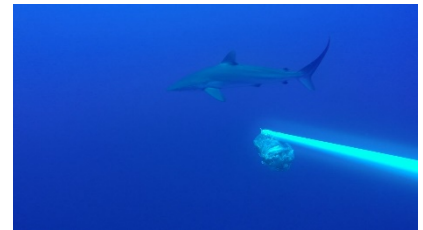UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO

CENTRO DE CIÊNCIAS HUMANAS E NATURAIS

DEPARTAMENTO DE OCEANOGRAFIA E ECOLOGIA

PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA AMBIENTAL

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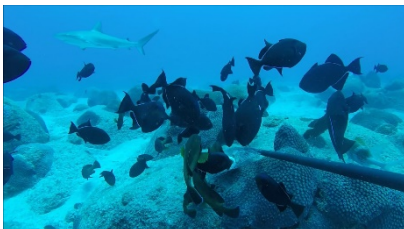
Caio Ribeiro Pimentel

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Tese apresentada ao Programa de Pós-Graduação em Oceanografia Ambiental da Universidade Federal do Espírito Santo, como requisito parcial para obtenção do título de Doutor em Oceanografia Ambiental.

Orientador: Dr. Jean-Christophe Joyeux
Coorientador: Dr. Tommaso Giarrizzo

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2021

UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO
Centro de Ciências Humanas e Naturais
Programa de Pós-Graduação em Oceanografia Ambiental

TESE DE DOUTORADO

"DISTRIBUIÇÃO E BIODIVERSIDADE DE PEIXES RECIFAIS BRASILEIROS: EXPLORANDO HABITATS BENTÔNICOS DA ZONA MESOFÓTICA"

por

Caio Ribeiro Pimentel

_____
Prof. Dr. Jean-Christophe Joyeux
Universidade Federal do Espírito Santo (via webconferência)

_____
Prof. Dr. Maurício Hostim Silva
Universidade Federal do Espírito Santo (via webconferência)

_____
Profa. Dra. Fernanda Andreoli Rolim
Universidade Estadual Paulista (via webconferência)

_____
Prof. Dr. Ricardo Clapis Garla
Universidade Federal do Rio Grande do Norte (via webconferência)

_____
Prof. Dr. Ciro Vilar
Universidade Federal do Espírito Santo (via webconferência)

Vitória, 30 de junho de 2021

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Resumo

Peixes recifais são eficientes modelos para a realização de estudos ecológicos em escalas espaciais e temporais relativamente pequenas, permitindo compreender como algumas características ambientais estruturam suas comunidades. Nesse sentido, a profundidade e o habitat bentônico (*e.g.*, recifes, bancos de rodolitos e macroalgas) são umas das características ambientais mais importantes. Apesar da singularidade e vulnerabilidade das comunidades de peixes recifais brasileiros, ainda sabemos pouco sobre a biodiversidade e os padrões de distribuição das espécies em habitats mesofóticos (que ocorrem entre 30 e 150 m de profundidade). Portanto, o principal objetivo desta tese foi analisar a composição e estrutura das assembleias de peixes em diferentes ilhas oceânicas brasileiras, visando entender principalmente como a profundidade e os habitats atuam na estruturação dessas assembleias. Foram utilizados sistemas de estéreo-vídeos subaquáticos com isca (*stereo*-BRUVS) para explorar diversos habitats bentônicos, ao longo de um amplo gradiente de profundidade (~ 10 a 90 m) nas ilhas oceânicas de Trindade, Arquipélago de Fernando de Noronha e Arquipélago de São Pedro e São Paulo (ASPSP). Inesperadamente, no ASPSP as assembleias de peixes recifais não apresentaram estruturação em função do gradiente de profundidade. A distribuição das espécies está mais associada a eventos de ressurgência e subsidência, que alteram drasticamente a temperatura da água e influenciam o movimento vertical das espécies no recife. Além disso, diversas espécies foram registradas tanto no ambiente pelágico quanto nos recifes, sugerindo a existência de conexão ecológica entre esses ambientes, por meio do fluxo de matéria e energia. Por sua vez, a plataforma insular da Ilha da Trindade compreende um mosaico de habitats bentônicos interconectados, os quais diferem em riqueza, abundância e biomassa das assembleias de peixes. Os recifes apresentaram maior riqueza e abundância, assim como maior proporção de espécies exclusivas, seguidos pelos bancos de rodolitos, bancos de macroalgas e fundos de areia. A profundidade foi considerada uma característica intrínseca dos habitats, uma vez que estes não se distribuem continuamente ao longo do gradiente batimétrico da plataforma. Essas características ambientais, portanto, atuam em sinergia na estruturação das assembleias de peixes. Em relação à biodiversidade, por meio dos *stereo*-BRUVS foi possível analisar a composição específica e abundância de tubarões nessas duas ilhas oceânicas, incluindo uma espécie considerada localmente extinta no ASPSP. Em Fernando de Noronha, dos 19 novos registros, três foram realizados por meio dos *stereo*-BRUVS. Esses resultados reforçam a necessidade de estratégias de gestão integrada dos habitats eufóticos e mesofóticos, bentônicos e pelágicos, recifais ou não-recifais, visando a conservação da biodiversidade, das funções ecológicas e da conectividade nos ambientes marinhos.

Palavras-chave: BRUVS, bancos de rodolitos, conservação, ecologia marinha, endêmicos, espécies ameaçadas, ilhas oceânicas, recifes.

Abstract

Reef fish are efficient models for carrying out ecological studies at relatively small spatial and temporal scales, allowing us to understand how some environmental characteristics structure their communities. In this sense, depth and benthic habitat (*e.g.*, reefs, rhodolith beds and macroalgae) are one of the most important environmental characteristics. Despite the uniqueness and vulnerability of Brazilian reef fish communities, we still know little about the biodiversity and distribution patterns of species in mesophotic habitats (which occur between 30 and 150 m deep). Therefore, the main objective of this thesis was to analyze the composition and structure of fish assemblages in different Brazilian oceanic islands, aiming to understand mainly how depth and habitats act structuring these assemblages. Baited remote underwater stereo-video systems (stereo-BRUVS) were used to explore diverse benthic habitats along a wide depth gradient (~10 to 90 m) at Trindade Island, Fernando de Noronha Archipelago and Saint Peter and Saint Paul's Archipelago (SPSPA), as well as on the east coast of Brazil. Unexpectedly, in SPSPA reef fish assemblages were not structured according to the depth gradient. Species distribution was more associated with up and down-welling events, which drastically change the temperature and influence the vertical movement of fishes along the reef. Furthermore, several species were recorded in both pelagic and reef environments, suggesting ecological connections between them, through the flux of matter and energy. In turn, the Trindade Island insular shelf comprises a mosaic of interconnected benthic habitats, which differ in richness, abundance and biomass of fish assemblages. Reefs showed greater richness and abundance, as well as a greater proportion of exclusive species, followed by rhodolith beds, macroalgae beds, and sandy bottoms. Depth was considered an intrinsic characteristic of habitats, as they are not continuously distributed along the bathymetric gradient of the insular shelf. These environmental characteristics, therefore, act in synergy in the structuring of fish assemblages. Regarding biodiversity, using stereo-BRUVS it was possible to analyze the composition and abundance of shark species in these two oceanic islands, including a species considered locally extinct in SPSPA. In Fernando de Noronha, stereo-BRUVS accounted for three new records. These results reinforce the need for integrated management strategies that include euphotic and mesophotic, benthic and pelagic habitats, reefs or non-reefs, aiming at the conservation of biodiversity, ecological functions and connectivity in marine environments.

Keywords: BRUVS, rhodolith beds, conservation, marine ecology, endemic, endangered species, oceanic islands, reefs.

Introdução geral

Peixe recifais possibilitam a realização de estudos ecológicos em escalas espaciais e temporais relativamente pequenas, permitindo compreender como as características ambientais estruturam suas assembleias (Sale, 1991). Dentre essas características, destacam-se o tipo de habitat e a profundidade como importantes preditores (Pearson & Stevens, 2015; Andradi-Brown *et al.*, 2016; Heyns-Veale *et al.*, 2016; Asher *et al.*, 2017). As assembleias podem responder a esses fatores desde variações na escala de microhabitats (Pereira, 2017; Brandl *et al.*, 2018), macrohabitats e ecossistemas (Harvey *et al.*, 2013; Longo *et al.*, 2015; Reis-Filho *et al.*, 2019; Moura *et al.*, 2021). Pequenas variações de profundidade, em particular na zona eufótica (até 30 m de profundidade), também podem influenciar as assembleias de peixes recifais (Krajewski & Floeter, 2011; Pinheiro *et al.*, 2011a; Luiz *et al.*, 2015), assim como variações em escalas maiores, como entre as zonas eufótica e mesofótica (31 a 150 m de profundidade), ou mesmo ao longo desta última (Pinheiro *et al.*, 2016; Rosa *et al.*, 2016; Rocha *et al.*, 2018; Andradi-Brown *et al.*, 2021).

Nesse sentido, ilhas oceânicas figuram como verdadeiros laboratórios naturais, onde a combinação de características intrínsecas como elevado isolamento e baixa riqueza de espécies, permite uma melhor compreensão das relações e processos ecológicos (Losos & Ricklefs, 2009). No Brasil, as ilhas e arquipélagos oceânicos apresentam características ambientais distintas, sobretudo o Arquipélago de São Pedro e São Paulo, único de origem e formação não vulcânica (Mohriak, 2020). Esses ambientes únicos apresentam biodiversidade peculiar e elevado endemismo de peixes recifais (Pinheiro *et al.*, 2018a). Espécies endêmicas das ilhas oceânicas apresentam elevada vulnerabilidade, devido à baixa variabilidade genética e distribuição geográfica restrita (Feitoza *et al.*, 2003). Tais características tornam as ilhas oceânicas brasileiras áreas prioritárias para a conservação da biodiversidade marinha, reforçando a necessidade de estudos que subsidiem estratégias de manejo adequadas às características de cada ilha.

Todavia, devido à complexidade dos ambientes recifais e às limitações das técnicas de amostragens normalmente utilizadas (*e.g.*, censo visual subaquático e artes de pesca), é difícil analisar de forma compreensível os padrões de distribuição e estrutura das assembleias de peixes (Harvey *et al.*, 2007). A elevada variabilidade nos dados coletados por essas técnicas diminui consideravelmente a capacidade estatística de detecção de alterações nas assembleias estudadas (Harvey *et al.*, 2007). Atualmente, sistemas de filmagens subaquáticas remotas com isca (*Baited Remote Underwater Video*

Systems - BRUVS) têm sido utilizados com intuito de minimizar esses problemas possibilitando, entre outros, realizar diversas amostragens padronizadas em diferentes habitats bentônicos, como recifes rochosos e carbonáticos, bancos de rodolitos, macroalgas e gramíneas marinhas, e substratos inconsolidados (*e.g.*, Reis-Filho *et al.*, 2019; Pimentel *et al.*, 2020b). Ao mesmo tempo, essa técnica não extrativa também possibilita explorar ambientes mais profundos (*e.g.*, recifes mesofóticos)(Asher *et al.*, 2017; Turner *et al.*, 2017; Andradi-Brown *et al.*, 2021) sem os riscos associados ao mergulho, além de não ter a necessidade de coletar os organismos e, portanto, eliminando a seletividade a pesca (Cappo *et al.*, 2004; Harvey *et al.*, 2007).

Além disso, trabalhos recentes demonstram que ainda podemos avançar muito no conhecimento acerca da biodiversidade de peixes recifais brasileiros (Pinheiro *et al.*, 2015; Pimentel *et al.*, 2019; Guabiroba *et al.*, 2020b; Pimentel *et al.*, 2020). A utilização de novas técnicas de pesquisa como BRUVS, ROVs (veículos operados remotamente) e mergulhos técnicos, tem proporcionado o estudo de habitats ainda pouco explorados, como os bancos de rodolitos e de macroalgas, além dos recifes mesofóticos (*e.g.*, Pimentel *et al.*, 2020b). Tal fato tem gerado a descoberta de novos registros de espécies e de novas espécies para a Província Brasileira (Pinheiro *et al.*, 2018a), como demonstrado por Pinheiro *et al.* (2020) explorando recifes rasos e profundos no Arquipélago de São Pedro e São Paulo por meio de técnicas diversas, assim como no caso da espécie *Tosanoides aphrodite* Pinheiro, Rocha & Rocha, 2018, recentemente descoberta nos recifes mesofóticos deste mesmo arquipélago (Pinheiro *et al.*, 2018b). Tais descobertas corroboram a necessidade de se aumentar os esforços de pesquisas nesses ambientes pouco estudados, com intuito de ampliarmos o conhecimento acerca da biodiversidade marinha local e regional.

Neste contexto, essa tese elaborada no âmbito do Programa de Pós-Graduação em Oceanografia Ambiental, da Universidade Federal do Espírito Santo, tem como objetivos analisar os processos ecológicos responsáveis pela estruturação das assembleias de peixes nas ilhas oceânicas brasileiras, principalmente em relação aos padrões de distribuição das espécies em diferentes habitats e ao longo do gradiente de profundidade da plataforma insular. Além disso, também visa expandir o conhecimento acerca da biodiversidade de peixes recifais da Província Brasileira. Desta forma, a tese está composta por 4 capítulos:

✓   **Capítulo 1** – *Pelagic and mesophotic reef fishes of the oceanic Saint Peter and Saint Paul's Archipelago (Equatorial Atlantic) suggest linked systems*

Neste trabalho, realizado no Arquipélago de São Pedro e São Paulo, focou-se nas variações das assembleias de peixes ao longo do gradiente de profundidade da zona mesofótica (entre 30 e 84 m de profundidade), e na identificação das espécies de peixes que conectam ecologicamente os ecossistemas pelágico e recifal. Este trabalho será submetido à edição especial *Biodiversity of Mesophotic Ecosystems* da revista *Diversity*.

✓ **Capítulo 2** – *Reef fish habitat use in a remote South Atlantic oceanic island*

Na isolada Ilha da Trindade, analisou-se a distribuição das assembleias de peixes para avaliar a resposta de características das espécies relacionadas à conservação (*e.g.*, abundância e biomassa, endemismo e vulnerabilidade), ao uso dos diferentes habitats bentônicos distribuídos ao longo gradiente de profundidade da plataforma insular.

✓ **Capítulo 3** – Pimentel, C. R., Rocha, L. A., Shepherd, B., Phelps, T. A. Y., Joyeux, J.-C., Martins, A. S., … Pinheiro, H. T. (2020). Mesophotic Ecosystems at Fernando de Noronha Archipelago, Brazil (South-Western Atlantic), Reveal Unique Ichthyofauna and Need for Conservation. **Neotropical Ichthyology**, 18, e200050.

Neste trabalho, publicado na *Neotropical Ichthyology* em 2020, foram utilizados mergulho autônomo e mergulho técnico, BRUVS e ROV, para registrar peixes de ambientes rasos (≤ 30 m de profundidade) e mesofóticos (31 a 150 m de profundidade) do Arquipélago de Fernando de Noronha. Os enfatizam a necessidade de proteção e atenção à ictiofauna única encontrada nos ecossistemas profundos.

✓ **Capítulo 4** – Pimentel, C. R., Andrades, R., Ferreira, C. E. L., Gadig, O. B. F., Harvey, E. S., Joyeux, J.-C., & Giarrizzo, T. (2020). BRUVS Reveal Locally Extinct Shark and the Way for Shark Monitoring in Brazilian Oceanic Islands. **Journal of Fish Biology**, 96, 539–542.

Publicado no *Journal of Fish Biology* em 2020, aqui são apresentadas as espécies de tubarões registradas por meio de BRUVS na Ilha da Trindade e no Arquipélago de São Pedro e São Paulo, e ressalta-se a importância da utilização de BRUVS conjuntamente com outros métodos não invasivos para monitorar as populações de tubarões.

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Capítulo 1 – Pelagic and mesophotic reef fishes of the oceanic Saint Peter and Saint Paul's Archipelago (Equatorial Atlantic) suggest linked systems

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Abstract

Due to intrinsic characteristics such as isolation, low species richness and high endemism, oceanic islands are natural laboratories for ecological and evolutionary studies. Here we used Baited Remote Underwater stereo-Video systems (stereo-BRUVS) to investigate the structure of pelagic and mesophotic reef fishes in the small and isolated Saint Peter and Saint Paul's Archipelago, equatorial Atlantic Ocean. We focused on the variations of fish assemblages along the mesophotic depth gradient (30 to 84 m depth) and the identification of potential fish species ecologically connecting (*i.e.*, co-occurring species) the pelagic and mesophotic reef ecosystems. We recorded 14 species in the pelagic ecosystem, carnivores being the most diverse and abundant trophic group. On the mesophotic reefs, we recorded 41 taxa. Carnivores and planktivores were the most diverse trophic groups, whereas omnivores were the most abundant. Nine species were recorded in both ecosystems, with *Melichthys niger*, *Caranx lugubris* and *Seriola rivoliana* being the main linking species. The connection between pelagic and reef ecosystems combined with the endangered status of some linking species, suggest the need for an integrated management strategy. Stricter fishing restrictions around the archipelago are suggested as the best alternative to reconcile biodiversity and ecological conservation with sustainable fishing activities.

Introduction

Oceanic islands often figure as natural laboratories for ecological and evolutionary studies (Losos & Ricklefs, 2009). The combination of intrinsic characteristics such as isolation, low species richness and high endemism allow a better understanding of ecological and evolutionary processes and patterns in these model systems (Vitousek, 2002; Pinheiro *et al.*, 2017b). Significant advances in the understanding of biogeographic and evolutionary processes such as colonization and speciation in reef fishes from oceanic islands have occurred in the past few years (Pinheiro *et al.*, 2015, 2017b; Barneche *et al.*, 2019; Quimbayo *et al.*, 2019), placing them as key regions for conservation. Ecological characteristics of oceanic reef fish communities are also being extensively studied, especially their bathymetric distribution and association with benthic habitats and organisms (Pinheiro *et al.*, 2011; Luiz *et al.*, 2015; Ilarri *et al.*, 2017; Maia *et al.*, 2018), in addition to the anthropogenic impacts (*e.g.*, fishing pressure and litter pollution) on the fish assemblages and species conservation measures (Luiz & Edwards, 2011; Rocha *et al.*, 2018; Guabiroba *et al.*, 2020). The study of pelagic fish assemblages is relatively more challenging, mainly due to inherent characteristics of the environment (*e.g.*, large spatial scale) and species (*e.g.*, low overall densities and heterogeneous distributions), which make it complex to sample consistently and accurately (Letessier *et al.*, 2013; Santana-Garcon *et al.*, 2014b; Clarke *et al.*, 2019).

Ecological connectivity between ecosystems driven by animal movements is an important ecological process influencing community structure and productivity, as well as species conservation and ecosystems health (Mcmahon *et al.*, 2012; Graham *et al.*, 2018; Williams *et al.*, 2018). Marine mammals, such as whales and seals, for example, are responsible for nutrient flow from deeper areas to the surface, contributing to local primary productivity (Roman & McCarthy, 2010). Even components from outside of a given ecosystem can influence the input of nutrients to it. For instance, seabirds' faeces can fertilize reefs adjacent to their colonies (Graham *et al.*, 2018). Many studies using different techniques, such as acoustic telemetry and stable isotope analyses, have shown that fish predators are important trophic links, making regular and periodic foraging movement between pelagic and reef ecosystems, and acting directly on nutrient cycling (*e.g.*, Beaudreau & Essington, 2011; Papastamatiou *et al.*, 2015; Williams *et al.*, 2018; Skinner *et al.*, 2019). However, despite understanding some emblematic cases of biotic connectivity and their influence in ecosystems functioning, we still do not know much about the connections between the reef and adjacent pelagic ecosystems. As many fish

species in oceanic islands presumably perform vertical water-column movements, they can be appropriated ecological models in such investigations.

The oceanic Saint Peter and Saint Paul's Archipelago (SPSPA), in the equatorial Atlantic Ocean, presents great ecological importance, which lies mainly in its high biomass (Morais *et al.*, 2017; Quimbayo *et al.*, 2019) and endemism of reef fishes (down to 150 m), despite the low species richness (Pinheiro *et al.*, 2020). In addition, many pelagic fishes use the SPSPA, including species of commercial interest (*e.g.*, tunas and wahoos) (Vaske Jr. *et al.*, 2008; Viana *et al.*, 2015) and locally or globally threatened with extinction, such as Galapagos sharks (Pimentel *et al.*, 2020) and whale sharks (Hazin *et al.*, 2008), respectively. However, although the shallow reef ichthyofauna (< 30 m depth) is relatively well studied (Lubbock & Edwards, 1981; Feitoza *et al.*, 2003; Vaske *et al.*, 2005; Luiz *et al.*, 2015), the structure of the pelagic fish assemblages immediately adjacent to the reefs has not been properly studied (but see Pinheiro *et al.*, 2020), nor the species that co-occur in these two neighbouring ecosystems, which potentially perform ecological connections. Similarly, the mesophotic reef fish assemblages need to be better studied, since only few projects about its biodiversity (Lubbock & Edwards, 1981) and some ecological aspects (Rosa *et al.*, 2016; Nunes *et al.*, 2019) have been carried out until nowadays.

Therefore, here we used pelagic and benthic Baited Remote Underwater stereo-Video systems (stereo-BRUVS) to investigate the taxonomic and trophic structure of pelagic and mesophotic reef fish assemblages at the small and isolated Saint Peter and Saint Paul's Archipelago. Our special interests were to analyse the variation of mesophotic fish assemblages along the depth gradient and to identify the potential fish species that ecologically connect (co-occurring species) pelagic and mesophotic reef ecosystems. The extremely steep local geomorphology promotes a great proximity between pelagic and mesophotic reef ecosystems, which favours studies on their inter-relationships. The conservation issues concerning the observed ecosystem connections are also discussed, aiming to contribute to fisheries management in the region.

Material and Methods

Study area

The remote Saint Peter and Saint Paul's Archipelago (SPSPA; Fig. 1) is located on the Mid-Atlantic Ridge, in the equatorial Atlantic Ocean, about 1,010 km from the Northeastern Brazilian coast (00° 55' N; 29° 21' W). This is one of the smallest and most isolated oceanic tropical archipelagos in the world, composed by a small group of islets

and rocks, and totalling an emerged area of *ca.* 15,000 m^2 and only about 0.5 km^2 of reefs shallower than 100 m depth (Luiz & Edwards, 2011; Luiz *et al.*, 2015; Rosa *et al.*, 2016). Shallow reefs (≤ 30 depth) are mostly found around a small bay, dominated by rocky reefs covered mainly by the zoanthid *Palythoa caribaeorum*, the fleshy algae *Caulerpa racemosa*, crustose coralline algae, and *Bryopsis spp.* (Magalhães *et al.*, 2015). Down to *ca.* 100 m, the mesophotic reef ecosystem has sharp relief and steep walls, covered by crustose calcareous algae, bryozoans, and scleractinian corals (*e.g. Madracis decactis* and *Scolymia wellsi*) up to around 40 m depth, while sponges and branching black corals (*Tanacetipathes* sp.) dominate deeper zones (Magalhães *et al.*, 2015; Rosa *et al.*, 2016; Pinheiro *et al.*, 2020). The surface South Equatorial Current, flowing westwards, and the Equatorial Undercurrent, flowing eastwards at depths between 40 and 150 m, directly influence the area (Campos *et al.*, 2005; Araujo *et al.*, 2018). The interaction of these currents with the local topography results in a complex hydrodynamic system, which can favour the occurrence of up and downwelling currents, influencing the reef assemblages and attracting many species from the pelagic ecosystem (Pinheiro *et al.*, 2020).

Until recently, this archipelago was part of the multiple-use Marine Protected Area (MPA) of Fernando de Noronha – Rocas – São Pedro and São Paulo Environmental Protected Area (Brasil, 1986). In March 2018, a large MPA including two categories of protected areas was created around the SPSPA: a multiple-use and a no-take area. The no-take area is nested within the multiple-use MPA, while most of the archipelago is part of the latter (see Giglio *et al.*, 2018).
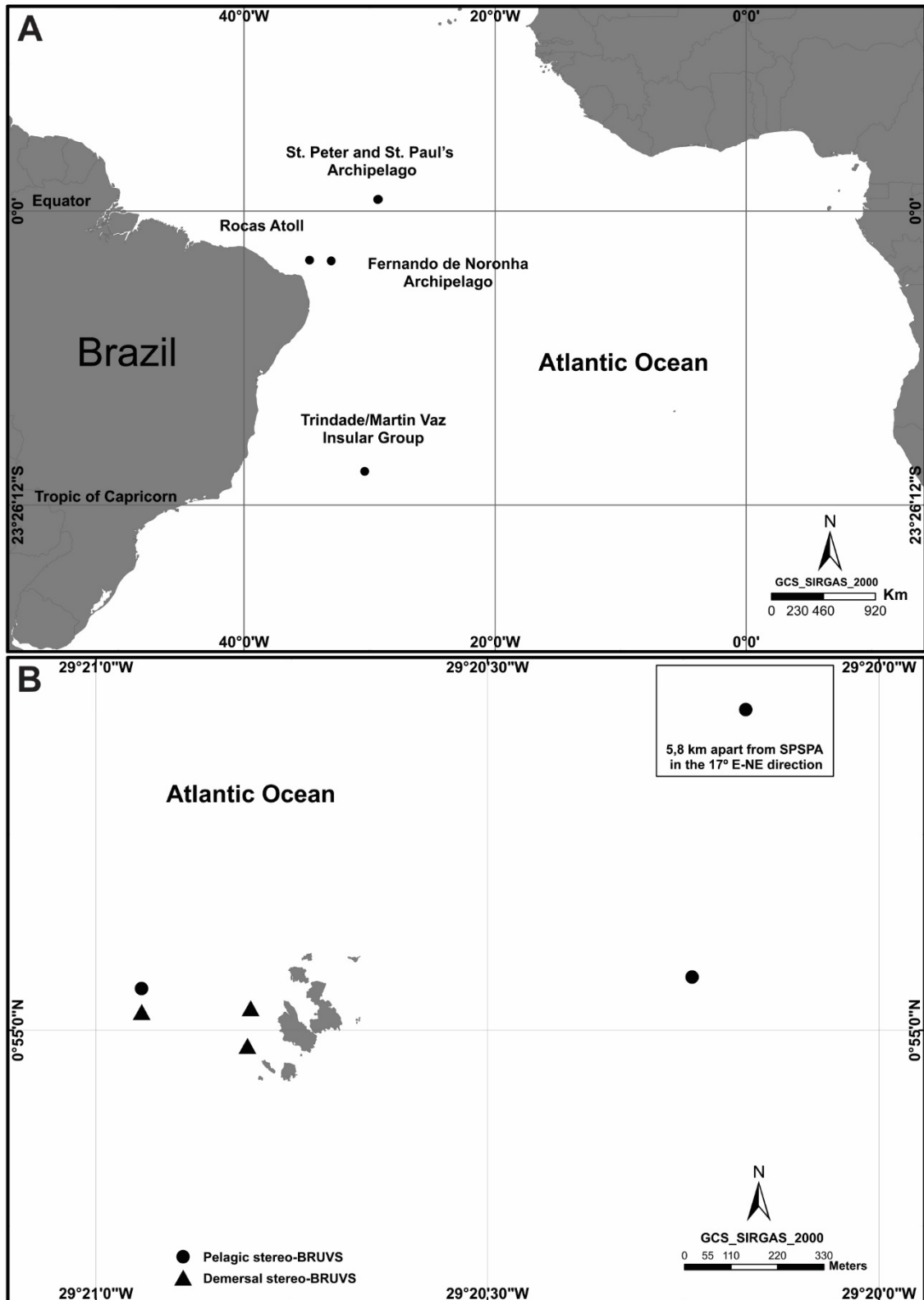
Figure 1: Map of the study area showing A) the location of Saint Peter and Saint Paul's Archipelago and other Brazilian oceanic sites in the Atlantic Ocean and B) the pelagic (black circle) and benthic (black triangle) stereo-BRUVS deployment sites.

Sampling procedures

During a two weeks expedition at SPSPA in September 2018, we performed five daytime (8 - 16 h) pelagic baited remote underwater stereo-video system (stereo-BRUVS) deployments *ca.* 20 to 30 m depth, and fourteen benthic stereo-BRUVS deployments between 30 and 84 m depth. Due to strong local currents, both pelagic and benthic stereo-BRUVS were attached to mooring buoys around the Archipelago (Fig. 1). Pelagic deployments were at least 50 m above the reefs. Benthic deployments lasted 60 minutes and were baited with 500 g of crushed false herring *Harengula clupeola* (Cuvier, 1829), while pelagic deployments lasted 120 minutes and were baited with 1,000 g of the same bait.

Video analysis

All fishes were identified to the lowest possible taxonomic level and the relative abundance of each species was recorded as MaxN, *i.e.*, the maximum number of individuals of a same given species present in a single frame (Cappo *et al.*, 2004). During the moment in which MaxN was recorded for each species, we measured the total or fork length of all possible fish, according to the distance (≤ 5 m) and angle (≤ 45°) to the cameras, as well as the measurement precision (≤ 1 cm). The lengths of two large *Mobula tarapacana* (Philippi, 1892) recorded in the pelagic system were visually estimated.

Data analysis

In order to analyse the trophic structure of the fish assemblages, species were classified into trophic groups as carnivores, mobile invertebrate feeders, sessile invertebrate feeders, planktivores, omnivores, territorial herbivores or roving herbivores (following Pinheiro *et al.*, 2018). Variation in taxonomic and trophic structure of the mesophotic reef fish assemblages along the depth gradient were examined using principal coordinate analysis (PCO), based on Bray-Curtis similarity matrix calculated from square root transformed MaxN data and Spearman's correlation overlaid vectors. Similarity Percentages (SIMPER) one-way analysis was conducted to evaluate the species contributions for the overall assemblage, as well as for the pelagic and mesophotic assemblages. These analyses were run in PRIMER version 6.1.13 and PERMANOVA+ version 1.0.3. The species contributions based on the SIMPER analysis were presented using an Alluvial diagram. For both taxonomic and trophic structures, generalized additive models (GAM) using Gaussian distribution and identity link were performed to analyse the correlation between PCO axes 1 and 2 with depth. Variation with depth in species richness, total relative abundance (TMaxN), and relative abundance (MaxN) of

the six most abundant species and trophic groups were explored using GAMs with Poisson distribution and log link (Guisan *et al.*, 2002). The GAMs were run in the R software using the package mgcv.

Results

Pelagic assemblages

In the pelagic system, we recorded 14 species belonging to eight families (Table S1). The most diverse families were Carangidae and Balistidae with four and three species, respectively. The most abundant species were *Elagatis bipinnulata* (Quoy & Gaimard, 1825), *Melichthys niger* (Bloch, 1786), and *Caranx crysos* (Mitchill, 1815), which together account for over 75% of the total relative abundance. Carnivores was the most diverse trophic group, represented by nine species, followed by planktivores with three species and omnivores with two (Fig. 2; Table S1). Carnivores was also the most abundant trophic group, composed mainly by *E. bipinnulata* and *C. crysos*, which accounted for over 60% of the total relative abundance. The carnivores *Acanthocybium solandri* (Cuvier, 1832), *Carcharhinus falciformis* (Müller & Henle, 1839), *E. bipinnulata,* and *Thunnus albacares* (Bonnaterre, 1788), and the planktivore *Mobula tarapacana* (Philippi, 1892) were the largest species (TL > 100 cm) recorded. Medium-sized (40 < TL < 101 cm) specimens were represented by the carnivores *C. crysos*, *Caranx lugubris* Poey, 1860, *Coryphaena hippurus* Linnaeus, 1758, *E. bipinnulata*, *Seriola rivoliana* Valenciennes, 1833 and *Sphyraena barracuda* (Edwards, 1771), and the planktivores *Canthidermis maculata* (Bloch, 1786) and *Canthidermis sufflamen* (Mitchill, 1815). The smallest species (TL ≤ 40 cm) were small-bodied *C. crysos*, *C. lugubris*, *C. maculata*, *C. sufflamen* and *S. rivoliana*, as well as the highly abundant omnivore *M. niger*.
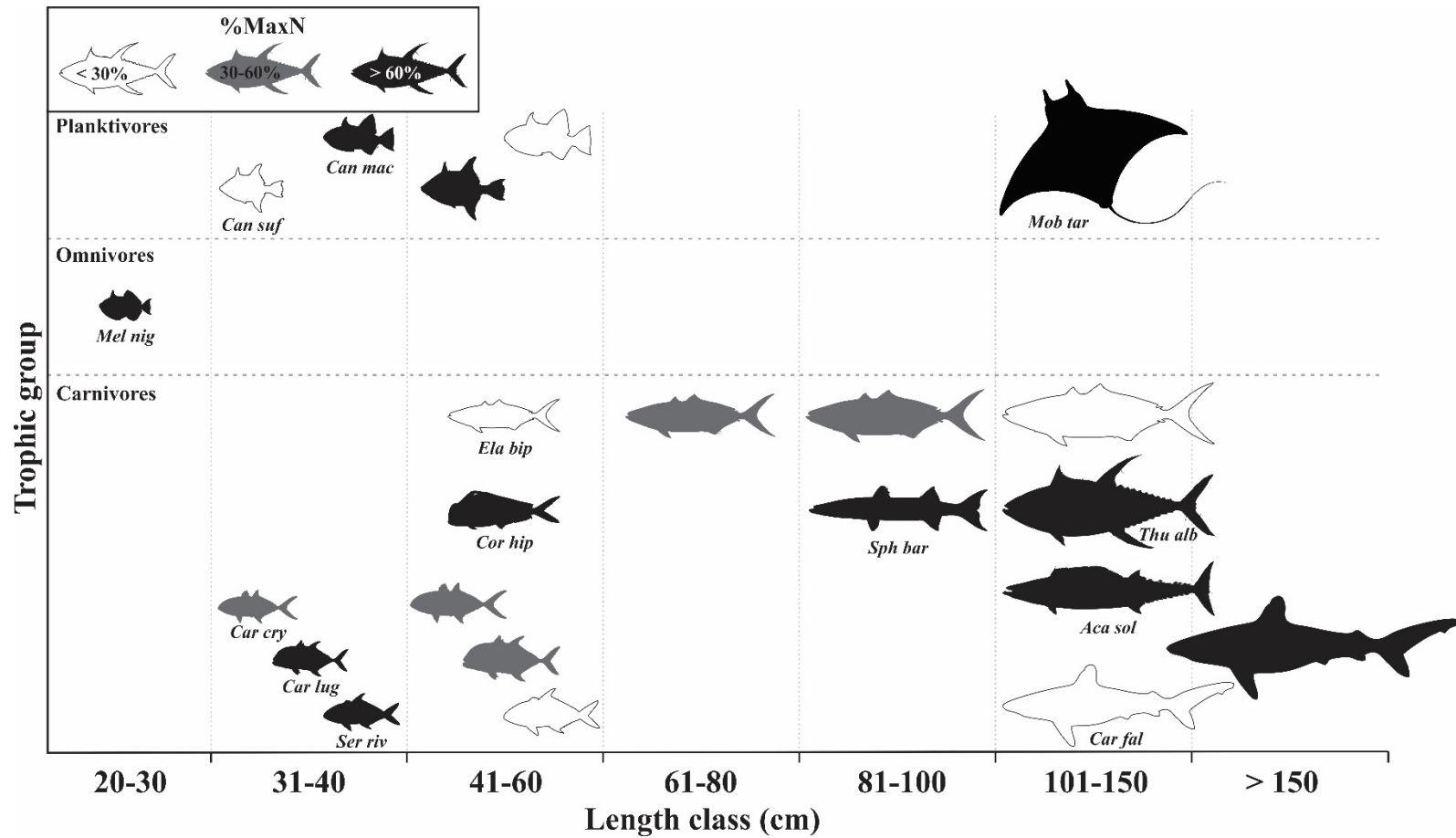
Figure 2: Intraspecific relative abundance percentage (%MaxN) by length class and trophic group of the pelagic fish assemblage of SPSPA. Aca sol: *Acanthocybium solandri*; Can mac: *Canthidermis maculata*; Can suf: *Canthidermis sufflamen*; Car cry: *Caranx crysos*; Car lug: *Caranx lugubris*; Car fal: *Carcharhinus falciformis*; Cor hip: *Coryphaena hippurus*; Ela bip: *Elagatis bipinnulata*; Mel nig: *Melichthys niger*; Mob tar: *Mobula tarapacana*; Ser riv: *Seriola rivoliana*; Thu alb: *Thunnus albacares*.

Mesophotic reef assemblages

On the mesophotic reef system, we recorded 41 taxa belonging to 19 families (Table S2). *Kyphosus* sp. and *Enchelycore* cf. *nycturanus* Smith, 2002, could not be identified to the species level. The most diverse families were Muraenidae (five taxa), Balistidae, Carangidae, and Pomacentridae (four species each). The most abundant species were *M. niger* with 808 individuals (mean ± standard deviation: 57.7 ± 23.6 individuals), *Azurina multilineata* (Guichenot, 1853) with 209 individuals (14.9 ± 17.9), *Chromis vanbebberae* McFarland, Baldwin, Robertson, Rocha & Tornabene 2020 with 123 individuals (8.8 ± 16.0), *S. rivoliana* with 90 individuals (6.4 ± 12.1), *C. lugubris* with 85 individuals (6.1 ± 8.7) and *Stegastes sanctipauli* Lubbock & Edwards, 1981 with 53 individuals (3.8 ± 5.6). We also recorded two sharks, one *Carcharhinus galapagensis* (Snodgrass & Heller, 1905) and one *C. falciformis* (Pimentel *et al.*, 2020). Carnivores (8 families and 16 species) and planktivores (6 families and 7 species) were the most diverse trophic groups. Omnivores, represented mainly by *M. niger*, was the most abundant trophic group on the mesophotic reefs, accounting for *ca.* 50% of the total fish abundance. Planktivores and carnivores represented about 21% and 18%, respectively. All other trophic groups represented less than 5% of the total abundance each.

The PCOs did not reveal a fish assemblage structured taxonomically or trophically by depth (Fig. 3A and B). This lack of taxonomic and trophic structure by depth were corroborated by GAMs, which did not show a significant relationship between the axes of the PCOs and depth (Table S3 and Table S4). The PCO1 axis of the taxonomic structure (Fig. 3A) evidenced two groups of deployments not related to depth differences. However, one group of deployments (on the left) was associated with species considered of shallow affinities (*i.e.*, species relatively more abundant in the shallows) such as *Abudefduf saxatilis* (Linnaeus, 1758), *A. multilineata*, *S. sanctipauli* and *Halichoeres radiatus* (Linnaeus, 1758). The other group (on the right) was correlated to demersal mesophotic specialists (*i.e.*, species relatively more abundant in the mesophotic reefs) such as *C. vanbebberae* and *Prognathodes obliquus* (Lubbock & Edwards, 1980), along with the benthopelagic species *S. rivoliana* and *C. lugubris*, besides *B. capriscus* and *Cantherhines macrocerus* (Hollard, 1853). The PCO2 axis separated the sample with greater abundance of *Kyphosus* spp. (above) from the others, which presented low or no individuals of this species. In the PCO based on the trophic structure (Fig. 3B), the first axis separated a sample (on the right) dominated by roving herbivores (*i.e.*, *Kyphosus* spp.) from others. The second axis partially separated samples associated with carnivores

and mobile invertebrate feeders (below) from those associated with planktivores and sessile invertebrate feeders (in the middle), and those associated with omnivores and territorial herbivores (above). Therefore, none of the PCOs presented a sample ordination according to the depth.
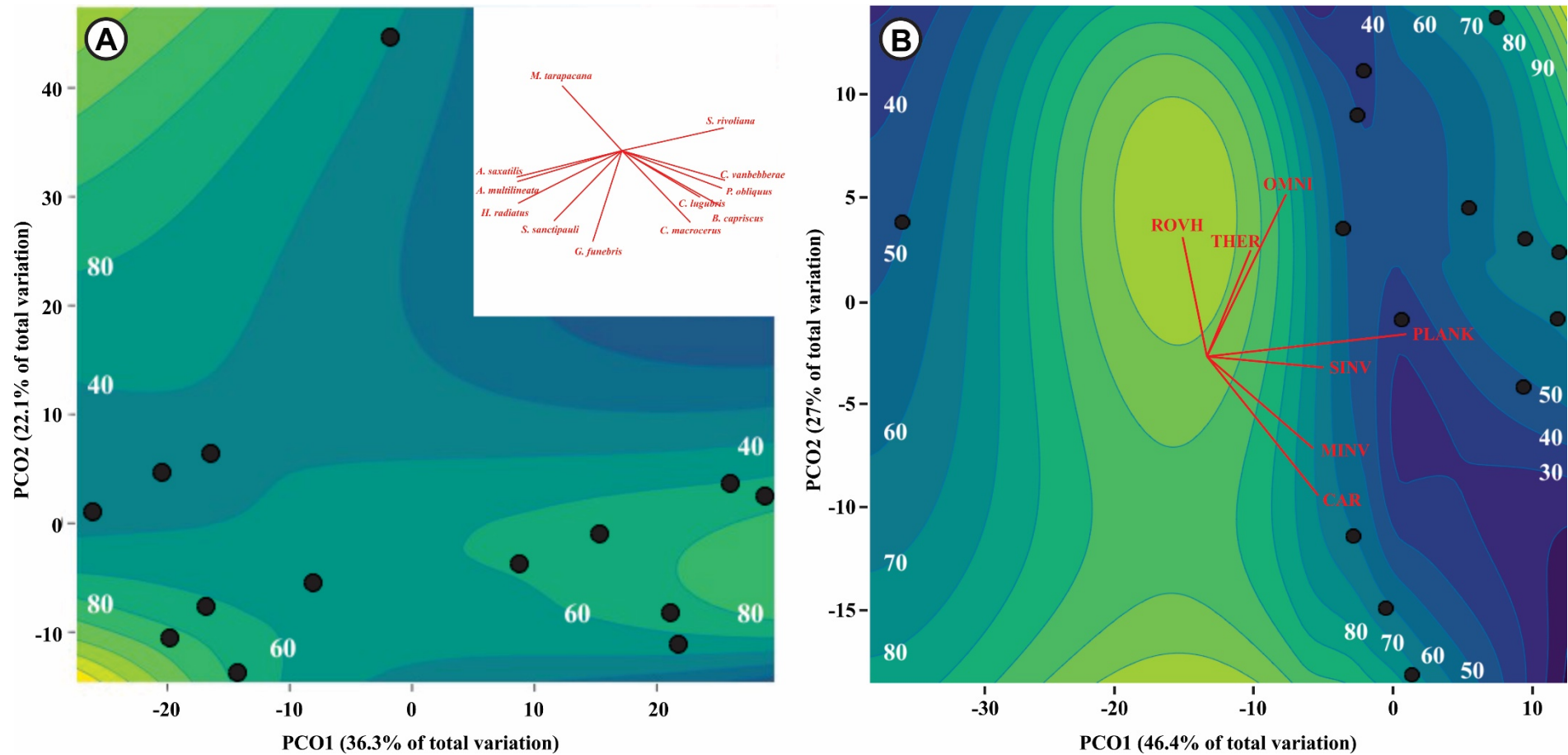
Figure 3: Principal coordinate analysis plots based on the relative abundance of A) species and B) trophic groups of the mesophotic assemblages. Species with Spearmen correlations > 0.65 and the trophic groups are overlaid with its respective vectors. White numbers indicate the depth gradient. CAR: carnivores; MINV: mobile invertebrate feeders; OMNI: omnivores; PLANK: planktivores; ROVH: roving herbivores; SINV: sessile invertebrate feeders; THER: territorial herbivores.

In contrast, species richness and TMaxN varied significantly with depth, as well as MaxN of the most abundant species, except *C. vanbebberae* (Fig. 4). Species richness and especially TMaxN showed a more evident increase along the depth gradient, whereas *S. rivoliana*, *C. lugubris* and *S. sanctipauli* did not show such an obvious pattern. *Azurina multilineata* presented a bimodal depth distribution, with higher MaxN occurring in the shallower and deeper zones. The distribution of trophic groups also showed significant variation with depth (Fig. 5). Carnivores, both mobile and sessile invertebrate feeders and, to a lesser extent, territorial herbivores, increased in abundance along the mesophotic depth gradient. Planktivores showed an evident bimodal depth distribution, while omnivores did not show a clear pattern of bathymetric distribution.
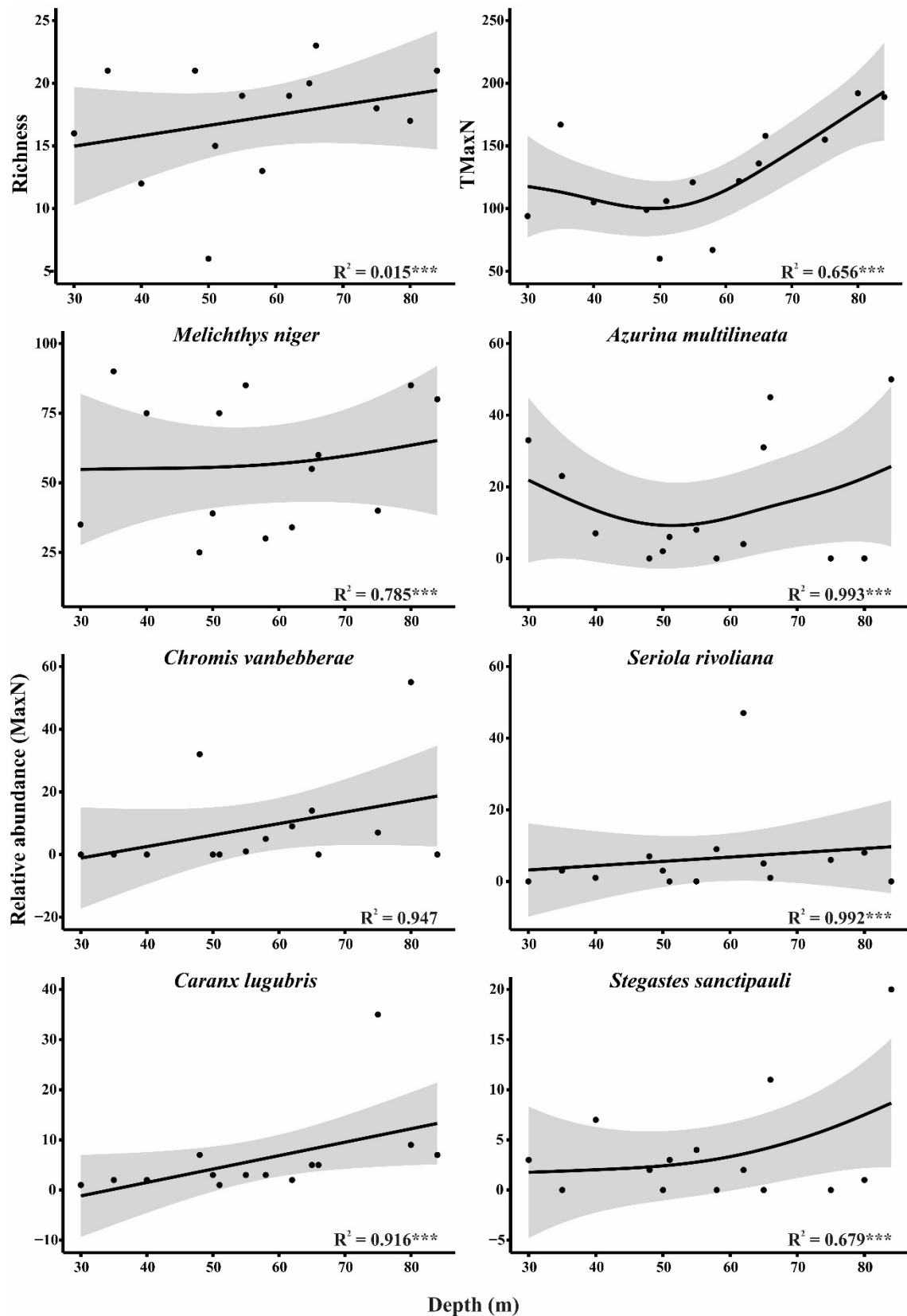
Figure 4: Relationship between species richness, total relative abundance (TMaxN) and relative abundance (MaxN) of the six most abundant species and depth according to the generalized additive models. 95 % confidence limits are shown in gray. *** $p < 0.001$.

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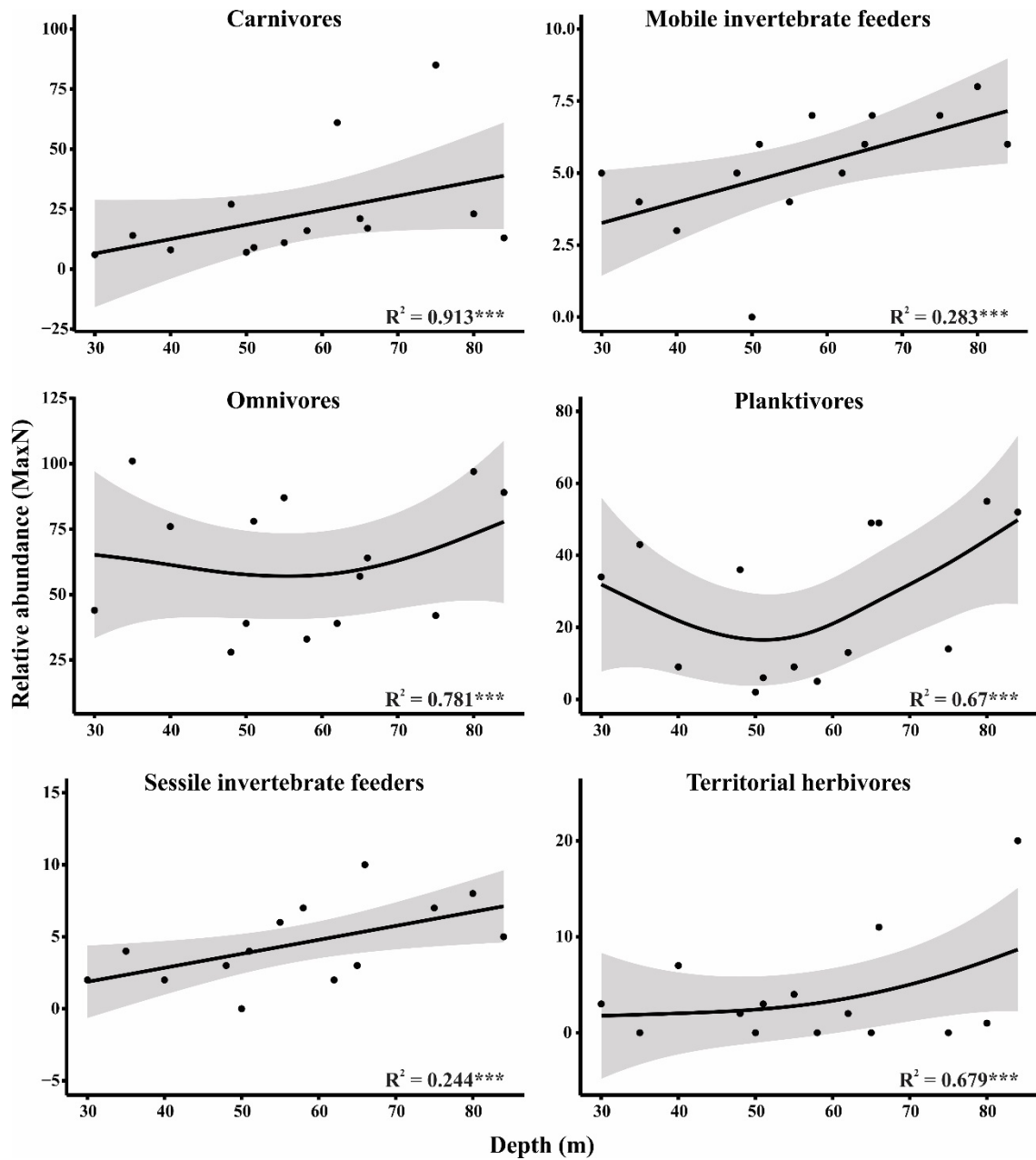
Figure 5: Relationship between relative abundance (MaxN) of the trophic groups and depth according to the generalized additive models. 95 % confidence limits are shown in gray. *** $p < 0.001$.

Ecosystems connections

Overall, 46 taxa were recorded in the SPSPA (Fig. 6). Nine fish species from six families were recorded in both systems, contributing 40.1% for the overall assemblage similarity (SIMPER analysis; Table S5). These same nine linking species contributed 33.8% for the pelagic and 34.4% for the mesophotic assemblages' similarities (Fig. 6). *Melichthys niger*, *C. lugubris* and *S. rivoliana* presented the greatest individual contributions for the overall assemblage, with 19.4%, 9.4% and 6.6%, respectively (SIMPER analysis; Table S5).
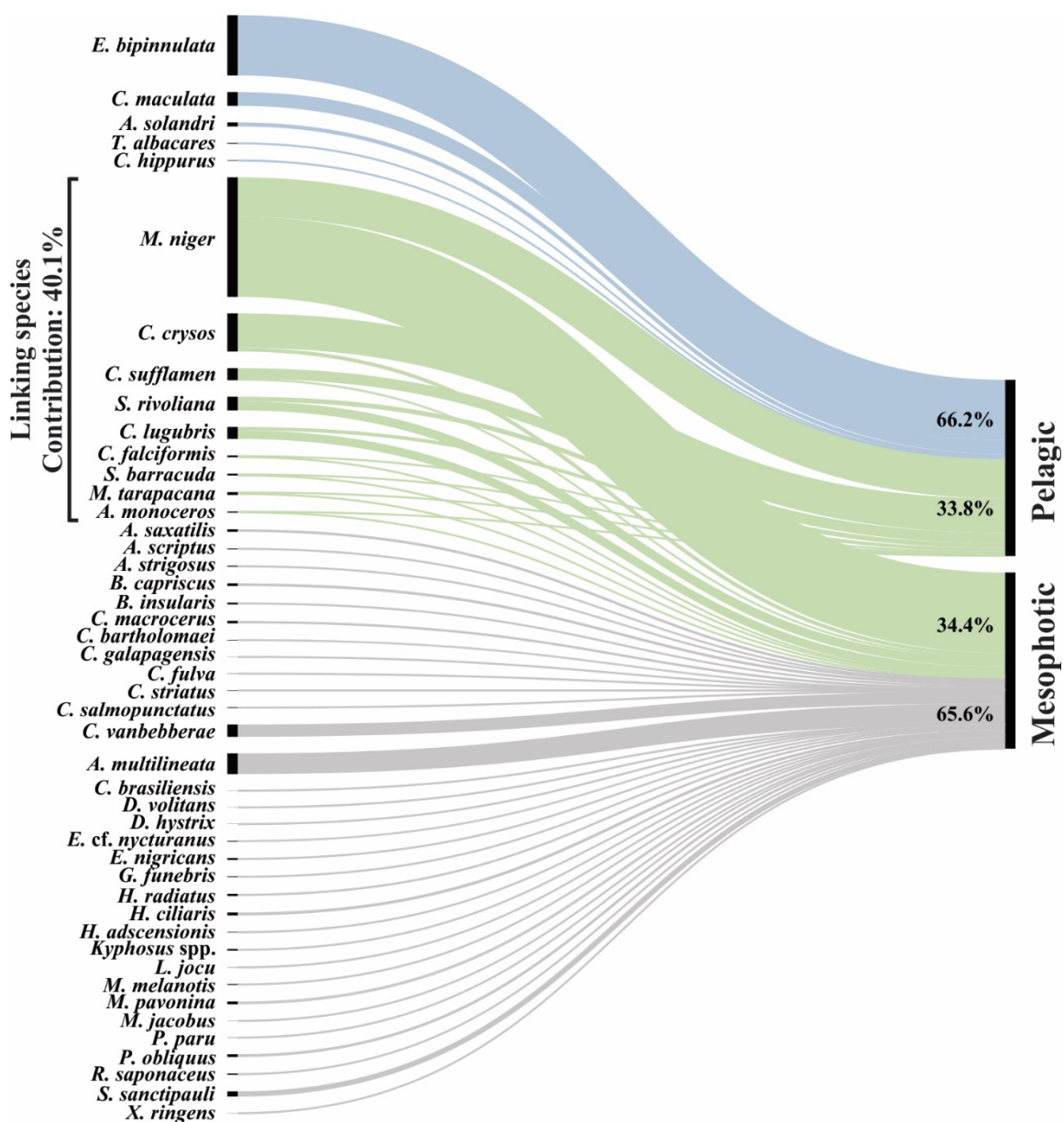
Figure 6: Alluvial plot based on the relative abundance percentage of the species, showing the contribution of linking species to pelagic and mesophotic reef fish assemblages, as well as the contribution of the other species to their respective assemblages.

Discussion

This study reinforces that BRUVS are adequate to provide fast and robust estimates of abundance, diversity and size structure of fish assemblages at remote and isolated oceanic islands, in addition to increasing our understanding about ecological connectivity between pelagic and reef ecosystems. Information that is crucial for managers and researchers to detect fish assemblage changes in response to multiple threats, such as overfishing and climate change (Chin *et al.*, 2010; Dulvy *et al.*, 2014). Moreover, our data revealed that although ichthyofauna is independently structured in pelagic and mesophotic reef systems, there is evidence of taxonomic and functional links in an ecological perspective, which can support local and regional conservation efforts.

Pelagic assemblages

This is one of the few fishery-independent ecological assessments of the pelagic fish assemblages in the southwestern Atlantic, which also explores the ecological connections between pelagic and mesophotic reef ecosystems (Papastamatiou *et al.*, 2015; Williams *et al.*, 2018; Madigan *et al.*, 2020). The study of pelagic fish assemblages presents challenges for accurate data collection and interpretation, partly due to the extensive area and the heterogeneous way in which the species are distributed in the environment (Letessier *et al.*, 2013, 2015; Santana-Garcon *et al.*, 2014c). In this sense, BRUVS is standing out as an efficient technique to study pelagic assemblages, presenting relatively fast deployment time, enabling many replications, and covering a large area, combined with a high capacity to record predators (Pimentel *et al.*, 2020). Since several pelagic species are elusive meso (*e.g.*, barracudas, tunas and wahoos) and large predators (*e.g.*, sharks), BRUVS are well suited to conduct surveys in marine protected areas as a non-extractive technique (Letessier *et al.*, 2013, 2015; Santana-Garcon *et al.*, 2014c).

Despite a relatively limited sampling effort, our BRUVS recorded about 25% of pelagic fish species known from the SPSPA, including some new records (Pinheiro *et al.*, 2020). Although researchers have investigated pelagic fishes in the SPSPA, their studies focused mainly on the trophic ecology of fisheries resources (*e.g.*, Vaske-Júnior *et al.*, 2003, 2006; Albuquerque *et al.*, 2019), where the assemblage structure was characterized through analyses of commercial fishing data (*e.g.*, Vaske Jr. *et al.*, 2008; Viana *et al.*, 2015). Fishery-dependent data is usually biased due to gear catchability and size-selectivity (Harvey *et al.*, 2012; Santana-Garcon *et al.*, 2014a). In SPSPA, for instance, previous studies based on commercial fishing data showed that mesopredators (*e.g.*, tunas and wahoos) dominate the pelagic assemblage (Vaske Jr. *et al.*, 2008; Viana *et al.*, 2015),

whereas our study disclosed a greater variety of trophic levels. In addition, due to the establishment of a large MPA around SPSPA, even if most of it is of multiple-use (Giglio *et al.*, 2018), fishing must be regulated, or allowed only for scientific purposes. Another point of concern is that a number of species targeted by fisheries show signs of overfishing and even hints of local extinction (Vaske Jr. *et al.*, 2008; Luiz & Edwards, 2011; Viana *et al.*, 2015).

In this context, despite the ban on longline fishing around the SPSPA since 2012 (SECIRM, 2012), the low species richness and abundance of sharks, as well as of *T. albacares* and *A. solandri*, is noteworthy. At least 10 species of pelagic sharks have been recorded for the SPSPA, not to mention *C. galapagensis*, which was considered very abundant few decades ago (Luiz & Edwards, 2011), but extremely rare nowadays (Pimentel *et al.*, 2020; Pinheiro et al., 2020). In turn, *T. albacares* and *A. solandri* are the main species caught by the commercial fishery in the SPSPA (Vaske Jr. *et al.*, 2008; Viana *et al.*, 2015), but the former is globally overfished and near endangered (Collette *et al.*, 2011). These results reinforce the importance of the ban on longline fishing in the SPSPA protection zone to restore local shark populations and other top predators, and achieve the conservation goals pursued by the creation of the MPA in this archipelago.

Mesophotic reef assemblages

The SPSPA reef fish fauna has been considered one of the poorest globally, due to the remoteness and small size of the archipelago (Pinheiro *et al.*, 2020). However, differently from previous studies on the fish assemblage structure of shallow and mesophotic reefs of the SPSPA (Luiz *et al.*, 2015; Rosa *et al.*, 2016), our study recorded a greater diversity of species (~20% and 53%, respectively), including new records (Pinheiro *et al.*, 2020). Such differences in the composition and structure of the fish assemblages among the studies could be related to the use of different sampling techniques and effort. Luiz *et al.* (2015) performed underwater visual censuses (UVCs), conducting 213 belt transects between 0 and 30 m depth, Rosa *et al.* (2016) analysed 230 minutes of footage acquired by remotely operated vehicle (ROV) between 30 and 90 m depth, while we used 840 minutes of BRUVS footage between 30 and 84 m depth. While UVCs and ROV can cause avoidance behaviour in some fish species, varying according to the size, intensity of noise and light emitted by the equipment and divers, BRUVS attracts carnivores and a great variety of fishes (*e.g.*, planktivores and omnivores), including rare and endangered species (Schramm *et al.*, 2020a, 2020b). Therefore, BRUVS are well suited and necessary

for biodiversity assessments and ecological studies in remote sites, especially where researchers have limited expedition time and restricted resources due to logistics.

Unexpectedly, we did not find fish assemblages clearly structured according to the depth gradient, as shown in Rosa *et al.* (2016) in the same archipelago and in other mesophotic reef ecosystems elsewhere (Pearson & Stevens, 2015; Pinheiro *et al.*, 2016; Asher *et al.*, 2017b, 2017a; Bond *et al.*, 2018). However, the structure we found was greatly driven by species with shallow and mesophotic affinities. Strong up and down-welling events were recorded between 50 and 100 m, switching drastically the temperature in a matter of minutes, and influencing the movement of fishes along the reef wall (H. T. Pinheiro and L. A. Rocha, pers. comm.). Such occasional oceanographic processes increase connectivity between shallow and mesophotic reef habitats, in addition to providing nutrients and rich plankton to local fish and benthic assemblages (Gove *et al.*, 2016). Mesophotic specialists possibly take advantage of cold ascendant currents that occur in the region (Travassos *et al.*, 1999) to briefly rise up and use some shallower resources not common in deeper reefs, such as turf and crustose calcareous algae, and scleractinian corals (Rosa *et al.*, 2016). According to Nunes *et al.* (2019), *P. obliquus* has a bathymetric distribution coincident with the temperature stratification, showing greatest abundances in deep (> 60 m) and cold (14-18 °C) waters, but with regular sightings at 40 m depth. Similarly, *C. vanbebberae* is also a mesophotic species associated with cold waters that can occur at depths of up to 10 m (McFarland *et al.*, 2020) under the right temperature conditions. Quick variation in temperature has also been observed in mesophotic reefs of Hawaii (Kahng *et al.*, 2019), and could drive the ephemeral occurrence of both assemblages at the same depth range. As shallow reefs are limited in the SPSPA (less than 0.5 km² of reefs < 50 m deep), competition for space and resources (*e.g.*, territory, food, shelter) could be intense, influencing the depth expansion of shallow affinity species, such as *S. sanctipauli*, to mesophotic reefs.

Ecosystems connections

The high number of linking species (*i.e.*, co-occurring) between pelagic and mesophotic reefs (~40% of the overall assemblages' similarity; Fig. 6) support the ecological connectivity between these ecosystems. Differently from previous studies that showed fish predators as important links between coral reefs and the pelagic environment (Papastamatiou *et al.*, 2015; Clarke *et al.*, 2019), our study showed that main linking species are omnivores. The abundant *M. niger* is considered a functional herbivore in the SPSPA, which play an important role by transferring nutrients from the benthic primary

production to higher trophic levels (Mendes *et al.*, 2019), through daily migrations among pelagic and reef systems. The enrichment of the pelagic ecosystem by nutrients from *M. niger* faeces could contribute to the primary productivity, in a similar process to the "whale pump", in which marine mammals that feed at great depths release faecal plumes near the surface, enhancing local primary productivity (Roman & McCarthy, 2010). On the other hand, *M. niger* also feeds on zooplankton in the pelagic system (Randall, 1967; Mendes *et al.*, 2019), thus possibly transferring pelagic nutrients back to the reefs, by providing extra fertilization for the primary producers or by serving as prey. In fact, pelagic subsidies can make a substantial contribution to reef fish productivity (Morais & Bellwood, 2019), which would contribute to the high reef fish abundance and biomass found in the SPSPA despite its small area (Morais *et al.*, 2017; Quimbayo *et al.*, 2019). Some large and high mobile predators also perform constant migrations between pelagic and reef ecosystems, thus influencing the energy flux and dynamics in both systems (Williams *et al.*, 2018; Skinner *et al.*, 2019). However, due to the current low abundance of large predators recorded in the SPSPA, this important trophic link may have been replaced by mesopredators that are still abundant in the region. For instance, in SPSPA, *C. lugubris* feeds mainly on pelagic prey (*e.g.*, small crustaceans and flyingfish), as well as reef fish such as *Myripristis jacobus* Cuvier, 1829, *A. multilineata* and *A. saxatilis* (Pinheiro *et al.*, 2017). Similarly, carangid species such as *C. crysos* and *S. rivoliana*, which are common in the SPSPA, have a diet based mainly on pelagic fish, but can also prey on a wide variety of demersal/reef fishes such as labrids, serranids, sparids, mullids and even gobies (Randall, 1967; Barreiros *et al.*, 2003; Sley *et al.*, 2009). Even exclusive pelagic species also opportunistically prey on fish and other reef organisms in SPSPA, including resident reef predators (Vaske-Júnior *et al.*, 2003, 2006; Albuquerque *et al.*, 2019). Therefore, our data hint at important ecosystem connections occurring through different species and trophic pathways (*i.e.*, herbivory, planktivory, piscivory). Even sustaining a low diversity reef fish assemblage, the ecological connectivity between the pelagic and reef ecosystems is a critical process, which probably help to sustain the high biomass and productive reef assemblages, even surrounded by oceanic poor waters.

The ecological connections between pelagic and mesophotic reef ecosystems inferred here based on species co-occurrences, as well as the endangered status of species found in both environments, suggest the need for an integrated management strategy. The very large MPA created in 2018, which included a no-take zone that encompasses only a tiny fraction of the SPSPA, need to be continually re-evaluated to verify if it is effectively

conserving reef biodiversity, as well as the pelagic fish assemblages and the important trophic connections they play. This research shows the importance of protecting not only the fragile and unique reef ecosystem, but also the pelagic environment around the SPSPA. Stricter fishing restrictions around the archipelago are suggested as the best alternative for biodiversity conservation and maintenance of critical ecological processes, thus helping system resilience.

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Acknowledgements

Supporting information

Table S1: Pelagic fish assemblage of the Saint Peter and Saint Paul's Archipelago. Families are in phylogenetic order according to Nelson *et al.* (2016). Trophic groups are following Pinheiro *et al.* (2018). Relative abundance (MaxN) and mean (MMaxN; ± standard deviation) relative abundance of the fish species.

Family / Species	Trophic group	MaxN	MMaxN
Carcharhinidae			
Carcharhinus falciformis	Carnivores	4	0.8 ± 1.1
Myliobatidae			
Mobula tarapacana	Planktivores	2	0.4 ± 0.9
Coryphaenidae			
Coryphaena hippurus	Carnivores	1	0.2 ± 0.5
Carangidae			
Caranx crysos	Carnivores	87	17.4 ± 32.4
Caranx lugubris	Carnivores	9	1.8 ± 4.0
Elagatis bipinnulata	Carnivores	153	30.6 ± 34.9
Seriola rivoliana	Carnivores	12	2.4 ± 3.9
Sphyraenidae			
Sphyraena barracuda	Carnivores	4	0.8 ± 1.3
Scombridae			
Acanthocybium solandri	Carnivores	10	2.0 ± 1.2
Thunnus albacares	Carnivores	2	0.4 ± 0.9
Balistidae			
Canthidermis maculata	Planktivores	35	7.0 ± 12.5
Canthidermis sufflamen	Planktivores	27	5.4 ± 7.9
Melichthys niger	Omnivores	100	20.0 ± 44.7
Monacanthidae			
Aluterus monoceros	Omnivores	1	0.2 ± 0.5

Table S2: Mesophotic reef fish assemblage of the Saint Peter and Saint Paul's Archipelago. Families are in phylogenetic order according to Nelson *et al.* (2016). Trophic groups are following Pinheiro *et al.* (2018). Relative abundance (MaxN) and mean (MMaxN; ± standard deviation) relative abundance of the fish species.

Family / Species	Trophic group	MaxN	MMaxN
Carcharhinidae			
Carcharhinus falciformis	Carnivores	1	0.07 ± 0.27
Carcharhinus galapagensis	Carnivores	1	0.07 ± 0.27
Myliobatidae			
Mobula tarapacana	Planktivores	21	1.50 ± 5.06
Muraenidae			
Enchelycore nigricans	Carnivores	18	1.29 ± 1.07
Enchelycore aff. nycturanus	Carnivores	8	0.57 ± 0.85
Gymnothorax funebris	Carnivores	8	0.57 ± 0.85
Muraena melanotis	Carnivores	9	0.64 ± 0.63
Muraena pavonina	Carnivores	28	2.00 ± 1.04
Holocentridae			
Holocentrus adscensionis	Mobile invertebrate feeders	4	0.29 ± 0.61
Myripristis jacobus	Planktivores	1	0.07 ± 0.27
Pomacentridae			
Chromis vanbebberae	Planktivores	123	8.79 ± 16.00
Azurina multilineata	Planktivores	209	14.93 ± 17.90
Abudefduf saxatilis	Omnivores	26	1.86 ± 3.23
Stegastes sanctipauli	Territorial herbivores	53	3.79 ± 5.63
Carangidae			
Caranx crysos	Carnivores	38	2.71 ± 10.20
Carangoides bartholomaei	Carnivores	4	0.29 ± 0.61
Caranx lugubris	Carnivores	85	6.07 ± 8.68
Seriola rivoliana	Carnivores	90	6.43 ± 12.10
Sphyraenidae			
Sphyraena barracuda	Carnivores	2	0.14 ± 0.36
Aulostomidae			
Aulostomus strigosus	Carnivores	10	0.71 ± 0.73
Dactylopteridae			
Dactylopterus volitans	Mobile invertebrate feeders	1	0.07 ± 0.27
Labridae			
Bodianus insularis	Mobile invertebrate feeders	18	1.29 ± 0.91
Clepticus brasiliensis	Planktivores	1	0.07 ± 0.27
Halichoeres radiatus	Mobile invertebrate feeders	22	1.57 ± 1.02
Kyphosidae			
Kyphosus sp.	Roving herbivores	17	1.21 ± 3.29
Epinephelidae			
Cephalopholis fulva	Carnivores	2	0.14 ± 0.36
Serranidae			
Choranthias salmopunctatus	Planktivores	7	0.50 ± 1.09
Rypticus saponaceus	Carnivores	12	0.86 ± 0.77
Chaetodontidae			
Chaetodon striatus	Sessile invertebrate feeders	4	0.29 ± 0.61
Prognathodes obliquus	Sessile invertebrate feeders	27	1.93 ± 2.09
Pomacanthidae			
Holacanthus ciliaris	Sessile invertebrate feeders	29	2.07 ± 1.64
Pomacanthus paru	Sessile invertebrate feeders	2	0.14 ± 0.36
Lutjanidae			
Lutjanus jocu	Carnivores	2	0.14 ± 0.36

Balistidae			
Balistes capriscus	Mobile invertebrate feeders	27	1.93 ± 1.73
Canthidermis sufflamen	Planktivores	14	1.00 ± 2.04
Melichthys niger	Omnivores	808	57.71 ± 23.60
Xanthichthys ringens	Mobile invertebrate feeders	1	0.07 ± 0.27
Monacanthidae			
Aluterus monoceros	Omnivores	8	0.57 ± 2.14
Aluterus scriptus	Omnivores	8	0.57 ± 0.65
Cantherhines macrocerus	Omnivores	24	1.71 ± 0.83
Diodontidae			
Diodon hystrix	Sessile invertebrate feeders	1	0.07 ± 0.27

Table S3: Generalized additive model results showing the correlations between the PCO axis 1 and 2 with depth, for the taxonomic structure (species MaxN) of the mesophotic reef fish assemblage.

PCO1	**Estimate**	**SE**	**t value**	**P**
Intercept	0.03462	4.50094	0.008	0.994
Depth	1.763	2.181	2.49	0.127
PCO2	**Estimate**	**SE**	**t value**	**P**
Intercept	0.2975	4.0296	0.074	0.942
Depth	1	1	1.137	0.307

Table S1: Generalized additive model results showing the correlations between the PCO axis 1 and 2 with depth, for the trophic structure (trophic group MaxN) of the mesophotic reef fish assemblage.

PCO1	**Estimate**	**SE**	**t value**	**P**
Intercept	$5.31*10^{-12}$	3202	0	1
Depth	1.269	1.487	0.734	0.372
PCO2	**Estimate**	**SE**	**t value**	**P**
Intercept	$8.429*10^{-09}$	2404	0	1
Depth	1.903	2.353	1.004	0.509

Table S5: Results of the Similarity Percentage (SIMPER) analysis showing the species contributions (70% cumulative) for the pelagic, mesophotic reef and overall fish assemblages of the Saint Peter and Saint Paul's Archipelago.

Species	Average Abundance	Average Similarity	Similarity standard deviation	Contribution (%)	Cumulative contribution (%)
Pelagic assemblage (Average similarity: 41.64)					
Elagatis bipinnulata	1.99	15.41	2.54	37.00	37.00
Acanthocybium solandri	1.00	8.84	1.11	21.24	58.24
Caranx crysos	1.37	6.77	1.12	16.25	74.49
Mesophotic reef assemblage (Average similarity: 58.35)					
Melichthys niger	2.71	11.28	4.93	19.34	19.34
Caranx lugubris	1.42	5.42	4.82	9.29	28.63
Muraena pavonina	1.11	4.02	2.25	6.88	35.51
Cantherhines macrocerus	1.07	3.89	2.31	6.67	42.18
Chromis multilineata	1.41	3.60	0.96	6.18	48.36
Holacanthus ciliaris	1.03	3.31	1.54	5.68	54.04
Halichoeres radiatus	0.98	3.17	1.54	5.44	59.48
Seriola rivoliana	1.10	2.82	0.93	4.84	64.32
Bodianus insularis	0.88	2.71	1.20	4.65	68.97
Balistes capriscus	0.89	2.27	0.95	3.90	72.87
Overall assemblage (Average similarity: 37.24)					
Melichthys niger	2.17	7.21	1.18	19.36	19.36
Caranx lugubris	1.14	3.49	1.18	9.37	28.73
Seriola rivoliana	0.97	2.44	0.74	6.56	35.29
Muraena pavonina	0.82	2.14	0.89	5.74	41.03
Cantherhines macrocerus	0.79	2.07	0.90	5.56	46.59
Chromis multilineata	1.04	1.92	0.58	5.15	51.74
Holacanthus ciliaris	0.76	1.76	0.77	4.74	56.48
Halichoeres radiatus	0.72	1.69	0.77	4.54	61.02
Bodianus insularis	0.65	1.44	0.68	3.88	64.89
Balistes capriscus	0.66	1.21	0.58	3.25	68.14
Enchelycore nigricans	0.60	1.18	0.59	3.17	71.32

Capítulo 2 – Fish assemblages habitat distribution in a remote South Atlantic oceanic island

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Abstract

Reef fish habitat use is highly associated with their environmental needs, and understanding fish-habitat associations is essential for efficient fisheries management and conservation of biodiversity. Depth is an important driver for reef fish assemblages, closely related to other environmental features including water temperature, hydrodynamics, light at bottom, benthic cover, and habitat type. Here, we analysed the fish assemblages distribution at Trindade Island to assess the response of conservation-related species traits (*e.g.*, biomass, endemism and species vulnerability) to habitat type and depth gradient. Using baited remote underwater stereo-video systems, we assessed reef fish over multiple habitats between 10 and 74 m deep. Multivariate analysis and data modelling reveal that fish assemblages at Trindade Island are structured according to the variation of benthic habitats across the depth gradient of the insular shelf. While species richness, total abundance and endemism were highly related towards reef habitats, total biomass and average vulnerability were more positively associated to increased depth. Therefore, an integrated management approach addressing the insular shelf gradient of benthic habitats is essential in order to guarantee the conservation of marine biodiversity and the ecological functions intrinsic to each habitat.

Keywords: BRUVS, conservation, depth gradient, endemism, reef fish, vulnerability.

Introduction

Understanding the distribution patterns of fish assemblages in relation to the environmental characteristics is essential for the conservation of biodiversity and an efficient fisheries management (Reis-Filho *et al.*, 2019a). The habitat type is an important structuring driver for fish assemblages, with more complex habitats often harbouring higher species richness and abundance than less complex ones (Gratwicke & Speight, 2005). However, far beyond this direct relationship with structural complexity, fish habitat use is highly associated with their environmental needs, especially in relation to feeding and growth, predation risk offset, competition mitigation, and reproductive necessities (Eggertsen *et al.*, 2017; Reis-Filho *et al.*, 2019a). Reef fishes may depend on many different essential habitats (*e.g.*, mangroves, rhodolith beds, tidepools) according to their life stages, whether as foraging, spawning or nursery grounds (Cocheret de la Morinière *et al.*, 2002; Papastamatiou *et al.*, 2015). As habitat requirements change, species may need to perform foraging movements (*e.g*., Beaudreau & Essington, 2011; Williams *et al.*, 2018), spawning migrations (*e.g.*, Feeley *et al.*, 2018; Bezerra *et al.*, 2021), or ontogenetic habitat shifts (Oliveira *et al.*, 2016; Reis-Filho *et al.*, 2019a), thus connecting habitats on different temporal and spatial scales.

Depth is also an important reef fish community driver (Asher *et al.*, 2017; Zintzen *et al.*, 2017), since it is closely related to many environmental characteristics including water temperature (Asher *et al.*, 2017), hydrodynamics (Maia *et al.*, 2018), light at bottom (Moura *et al.*, 2021), as well as benthic cover (Rosa *et al.*, 2016), and habitat type (Bond *et al.*, 2018). Change in habitat type along the depth gradient is a common feature of continental or insular shelves (Pimentel *et al.*, 2020; Moura *et al.*, 2021), which can strongly influence the fish assemblage structure (Cappo *et al.*, 2011; Bond *et al.*, 2018). However, co-variation lowers the distinctiveness between the influences that each factor exerts on the assemblages. Nevertheless, understanding complex species distribution over multiple benthic habitats across the depth gradient is crucial for marine biodiversity conservation. The integration of marine reserves into connected networks encompassing all habitats and a broad depth range has been proved to be more efficient to preserve higher abundance and biomass of fished species, as they experience relatively stronger fishing pressure in shallow water and the larger fish are usually at greater depths (Goetze *et al.*, 2021).

The farthest oceanic island off the Brazilian coast, Trindade Island, harbours a relatively high reef fish richness (194 species) and endemism rate (9.6%) compared to other south

Atlantic oceanic localities, being considered a hotspot of biodiversity (Pinheiro *et al.*, 2015; Guabiroba *et al.*, 2020b). Trindade Island also supports one of the greatest biomass of reef fishes of the Brazilian coast, and the highest among Brazilian oceanic islands (Morais *et al.*, 2017). While any of these characteristics would make the island a high priority for conservation, it was only in 2018 that a marine protected area (MPA) was established in the region. However, the establishment process and geographic delineation have suffered heavy criticism from the scientific community (Giglio *et al.*, 2018; Vilar *et al.*, 2020). While the concerns from the scientific community remain unanswered, one needs to admit that no fishing management strategy regulated fishing activities in the region prior to MPA creation. Lack of rules adapted to the remoteness, isolation and singularity of assemblages resulted in overfishing and a severe decrease in the populations of many species, including nurse and reef sharks, yellowfin grouper, rock hind grouper, coney, and black jack (Pinheiro *et al.*, 2010a; Guabiroba *et al.*, 2020a).

A number of studies have brought up our knowledge of the biodiversity (Pinheiro *et al.*, 2010b; Simon *et al.*, 2013; Smith-Vaniz *et al.*, 2018; Guabiroba *et al.*, 2020b) and distribution patterns (Pereira-Filho *et al.*, 2011; Pinheiro *et al.*, 2011) of reef and shallow fish assemblages of Trindade Island. Other habitats and depths remain knowledge-deficient and assemblage connectivity patterns remain fully unknown. Therefore, we analysed the structure and distribution of fish assemblages over the mosaic of benthic habitats of the Trindade Island insular shelf to assess the response of conservation-related species traits (*e.g.*, biomass, endemism and species vulnerability) to habitat type and depth gradient, in order to collaborate with a successful marine conservation and fishery management.

Material and Methods

Study area

Volcanic Trindade Island (20°30' S, 29°20' W) is located about 1140 km off the south-eastern Brazilian coast (Fig. 1), at the east end of the Vitória-Trindade Chain, Southwestern Atlantic. Together with the Martin Vaz Archipelago, located 47 km east of Trindade Island, they constitute the youngest (younger than 1 Ma) and the easternmost oceanic islands in Brazil (Hasen *et al.*, 1998; Mohriak, 2020). Currently, Trindade Island has an emerged area of approximately 9.3 km^2, with extremely rugged and mostly unvegetated relief, whereas the shallow insular shelf (down to *ca.* 50 m depth) was estimated to be 32 km^2 (Gasparini & Floeter, 2001). A mosaic of benthic habitats typifies the insular shelf seascape, including carbonate and rocky reefs, rhodolith and macroalgae

beds, and sandy bottoms. The fringing carbonate reefs can be extremely complex, with interconnected holes and crevices, or completely flat, showing almost no structural complexity. Volcanic boulders compose the rocky reefs, adding high structural complexity to the seascape of the shallow insular shelf. These reef habitats are interspersed by sand, rhodolith and macroalgae beds, which are most common below 30 m. In relation to environmental conservation, two large Marine Protected Areas (MPAs) were recently (March 2018) created around Trindade Island and Martin Vaz Archipelago, a larger multiple-use area, and a relatively smaller and supposedly no-take area. However, surprisingly, most part of the island was excluded even from the multiple-use MPA, leaving only a tiny part as a no-take area (Giglio *et al.*, 2018; Vilar *et al.*, 2020).
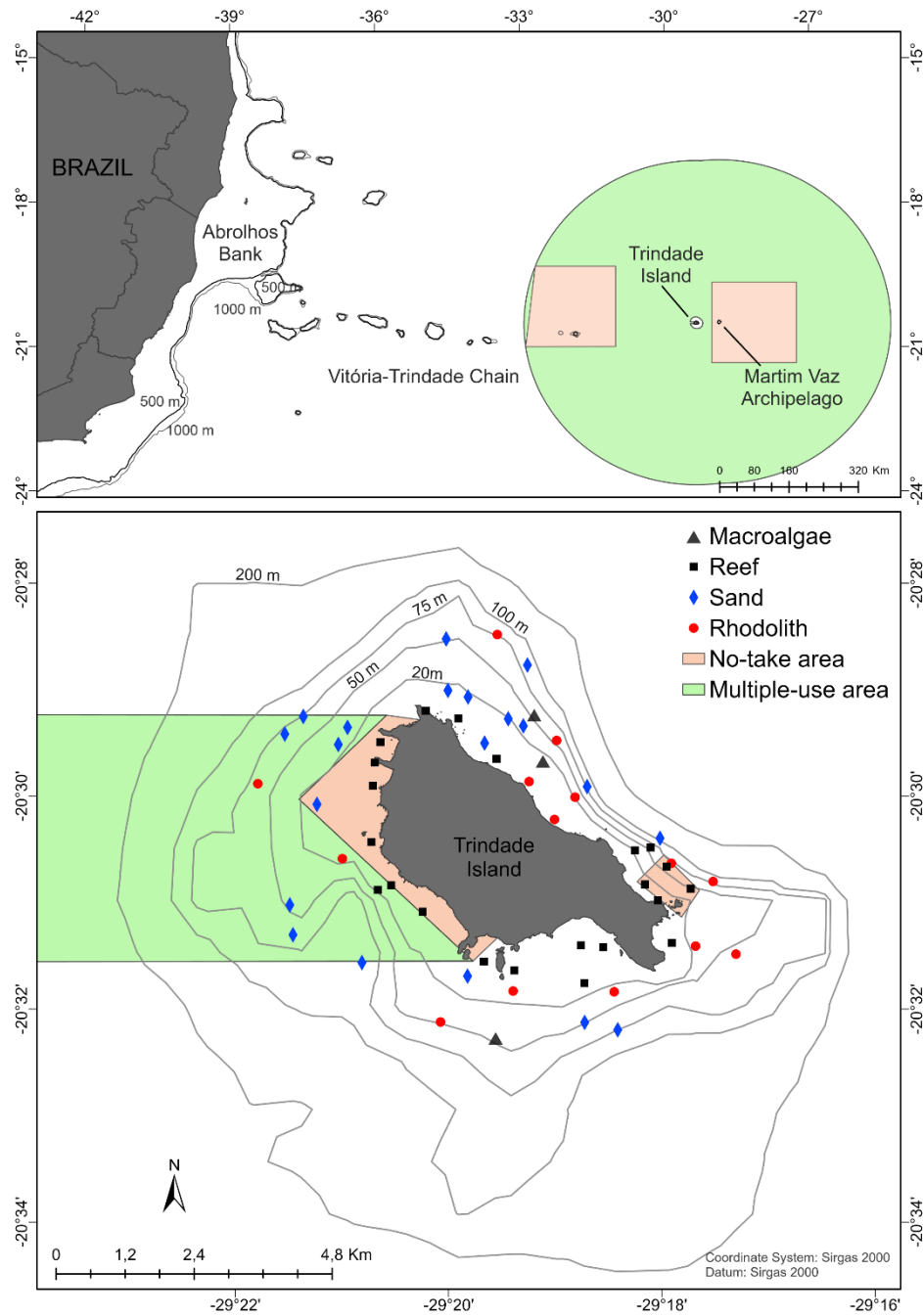
Figure 1: Location of Trindade Island at the eastern end of the Vitória-Trindade Chain, Southwestern Atlantic. Gray triangles, black squares, blue diamonds and red circles indicate the position of the BRUVS deployments according to the dominant benthic habitat: macroalgae (n = 3), reef (n = 22), sand (n = 21), and rhodolith (n = 14). Gray lines indicate isobaths. The No-take and Multiple-use areas are shown in pink and green, respectively.

Sampling procedures

During a expedition in November 2017, 60 daytime (8 - 16 h) deployments of benthic baited remote underwater stereo-video systems (hereafter BRUVS) were realized around the island, 30 on each island side (*i.e.* leeward - southwest and windward - northeast), distributed from 10 to 74 m depth. The depth gradient was defined based on arbitrary depth zones, being shallow (< 30 m), middle (30 to 50 m) and deep (> 50 m). The BRUVS were baited with 500 g of crushed Brazilian sardine *Sardinella brasiliensis* (Steindachner, 1879), and arranged at least 500 m apart from each other to avoid overlapping bait plumes. Each deployment lasted 60 minutes (Whitmarsh *et al.*, 2017).

Video analysis

Fishes were identified to the lowest possible taxonomic level and the relative abundance of each species was recorded as MaxN, *i.e.* the maximum number of individuals of the same species present in a single frame (Cappo *et al.*, 2004). In the MaxN frame of each species, we measured the total or fork length of all fish, according to their distance (≤ 5 m) and angle ($\leq 45°$) to the cameras. We also pre-established the measurement precision ≤ 1 cm as a necessary requirement. The criteria for measuring fishes were entered and verified by the software used to analyze the videos (EventMeasure). The proportion of each benthic habitat (*i.e.*, reef, rhodolith, sand and macroalgae) was assessed through the seabed image of the samples. The seabed images were divided into a 5 x 4 grid and, for each grid square, the dominant benthic habitat (*i.e.*, the one with greatest coverage) was recorded. The total grid squares that each habitat was dominant represented its proportion in the sample.

Data analysis

Fish biomass was estimated through the allometric length–weight relationship of each species, using the parameters presented by FishBase (Froese & Pauly, 2021). When the species parameters were not available, were used parameters of congeneric morphologically similar species. Species were classified into trophic groups as carnivores, mobile invertebrate feeders, sessile invertebrate feeders, planktivores, omnivores and herbivores (following Pinheiro *et al.*, 2018). To analyse species vulnerability, the FishBase vulnerability index was used (Froese & Pauly, 2021). This intrinsic vulnerability index is based on life history and ecological characteristics (*e.g.*, length, maturity, longevity, mortality, fecundity, and geographic range), and is expressed on a scale ranging from 1 to 100, with 100 being the most vulnerable (Cheung *et al.*, 2005). A principal coordinate analysis (PCO) was used to construct an unconstrained

ordination of the samples, based on a Bray-Curtis similarity matrix, calculated from the fourth root-transformed relative abundance (MaxN) dataset. A Spearman correlation of 0.6 was used to display potential relationships between fish species and the axes of PCO (Clarke & Gorley, 2006). A RELATE test, based on the Spearman correlation, was used to verify the correlation between relative abundance and relative biomass similarity matrices (Rho = 0.923) (Clarke & Gorley, 2006). Therefore, relative abundance data of fish assemblages were used in the multivariate statistical analyses. These analyses were run in PRIMER 6.1.13 with PERMANOVA+ 1.0.3 (Clarke & Gorley, 2006). To analyse the association of species with benthic habitats along the depth gradient, a shade plot was produced by clustering the samples on the x-axis, based on Bray–Curtis similarity, and the 15 most important species on the y-axis, based on Whittaker's index of association (Clarke & Gorley, 2015). To detect significantly different sample clusters and to identify fish species groups with habitat/depth gradient partitioning, we used the similarity profile test (SIMPROF). All analyses were run in PRIMER 7 with PERMANOVA (Clarke & Gorley, 2015).

Overall and between benthic habitats beta diversity was calculated with the Sorensen dissimilarity index, using the betapart package in R (Baselga & Orme, 2012; Baselga *et al.*, 2013). Generalized additive models (GAM) were performed to analyse the relationships between the PCOs' axes with the depth gradient and the proportion of each benthic habitat (*i.e.*, reef, rhodolith and sand). Macroalgae proportion was not tested due to its low representativeness in samples. Gaussian distribution and identity link were used in the GAMs, through the mgcv package in R (Wood, 2011, 2012). Generalised additive models were also used to test for relationships between explanatory variables (*i.e.*, depth, and proportion of reef, rhodolith, and sand) and untransformed species richness, total abundance and biomass, biomass of trophic groups, average vulnerability, and richness and abundance of endemic species. Poisson distribution and log link were used with the mgcv package (Wood, 2011, 2012). Models were selected according to Akaike Information Criterion (AICc) values, and the percentage of explained variance was used as secondary criterion. The dredge function was used for the model selection procedure, using MuMIn package in R (Bartón, 2014; Kamil, 2016).

Results

A total of 4,832 individuals were recorded belonging to 79 taxa from 35 families (Supporting Information Table S1). Seventy-two species were identified, while five taxa remain at the genus level, and one at the family level. The well-known hybrid of

Cephalopholis fulva (Linnaeus, 1758) with *Paranthias furcifer* (Valenciennes, 1828) (Bostrom *et al.*, 2002) was counted as one taxa of its own. *Aluterus monoceros* (Linnaeus 1758) was recorded for the first time at Trindade Island (Guabiroba *et al.*, 2020b). The most diverse families were Labridae, Epinephelidae and Carangidae with 11, 7 and 6 taxa each, respectively. The most abundant taxa were *Melichthys niger* (Bloch, 1786), representing 58.2% of total MaxN, *Kyphosus* spp. with 4.8%, *P. furcifer* with 4.5%, and *C. fulva* with 4.2%. Five elasmobranch species were also recorded, one individual of *Aetobatus narinari* (Euphrasen, 1790), 18 of *Carcharhinus perezi* (Poey, 1876), four of *Galeocerdo cuvier* (Péron & Lesueur, 1822), two of *Ginglymostoma cirratum* (Bonnaterre, 1788), and five of *Sphyrna lewini* (Griffith & Smith, 1834).

The richest (mean S ± standard error: 19.2 ± 1.1) and most abundant (mean MaxN ± standard error: 121.4 ± 6.1) benthic habitat was the reef environment, followed by rhodolith beds (S: 11.8 ± 0.9; MaxN: 91.4 ± 15.4), macroalgae beds (S: 9.7 ± 2.4; MaxN: 41.7 ± 21.0), and sandy bottoms (S: 6.1 ± 0.6; MaxN: 36.1 ± 6.2) (Fig. 2). Reef habitat also showed the most exclusive ichthyofauna, with almost 30% of the taxa (n = 24) occurring only in this habitat (Supporting Information Table S1). In turn, five species (6%) were exclusive of rhodolith beds, three (4%) of sandy bottoms, and other three of macroalgae beds. On the other hand, only nine species were recorded in all benthic habitats, and 17 species in three habitats. Concerning the depth gradient, species richness, and relative abundance were considerably higher in the shallow zone (S: 17.5 ± 1.2; MaxN: 118.8 ± 5.4; n = 24) than in the middle (S: 9.8 ± 1.1; MaxN: 57.6 ± 7.1; n = 21) and deep zones (S: 7.3 ± 1.2; MaxN: 46.6 ± 18.3; n = 15). Nineteen species were recorded only in the shallow zone, eight were exclusive of the middle zone, and no species was exclusively detected in the deep zone. Most fish was unspecialized toward particular depth (within the range explored), since 26 species were widely distributed throughout the bathymetric range.
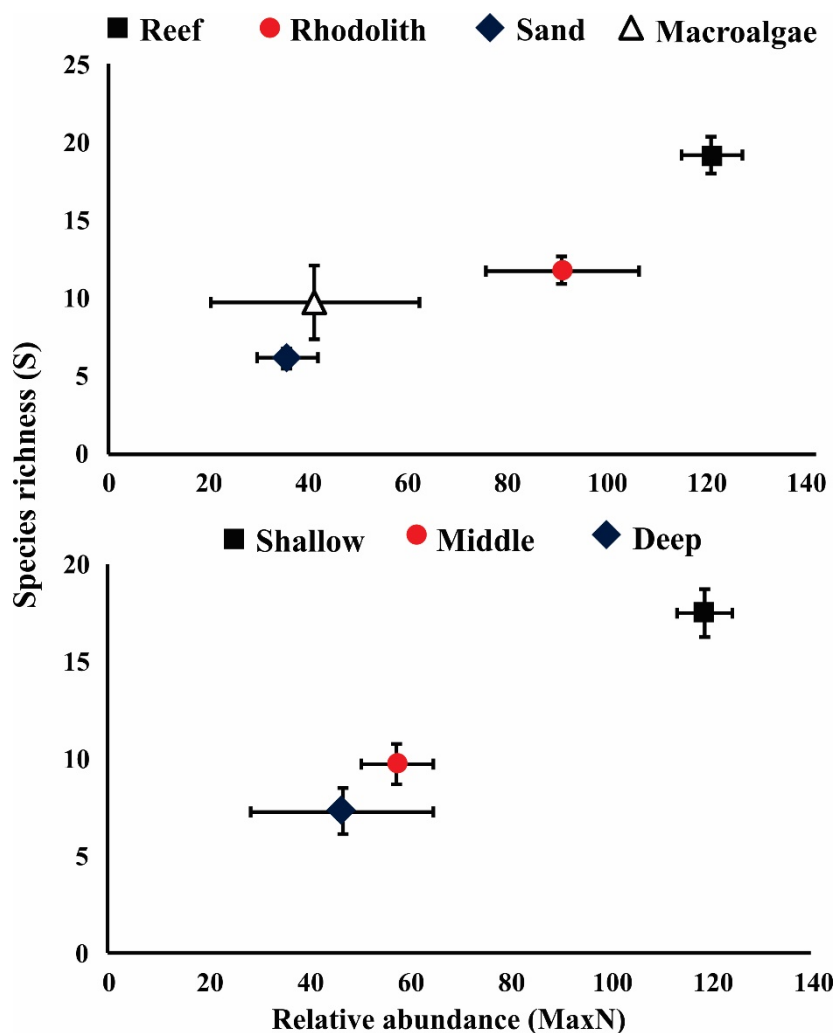
Figure 2: Mean (± standard error) species richness (S) and relative abundance (MaxN) of the fish assemblages recorded on the different benthic habitats and depth zones (shallow: < 30 m; middle: 30 to 50 m; > 50 m deep). Black vertical and horizontal bars indicate standard error.

The overall variation in assemblage composition was very high (beta diversity = 0.95). The highest compositional variation was detected between reef and macroalgae beds, and between reef and sand bottoms (Table 1). The lowest values were recorded between reef and rhodolith beds, and sand bottoms and macroalgae beds.

Table 1: Mean beta diversity (± standard deviation) among benthic habitats calculated with the Sorensen dissimilarity index.

Benthic habitat	Reef	Rhodolith	Sand
Rhodolith	0.66 (± 0.10)		
Sand	0.82 (± 0.13)	0.70 (± 0.17)	
Macroalgae	0.85 (± 0.12)	0.74 (± 0.15)	0.67 (± 0.18)

The variation on the fish assemblages among benthic habitats through the depth gradient is clearly evidenced in the PCO (Fig. 3). The first axis explained 38.3% of total variation, and mainly opposed reefs against sand bottoms. The second axis explained 16.1% of total variation, and segregated rhodolith beds from reef and sand bottoms. Macroalgae beds were poorly evidenced but appear to share some characteristics with sand bottoms. Most species (10) showed high correlation (> 0.6) with reefs, while only *M. plumieri* was highly associated to rhodolith beds, and *Xyrichtys* spp. to sandy bottoms (Fig. 3). Generalized additive models resulted in significant relationships between both PCO axes with depth and reef proportion, as well as between the proportion of rhodolith and sand with PCO1 and PCO2 axes, respectively (Supporting information Table S2 and Fig. S1). These significant relationships corroborated that fish assemblages are structured according to the benthic habitats through the depth gradient.
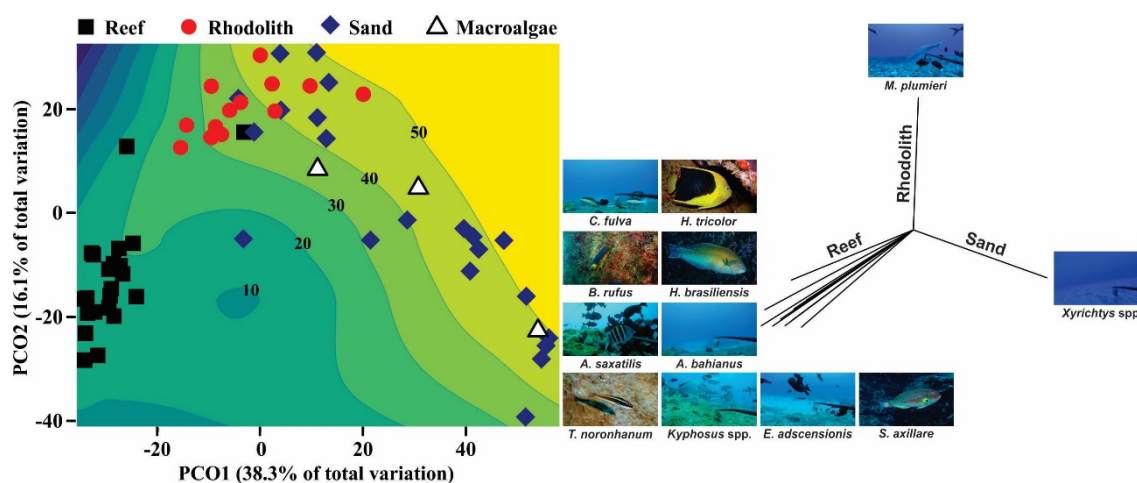
Figure 3: Principal coordinate analysis plot based on the relative abundance (MaxN) of the fish assemblages. Numbers arranged within the figure on the left indicate the depth gradient, and symbols the sampled benthic habitats. Vectors on the right indicate the species with Spearman correlation > 0.60 with the axes of PCO. Photos of *Bodianus rufus* and *Holacanthus tricolor* by Raphael Macieira, and photos of *Halichoeres brasiliensis*, *Thalassoma noronhanum*, and *Sparisoma axillare* by Luiz Rocha.

The shade plot with the cluster analyses identified five groups of benthic habitats/depth zones (top clusters) associated to three groups (left clusters) of fish taxa (Fig. 4). Reef and rhodolith habitats formed distinct groups regardless of depth zone. Sandy bottoms and macroalgae beds were distributed among three groups of benthic habitats, with deep macroalgae beds singled out. Regarding the fish species-habitat association, *Kyphosus* spp., *Sparisoma amplum* (Ranzani, 1841), *Thalassoma noronhanum* (Boulenger, 1890), *C. fulva*, *M. niger* and *Seriola rivoliana* Valenciennes, 1833, formed a group more

associated with reef habitat. A second group composed by *P. furcifer* and *Holocentrus adscensionis* (Osbeck, 1765), mostly small individuals, was related to rhodolith beds, especially the deepest ones. The third significant group was formed by seven species, some of them with great affinity for unconsolidated substrates, such as *Pseudupeneus maculatus* (Bloch, 1793) and *Xyrichtis* spp., and other species more associated with macroalgae beds, such as *Sphoeroides spengleri* (Bloch, 1785), *Aluterus scriptus* (Osbeck, 1765), and *Bothus* sp.. Species with greater mobility such as *Fistularia petimba* Lacepède, 1803 and *Caranx crysos* (Mitchill, 1815) also composed this group.
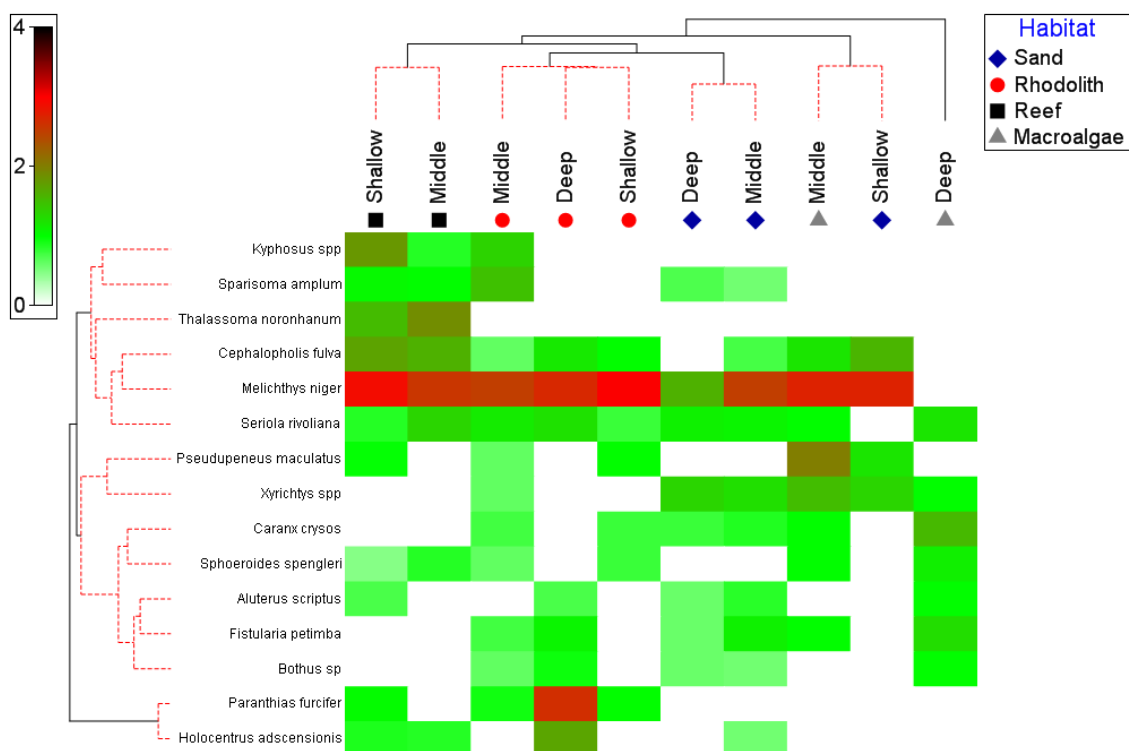
Figure 4: Shade plot showing the association of fish species (left clusters) with the benthic habitats/depth zones (top clusters). The colour gradient from black (strong correlation) to white (no correlation) indicates the strength of species-habitat/depth association. The dashed red lines indicate the significant groups according to the SIMPROF test.

The selected models (Supporting information Table S3) for species richness, total abundance and biomass contrasted reef and rhodolith beds from sand bottoms (Fig. 5 A-D, F), albeit details differed among dependent variables. Total biomass also varied with depth (Fig. 5 E) in a response strongly linked to carnivores biomass (Fig. 6 A). The AICc-selected model also included reef proportion as a predictor variable for carnivores distribution (Supporting information Table S3), but GAM was not performed with both predictor variables because there were fewer unique covariate combinations than specified maximum degrees of freedom. Omnivores biomass only varied in proportion of sand, but results interpretation is neither straightforward nor intuitive (Fig. 6 B). The biomass of mobile invertebrate feeders and planktivores decreased with depth but bottom nature (*i.e.*, sand proportion) did not influence planktivores (Fig. 6 C-E). For herbivores and sessile invertebrate feeders, GAMs were not run because there were fewer unique covariate combinations than specified maximum degrees of freedom. The average vulnerability showed a positive relationship with depth (Fig. 7 A), following the pattern of carnivores. The richness and abundance of endemic species are strongly related to the proportion of reef. However, some endemic species (*e.g.*, wrasses and parrotfish) also use other benthic habitats, such as rhodolith and macroalgae beds, mainly as juveniles. Sandy bottoms, on the other hand, had a negative relationship with the richness of endemic species.
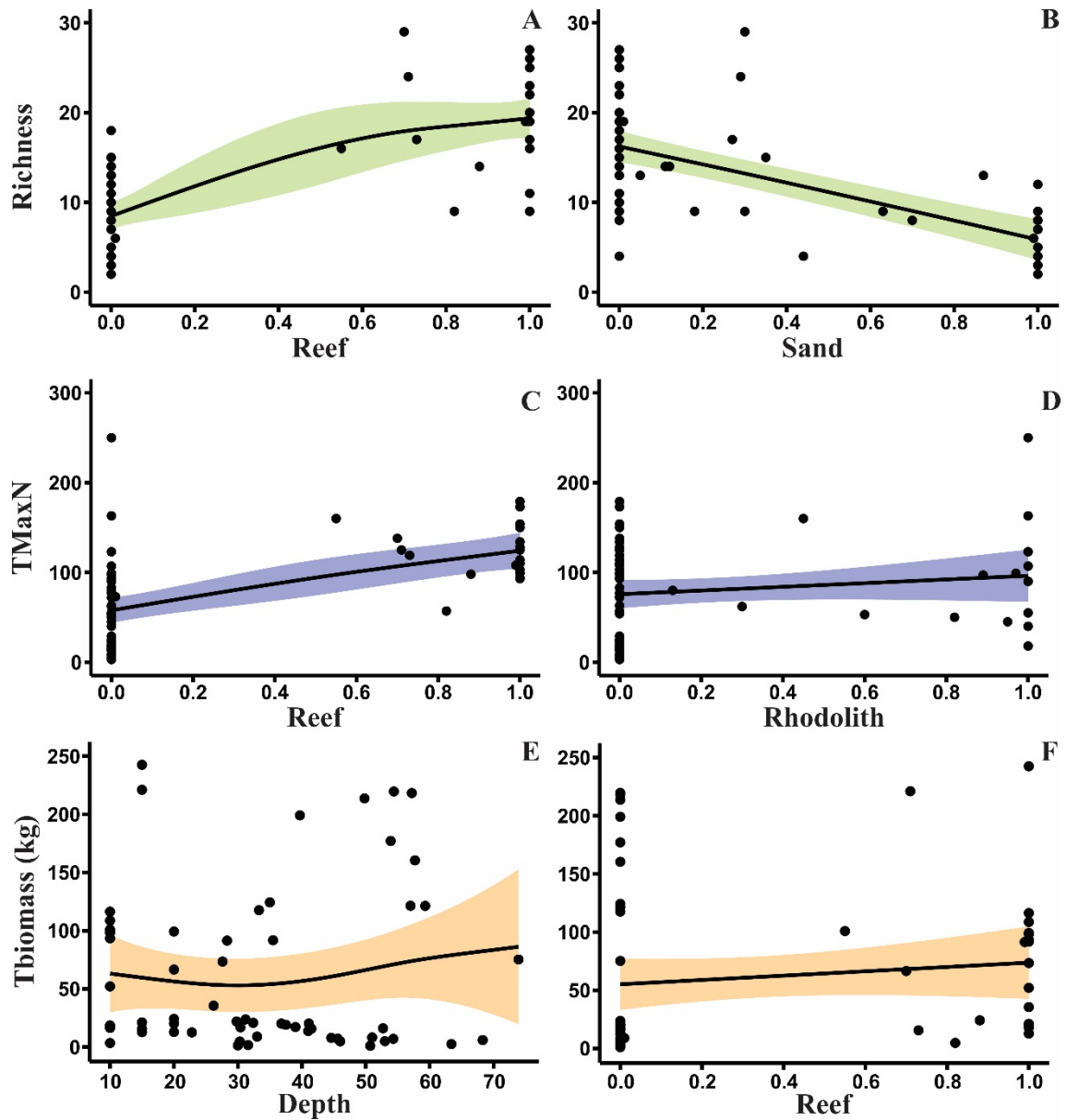
Figure 5: Relationships between richness (A and B), total abundance (TMaxN; C and D) and total biomass (TBiomass; E and F) with the depth gradient and the proportion of benthic habitats obtained by the selected generalized additive models. The coloured areas represent 95% confidence interval. All models are significant ($p < 0.05$).
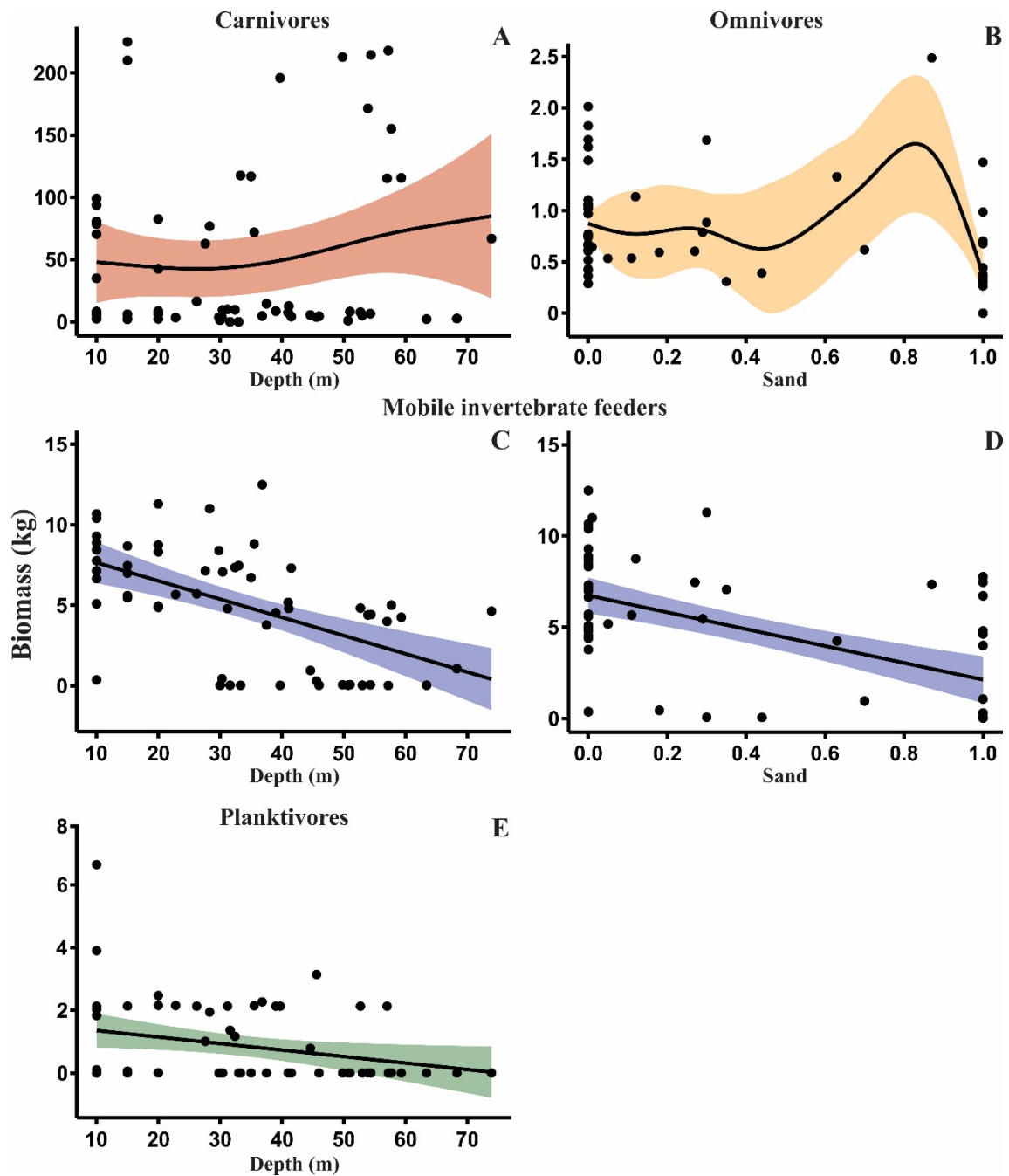
Figure 6: Relationships between the biomass (kg) of trophic groups with the depth gradient and the proportion of benthic habitats obtained by the selected generalized additive models. The coloured areas represent 95% confidence interval. All models presented are significant ($p < 0.05$).
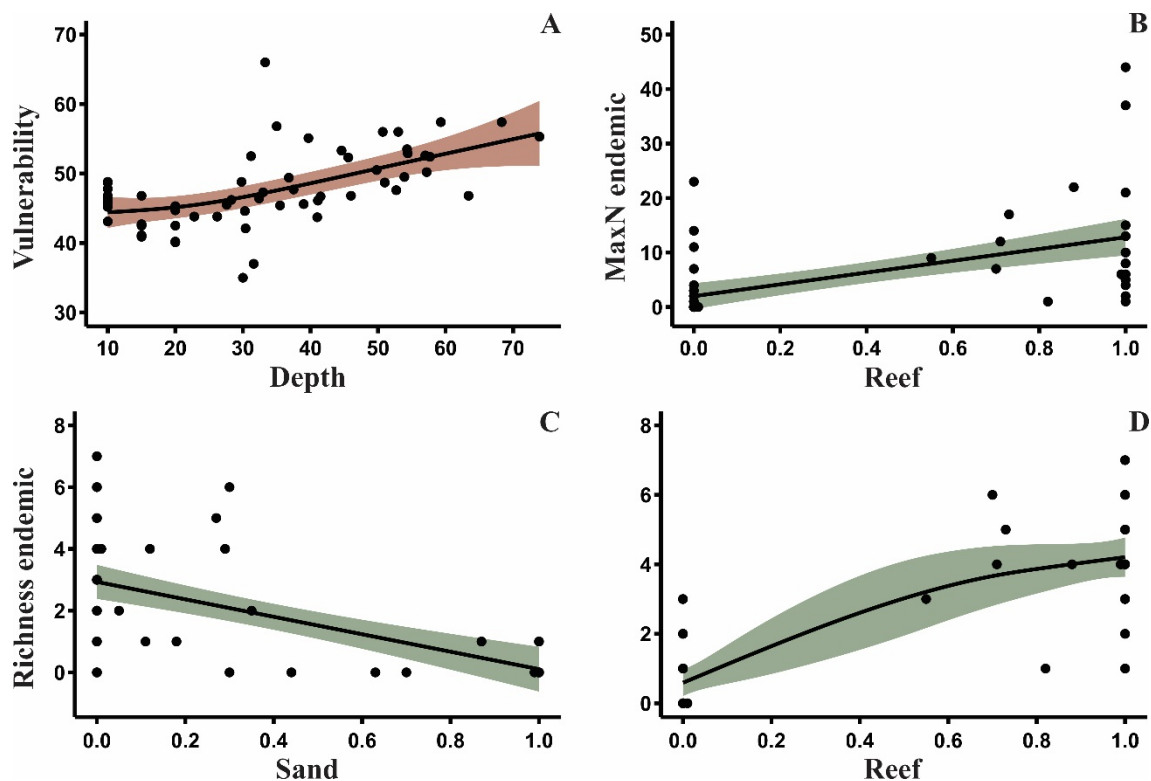
Figure 7: Relationships between the average vulnerability (A), abundance (MaxN; B) and richness (C and D) of endemic species with the depth gradient and the proportion of benthic habitats obtained by the selected generalized additive models. The coloured areas represent 95% confidence interval. All models presented are significant ($p < 0.05$).

Discussion

Depth gradient and benthic habitats are the most important environmental drivers in the structuring of marine fish assemblages (Reis-Filho *et al.*, 2019a; Moura *et al.*, 2021). The influence of these drivers on the structure of the assemblages is common knowledge and has been reported on several spatial scales. Fish can respond even to small depth variations within the euphotic zone (Krajewski & Floeter, 2011; Pinheiro *et al.*, 2011; Luiz *et al.*, 2015), passing through intermediate variations, such as from the euphotic to the mesophotic zone and within the latter (Pinheiro *et al.*, 2016; Rosa *et al.*, 2016; Rocha *et al.*, 2018; Andradi-Brown *et al.*, 2021), to large-scale variations from the mesophotic to aphotic zone (Semmler *et al.*, 2017; Zintzen *et al.*, 2017). Likewise, fish can exhibit microhabitat partitioning (Pereira, 2017; Brandl *et al.*, 2018), as well as variations in macrohabitat and ecosystem scale (Harvey *et al.*, 2013; Longo *et al.*, 2015; Reis-Filho *et al.*, 2019a; Moura *et al.*, 2021). Often the influence of depth and habitat on fish assemblages occurs simultaneously, since habitat variation across the depth gradient is a common characteristic of marine ecosystems (*e.g.*, Pereira-Filho *et al.*, 2011; Pimentel *et al.*, 2020; Moura *et al.*, 2021).

Here we demonstrate how the fish assemblages at Trindade Island are structured according to the benthic habitats variation along the depth gradient of the insular shelf. Differences in the fish assemblages between types of shallow fringing reefs (*i.e.*, volcanic rocky and coralline algae reefs) (Pinheiro *et al.*, 2011) and other species-habitat associations (Gasparini & Floeter, 2001) have been shown, but not the association of fish species with benthic habitats through the euphotic-mesophotic depth gradient (but see Pereira-Filho *et al.*, 2011; Meirelles *et al.*, 2015). The structural complexity of the benthic habitat is one of the strongest and most consistent predictors of composition and structure of fish assemblages (Gratwicke & Speight, 2005; Darling *et al.*, 2017). This factor seems to be driving the taxonomic structure of Trindade fish assemblages (see Fig. 3 and 4). The coralline algae reefs can exhibit relatively high structural complexity, forming a labyrinth of crevices and holes, while the rocky reefs are made of large volcanic boulders (Pinheiro *et al.*, 2011). In turn, rhodolith beds provide much greater structural complexity than sand bottoms (Holz *et al.*, 2020), due to the small crevices and holes between and within the calcareous nodules, while the complexity is low in sand bottoms, despite ripple marks and distinct texture due to varying grain size, nature and density.

Assessing fish assemblages in shallow reefs and rhodolith beds across the Abrolhos Shelf, on the east coast of Brazil, Moura *et al.* (2021) stated that the variation in the fish assemblages' composition at seascape level was also associated to the habitat structure, as well as to the amount of light reaching the bottom. According to the same authors, light at bottom integrates depth and turbidity in a single ecological variable, whose effects over reef fishes seems to be indirectly associated with trophic (*e.g.*, grazing and predation) and non-trophic (*e.g.*, shelter) interactions with the benthos. Similarly, benthic habitats and depth also influenced the composition and structure of the fish assemblages on the insular shelf of Trindade Island. However, since benthic habitats do not have a continuous distribution across the entire depth gradient, with reefs occurring predominantly in the shallow zone (< 30 m depth) and other habitats mainly in middle (30 to 50 m) and deep zones (> 50 m), depth is considered an intrinsic characteristic of habitats, acting in synergy with them on the distribution of the fish assemblages. In this sense, Reis-Filho *et al.* (2019) considered the range in temperature and salinity as components of the respective habitats, when analysing the distribution of fish assemblages along an ecosystem gradient.

Understanding the patterns of association and distribution of fish assemblages with habitats is essential for the management of natural resources in an ecosystem approach, especially in relation to the conservation of biodiversity (*e.g.*, species richness and endemic species) and fishery resources (*e.g.*, endangered and target species) (Reis-Filho *et al.*, 2019a). In this context, our results demonstrate that the insular shelf of Trindade Island comprises a mosaic of interconnected benthic habitats, which differ widely in terms of fish species richness, abundance, and biomass (Fig. 5), as well as in biomass of trophic groups (Fig. 6). The high beta diversity values (*i.e.*, dissimilarity), both overall and among benthic habitats, also support taxonomically distinct fish assemblages, which associated with the trophic structure differences, may indicate functionally distinct habitats (Moura *et al.*, 2021). In a conservation context, an integrated management approach that addresses all this diversity of habitats is essential, in order to guarantee the conservation of the biodiversity, as well as the ecological functions intrinsic to each habitat. Thus, there is an urgent need to reconfigure the recently created MPAs around the Trindade Island, which fail even to protect the relatively well known shallow reef biodiversity and endemism.

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Supporting information

Table S1: Total and mean (± standard deviation) relative abundance (MaxN) of the fish assemblages recorded in each benthic habitat from the oceanic Trindade Island.

	Reef		Rhodolith		Sand		Macroalgae		Total	
Taxa	**N = 22**		**N = 14**		**N = 21**		**N = 3**		**N = 60**	
	MaxN	**Mean ± SD**	**MaxN**	**Mean ± SD**	**MaxN**	**Mean ± SD**	**MaxN**	**Mean ± SD**	**MaxN**	**Mean ± SD**
Abudefduf saxatilis	112	5.09 ± 6.44			1	0.05 ± 0.21			113	1.88 ± 4.60
Acanthostracion polygonius							1	0.33 ± 0.47	1	0.02 ± 0.13
Acanthostracion sp.	2	0.09 ± 0.29	2	0.14 ± 0.35	1	0.05 ± 0.21			5	0.08 ± 0.28
Acanthurus bahianus	38	1.73 ± 1.71							38	0.63 ± 1.33
Acanthurus coeruleus	12	0.55 ± 0.72							12	0.20 ± 0.51
Aetobatus narinari					1	0.05 ± 0.21			1	0.02 ± 0.13
Aluterus monoceros	3	0.14 ± 0.62	12	0.86 ± 2.39	4	0.19 ± 0.85			19	0.32 ± 1.35
Aluterus scriptus	5	0.23 ± 0.52	1	0.07 ± 0.26	6	0.29 ± 0.63	2	0.67 ± 0.47	14	0.23 ± 0.53
Anisotremus surinamensis	4	0.18 ± 0.49							4	0.07 ± 0.31
Balistes vetula	31	1.41 ± 0.83	39	2.79 ± 1.78	12	0.57 ± 0.95	1	0.33 ± 0.47	83	1.38 ± 1.44
Bodianus pulchellus	3	0.14 ± 0.34							3	0.05 ± 0.22
Bodianus rufus	21	0.95 ± 0.82							21	0.35 ± 0.68
Bothus lunatus					2	0.10 ± 0.29			2	0.03 ± 0.18
Bothus sp.			4	0.29 ± 0.59			2	0.67 ± 0.94	6	0.10 ± 0.40
Cantherhines macrocerus	17	0.77 ± 0.6	15	1.07 ± 0.80	7	0.33 ± 0.56	1	0.33 ± 0.47	40	0.67 ± 0.70
Cantherhines pullus	1	0.05 ± 0.21							1	0.02 ± 0.13
Canthidermis sufflamen	13	0.59 ± 0.72	5	0.36 ± 0.48	8	0.38 ± 0.58			26	0.43 ± 0.62
Caranx crysos			3	0.21 ± 0.41	9	0.43 ± 0.66	12	4 ± 4.24	24	0.40 ± 1.34
Caranx lugubris	14	0.64 ± 0.98	19	1.36 ± 3.08	6	0.29 ± 0.76			39	0.65 ± 1.72
Caranx ruber	6	0.27 ± 0.45	27	1.93 ± 1.87	8	0.38 ± 0.79	2	0.67 ± 0.94	43	0.72 ± 1.27

Carcharhinus perezii	15	0.68 ± 0.92	2	0.14 ± 0.35	1	0.05 ± 0.21			18	0.30 ± 0.67
Centropyge aurantonotus			12	0.86 ± 1.81					12	0.20 ± 0.95
Cephalopholis fulva	180	8.18 ± 5.16	11	0.79 ± 1.37	9	0.43 ± 1.33	2	0.67 ± 0.94	202	3.37 ± 4.93
Chaetodon striatus	4	0.18 ± 0.49							4	0.07 ± 0.31
Chilomycterus reticulatus	1	0.05 ± 0.21	2	0.14 ± 0.52	1	0.05 ± 0.21			4	0.07 ± 0.31
Chromis multilineata	61	2.77 ± 6.26							61	1.02 ± 4.02
Clepticus brasiliensis	1	0.05 ± 0.21							1	0.02 ± 0.13
Congridae					2	0.10 ± 0.29			2	0.03 ± 0.18
Cryptotomus roseus							1	0.33 ± 0.47	1	0.02 ± 0.13
Dactylopterus volitans			1	0.07 ± 0.26					1	0.02 ± 0.13
Dermatolepis inermis	1	0.05 ± 0.21							1	0.02 ± 0.13
Diodon holocanthus			2	0.14 ± 0.35					2	0.03 ± 0.18
Diodon hystrix	1	0.05 ± 0.21	1	0.07 ± 0.26					2	0.03 ± 0.18
Diplodus argenteus	5	0.23 ± 0.52							5	0.08 ± 0.33
Echeneis naucrates	1	0.05 ± 0.21							1	0.02 ± 0.13
Echidna catenata	2	0.09 ± 0.42							2	0.03 ± 0.26
Elagatis bipinnulata					2	0.10 ± 0.29	1	0.33 ± 0.47	3	0.05 ± 0.22
Epinephelus adscensionis	29	1.32 ± 0.87							29	0.48 ± 0.83
Fistularia petimba			7	0.5 ± 0.73	17	0.81 ± 2.65	6	2.00 ± 2.16	30	0.50 ± 1.75
Galeocerdo cuvier	1	0.05 ± 0.21			2	0.10 ± 0.29	1	0.33 ± 0.47	4	0.07 ± 0.25
Ginglymostoma cirratum	1	0.05 ± 0.21	1	0.07 ± 0.26					2	0.03 ± 0.18
Gymnothorax moringa	17	0.77 ± 0.6	7	0.50 ± 0.73	2	0.10 ± 0.29			26	0.43 ± 0.62
Halichoeres brasiliensis	28	1.27 ± 0.62	2	0.14 ± 0.35					30	0.50 ± 0.72
Halichoeres penrosei	14	0.64 ± 2.31	1	0.07 ± 0.26					15	0.25 ± 1.43
Halichoeres poeyi	7	0.32 ± 0.76							7	0.12 ± 0.49
Halichoeres rubrovirens	6	0.27 ± 0.54	1	0.07 ± 0.26			3	1.00 ± 1.41	10	0.17 ± 0.52
Holacanthus tricolor	20	0.91 ± 0.51	7	0.50 ± 0.73					27	0.45 ± 0.62
Holocentrus adscensionis	13	0.59 ± 0.72	32	2.29 ± 8.24	1	0.05 ± 0.21			46	0.77 ± 4.10

Species										
Hybrid (*C. fulva* and *P. furcifer*)	5	0.23 ± 0.52							5	0.08 ± 0.33
Kyphosus cinerascens	1	0.05 ± 0.21							1	0.02 ± 0.13
Kyphosus spp.	212	9.64 ± 17.94	22	1.57 ± 5.39					234	3.90 ± 12.01
Malacanthus plumieri	9	0.41 ± 0.58	23	1.64 ± 1.44	16	0.76 ± 1.02	2	0.67 ± 0.94	50	0.83 ± 1.11
Malacoctenus brunoi	1	0.05 ± 0.21							1	0.02 ± 0.13
Melichthys niger	1493	67.86 ± 22.97	721	51.5 ± 26.59	542	25.81 ± 26.93	55	18.33 ± 25.93	2811	46.85 ± 31.75
Mulloidichthys martinicus	2	0.09 ± 0.42							2	0.03 ± 0.26
Mycteroperca interstitialis	2	0.09 ± 0.42							2	0.03 ± 0.26
Myrichthys breviceps	3	0.14 ± 0.34							3	0.05 ± 0.22
Myripristis jacobus	2	0.09 ± 0.29							2	0.03 ± 0.18
Opistognathus aurifrons			2	0.14 ± 0.52	2	0.10 ± 0.43			4	0.07 ± 0.36
Paranthias furcifer	21	0.95 ± 2.14	198	14.14 ± 35.59					219	3.65 ± 18.19
Pseudupeneus maculatus	18	0.82 ± 1.07	4	0.29 ± 0.59	2	0.10 ± 0.43	16	5.33 ± 7.54	40	0.67 ± 2.16
Rypticus saponaceus	7	0.32 ± 0.47	13	0.93 ± 0.80					20	0.33 ± 0.60
Scorpaena plumieri			2	0.14 ± 0.35					2	0.03 ± 0.18
Scorpaena sp.			1	0.07 ± 0.26	1	0.05 ± 0.21			2	0.03 ± 0.18
Seriola dumerili	1	0.05 ± 0.21							1	0.02 ± 0.13
Seriola rivoliana	16	0.73 ± 1.17	22	1.57 ± 1.55	27	1.29 ± 0.88	5	1.67 ± 0.94	70	1.17 ± 1.23
Serranus annularis			4	0.29 ± 0.70					4	0.07 ± 0.36
Sparisoma amplum	24	1.09 ± 1.68	32	2.29 ± 5.91	3	0.14 ± 0.47			59	0.98 ± 3.15
Sparisoma axillare	15	0.68 ± 0.70	1	0.07 ± 0.26					16	0.27 ± 0.54
Sparisoma rocha	1	0.05 ± 0.21	1	0.07 ± 0.26			1	0.33 ± 0.47	3	0.05 ± 0.22
Sphoeroides spengleri	2	0.09 ± 0.29	2	0.14 ± 0.35			4	1.33 ± 1.25	8	0.13 ± 0.46
Sphyraena barracuda	6	0.27 ± 0.45	2	0.14 ± 0.35	2	0.10 ± 0.29			10	0.17 ± 0.37
Sphyrna lewini	1	0.05 ± 0.21			4	0.19 ± 0.39			5	0.08 ± 0.28
Stegastes pictus	4	0.18 ± 0.57	13	0.93 ± 1.49					17	0.28 ± 0.88
Stegastes trindadensis	3	0.14 ± 0.46							3	0.05 ± 0.28
Thalassoma noronhanum	131	5.95 ± 9.40							131	2.18 ± 6.38

Xyrichtys novacula					55	2.62 ± 2.68	1	0.33 ± 0.47	56	0.93 ± 2.02
Xyrichtys sp.			1	0.07 ± 0.26	1	0.05 ± 0.21	1	0.33 ± 0.47	3	0.05 ± 0.22
Xyrichtys splendens							5	1.67 ± 2.36	5	0.08 ± 0.64
Total	**2670**	**121.36 ± 28.56**	**1280**	**91.43 ± 57.51**	**757**	**36.05 ± 28.38**	**125**	**41.67 ± 36.33**	**4832**	**80.53 ± 53.16**

Table S2: Generalized additive models presenting the approximate significance of smooth terms for the correlations between the PCO's axes and the depth gradient and the proportion of benthic habitats for the taxonomic structure of the fish assemblages.

PCO1	edf	Ref.df	F	P-value
s(Depth)	3.978	4.877	4.670	**0.002**
s(Reef)	10.000	10.000	9.184	**0.004**
s(Rhodolith)	1.907	2.270	2.845	**0.055**
s(Sand)	1.700	2.054	1.200	0.284
PCO2	**edf**	**Ref.df**	**F**	**P-value**
s(Depth)	4.499	5.476	3.043	**0.014**
s(Reef)	10.000	10.000	49.000	**0.051**
s(Rhodolith)	10.000	10.000	01.000	0.975
s(Sand)	4.398	5.306	39.000	**0.018**

Table S3: Top-ranked generalized additive models used to analyse the relationships between the explanatory variables and the species richness, total abundance and biomass, biomass of the trophic groups, average vulnerability, abundance and richness of endemic species.

| Dependent variables	Best model	AICc	ΔAICc	AICc weight
Richness	Reef + Sand	351.6	0	0.402
TMaxN	Reef + Rhodolith	612.8	0	0.312
TBiomass	Depth + Reef	1512.7	1.11	0.098
Trophic group				
Carnivores	Depth	1512.1	1.18	0.101
	Depth + Reef	1512.1	1.18	0.101
Mobile invertebrate feeders	Depth + Sand	1125.9	0	0.399
Omnivores	Sand	921.6	0	0.212
Planktivores	Depth	1032.2	0	0.251
Average vulnerability	Depth + Sand	357.9	0	0.260
Abundance endemic	Reef + Rhodolith	415.9	0	0.224
Richness endemic	Reef + Sand	194.7	0	0.301
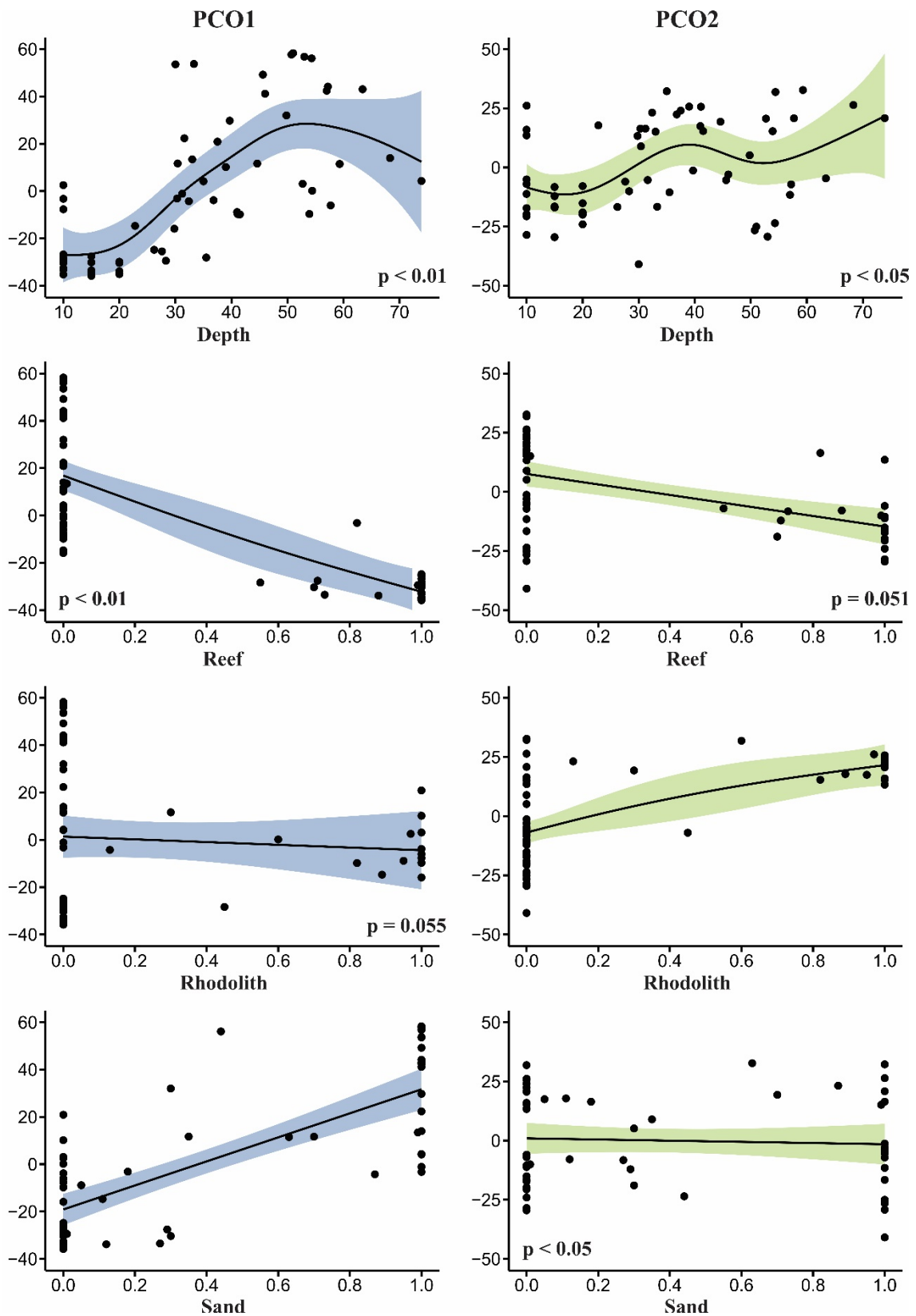
Figure S1: Generalized additive model plots showing the relationships between PCOs' axes with the depth gradient and the proportion of each benthic habitat. Confidence limits of 95% are shown in blue and green. P values indicate significant relationships.

Capítulo 3 - Mesophotic ecosystems at Fernando de Noronha Archipelago, Brazil (Southwestern Atlantic), reveal unique ichthyofauna and need for conservation

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Mesophotic ecosystems at Fernando de Noronha Archipelago, Brazil (Southwestern Atlantic), reveal unique ichthyofauna and need for conservation

Caio R. Pimentel[1,2], Luiz A. Rocha[2], Bart Shepherd[2], Tyler A. Y. Phelps[2], Jean-Christophe Joyeux[1], Agnaldo S. Martins[1], Carlos Eduardo Stein[3], João B. Teixeira[1,3], João Luiz Gasparini[1,4], José Amorim Reis-Filho[5], Ricardo C. Garla[6], Ronaldo B. Francini-Filho[7], Stephanie D. T. Delfino[1], Thayná J. Mello[8], Tommaso Giarrizzo[9] and Hudson T. Pinheiro[2,3]

Correspondence:
Caio R. Pimentel
caiopimentelr@gmail.com

Although several studies on the ichthyofauna of the Fernando de Noronha Archipelago have been carried out, its mesophotic fish diversity has never been surveyed before. Here we used SCUBA and technical rebreather diving, baited remote underwater videos and remotely operated vehicle to record shallow (≤ 30 m depth) and mesophotic (31 to 150 m depth) fishes. Nineteen fish species belonging to 14 families are reported here as new records, representing an increase of 8.2% in marine fish richness for the region, which now has a total of 250 species and 77 families. These new records include four potential new species and highlight the importance of surveying mesophotic ecosystems, even in well studied sites. Our results also emphasize the need for protection and attention to the unique ichthyofauna found at mesophotic depths.

Keywords: BRUVS, Marine Protected Area, Oceanic Island, Rebreather, Remotely Operated Vehicle.

1 Programa de Pós-Graduação em Oceanografia Ambiental, Dep. de Oceanografia e Ecologia, Univ. Federal do Espírito Santo, Av. Fernando Ferrari, 514, Goiabeiras, 29075-910 Vitória, ES, Brazil. (CRP) caiopimentelr@gmail.com, (JCJ) jean.joyeux@ufes.br, (ASM) agnaldo.ufes@gmail.com, (JBT) jboceano@gmail.com, (JLG) gaspa.vix@gmail.com, (SDTD) dtdstephanie@gmail.com.

2 California Academy of Sciences, 94118 San Francisco, CA, USA. (LAR) lrocha@calacademy.org, (BS) bshepherd@calacademy.org, (TP) tphelps@calacademy.org, San Francisco State University, 94132 San Francisco, CA, USA, (HTP) htpinheiro@gmail.com.

3 Associação Ambiental Voz da Natureza, Rua Coronel Shuwab Filho, 104, 29052-070 Vitória, ES, Brazil. (CES) stein.ce@gmail.com.

4 Programa de Pós-Graduação em Ciências Ambientais e Conservação, Instituto de Biodiversidade e Sustentabilidade, Univ. Federal do Rio de Janeiro, 29910-970 Macaé, RJ, Brazil.

5 ICHTUS Soluções em Meio Ambiente, R. Dep. Herculano Menezes, 10, 41335-400 Salvador, BA, Brazil. (JARF) amorim@icthusambiental.com.br.

6 Departamento de Botânica e Zoologia, Univ. Federal do Rio Grande do Norte, 59078-970 Natal, RN, Brazil. (RCG) rgarla@hotmail.com.

7 Centro de Biologia Marinha, Univ. de São Paulo, 11612-109 São Sebastião, SP, Brazil. (RBFF) francinifilho@usp.br.

8 Programa de Pós-Graduação em Ecologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, 59072-970 Natal, RN, Brazil (TJM) thaynajm@gmail.com.

9 Núcleo de Ecologia Aquática e Pesca da Amazônia, Univ. Federal do Pará, Av. Perimetral, 2651, Terra Firme, 66040-170 Belém, PA, Brazil. (TG) tgiarrizzo@gmail.com.

Apesar de muitos estudos sobre a ictiofauna do Arquipélago de Fernando de Noronha terem sido realizados, sua diversidade de peixes mesofóticos nunca foi estudada antes. Neste estudo utilizamos mergulho autônomo e mergulho técnico, vídeos subaquáticos remotos com isca e veículo operado remotamente para registrar peixes de ecossistemas rasos (≤ 30 m de profundidade) e mesofóticos (31 a 150 m de profundidade). Dezenove espécies de peixes pertencentes a 14 famílias são apresentadas aqui como novos registros, representando um aumento de 8,2% na riqueza de peixes marinhos da região, que agora possui um total de 250 espécies e 77 famílias. Esses novos registros incluem quatro prováveis novas espécies e reforçam a importância de estudos em ecossistemas mesofóticos. Nossos resultados também enfatizam a necessidade de proteção e atenção à essa ictiofauna única encontrada nesses ecossistemas profundos.

Palavras-chave: Área Marinha Protegida, BRUVS, Ilha Oceânica, Rebreather, Veículo Operado Remotamente.

INTRODUCTION

Due to their geographical isolation, oceanic islands are often unique environments with biodiversity characterized by high endemism (Vaske Jr *et al.*, 2005; Macieira *et al.*, 2015; Kosaki *et al.*, 2017; Pinheiro *et al.*, 2018a). These environments function as true natural laboratories for evolutionary and ecological studies (Pinheiro *et al.*, 2017) and are important for understanding patterns of species dispersal and establishment (Losos, Ricklefs, 2009). Recent studies are revealing many new species and new occurrences, filling gaps in the biodiversity knowledge and increasing our understanding about the biogeographic patterns of oceanic islands (*e.g.*, Simon *et al.*, 2013; Macieira *et al.*, 2015; Carvalho-Filho *et al.*, 2016; Pinheiro *et al.*, 2018a).

Knowledge about reef fish biodiversity and biogeographic patterns of South Atlantic oceanic islands has steadily increased over the past two decades (*e.g.*, Batista *et al.*, 2012; Wirtz *et al.*, 2017; Hachich *et al.*, 2015; Pinheiro *et al.*, 2015, 2018a; Quimbayo *et al.*, 2019). However, mesophotic ecosystems (between 31 – 150 m depth) remain largely unknown and are only now receiving some scientific attention (*e.g.*, Rocha *et al.*, 2018). Even though these ecosystems have been recognized since the 19th century (Sinniger *et al.*, 2016), the first studies in Brazil date back only to the 1960s (Francini-Filho *et al.*, 2019). Systematic studies of the mesophotic ecosystems have however increased worldwide (*e.g.*, Rosa *et al.*, 2015; Andradi-Brown *et al.*, 2016; Pyle *et al.*, 2016; Simon *et al.*, 2016; Rocha *et al.*, 2018; Pinheiro *et al.*, 2019; Pimentel *et al.*, 2020). Such pioneer studies have provided important baseline information, such as richness and diversity of species, and form the basis for more complex ecological and evolutionary studies.

Fernando de Noronha Archipelago (FN) is the most accessible oceanic island in Brazil, as it is relatively close to the mainland and has an airport. It also offers logistical support due to the presence of a research station and several dive shops and boats. Part of the Archipelago comprises a no-take Marine Protected Area (MPA), the Fernando de

Noronha Marine National Park, which protects near-shore ecosystems (*e.g.*, tidepools, rocky shores, and reefs) to around 50 m depth. Most of the mesophotic ecosystems are located in a sustainable use MPA, the Fernando de Noronha – Rocas – São Pedro and São Paulo Environmental Protected Area, where fishing is allowed with some restrictions (ICMBio, 2017). Nearly all biodiversity and ecological studies of FN's ichthyofauna to date have been carried out in the intertidal (*e.g.*, Andrades *et al.*, 2018; Rodríguez-Rey *et al.*, 2018) and shallow (≤ 20 m deep) environments (*e.g.*, Krajewski, Floeter, 2011; Medeiros *et al.*, 2011; Ilarri *et al.*, 2017; Smith-Vaniz *et al.*, 2018; but see Garla *et al.*, 2006; Sazima *et al.*, 2010; Afonso *et al.*, 2017).

Therefore, to fill the knowledge gap about fish biodiversity from mesophotic ecosystems of the Fernando de Noronha Archipelago, we carried out a large-scale survey using sampling techniques including technical rebreather diving, baited remote underwater stereo-video systems (stereo-BRUVS) and remotely operated vehicles (ROVs). Here, we present new records and new species of fishes discovered during our expedition, discuss aspects related to the island's biodiversity and biogeography, and highlight the need to protect insular mesophotic ecosystems.

MATERIAL AND METHODS

Study area. Fernando de Noronha Archipelago is located 345 km off the north-eastern Brazilian coast (03°50'S 32°25'W), on the Fernando de Noronha Submarine Ridge (Fig. 1). It is the largest Brazilian oceanic archipelago, composed by a volcanic island (16.4 km^2) and 18 small islets (Almeida, 2006). The shallow reefs (≤ 30 m depth) are mainly composed by volcanic rocks predominantly covered by algal turfs and brown macroalgae, with low coral cover (Krajewski, Floeter, 2011). Following the pattern of low diversity typical of Atlantic oceanic islands (Ferreira *et al.*, 2004; Floeter *et al.*, 2008), the fish assemblages are dominated by a few very abundant species (Krajewski, Floeter, 2011; Ilarri *et al.*, 2017). Compared to shallow reefs, the upper mesophotic reefs (31 to 60 m depth) show higher cover of sponges and the scleractinian coral *Montastraea cavernosa* (Linnaeus, 1767) (Matheus *et al.*, 2019). A mosaic of habitats such as patch reefs, sand bottoms and rhodolith beds compose the middle mesophotic zone (61 to 90 m depth; Fig. 2). Below 90 m depth, the edge of the insular shelf followed by a steep wall characterizes the lower mesophotic zone (91 to 150 m; Fig. 3). A strong thermocline is found just below the shelf edge, where the temperature drops from ~27 to ~14 °C. The ecosystem at the lower mesophotic zone is highly complex, formed by rocky reefs covered mostly by crustose coralline algae, black corals and sponges.

Regarding environmental management, the Archipelago encompasses two different types of Marine Protected Areas, the no-take zone of the Fernando de Noronha Marine National Park (Brasil, 1988), and the sustainable use zone of the Fernando de Noronha – Rocas – São Pedro and São Paulo Environmental Protected Area (Brasil, 1986) (Fig. 1). The Marine National Park comprises about 70% of the main island (*i.e.*, all the windward coast and part of the leeward coast), all smaller islands and extends to around the 50 m isobath, with fishing prohibited and tourism regulated (Brasil, 1988; Ibama, 1990). The area of sustainable use aims to make human occupation, tourism and fishing compatible with environmental protection and preservation of natural
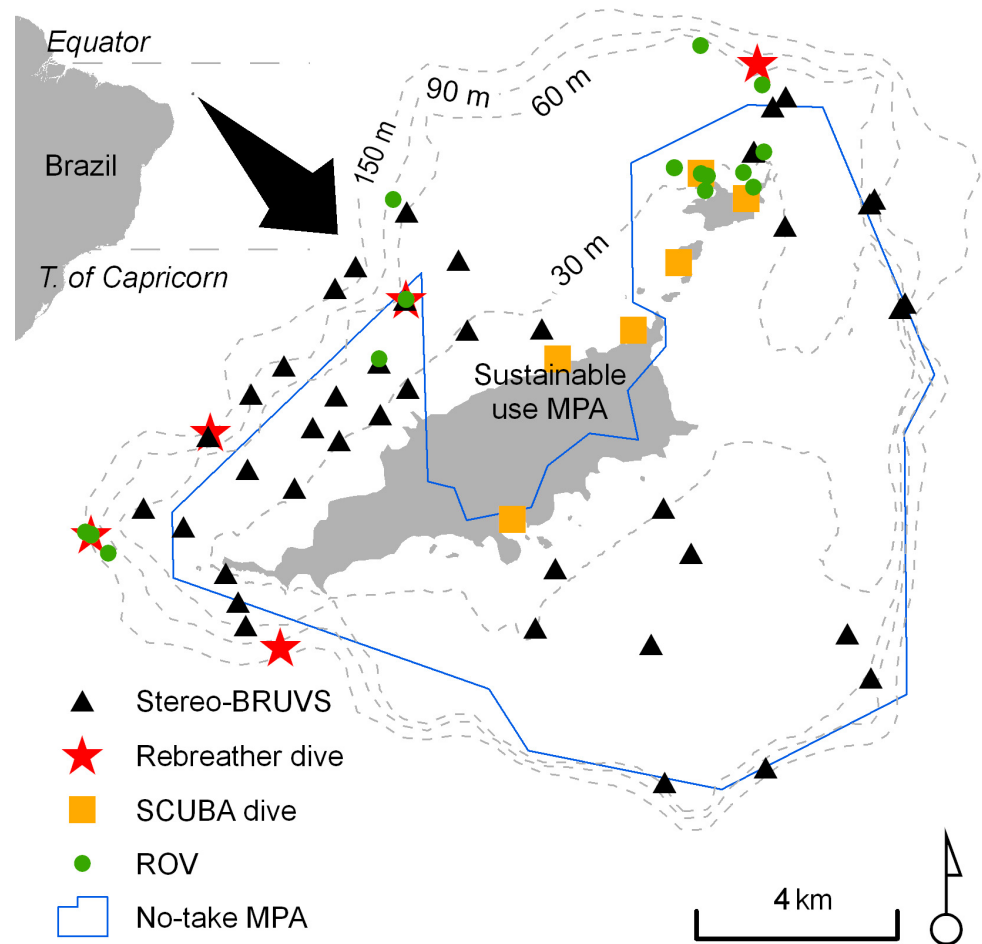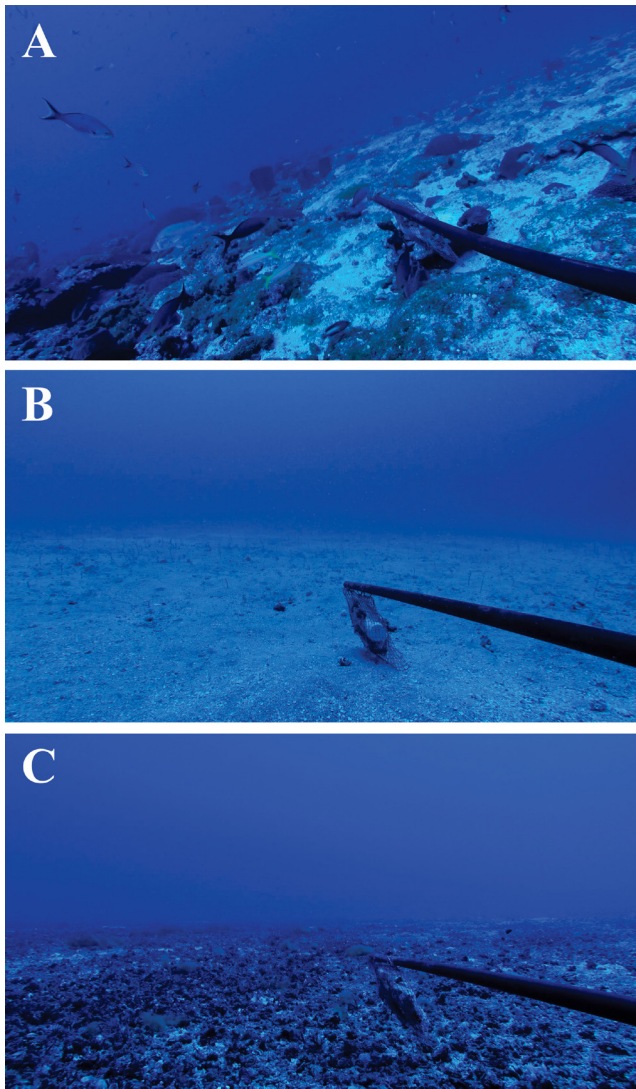
FIGURE 1 | Location of the Fernando de Noronha Archipelago, Brazil (South-western Atlantic). Blue line indicates the area of the Marine National Park of Fernando de Noronha (no-take MPA). Dashed lines indicate the 30, 60, 90 and 150 m isobaths. Black triangles, red stars, golden squares and green dots indicate the position of stereo-BRUVS deployments, rebreather dives, SCUBA dives and ROV footages, respectively.

resources (Brasil, 1986; ICMBio, 2017). The use of trawl nets, longlines, drift nets and spears, as well as the capture of sharks, rays and parrotfishes are not allowed (Brasil, 1986; ICMBio, 2017).

Sampling procedures. The data presented here were obtained during a 15-day expedition in October 2019. Fish were recorded with SCUBA (*ca*. 30 h sampling in the euphotic zone) and technical rebreather diving (*ca*. 6 h sampling in the upper and 2 h in the lower mesophotic zone), remotely operated vehicle (ROV – *ca*. 8 h of footage) and baited remote underwater stereo-video systems (stereo-BRUVS – 42 deployments of 1 h footage each). Some fishes were collected using hand-nets and pole-spears, and voucher specimens were deposited in the ichthyological collection of the Universidade Federal do Espírito Santo (CIUFES; see Tab. 1 for catalogue numbers).

Data analysis. Species identification was performed using taxonomic keys (*e.g.*,

FIGURE 2 | Middle mesophotic (61 to 90 m depth) mosaic of habitats sampled with stereo-BRUVS around the Fernando de Noronha Archipelago. **A.** Patch reefs; **B.** Sand bottoms; and **C.** Rhodoliths beds.
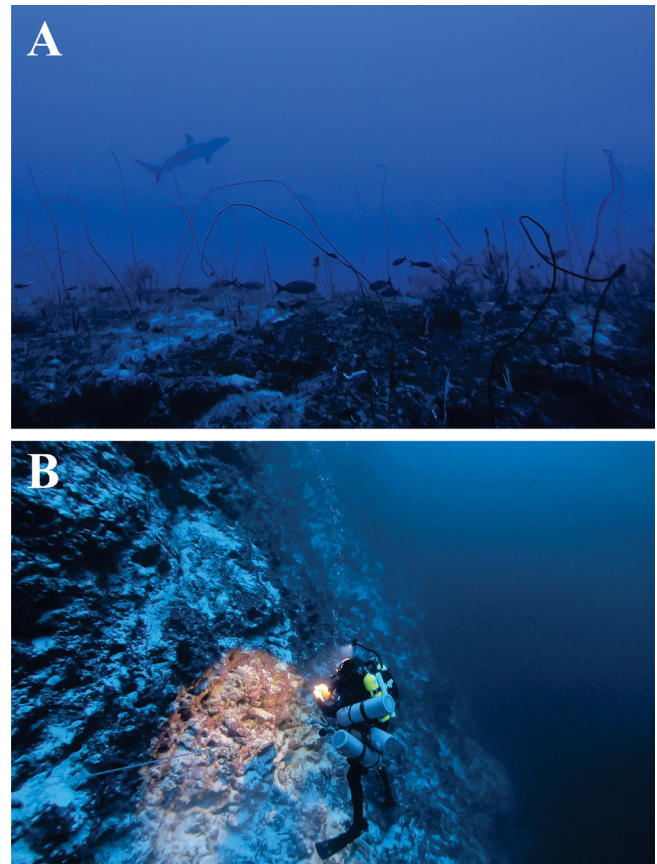
FIGURE 3 | Lower mesophotic (below 90 m depth) ecosystems explored through technical rebreather diving around the Fernando de Noronha Archipelago. **A.** The insular shelf edge; and **B.** The steep wall.

Menezes, 1971; Knudsen, Clements, 2013) and, when necessary, comparing our collected specimens with others available at the ichthyological collection of CIUFES. We then classified the species according to: 1) depth zone of the record, *i.e.*, euphotic (≤ 30 m) or mesophotic (> 30 – 150 m), 2) habitat (reef or rhodolith), 3) the type of the record (collected, photographed or filmed with ROV or stereo–BRUVS), 4) geographic range (following Pinheiro *et al.*, 2018a), and 5) conservation status, following the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (https://www.iucnredlist.org).

RESULTS

Nineteen fish species belonging to 14 families are reported here as new records for FN (Tab. 1). The most speciose families were Kyphosidae and Serranidae, with three new records each, followed by Pomacentridae, with two new records. Fourteen new records (74% of total) were from the mesophotic ecosystems (Figs. 4–5; Tab. 1) and five (26%) from the euphotic zone (Fig. 6; Tab. 1). Seven species are distributed throughout the Western Atlantic, and the three Kyphosidae are circumtropical species. Three other species are amphi–Atlantic, one of which also occurs in the Mediterranean (*Balistes capriscus* Gmelin, 1789). *Aulotrachichthys argyrophanus* (Woods, 1961) occurs only in the South–western Atlantic and *Chromis scotti* Emery, 1968 is found in the Caribbean Sea and Northern Brazil (Moura *et al.*, 1999). Four new records are probable new species (*Synodus* sp., *Scorpaena* sp., *Psilotris* sp., and *Tosanoides* sp.) with unknown geographic range (Fig. 4E–G; Tab. 1). In terms of conservation status, only *B. capriscus* is listed as threatened, being currently classified as vulnerable in the IUCN Red List (Liu *et al.*, 2015).

TABLE 1 | New records of fishes from Fernando de Noronha Archipelago, north-eastern Brazil. Families are presented in phylogenetic order according to Nelson *et al.* (2016). Information about depth zone, habitat, record type and voucher of the new records, as well as distribution and conservation status of the species are presented. Depth zone of the record: euphotic (≤ 30 m deep) and mesophotic (31 to 150 m deep). Geographic range: amphi-Atlantic (AA), Caribbean Sea (CS), Circumtropical (CT), Mediterranean (M), Northern Brazil (NB), South-western Atlantic (SW) and Western Atlantic (WA). International Union for Conservation of Nature and Natural Resources (IUCN) conservation status: data deficient (DD), least concern (LC), and vulnerable (VU); N/A: not applicable.

| Family	Species	Depth zone	Habitat	Record type	Voucher	Geographic range	Conservation status
Synodontidae	*Synodus* sp.	Mesophotic	Reef	Photo	Fig. 4	Unknown	N/A
Holocentridae	*Corniger spinosus* Agassiz, 1831	Mesophotic	Reef	Collected / Photo	CIUFES 3922 / Fig. 5	AA	LC
Trachichthyidae	*Aulotrachichthys argyrophanus* (Woods, 1961)	Mesophotic	Reef	Collected / Photo	CIUFES 3909 / Fig. 5	SW	DD
Apogonidae	*Apogon pseudomaculatus* Longley, 1932	Euphotic	Reef	Collected	CIUFES 3957	WA	LC
Gobiidae	*Psilotris* sp.	Mesophotic	Reef	Photo	Fig. 4	Unknown	N/A
Pomacentridae	*Chromis enchrysura* Jordan & Gilbert, 1882	Mesophotic	Reef	Collected / Photo	CIUFES 3902 / Fig. 4	AA	LC
Pomacentridae	*Chromis scotti* Emery, 1968	Mesophotic	Reef	Photo	Fig. 4	CS / NB	LC
Syngnathidae	*Cosmocampus profundus* (Herald, 1965)	Mesophotic	Rhodolith	Stereo-BRUVS	Fig. 4	WA	DD
Labridae	*Decodon puellaris* (Poey, 1860)	Mesophotic	Reef	Collected	CIUFES 3914 / Fig. 5	WA	LC
Kyphosidae	*Kyphosus bigibbus* Lacepède, 1801	Euphotic	Reef	Photo	Fig. 6	CT	LC
Kyphosidae	*Kyphosus cinerascens* (Forsskål, 1775)	Euphotic	Reef	Photo	Fig. 6	CT	LC
Kyphosidae	*Kyphosus vaigiensis* (Quoy & Gaimard, 1825)	Euphotic	Reef	Collected / Photo	CIUFES 4050 / Fig. 6	CT	LC
Serranidae	*Pronotogrammus martinicensis* (Guichenot, 1868)	Mesophotic	Reef	Collected / Photo	CIUFES 3939 / 3960 / Fig. 5	WA	LC
Serranidae	*Pseudogramma gregoryi* (Breder, 1927)	Euphotic	Rhodolith	Collected / Photo	CIUFES 4029 / Fig. 6	WA	LC
Serranidae	*Tosanoides* sp.	Mesophotic	Reef	Collected	CIUFES 3892 / 3893 / 3894 / 3912 / 3913 / 3952	Unknown	N/A
Chaetodontidae	*Prognathodes guyanensis* (Durand, 1960)	Mesophotic	Reef	Collected / Photo / ROV	CIUFES 3959 / Fig. 4	WA	LC
Lutjanidae	*Lutjanus buccanella* (Cuvier, 1828)	Mesophotic	Rhodolith	Stereo-BRUVS	Fig. 4	WA	DD
Scorpaenidae	*Scorpaena* sp.	Mesophotic	Reef	Photo	Fig. 4	Unknown	N/A
Balistidae	*Balistes capriscus* Gmelin, 1789	Mesophotic	Rhodolith	Stereo-BRUVS	Fig. 3	AA / M	VU

FIGURE 4 | New records of fishes at the mesophotic ecosystems. **A.** *Chromis enchrysura* (~ 10 cm total length); **B.** *Balistes capriscus* (~ 30 cm total length); **C.** *Chromis scotti* (~ 7.5 cm total length); **D.** *Prognathodes guyanensis* (~ 15 cm total length); **E.** *Synodus* sp. (~ 15 cm total length); **F.** *Scorpaena* sp. (~ 7.5 cm total length); **G.** *Psilotris* sp. (~ 5 cm total length); and **H.** *Cosmocampus profundus* (white arrow; ~ 15 cm total; *I. Lutjanus buccanella* (~ 50 cm total length). Photos by L. A. Rocha (**A**, **C**-**G**) and stereo-BRUVS (**B**, **H** and **I**). *Tosanoides* sp. is under description and its picture is not shown.
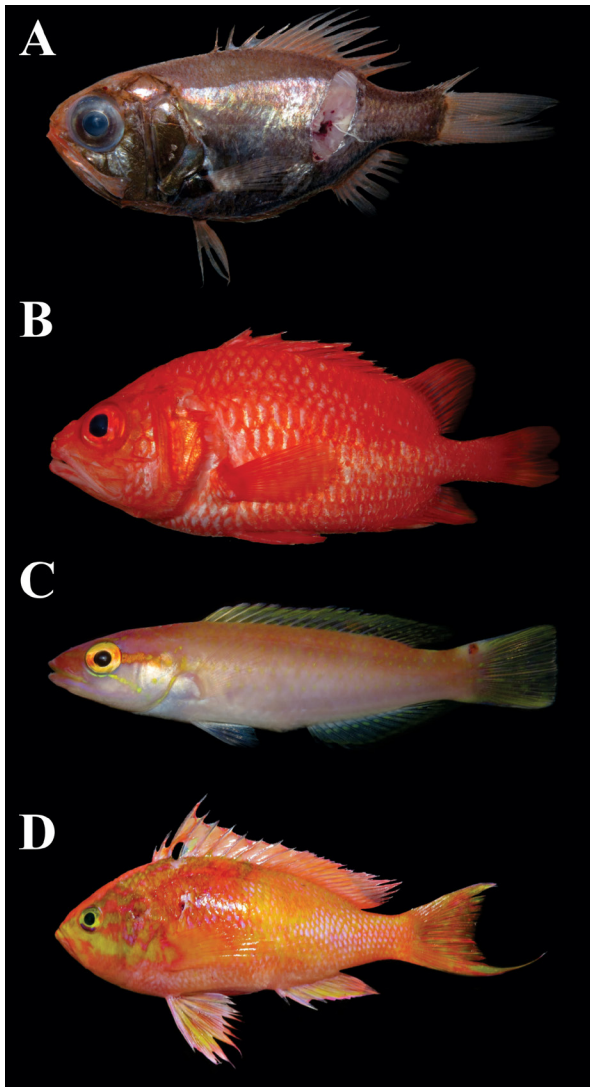
FIGURE 5 | New records of fishes from the mesophotic ecosystems collected and photographed in aquarium. **A.** *Aulotrachichthys argyrophanus* (~ 6.5 cm total length; CIUFES 3909); **B.** *Corniger spinosus* (~ 15 cm total length; CIUFES 3922); **C.** *Decodon puellaris* (~ 7.5 cm total length; CIUFES 3914); and **D.** *Pronotogrammus martinicensis* (~ 20 cm total length; CIUFES 3939 / 3960). Photos by J. L. Gasparini.
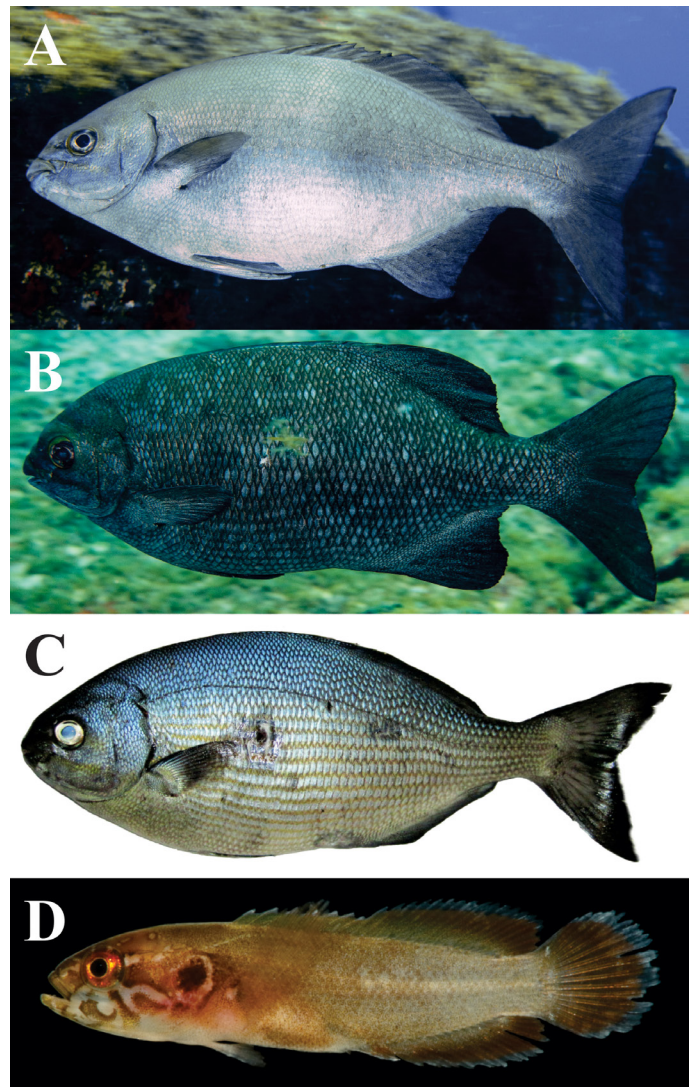
FIGURE 6 | New records of fishes from the euphotic ecosystems. **A.** *Kyphosus bigibbus* (~ 25 cm total length); **B.** *Kyphosus cinerascens* (~ 25 cm total length); **C.** *Kyphosus vaigiensis* (~ 25 cm total length; CIUFES 4050); and **D.** *Pseudogramma gregoryi* (~ 6.5 cm total length; CIUFES 4029). Photos **A**, **B** and **C** by J. L. Gasparini and photo **D** by R. M. Macieira. *Apogon pseudomaculatus* (CIUFES 3957) is not shown.

DISCUSSION

Fernando de Noronha Archipelago harbours the greatest richness of marine fish among the oceanic islands of the South Atlantic (Floeter *et al*., 2008; Pinheiro *et al*., 2018a). The 19 new records presented here represent an increase of 8.2% in its marine ichthyofauna, now composed of 250 species and 77 families. Fernando de Noronha Archipelago is now between 22% and 36% richer, in fishes, than Trindade Island, Santa Helena Island,

Ascension Island, Rocas Atoll and St. Paul's Archipelago (see Wirtz *et al.*, 2017; Pinheiro *et al.*, 2018a, 2020; Brown *et al.*, 2019). This higher fish richness is probably related to FN being the largest and oldest island, situated relatively close to the continental shore, and being the most studied oceanic island in Brazil.

Even though we have also explored shallow ecosystems, this is the first systematic survey of the fish biodiversity of FN mesophotic ecosystems. Despite the logistical difficulties and risks associated with this type of exploration, our effort was rewarded as most of the new records (74%) came from the mesophotic ecosystems. In fact, we still know very little about mesophotic reefs in comparison to shallow ones, albeit they represent about 80% of the potential reef habitat worldwide (Pyle, Copus, 2019). Although they have been considered potential refuges for shallow water organisms and less susceptible to human and natural impacts, mesophotic reefs are increasingly being recognized as unique ecosystems, home to largely distinct and independent communities that are also impacted and in need of protection as much as shallow reefs (Rocha *et al.*, 2018; Pyle, Copus, 2019). As reported elsewhere (Rocha *et al.*, 2018), we found plastic trash and fishing debris (in 6% and 18% of the visual censuses, respectively) in mesophotic ecosystems explored around FN (Fig. 7), evidence of human impacts, which are even more noticeable in the intertidal and shallow ecosystems. Despite an island–wide ban on single use plastics (Pernambuco, 2018) and the presence of a program to eliminate plastic bags from the island, most of the goods that can be obtained in stores come wrapped in plastic.
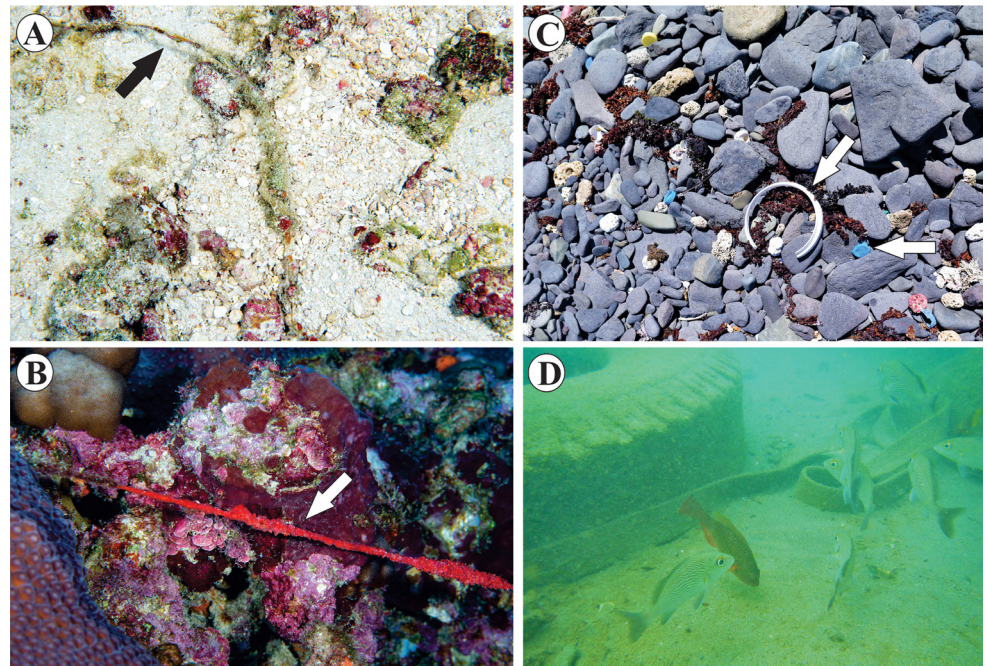
FIGURE 7 | Evidence of human impacts (arrows) by fishing debris, plastics and other trash found in the ecosystems explored around the Fernando de Noronha Archipelago. **A.** and **B.** Mesophotic (> 30 m deep); **C.** Intertidal; and **D.** Shallow ecosystems (≤ 30 m deep). Photos **A** and **B** by L. A. Rocha and photos **C** and **D** by J. L. Gasparini.

Several studies addressing the diversity, biology and ecology of the shallow water fish assemblages of FN have been carried out (*e.g.*, Krajewski, Floeter, 2011; Ilarri *et al.*, 2017). However, even for the relatively well explored euphotic zone, we obtained new records such as *Apogon pseudomaculatus* Longley, 1932 and *Pseudogramma gregoryi* (Breder, 1927) (Tab. 1), reinforcing the need for further studies and a better understanding of the local cryptobenthic fish diversity. Currently, the cryptobenthic fishes represent only about 17% (~ 42 species) of the ichthyofauna of FN. Due to its small size and cryptic behaviour, most cryptobenthic fishes cannot be properly accessed by standard technics (*e.g.*, underwater visual censuses and videos). Thus, in order to increase our knowledge of this hidden fish diversity, the scientific use of anaesthetics to collect specimens should be promoted (Collette *et al.*, 2003; Williams *et al.*, 2010). The importance of these underestimated assemblages of cryptobenthic fishes goes far beyond diversity. In a recent study, Brandl *et al.* (2019) showed that through their extraordinary larval dynamics, rapid growth, and extreme mortality, the hyperdiverse assemblages of abundant, small, and short-lived cryptobenthic species appear to be a critical functional group on the trophodynamics of coral reefs.

Regarding the species registered in the mesophotic ecosystems, we emphasize that this is only the second record of the genus *Tosanoides* for the Atlantic Ocean, with a new species previously recorded on mesophotic reefs of St. Paul's Archipelago (Pinheiro *et al.*, 2018b). The present record corroborates the hypothesis that this genus is probably widely distributed in peripheral Atlantic sites (Pinheiro *et al.*, 2018b). Differences in colour pattern suggest *Tosanoides* sp. from FN might be a new species, different from *Tosanoides aphrodite* Pinheiro, Rocha & Rocha, 2018, and genetic analyses are being carried out to confirm the species identity. Similarly, *Aulotrachichthys argyrophanus* (Woods, 1961) was previously known only from the type locality in the Southwest Atlantic, on the continental shelf slope off the Amazon River mouth, northern Brazil (Froese, Pauly, 2019; Moore, 2019). Finally, *Cosmocampus profundus* (Herald, 1965) is for the first time recorded in Brazil, previously known to occur only from eastern Florida to south Caribbean (Robertson, Van Tassell, 2019).

Another curious new record is the common *B. capriscus*, an amphi–Atlantic species widespread in the Atlantic Ocean (Liu *et al.*, 2015; Froese, Pauly, 2019), which is also present at Trindade Island (Miranda Ribeiro, 1919) and St. Paul's Archipelago (Pinheiro *et al.*, 2020). At FN and St. Paul's Archipelago, the species has been observed several times in groups of up to four individuals. In contrast, the only record of this species on Trindade Island dates from 1916, when one individual was collected during a scientific expedition by the National Museum of Rio de Janeiro (Miranda-Ribeiro, 1919). All recent extensive samplings around Trindade, in both euphotic and mesophotic ecosystems, including the use of technical dive (Pereira-Filho *et al.*, 2011) and BRUVS (Pimentel *et al.*, 2020), yielded no record for this species. New records of common and large fishes such as *B. capriscus* may result from the attractiveness of the BRUVS bait and sampling in the mesophotic ecosystems, however this does not appear to be the case here. Alternatively, this could represent a recent colonization and successful establishment in these oceanic islands (*e.g.*, Mazzei *et al.*, 2019). These observations involving colonization, establishment and extinction are in accordance with the Theory of Island Biogeography (*e.g.*, Pinheiro *et al.*, 2017), representing the main drivers balancing island diversity.

Other probable new species include *Psilotris* sp., *Scorpaena* sp. and *Synodus* sp., which have been only photographed. The goby resembles a *Psilotris* species (Luke Tornabene, 2020, pers. comm.), both in colour/appearance and in meristics: VII, 10 dorsal fin spines, with no visible scales and split pelvic fins. *Psilotris* sp. is closest in appearance to *Psilotris kaufmani* Greenfield, Findley & Johnson, 1993, but differs from it in having a unique body coloration, and not having a dark upper pectoral fin. The scorpaenid seems to belong to the genus *Scorpaena* (Alfredo Carvalho-Filho, 2020, pers. comm.) because the specimen has several pectoral fin rays well branched, especially the lower ones, whereas species of *Pontinus* have all rays unbranched. This *Scorpaena* sp. is different from the undescribed St. Paul's Archipelago species (Feitoza *et al.*, 2003; CIUFES 0349), which has a snout larger than the eye. The synodontid is different from all other species occurring in Brazil (Alfredo Carvalho-Filho, 2020, pers. comm.). It differs from *Synodus synodus* (Linnaeus, 1758) in not having a characteristic black spot at the tip of the snout; from *Synodus intermedius* (Spix & Agassiz, 1829) and *Synodus macrostigmus* Frable, Luther & Baldwin, 2013 in not having a dark spot at upper right corner of the operculum; and from *Synodus poeyi* Jordan, 1887 in overall coloration, the latter being bluish. Therefore, these three species are likely undescribed. Considering that four possible new species were disclosed in two hours of exploration of the lower mesophotic ecosystems (four divers with an average of 30 min each), the discovery rate herein reported is of two new species per hour, which is consistent with recent findings in other unexplored mesophotic ecosystems of the world (Pinheiro *et al.*, 2019; Pyle *et al.*, 2019).

Here we have shown that the mesophotic ecosystems and the shallow cryptobenthic ichthyofauna need to be better studied, even in well-studied oceanic islands such as FN. We emphasize the need for protection of the mesophotic ecosystems of FN, looking for ways to conciliate activities such as fishing and tourism, with the preservation of the unique biodiversity and ecosystems found at mesophotic depths. As with shallow reefs, significant progress in the conservation of mesophotic ecosystems of FN could be reached by expanding the no-take zone of the Marine National Park beyond the 50 m isobath, or by creating some fishing exclusion zones inside the sustainable use MPA (Araújo, Bernard, 2016).

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AUTHOR'S CONTRIBUTION ⓒ

Caio R. Pimentel: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing–review and editing.

Luiz A. Rocha: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing–review and editing.

Bart Shepherd: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing–review and editing.

Tyler A. Y. Phelps: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing–review and editing.

Jean–Christophe Joyeux: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing–review and editing.

Agnaldo S. Martins: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing–review and editing.

Carlos Eduardo Stein: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing–review and editing.

João B. Teixeira: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing–review and editing.

João Luiz Gasparini: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing–review and editing.

José Amorim Reis–Filho: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing–review and editing.

Ricardo C. Garla: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software,

Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

Ronaldo B. Francini-Filho: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

Stephanie D. T. Delfino: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

Thayná J. Mello: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

Tommaso Giarrizzo: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

Hudson T. Pinheiro: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

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ETHICAL STATEMENT

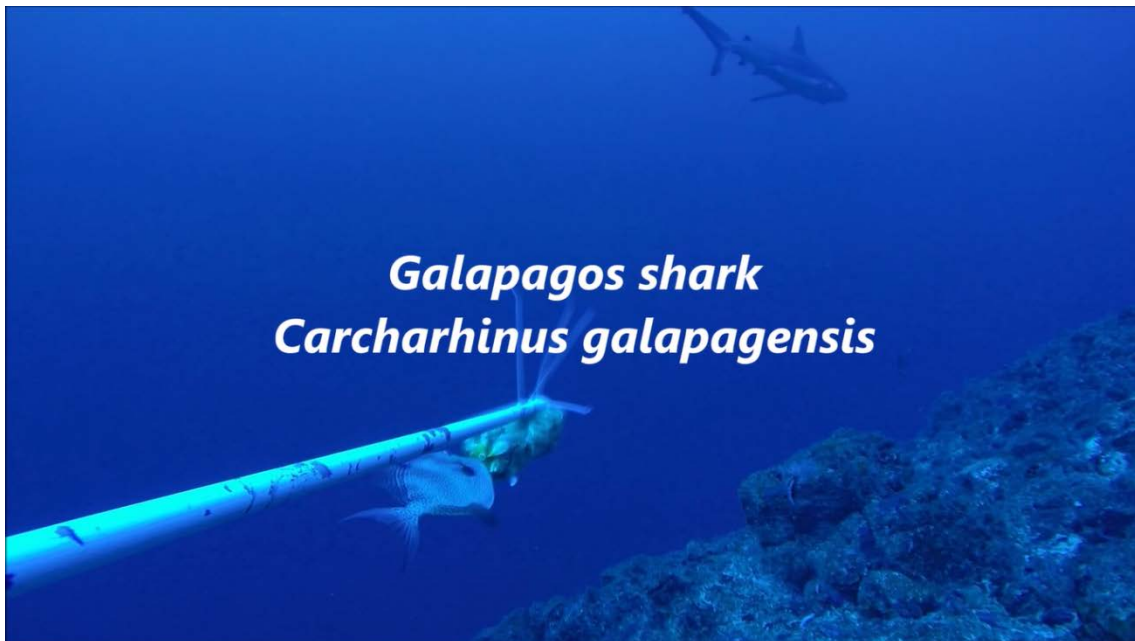The Brazilian Environmental Agency (ICMBio, license #64991-3).

COMPETING INTERESTS

The authors declare no competing interests.

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Capítulo 4 - BRUVS reveal locally extinct shark and the way for shark monitoring in Brazilian oceanic islands

BRIEF COMMUNICATION

BRUVS reveal locally extinct shark and the way for shark monitoring in Brazilian oceanic islands

Caio R. Pimentel[1] | Ryan Andrades[1] | Carlos E. L. Ferreira[2] |
Otto B. F. Gadig[3] | Euan S. Harvey[4] | Jean-Christophe Joyeux[1] |
Tommaso Giarrizzo[5]

[1]Programa de Pós-Graduação em Oceanografia Ambiental, Departamento de Oceanografia, Universidade Federal do Espírito Santo, Vitória, Brazil

[2]Departamento de Biologia Marinha, Universidade Federal Fluminense, Niterói, Brazil

[3]Instituto de Biociências, Universidade Estadual Paulista, São Paulo, Brazil

[4]School of Molecular and Life Sciences, Curtin University, Perth, Western Australia, Australia

[5]Universidade Federal do Pará (UFPA), Núcleo de Ecologia Aquática e Pesca da Amazônia, Aquatic Ecology Group's Lab, Belém, Brazil

Correspondence

Caio R. Pimentel, Departamento de Oceanografia, Universidade Federal do Espírito Santo, Avenida Fernando Ferrari, 514, Goiabeiras, 29075-910 Vitória, ES, Brazil.
Email: caiopimentelr@gmail.com

ABSTRACT

Here we present records of sharks obtained using baited remote underwater stereo-video systems (stereo-BRUVS) at two Brazilian oceanic islands. Fourteen of the 60 deployments recorded 19 sharks in Trindade Island. In Saint Peter and Saint Paul Archipelago (SPSPA), two pelagic and two demersal deployments recorded two and one shark, respectively, including the locally extinct Galapagos shark *Carcharhinus galapagensis*. Stereo-BRUVS should be considered as adjuncts to other non-invasive methods to monitor shark populations.

KEYWORDS

Carcharhinus galapagensis, conservation status, elasmobranch, reef fish, south-western Atlantic Ocean

One hundred and sixty-five species of elasmobranchs have been recorded off the Brazilian coast (Rosa & Gadig, 2014). Although representing only *c.* 13% of the fish species (Menezes *et al.*, 2003), sharks and rays species account for 55% of the endangered Brazilian marine ichthyofauna (ICMBio, 2018), with 54 species classified in the IUCN threat categories: Vulnerable, Endangered or Critically Endangered. The main challenge for assessing population trends and conservation statuses of many shark species is the lack of population data (Rosa & Gadig, 2014).
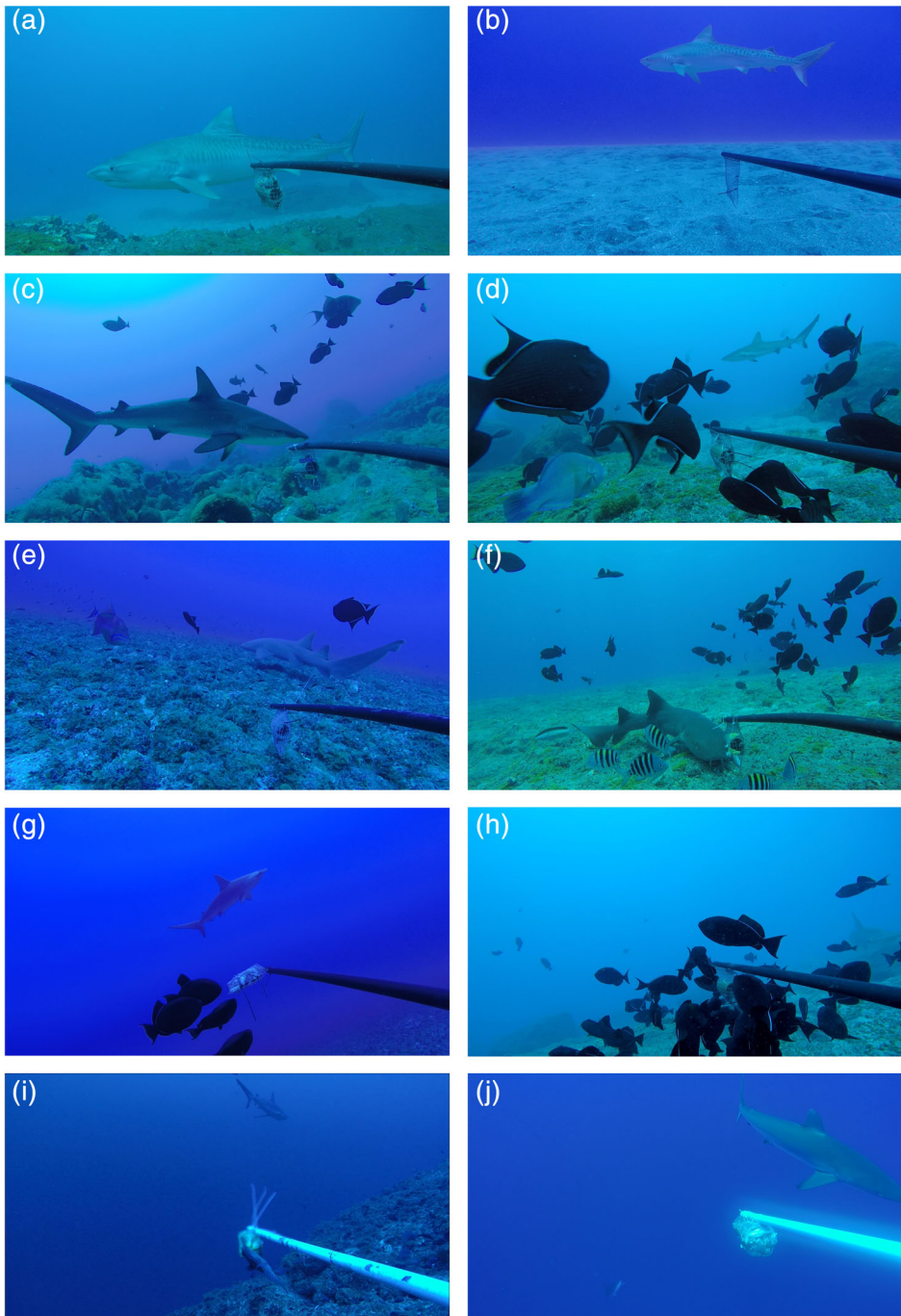
Here, we present records of sharks obtained from surveys using baited remote underwater stereo-video systems (stereo-BRUVS) at the Brazilian oceanic islands of Trindade (October 2017) and Saint

Peter and Saint Paul Archipelago (SPSPA; September 2018; Supporting Information Video V1). Trindade (20° 30′ S; 29° 20′ W) is a volcanic island located 1160 km off the coast of Espírito Santo state, south-western Atlantic Ocean, and together with Martin Vaz Archipelago constitutes the eastern end of the Vitória-Trindade Chain. The SPSPA (0° 55′ N; 29° 21′ W) is a small group of rocky islets located about 1000 km off the north-eastern Brazilian coast, on the Mid-Atlantic Ridge in the central equatorial Atlantic Ocean.

Sampling complied with Brazilian laws and was authorized by the Federal Government under the environmental permits #403740/2012–6 and #405426/2012-7.

TABLE 1   Length measurements of the shark species recorded at the Brazilian oceanic islands of Trindade and Saint Peter and Saint Paul Archipelago (SPSPA)

	Fork length (m)							
Trindade								
Carcharhinus perezi	0.79	0.82	0.90	0.95	1.01	1.12	1.29	1.48
Galeocerdo cuvier	2.57	2.69						
Ginglymostoma cirratum	1.10	2.05						
Sphyrna lewini	2.08							
SPSPA								
Carcharhinus falciformis	1.22	1.27	1.41	1.46				
Carcharhinus galapagensis	2.19							

FIGURE 1   Shark species recorded using baited remote underwater stereo-video systems (stereo-BRUVS) at the Brazilian oceanic islands of Trindade: a and b) tiger shark *Galeocerdo cuvier*; c and d) caribbean reef shark *Carcharhinus perezi*; e and f) nurse shark *Ginglymostoma cirratum*; g and h) scalloped hammerhead shark *Sphyrna lewini*; and Saint Peter and Saint Paul Archipelago: i) Galapagos shark *Carcharhinus galapagensis* and j) silky shark *Carcharhinus falciformis*

Demersal stereo-BRUVS were deployed at depths of 10 – 74 m in Trindade (60 h of footage; n = 60 samples) and 30 – 85 m in SPSPA (14 h of footage; n = 14). Pelagic stereo-BRUVS were deployed in SPSPA (10 h of footage; n = 5) at 20 and 30 m depths. In Trindade, stereo-BRUVS were baited with 500 g of small pieces of thawed Brazilian sardinella *Sardinella brasiliensis* (Steindachner 1879), and with 500 g (demersal) or 1 kg (pelagic) of crushed thawed herring *Harengula* sp. in SPSPA. We calibrated the stereo-BRUVS using the CAL software and analysed the video samples using the EventMeasure software (www.seagis.com.au). We identified the sharks at the species level and recorded the relative abundance as the maximum number of individuals of the same species present in a single frame (N_{max}; Cappo *et al.*, 2004). We measured the fork length (L_F) of all individuals according to the distance (≤ 7 m) and angle (≤ 45°) to the cameras and the measurement precision (≤ 1 cm).

Fourteen of the 60 deployments recorded 19 sharks in Trindade Island, including two tiger sharks *Galeocerdo cuvier* (Péron & LeSueur 1822) (mean L_F = 2.63 m; Table 1), 11 Caribbean reef sharks *Carcharhinus perezi* (Poey 1876) (mean L_F = 1.05 m), two nurse sharks *Ginglymostoma cirratum* (Bonnaterre 1788) (mean L_F = 1.57 m) and three scalloped hammerhead sharks *Sphyrna lewini* (Griffith & Smith 1834) (L_F = 2.08 m; Figure 1a–h). In SPSPA, only two of five pelagic deployments recorded sharks, two silky sharks *Carcharhinus falciformis* (Müller & Henle 1839) (mean L_F = 1.34 m) in each deployment, and two of 14 demersal deployments recorded one silky shark (not measured) and one Galapagos shark *Carcharhinus galapagensis* (Snodgrass & Heller 1905) (L_F = 2.19 m) (Figure 1i,j).

The main diagnostic characteristics that allowed us to differentiate the Galapagos shark from its congener, the dusky shark *Carcharhinus obscurus* (LeSueur 1818), were the first dorsal fin rather high and straight (only slightly curved near the tip), and a relatively high and short second dorsal fin, as is observed for the anal fin (Garrick, 1982; Voigt & Weber, 2011). Galapagos sharks were regarded as locally extinct in SPSPA (Luiz & Edwards, 2011), although this archipelago has been a designated multiple-use marine protected area (MPA) since 1986 (Brasil, 1986). The main threats are longline and hand line fishing, which until the 1970s caught large quantities of these sharks with low reproductive capacity and limited intrinsic rebound potential (Luiz & Edwards, 2011).

Systematic fish and shark studies using other non-invasive methods (*e.g.*, underwater visual census (UVC) and remotely operated vehicle (ROV)) in these two Brazilian oceanic islands have not recorded sharks in recent decades (Pinheiro *et al.*, 2011; Luiz *et al.*, 2015; Rosa *et al.*, 2016). However, it is noteworthy that a small number of sharks have been occasionally sighted, such as nurse and Caribbean reef sharks at Trindade, as well as a hammerhead shark (in 2009; C. E. L. Ferreira, pers. comm.) and a six-gill shark *Hexanchus griseus* (Bonnaterre 1788) (in 2018; H. T. Pinheiro & L. A. Rocha, pers. comm.) in SPSPA. Our data demonstrate the advantages of using stereo-BRUVS for sampling sharks and rays (Harvey *et al.*, 2018) as a complementary tool to more traditional methods (Langlois *et al.*, 2010; Rolim *et al.*, 2019), particularly in fishery-affected ecosystems. Despite the

overfishing of sharks at these Brazilian oceanic islands (Luiz & Edwards, 2011; Pinheiro *et al.*, 2011), these results demonstrate that a few have remained or occasional individuals have migrated from outer areas.

Long-term monitoring with stereo-BRUVS would confirm local extinctions, indicate stray specimens or follow population recovery. For example, while a few fishery-dependent records of Galapagos sharks near SPSPA have been published subsequent to Luiz & Edwards (2011) paper (Hazin *et al.*, 2018), neither those nor our record indicate a recovery of the population. Instead, it brings attention to the urgent need to monitor and assess the population trends of this Critically Threatened species (ICMBio, 2018), especially now that part of these two oceanic islands have been established as no-take areas (Brasil, 2018; Giglio *et al.*, 2018).

ORCID

Caio R. Pimentel https://orcid.org/0000-0003-4110-1249
Ryan Andrades https://orcid.org/0000-0003-2418-1072
Carlos E. L. Ferreira https://orcid.org/0000-0002-4311-0491
Otto B. F. Gadig https://orcid.org/0000-0002-8109-5085
Euan S. Harvey https://orcid.org/0000-0002-9069-4581
Tommaso Giarrizzo https://orcid.org/0000-0002-5116-5206

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Conclusão geral

Por meio dos estudos que compõem essa tese, foi possível avançarmos de forma substancial no entendimento sobre os processos ecológicos responsáveis pela estruturação das assembleias de peixes recifais em ilhas oceânicas, como também contribuirmos para aumentar o nosso conhecimento sobre a biodiversidade de peixes da Província Brasileira. Demonstramos que as assembleias de peixes respondem de forma distinta ao gradiente de profundidade e mudanças de habitats. No Arquipélago de São Pedro e São Paulo, inesperadamente, não encontramos assembleias de peixes claramente estruturadas de acordo com o gradiente de profundidade. Porém, a estrutura das assembleias estava altamente associada a espécies com afinidades a recifes rasos em oposição a espécies mais comuns em recifes profundos/mesofóticos. Esses grupos de espécies, possivelmente, estão mais relacionados a mudanças drásticas na temperatura da água, causadas por fortes eventos de ressurgência e subsidência entre 50 e 100 m de profundidade, influenciando assim o movimento vertical dos peixes ao longo do gradiente de profundidade. Além disso, a alta co-ocorrência de espécies nos ecossistemas pelágico e recifal indicam processos de conectividade ecológica entre esses ecossistemas. Portanto, nossos resultados demonstram que para a conservação da biodiversidade e manutenção dos processos ecológicos, é necessário protegermos não apenas as áreas recifais, mas também o ambiente pelágico ao seu redor. Na Ilha da Trindade as assembleias de peixes estão estruturadas de acordo com a variação dos habitats bentônicos ao longo do gradiente de profundidade da plataforma insular. A riqueza de espécies, a abundância total e o endemismo foram altamente relacionados ao habitat recifal, enquanto a biomassa total e a vulnerabilidade média apresentaram relação direta ao aumento da profundidade. Portanto, sugere-se que para garantir a conservação da biodiversidade marinha e das funções ecológicas intrínsecas a cada habitat, é necessária uma gestão integrada destes ambientes, abrangendo todo o gradiente de habitats bentônicos da plataforma insular. Em termos de biodiversidade, nossas descobertas e avanços demonstram a necessidade de continuarmos e ampliarmos nossos esforços de pesquisas nesses ecossistemas profundos e pouco estudados, assim como de proteção e atenção à essa ictiofauna única encontrada nesses ecossistemas.