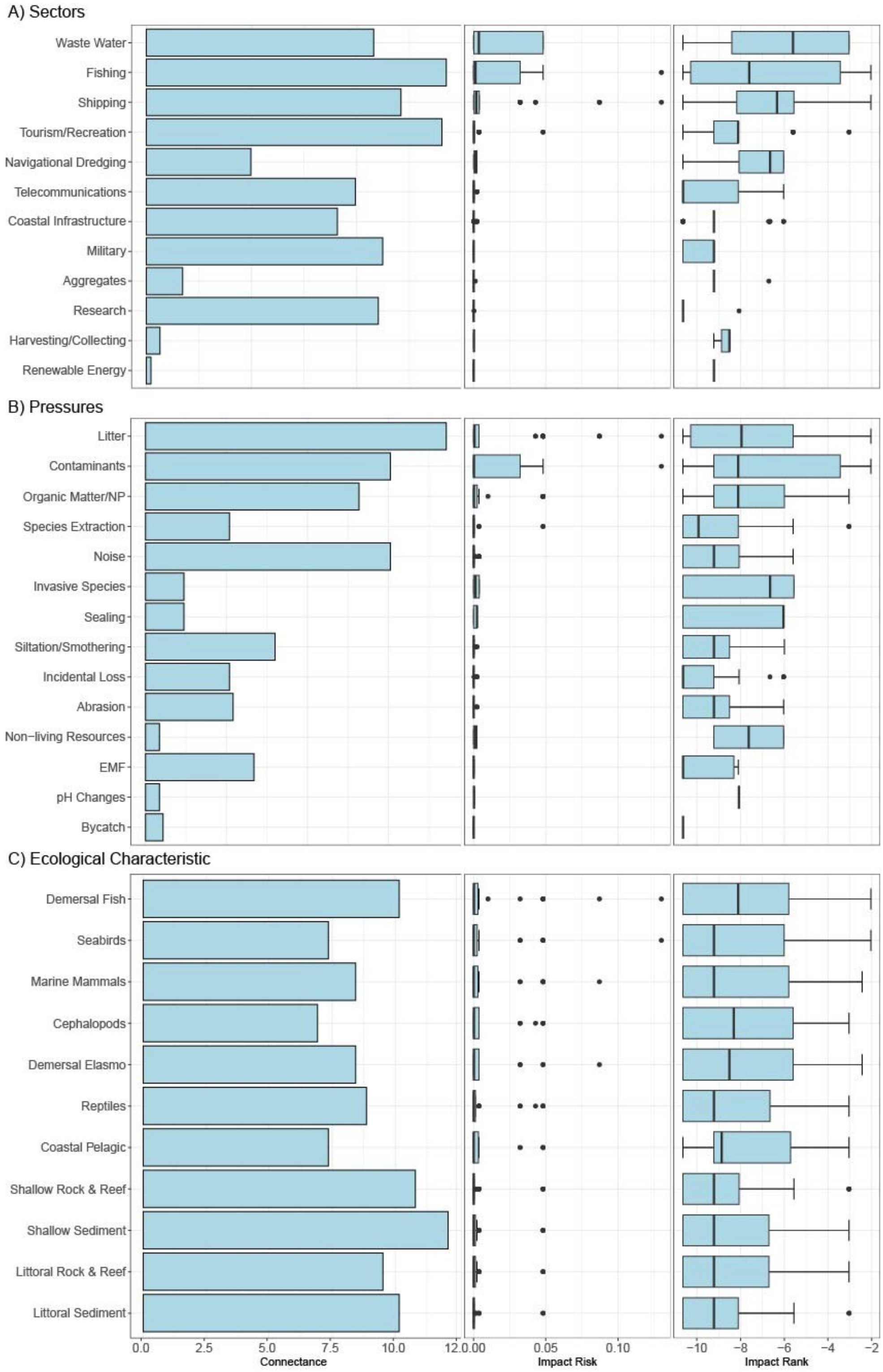

Fig. 4. Proportional Connectance, Impact Risk, Impact Rank Boxplots. Components are ordered according to impact risk. The thick black vertical lines on the boxplots indicate the median values, box lengths representing the 25% quartiles, whiskers representing 1.5 times the interquartile range and outliers are shown as black dots. The small Impact Risk scores have been log-transformed ('Impact Rank') to allow visual comparison between the assessed components.

Table 3 Rankings of sectors, pressures, and ecological components classified by the sum and average impact risk rank. The total links represent the number of linkage chains for each component. PC stands for proportional connectance, and IR represents the impact risk (average and sum).

Sectors	Pressures (count)	EcoCom (count)	Total Links	PC (%)	IR (average)	IR (sum)	IR Rank (Average)	IR Rank (sum)
Waste Water	6	11	50	10,80	0,0220	1,1008	1	1
Fishing	9	11	66	14,25	0,0152	1,0014	2	2
Shipping	8	11	56	12,10	0,0138	0,7745	3	3
Tourism/Recreation	8	11	65	14,04	0,0022	0,1405	4	4
Navigational Dredging	6	8	23	4,97	0,0012	0,0270	5	5
Telecommunications	7	11	46	9,94	0,0003	0,0152	7	6
Coastal Infrastructure	7	11	42	9,07	0,0004	0,0150	6	7
Military	8	11	52	11,23	0,0001	0,0038	11	8
Aggregates	5	4	8	1,73	0,0002	0,0019	8	9
Research	6	11	51	11,02	0,0000	0,0015	12	10
Harvesting/Collecting	1	3	3	0,65	0,0002	0,0005	9	11
Renewable Energy	1	1	1	0,22	0,0001	0,0001	10	12

Pressures	EcoCom (count)	Sectors (count)	Total Links	PC (%)	IR (average)	IR (sum)	IR Rank (Average)	IR Rank (sum)
Litter	11	8	86	18,57	0,0143	1,2258	2	1
Contaminants	11	8	70	15,12	0,0156	1,0932	1	2
Organic Matter/NP	11	6	61	13,17	0,0085	0,5200	3	3
Species Extraction	7	5	24	5,18	0,0046	0,1093	4	4
Noise	11	9	70	15,12	0,0009	0,0600	8	5
Invasive Species	7	3	11	2,38	0,0016	0,0181	5	6
Sealing	5	3	11	2,38	0,0015	0,0169	6	7
Siltation/Smothering	10	5	37	7,99	0,0003	0,0113	12	8
Incidental Loss	9	9	24	5,18	0,0004	0,0095	9	9
Abrasion	6	8	25	5,40	0,0003	0,0083	10	10
Non-living Resources	3	2	4	0,86	0,0012	0,0050	7	11
EMF	11	4	31	6,70	0,0001	0,0035	13	12
pH Changes	4	1	4	0,86	0,0003	0,0012	11	13
Bycatch	5	1	5	1,08	0,0000	0,0001	14	14

Ecological components	Pressures (count)	Sectors (count)	Total Links	PC (%)	IR (average)	IR (sum)	IR Rank (Average)	IR Rank (sum)
Demersal Fish	11	10	47	10,15	0,0113	0,5296	2	1
Seabirds	9	10	34	7,34	0,0118	0,3995	1	2
Marine Mammals	8	9	39	8,42	0,0093	0,3618	3	3
Cephalopods	8	9	32	6,91	0,0086	0,2758	4	4
Demersal Elasmo	8	9	39	8,42	0,0071	0,2757	5	5
Reptiles	9	10	41	8,86	0,0067	0,2729	7	6
Coastal Pelagic	9	9	34	7,34	0,0068	0,2300	6	7
Shallow Rock & Reef	12	10	50	10,80	0,0044	0,2190	8	8
Shallow Sediment	13	10	56	12,10	0,0032	0,1781	11	9
Littoral Rock & Reef	11	9	44	9,50	0,0040	0,1748	9	10
Littoral Sediment	13	9	47	10,15	0,0035	0,1652	10	11

4. Discussion

This study represents the first risk assessment of the reef system of St. Helena Island and applies to the early stages of the Integrated Ecosystem Assessment (IEA). It reveals the cumulative effects of key pressure pathways and identifies the main sectors and the pressures they generate. These pressures, in turn, have a significant influence on the ecological components within the reef system of St. Helena Island. Applying the ODEMM approach, our results have highlighted that wastewater, fishing and shipping are the predominant sectors, contributing to pressures like litter and contaminants, ultimately affecting demersal fish, seabirds and marine mammals. These results corroborated with patterns found in other areas, encompassing not only other oceanic islands (i.e., Rodrigues et al. 2023; Suhet et al., *in prep*) but also densely populated coastal areas (i.e., Pedreschi et al., 2019; Skein et al. 2022; Scherer et al., 2024). This demonstrates that oceanic islands are already being affected by the main sources of anthropogenic activities (Alava et al., 2023).

The lack of adequate treatment took the wastewater sector in the first place among the sectors exerting the most significant pressure on the reef ecosystem. While there is no available data on the effects of this pressure on the reef system of St. Helena, it is acknowledged that the disposal of sewage, entailing the release of raw organic matter with associated pathogens (Wear, 2019), and the additional greywater discharge from both residential and commercial sources, introduce chemical contaminants, sediments, pathogens, and heavy metals (Wear & Thurber, 2015). The combined impact of these elements introduced into the marine environment can trigger eutrophication, leading to an excessive growth of organisms like algae and cyanobacteria (Smith, 2003). The exposure to these multiple stressors can lead to a decrease in certain marine species, consequently causing changes in the structure of reef communities and in the marine ecosystem (Wear and Thurber, 2015). The possibility of these cumulative and profound effects on the reefs of St. Helena, resulting from the lack of wastewater treatment, emphasize the need to prioritize the proper management of this sector on St. Helena Island.

Besides the wastewater sector affecting the St Helena reef environment, other sectors also deserve attention. Fishing is becoming a growing concern for the risk in ecosystems, as is similarly observed in other regions of the Atlantic Ocean, including the Southern Brazilian continental shelf (Scherer et al., 2024), South Africa (Skein et al., 2022), Irish (Pedreschi et al., 2019), and other Atlantic oceanic islands (Rodrigues et al., 2023; Suhet et al., *in prep*). Fishing activities may remove species from the ecosystem through different manners, such as types of fishing gear, bycatch, and ghost nets (Macfadyen et al., 2009). However, the reef system of St.

Helena is situated within a marine protected area designated for sustainable use (St. Helena Government, 2022). As a result, fishing is limited to specific methods, with only one-by-one fishery methods being permitted, thus, this type of fishing reduces bycatch, as reported in a preliminary risk analysis (see St. Helena Government, 2022), and prevents ghost fishing. St. Helena still lacks designated no-take zones, however, due to the challenging access to some areas of the island, this has resulted in natural no-take zones (St. Helena Government, 2022). While commercial inshore fishing typically occurs when tuna catches are poor or when the local market demands other species (St. Helena Government, 2022), there is still fishing pressure from both sport fishing and recreational fishing, with the latter being pursued for either recreational purposes or subsistence. Recreational fishing is recognized for being highly selective and depleting important species, as seen in Ascension Island, which was reported affecting the decline of marine biodiversity (Hardman et al., 2022). Besides that, we cannot ignore that all types of ongoing one-by-one fishing exerts pressure on the reef fish population, particularly the targeted reef species, such as the Spotted moray (commonly referred to as Conger) and Groupers.

In addition to fishing, the sector shipping, which includes vessels and boats, can exert a range of pressures on the environment (Jaügerbrand et al., 2019; Ytreberg et al., 2021). These include the release of contaminants through oil spills, underwater noise, habitat damage through anchoring, the generation of waste and plastic pollution, as well as collisions with marine fauna, among other impacts (Walker et al., 2019). St. Helena is a well-known shipping route, crossing both their Exclusive Economic Zone (EEZ) and Marine Protected Area (MPA) boundaries (Rodrigues et al., 2023). While shipping routes are typically offshore, more than 30 miles away from the island, the impacts of these vessels can affect the inshore environment, particularly in terms of pressures with widespread effects, such as contaminants. Furthermore, there are commercial ships that deliver supplies to the island by entering and anchoring near the coast. It's not only the offshore shipping traffic that may impact the environment, both cruise ships that stay in St. Helena and small vessels require anchoring, which has the potential to cause habitat damage to the reefs and their organisms (St. Helena Government, 2022). In addition to habitat damage, other impacts on the reef environment, such as pollution and collisions, are also a concern.

The tourism and recreation sector, though ranking fourth in terms of risk impact, demonstrates a positive correlation with the fishing and shipping sectors. Tourism and recreational activities are intrinsically linked to the marine environment, encompassing endeavors such as snorkeling, sport fishing, and scuba diving. Consequently, as the number of tourists on the island grows, it leads to an increased use of boats and greater demand for seafood consumption. Furthermore, this results in a growing inflow of sewage on an island that already has a population of ~4,000 residents and lacks proper sewage treatment facilities.

Among the consequences created by the sectors mentioned, marine pollution poses the major concern. Litter and contaminants ranked the top of pressures impacting the ecological components. Marine litter is primarily made of plastic materials, being plastic pollution globally recognized as one of the most significant pressures on the ocean (Morales-Caselles et al., 2021). Beyond that has been identified as the primary pressure in risk assessments conducted in various locations, such as Ireland's marine waters (Pedreschi et al., 2019), the Southern Brazilian continental shelf (Scherer et al., 2024), and Trindade Island (Suhet et al., *in prep*). In our study, litter was mainly associated with fishing and shipping activities, although not necessarily local activities, as the majority of the waste comes from open sea waters through marine currents (Morales-Caselles et al., 2021). A recent study noted that the majority of litter originating from the open sea is primarily composed of fishing materials (e.g., fishing nets, fishing-related items), and ropes (see Morales-Caselles et al., 2021). Furthermore, concerning plastic litter, there is evidence indicating that ships are responsible for the majority of the bottles found floating in the central South Atlantic Ocean (Ryan et al., 2019). Regarding plastic materials in St. Helena, it originates from both local and international sources, being the bulk of plastic litter that comes from beyond the island are primarily of Asian origin (St. Helena Government, 2022). This trend is similarly observed in Inaccessible Island within the Tristan da Cunha archipelago, another central Atlantic oceanic island (Ryan et al., 2019).

When it comes to contaminants, apart from untreated sewage, the surface runoff loaded with pesticides, fertilizers, and car oil becomes notably pronounced after heavy rain periods (St. Helena Government, 2022). Vessels also contribute to the issue by releasing contaminants (Ytreberg et al., 2020). Specifically in St. Helena, there is a concern about possible fuel spills or leaks during the transfer of the island's fuel supplies from ship to shore (St. Helena Government, 2022). The highest maritime activity in St. Helena occurs around Jamestown and Rupert's Bays, and concerns arise due to the impact of anti-fouling paint in shallow areas caused by the cleaning of boat encrustations (St. Helena Government, 2022). Furthermore, there is evidence suggesting that anti-fouling has an adverse effect on fish (Amara et al., 2018).

The main ecological components impacted were demersal fish, seabirds and marine mammals, particularly due to pressures from litter and contaminants. Coastal areas and shallow rock and reef exhibited substantial connectivity with diverse pressures, with a higher risk of impact from litter, contaminants, organic matter, mainly because these pressures exhibit a widespread spatial extent, thereby intensifying their overall impact. While littoral rock areas may not have as pronounced an impact as coastal and shallow areas, it is crucial not to overlook the high connectivity of this environment with potential pressures.

The synergy of these impacts in the shallow environment has the potential to create environmental imbalance, triggering a cascade of effects, both bottom-up (e.g., eutrophication) and top-down (e.g., loss of top predators). The impact of marine litter on marine animals and the entire ecosystem is substantial (Barnes et al., 2018; Thushari and Senevirathna, 2020; Pinheiro et al., 2023). At a global scale, marine litter is predominantly composed of plastic (Morales-Caselles et al., 2021), and there has been a documented increase in the effects of plastic ingestion on marine organisms (Markic et al., 2020).

The impact of plastic on marine species extends throughout the entire trophic chain, affecting species from small cryptic fish to reef sharks (Markic et al. 2020), and marine mammals (Zantis et al., 2021). The ingestion of plastic by these species can impact them physically, either by directly obstructing their digestive system with pieces of plastic or indirectly through the presence of micro and nanoplastics, diminishing their mobility, feeding, and growth (Baulch and Perry, 2014; Critchell and Hoogenboom, 2018; Nunes et al., 2019). Moreover, plastic ingestion can introduce toxic components adsorbed onto the plastic (Markic et al., 2020). Regarding seabirds, they are highly associated with the marine environment and are part of its food chain (Signa et al., 2021). Moreover, the excrement released by seabirds is a rich source of essential nutrients for reefs stimulating primary production (Otero et al., 2018). Despite their critical role, seabirds are frequently impacted, primarily by litter (Pierce et al., 2004). It is recognized that seabirds carry litter found on beaches and in the sea (e.g. packaging, bottle caps) into their nests. Additionally, seabirds often mistake floating plastic pieces for food, leading to the ingestion of small plastic fragments, such as microplastics, or larger items like plastic bags. This can result in direct mortality due to complications such as gut obstruction and perforation (Pierce et al., 2004).

Despite elasmobranchs ranking fifth in the risk impact, it is worth noting that historically in St. Helena, reef sharks are rarely sighted in the waters, and there is no evidence of overfishing effects (St. Helena Government, 2022). Therefore, in this study, we consider Devil Rays and whale sharks within this group. Although they are pelagic species, they are commonly observed in the reefs of St. Helena, directly experiencing the impacts generated on the reef environment. Both species are planktivorous, filtering planktonic species from the water column. The accidental ingestion of microplastics dissolved in the water column is known to be one of the major impacts caused by pollution on filter-feeding species (Germanov et al., 2019; Yong et al., 2021). Furthermore, whale shark observation tourism holds great significance for the economy of St. Helena. This activity involves daily boat excursions navigating the area where these animals reside during the season from November to April, potentially generating both noise pollution and collision risks (Womersley et al., 2022).

Beyond revealing the complexities of the main interactions and their impacts, this study aids in identifying knowledge gaps and underscores the necessity for ongoing studies and management monitoring. For instance, in our study, the electromagnetic field (EMF) sector was identified as an emerging issue due to the lack of knowledge about the potential impacts of this sector operating in the shallow environments of the St. Helena Island, particularly considering the planned implementation of submarine cables around St. Helena waters (St. Helena Government, 2022). Although the effects of EMF on the ecosystem are known, such as influencing migration and predatory behavior in marine fauna (Tricas and Gill, 2011), the potential impacts during implementation and after long exposures in the St. Helena reef system remains uncertain, requiring prior studies and monitoring.

It is noteworthy that studies requiring the compreension of all aspects of the ecosystem often encounter challenges due unavaiable quantitative data. This challenge becomes more pronounced in studies conducted in remote and understudied locations, such as oceanic islands, where the lack of available data or literature leading the use of a semi-quantitative approach. Although be considered a subjective methodology, when applied in a standardized manner, the semi-quantitative approach emerges as a valuable tool for enhancing the overall understanding of the studied system (Scherer et al., 2024). Due to the necessary to use a methodology that incorporates different levels of knowledge and data availability, the ODEMM methodology has been identified as a suitable option due to its adaptability and iterative process, which can be updated as new data and knowledge become available (Robinson et al., 2014; Pedreschi et al., 2023). Additionally, through this methodology, it is possible to identify knowledge gaps and areas that require quantitative studies. Although the lack of quantitative data is a limitation in studies with a holistic approach, there is an emerging need to take action now, and this can be done based on the best science and evidence available until the moment (Pedreschi et al. 2023)

Fig. 1. Human activities at St. Helena Island: A) Coastal infrastructure, B) Boats anchored, C) Harbour, D) Oil storage, E) Fishing, F) Wind power plant, G) Litter into the sea, H) Litter onto the beach. Photos by LA Rocha, JL Gasparini, SR Floeter.

5. Conclusion

The application of the integrated ecosystem assessment in this study provided a comprehensive understanding of the main intricate interactions between human activities and the ecological components of the St. Helena reef system, as well as corroborated with the pattens found in both isolated and densely populated areas. Studies highlighting the human impacts on reef environments have been growing (Hoegh-Guldberg, 2011; Bahr et al., 2015; El-Naggar, 2020). Although the impacts are more pronounced in coastal environments, isolated oceanic islands, as St. Helena Island, still considered pristine compared to the mainland, are already being affected by anthropogenic activities (Alava et al., 2023). Thus, studies revealing these impacts in these isolated and understudied areas are crucial for prioritizing management of the key threats to this ecosystem. The risk analysis undertaken in this study, using the ODEMM methodology, not only enables the identification of key sectors and pressures with potential impacts but also reveals the chains of more severe impacts. Furthermore, the methodology is adaptable and replicable, allowing updates when necessary (Robinson et al., 2014). Additionally, this study emphasizes the importance of cooperation among various institutions, including scientific research, interdisciplinary projects, and stakeholders, underscoring the need for interactions across different sectors of society. Furthermore, we highlight that the ongoing engagement of diverse institutions and sectors is critical to the formulation of effective conservation policies and management actions for mitigating the impact on the reef ecosystem of St. Helena Island.

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Supplementary Material

Table S1 Definitions of each sector and pressure that were considered in the study.

Sector	Definition
Aggregates	Inorganic mine and particulate waste, rock/minerals (coastal quarrying), sand/gravel.
Coastal Infrastructure	Beach replenishment, dock/port facilities, infrastructure found on the coast rather in the marine environment, urban dwellings (i.e., housing and other buildings).
Fishing	Harvest of marine resources for commercial purposes.
Harvesting/Collecting	Hand collecting of living marine resources (e.g., seaweed and shellfish).
Military	Activities to supply, maintain or enhance any aspect of the military.
Navigational Dredging	Capital dredging, maintenance dredging, removal of substrate, spoil dumping.
Renewable Energy	Renewable (tide/wave/wind) power stations.
Research	Activities undertaken as part of marine research (e.g., survey cruises, grab sampling, trawls).
Shipping	Domestic and global trade via transportation of commodities and products.
Telecommunications	Communication cables.
Tourism/Recreation	Boating/yachting, diving/dive site, public beach, tourist resort, water sports, Recreational fishing, cruise ship.
Wastewater Treatment	Sewage discharge, thermal discharge.
Pressure	**Definition**
Abrasion	Physical interaction of human activities with the seafloor and with seabed fauna/flora causing physical damage and/or mortality (e.g., from trawling or anchoring), excluding death or injury due to collision.
Bycatch	Unwanted/illegal catch (that ends up in the net/on board)
Contaminants	Introduction of pesticides, antifoulants, pharmaceuticals, heavy metals, and hydrocarbons into marine waters.
Electromagnetic Field (EMF)	Change in the amount and/or distribution and/or periodicity of electromagnetic energy emitted in a marine area (e.g., from electrical sources such as underwater cables).
Incidental Loss	Collateral damage of all species (e.g., collisions with ships/gear). Entanglement in fishing nettings.
Invasive Species	Introduction of non-indigenous species and translocations of species by the activities of a particular sector (e.g., through shipping).
Litter	Marine litter originates from numerous sources and consists of different materials including metal, glass, rubber, wood, cloth, and plastics (including microparticles of plastics and lost or discarded fishing gear).
Noise	Underwater sound from anthropogenic sources (e.g., shipping, fishing, geological investigations, harbor operations).
Non-living Resources	Sand and gravel (aggregates) extraction, or removal of surface substrates for exploration of subsoil.
Organic Matter/NP	Organic enrichment e.g., from industrial and sewage effluent input and/or fertilizers, and other nitrogen and phosphorous rich substances into rivers and coastal areas. Include organic discards.
pH Changes	Change in pH (average, range, or variability) due to runoff from land-based industry or point-source discharges. Here, pH changes exclude ocean acidification (i.e., the reduction in pH of the ocean over an extended period, typically decades or longer, caused primarily by the uptake of anthropogenic carbon dioxide from the atmosphere)
Sealing	Substrate loss. Sealing by permanent construction (e.g., coastal defences, wind turbines) or change in substrate type due to loss of key characteristic features (physical and/or biological). Natural substrate loss and replacement by a different kind of substrate. Loss of roosting/nesting/foraging areas of bird. Loss of nursery grounds for fish.
Siltation/Smothering	Change in the concentration and/or distribution of suspended sediments in the water column from runoff, dredging etc. or smothering by man-made structures or disposal of materials to the seafloor.
Species Extraction	Targeted extraction of species.

Supplementary Material - Literature review

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CONCLUSÃO GERAL

Essa tese de doutorado demonstrou que a sinergia entre diferentes processos ecológicos e fatores ambientais moldam os padrões de diversidade encontrados nas comunidades recifais das ilhas oceânicas do Atlântico sul. Os resultados da tese também evidenciaram a importância de incorporar medidas clássicas na avaliação das comunidades biológicas. Adicionalmente, por meio de uma abordagem socioecológica, foram evidenciadas as principais atividades antropogênicas e as pressões por elas geradas. Cada capítulo proporcionou uma investigação aprofundada do ecossistema recifal em ilhas oceânicas por meio de diferentes perspectivas e partindo do nível de comunidades para o nível de ecossistema.

Inicialmente, no primeiro capítulo, por meio da perspectiva das interações tróficas, evidenciou-se que a pressão alimentar dos peixes é influenciada tanto pelas características do habitat quanto pela biomassa dos peixes. Além disso, foi observado que cada grupo trófico é dominado por poucas espécies em termos de biomassa, resultando em um padrão de hiperdominância de espécies dentro da comunidade. Este achado tem implicações importantes para a gestão marinha, enfatizando a necessidade de considerar a heterogeneidade do habitat e a dominância de certas espécies no planejamento de conservação do ecossistema recifal. Dada a presença de diferentes Áreas Marinhas Protegidas (AMPs) nas áreas estudadas, é recomendável concentrar-se no desenvolvimento de estratégias de gestão não apenas para as espécies alvo da pesca, mas também para aquelas que promovem a diversidade do habitat, bem como para as espécies hiperdominantes que desempenham papel importante na teia trófica do ecossistema recifal.

Adicionalmente, no Capítulo 2, foram evidenciadas variações na estrutura das comunidades de peixes recifais em termos de composição, abundância, biomassa, estrutura trófica e tamanho corporal entre as três ilhas da Cordilheira Meso-Atlântica. Os padrões identificados indicam que uma combinação de fatores ambientais, com ênfase particular na interação entre as temperaturas da superfície do mar e a tolerância térmica das espécies, desempenha um papel crucial na formação dessas comunidades insulares. Esses resultados destacam a importância de estabelecer uma compreensão básica, como a quantificação de assembleias de peixes recifais, incluindo a estimativa de abundância e biomassa, bem como a variação de temperatura. Isso é essencial para monitorar a dinâmica da comunidade ao longo do tempo e identificar sinais precoces de mudanças no ecossistema decorrentes do aumento da temperatura do mar ou de outros fatores.

Nas últimas décadas, a compreensão de como as atividades antrópicas podem afetar o ambiente recifal tornou-se uma preocupação emergente. Dessa forma, no terceiro capítulo, foi adotada uma abordagem holística por meio de uma avaliação integrada do ecossistema. No capítulo 3, ficou evidente que a aplicação da avaliação integrada do ecossistema proporcionou uma maior compreensão das intricadas inter-relações entre as atividades humanas e os componentes ecológicos do sistema de recifes de St. Helena. Isso inclui, por exemplo, a influência das águas residuais e da pesca, que geram resíduos e contaminantes, impactando, por sua vez, os peixes demersais, aves marinhas e mamíferos marinhos. Além de revelar as complexidades dessas interações e seus impactos, essa abordagem auxilia na identificação de lacunas de conhecimento e destaca a necessidade de estudos contínuos e monitoramento. Assim, estudos que revelam esses impactos em áreas isoladas e pouco estudadas são cruciais para priorizar a gestão das principais ameaças a esse ecossistema, permitindo que os gestores tenham as ferramentas e informações necessárias para desenvolver estratégias de gestão e monitoramento para mitigar o impacto no ecossistema recifal.

Finalmente, esta tese contribuiu para um entendimento mais holístico das comunidades de peixes recifais em ilhas oceânicas do Atlântico Sul, e evidenciou os possíveis impactos causados pelas atividades humanas. Embora os impactos sejam mais evidentes em ambientes costeiros, as ilhas oceânicas isoladas, geralmente consideradas intocadas em comparação com o continente, já estão sendo afetadas por atividades humanas. Investigar diferentes aspectos, como a estrutura e o funcionamento das comunidades, assim como a dinâmica entre os setores antrópicos e as pressões que eles criam, proporciona uma compreensão mais ampla do ecossistema recifal nessas ilhas isoladas. A partir desse conhecimento, é possível desenvolver estratégias de monitoramento e manejo embasadas em evidências científicas. Por exemplo, concentrar-se em espécies-chave para a preservação do recife, como as hiperdominantes e herbívoros (Capítulo 1). Além disso, monitorar possíveis aumentos nas temperaturas superficiais do mar e utilizar esses dados como base para estratégias de conservação (Capítulo 2). Por fim, monitorar as principais cadeias de impacto, ou seja, os setores-pressões-componente ecológico, e desenvolver estratégias para mitigar alguns impactos mais severos, como, por exemplo, a ausência de tratamento das águas residuais, que gera contaminantes capazes de provocar a eutrofização do sistema recifal (Capítulo 3).

APÊNDICE

Artigos publicados durante o andamento desta tese (no período de 2020 a 2024).

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

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RESEARCH ARTICLE

A trait-based approach to marine island biogeography

Débora S. Ferrari, Sergio R. Floeter, Fabien Leprieur, Juan P. Quimbayo

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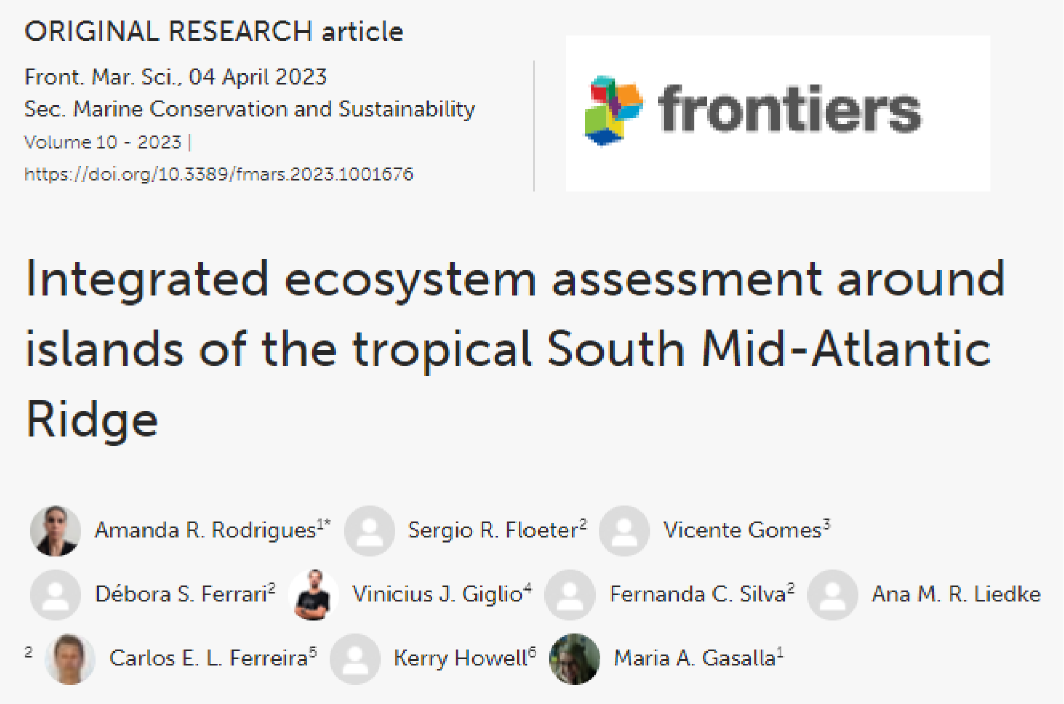

ORIGINAL RESEARCH article

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

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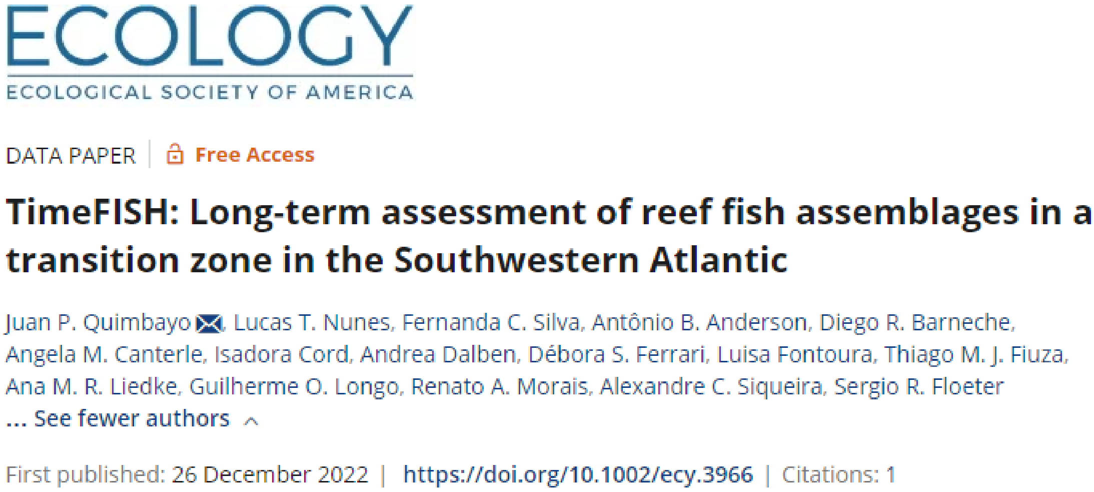

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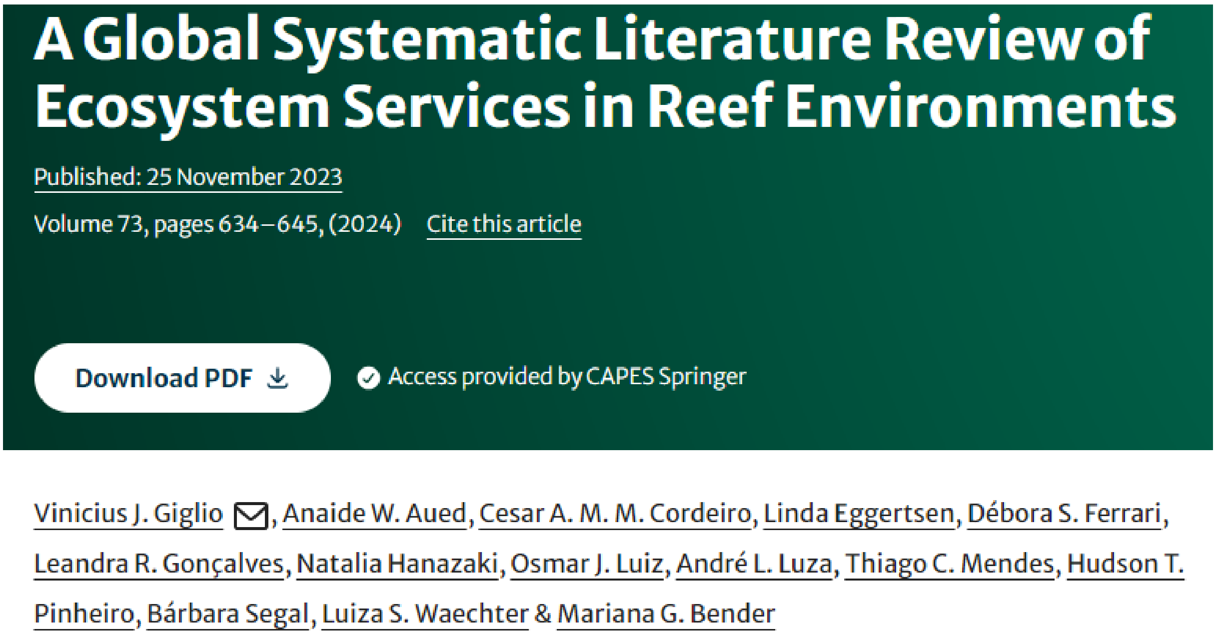

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