Vol. 726: 1–15, 2024
https://doi.org/10.3354/meps14483

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 11

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

Débora S. Ferrari[1,*], Lucas T. Nunes[1,2], Thiago C. Mendes[2], Carlos E. L. Ferreira[2], Sergio R. Floeter[1]

[1]Marine Macroecology and Biogeography Lab, Department of Ecology and Zoology, Universidade Federal de Santa Catarina, Florianópolis, SC 88010-970, Brazil

[2]Reef Systems Ecology and Conservation Lab, Department of Marine Biology, Universidade Federal Fluminense, Niterói, RJ 24210-201, Brazil

---

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

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

1. INTRODUCTION

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

Niche diversity facilitates the partitioning of resources among species and regulates population sizes through predation and herbivory, effectively mitigating the dominance of any particular species and fostering overall ecological diversity (Estes et

---

*Corresponding author: ferrari.silva.debora@gmail.com al. 2011). However, disproportionate dominance in abundance or biomass by a few species is well-known in both terrestrial (ter Steege et al. 2013, Fauset et al. 2015, Rodrigues et al. 2019) and coral reef communities (Dietzel et al. 2021). In ecological studies, the term 'hyperdominance' has been employed to describe this differential high abundance or biomass of organisms within a community (Lohbeck et al. 2016, Tebbett et al. 2023). In the marine environment, Dietzel et al. (2021) reported that of 318 species examined in the Indo-Pacific coral fauna, only 17 hyperdominant species accounted for half of the total community abundance. These species have a disproportionate influence on the structure and functioning of shallow coral reef ecosystems across the Indo-Pacific.

Hyperdominant species typically exhibit characteristics that confer a competitive advantage over other species, such as rapid growth, efficient resource use, resistance against environmental disturbances and enhanced dispersal abilities (Dietzel et al. 2021, De Souza et al. 2022). As a result, hyperdominant species outcompete and surpass other species, leading to their increased abundance and biomass within the community (De Souza et al. 2022). Since trophic interactions are highly correlated to either species abundance or biomass (Elmhagen & Rushton 2007, Longo et al. 2014, Nunes et al. 2020), hyperdominant species can monopolise these trophic functions, facilitated by characteristics such as a more generalist diet and habitat use. These characteristics are especially prevalent within groups at lower trophic levels (Kavanagh & Olney 2006, Mendes et al. 2019), while they facilitate the establishment of populations in remote locations, such as oceanic islands (Hachich et al. 2020, Ferrari et al. 2023). However, our current understanding of the potential impact of hyperdominance on trophic interactions and energy flow in bottom-up processes, particularly in highly diverse systems like reefs, remains insufficient and requires large-scale comparisons.

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

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

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

2. MATERIALS AND METHODS

2.1. Study area

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

2.2. Sampling and laboratory procedures

On each island, we recorded remote underwater videos (RUVs) to quantify feeding pressure of fishes on the benthic community (following Longo et al. 2014). Sampling was conducted during the daytime (between 09:00 and 15:00 h) in the consolidated substrate of shallow reefs (between 3 and 15 m deep). Sampling was conducted at different locations within each island based on accessibility factors such as wave and current conditions, while also adhering to a specific depth pattern. Subsequent data analyses involved comparisons within individual sites on each island, revealing no notable distinctions of significance. Videos were recorded with a digital camera (GoPro Hero #3 model) focused on a 2 m^2 reef area, previously demarcated with a measuring tape. Each area was recorded for 15 min, with the central 10 min of each video used for analysis (i.e. discarding the first and last 2 min and 30 s of each recording). A minimum separation of 3 m between plot areas was applied to avoid overlapping.

For each video, we identified all individual fishes that exhibited foraging (i.e. biting the substrate) inside the focal area. We emphasize that the RUV method filters species that feed in the benthos, excluding other groups such as planktivores and carnivores. For each individual, we counted the number of bites, estimated its total length (TL) and assigned it to a trophic group (Ferreira et al. 2004, Longo et al. 2014). The individual TL was used to calculate its biomass, which was obtained from length–weight relationships retrieved from the literature (Quimbayo et al. 2021). To determine the individual feeding pressure (FP), we com-

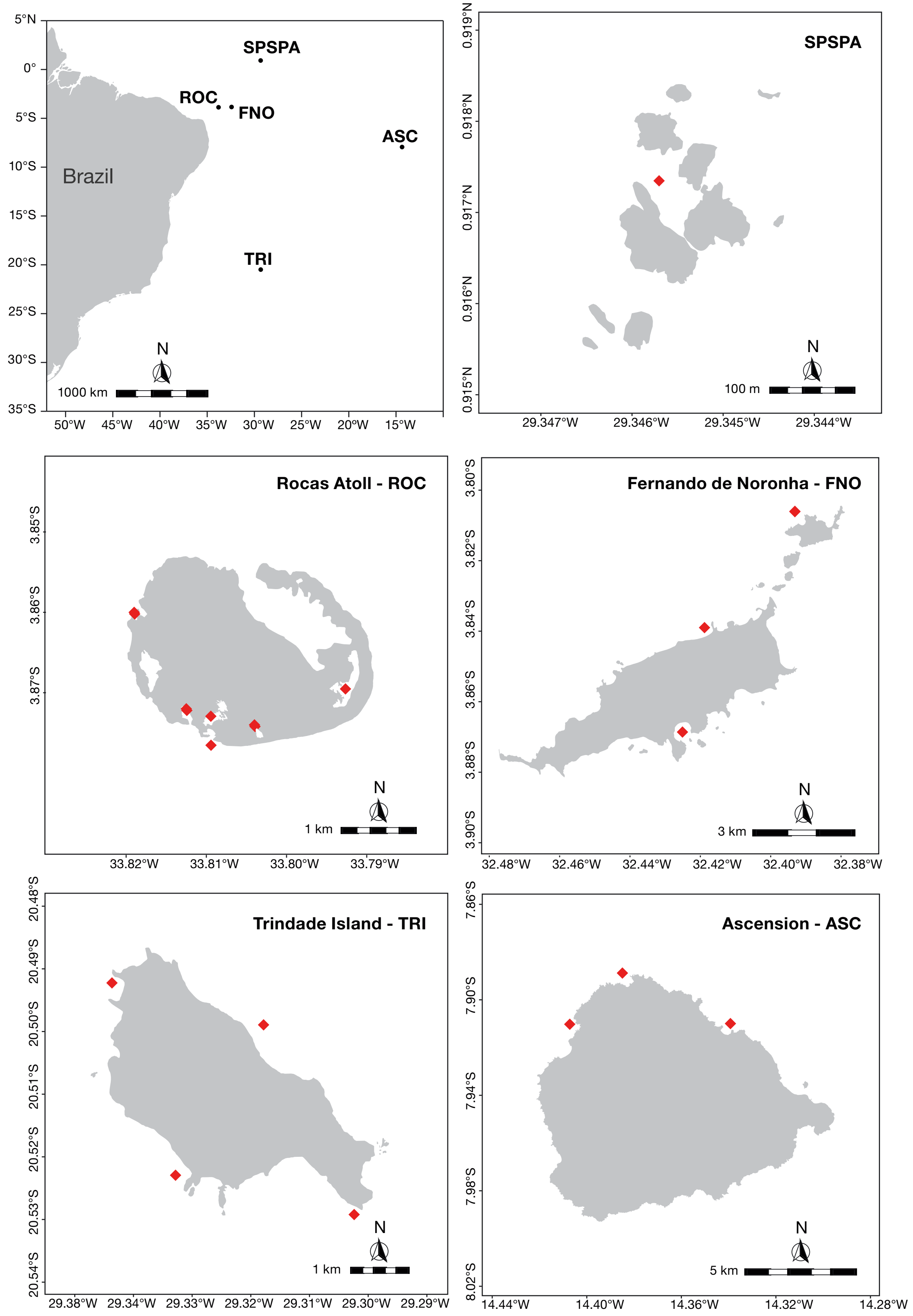

Fig. 1. Geographical location of sampled oceanic islands on the Atlantic Ocean. SPSPA: St Peter and St Paul's Archipelago; FNO: Fernando de Noronha; ROC: Rocas Atoll; ASC: Ascension Island; TRI: Trindade Island. Red diamonds represent the sampled sites on each island

bined the number of bites and biomass of each individual through the equation FP = (bites × biomass) / (2 m^2 × 10 min). For each video (i.e. sample), we obtained the feeding pressure for each trophic group, by summing the feeding pressure of all individuals within the same species and trophic group based on literature (Ferreira et al. 2004, Longo et al. 2014).

Within the designated area of 2 m^2, the photoquadrat method was employed after the RUVs to estimate the percentage cover of each benthic group on the substrate. Five photos (25 × 25 cm) were taken inside each RUVs' area. In the laboratory, the proportion of coverage for each benthic group was estimated using PhotoQuad software (Trygonis & Sini 2012). In each photo, 50 points were randomly distributed, and the organism below each point was identified to the lowest possible taxonomic level. When it was unfeasible to identify an organism to the lowest taxonomic level, we categorized it into a functional group based on Aued et al. (2018). The percentage cover of each group is equivalent to the total number of points overlying that group divided by the total points analysed in the photoquadrat. We then calculated a mean occurrence for benthic substrates in each video by dividing the sum of each benthic substrate by the total number of photos per video (i.e. 5 photos).

For Brazilian oceanic islands, we used published data on species abundance and individual TL from visual censuses recorded in the literature (i.e. Cordeiro et al. 2021), and for Ascension Island, we performed visual censuses. This method consists of a linear transect of 40 m^2 (20 × 2 m), carried out close to the RUV area, in which a diver constantly swims, counting the number and estimating the TL of each fish (Morais et al. 2017). The TL was also used to calculate the corresponding biomass of fish obtained from length—weight relationships from the literature (Quimbayo et al. 2021). The species that collectively accounted for at least 50% of the biomass were considered hyperdominant species.

RUVs, photoquadrats and visual census techniques were performed concomitantly during sampling by different divers. The specific sampling dates for each location were as follows: Fernando de Noronha in October 2011, Rocas Atoll in February 2012, Trindade Island in July 2012, SPSPA in November 2013 and Ascension Island in August 2015.

2.3. Statistical analysis

We first used the benthic composition data, obtained from the photoquadrats, to group each video plot into a specific habitat according to the prevalence of a benthic component within the 2 m^2 video area. For this, we performed a cluster analysis for each oceanic island, by using Euclidean distance and the UPGMA clustering method. We then 'cut' the dendrogram resulting from the clusters into 5 groups based on a 50% distance height (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m726p001_supp.pdf). We also performed a principal coordinate analysis (PCoA) followed by a permutational multivariate analysis of variance (PERMANOVA) to validate our habitat clustering (Fig. S2).

Descriptive analyses were employed to illustrate the percentage cover of benthic substrate on each island (Fig. S3). Additionally, a stacked plot was generated to visually represent the relative proportions of benthic composition and feeding pressure on each oceanic island, and feeding pressure across the habitats. Furthermore, a barplot was constructed to display the mean biomass of reef fish species on each sampled oceanic island. A scatterplot was generated to visually represent the relationship between relative biomass and relative feeding pressure on each oceanic island. Additionally, another scatterplot was created to illustrate the relationship among the mean biomass, mean feeding pressure and number of habitats.

Due to the different total number of samples among habitats, we randomly sorted out 30 samples as a minimum sample effort for each habitat and calculated the average frequency for the benthic substrates and feeding pressure of fish trophic groups. For this, the feeding pressure matrix (response variable) was transformed to a proportion. We then repeated this procedure 1000 times for each habitat, resulting in a matrix of 4000 observations (i.e. 1000 for each habitat). The habitat dominated by zoanthids was not used due to the limited number of available samples, of which there were only 3 (Fig. S2). To understand the influence of benthic composition on fish feeding pressure, we performed a canonical correlation analysis, with a subsequent ANOVA of the canonical axes.

To examine how species' feeding pressure is influenced by fish biomass, trophic group and the number of feeding habitats used (i.e. as a proxy indicating a generalist and plastic feeding habit), we fitted a general linear model (GLM) with a Gaussian distribution. All analyses were performed using the 'clustsig' (Whitaker & Christman 2014), 'dplyr' (Wickham et al. 2021), 'vegan' (Oksanen et al. 2020), 'ggdendro' (Vries & Ripley 2020), 'ggplot2' (Wickham 2016), 'ISLR' (James et al. 2021) and 'tidyr' (Wickham 2021) packages of R software (R Core Team 2021).

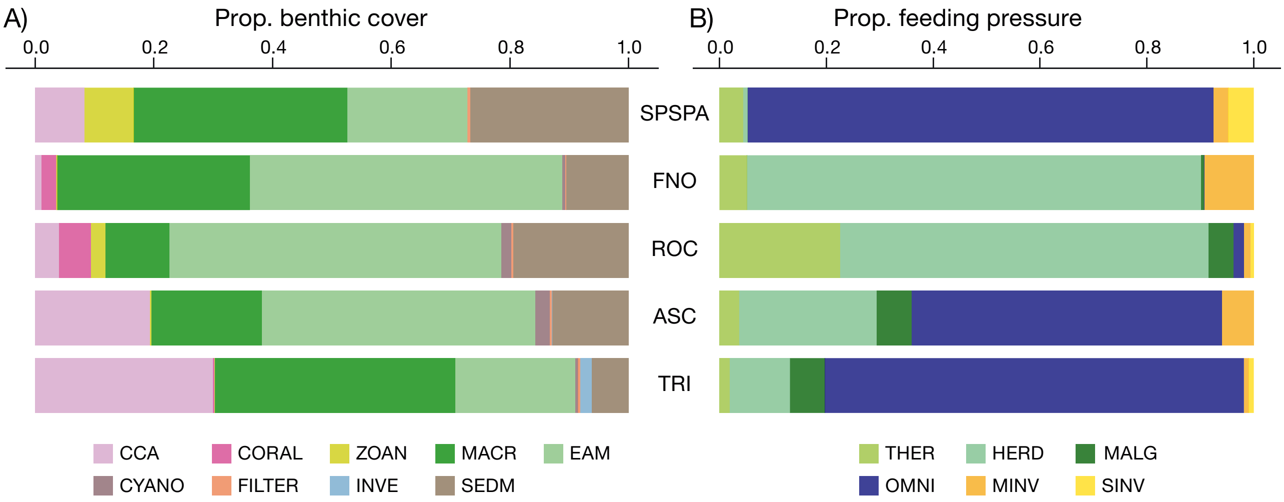

Fig. 2. (A) Relative proportion of benthic cover and (B) fish feeding pressure on 5 oceanic islands (abbreviations as in Fig. 1). Colours represent different benthic components and fish trophic groups. CCA: crustose coralline algae; CYANO: Cyanobacteria; CORAL: scleractinian coral; FILTER: suspension/filter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

3. RESULTS

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

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

A total of 6 fish trophic groups were observed feeding on the habitats at all oceanic islands (Fig. 2B). Omnivores (OMNI) were the dominant group in terms of feeding pressure in SPSPA (87%), Ascension (58%) and Trindade (78%), whereas herbivores/detritivores (HERD) were the most important group in Fernando de Noronha (85%) and Rocas Atoll (68%). Territorial herbivores (THER), macroalgivores (MALG), mobile invertebrate feeders (MINV) and sessile invertebrate feeders (SINV) were the groups with the lowest values of feeding pressure at all of the islands (Fig. 2B).

The predominant habitat foraged by all trophic groups in SPSPA was the habitat dominated by macroalgae (Fig. 3). In Fernando de Noronha, all trophic groups foraged almost exclusively in the habitat dominated by EAM. In Rocas Atoll, there was a difference in the habitat use among trophic groups, but habitats dominated by sand and EAM were the predominant habitats explored by fishes (Fig. 3). The habitat dominated by CCA was highly foraged by omnivores in Ascension and by macroalgivores and sessile invertebrate feeders in Trindade Island (Fig. 3). Benthic habitats explained approximately 81% of the observed fish feeding pressure patterns (Fig. 4). In general, the proximity of all fish trophic groups to the centroid of canonical correlation analysis indicated a correlation between their feeding pressure pattern and the different habitats. Notably,

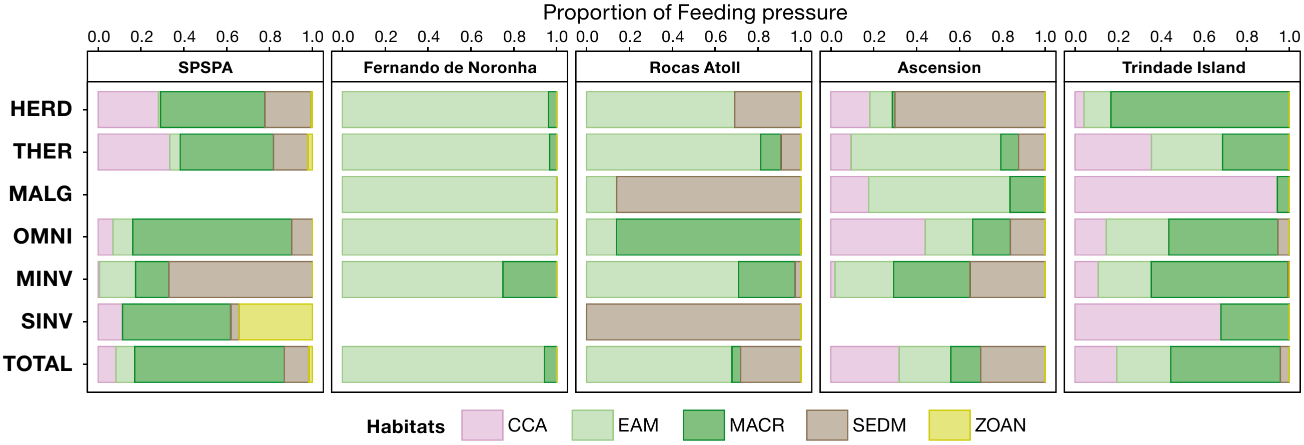

Fig. 3. Relative proportion of feeding pressure performed by different fish trophic groups on the 5 habitats. Colours represent different habitats. Abbreviations as in Figs. 1 & 2

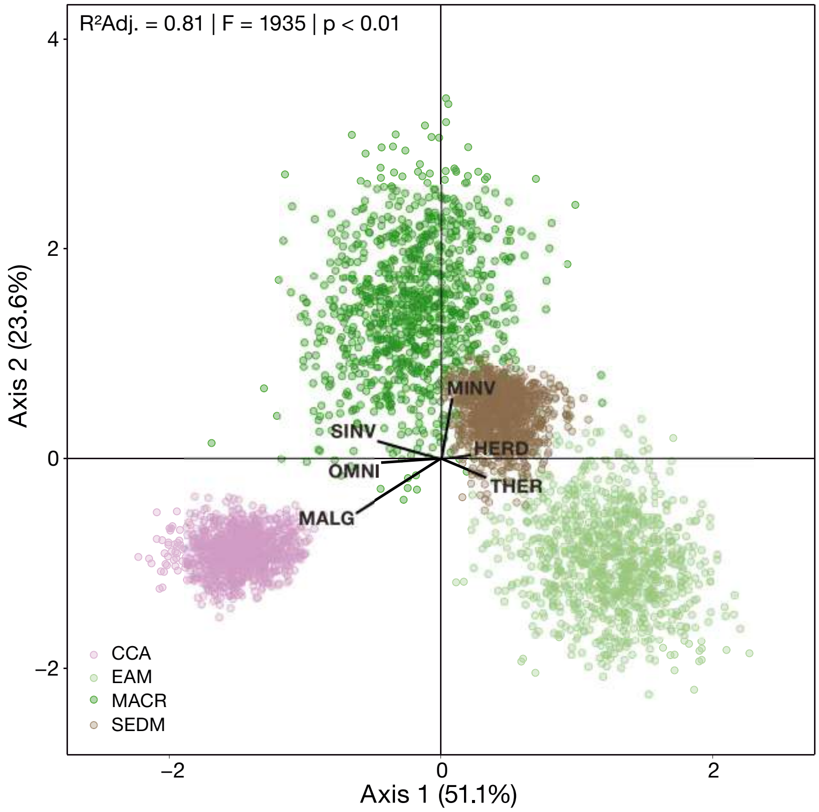

Fig. 4. Canonical correlation analysis (CCoA) between the benthic-dominated habitats and the feeding pressure of fishes in all 5 islands. Colours indicate habitats. Abbreviations as in Fig. 2

specific patterns emerged, such as macroalgivores and omnivores being more closely associated with habitats dominated by CCA, territorial herbivores exhibiting associations with habitats dominated by EAM, and mobile invertebrate feeders associated with habitats dominated by sand and macroalgae.

There was a positive correlation between feeding pressure and fish biomass (Table S1, Figs. S4 & S5), particularly within the herbivore and omnivore groups (Fig. 5A). However, we found no significant effect of trophic group or the number of habitats used on the feeding pressure. Omnivores and territorial herbivores generally accounted for higher biomass and interacted with more habitats. In terms of biomass, the omnivore group was mainly composed of the species *Melichthys niger*, which interacted with up to 4 different habitats. The herbivore—detritivore group was mainly composed of 2 species from the genus *Acanthurus* (Fig. 5A). A hyperdominance of omnivores was observed in Rocas, SPSPA and Trindade in terms of relative biomass and feeding pressure, while herbivores—detritivores were predominant in Rocas Atoll (Fig. 5B).

In terms of the hyperdominance of reef fish, our observations revealed that the black triggerfish *M. niger*, an omnivore, exhibited the highest biomass among all species in SPSPA, Trindade Island and Ascension, accounting for 85.2, 61.5 and 85.5% of the total fish biomass at each island, respectively (Fig. 6). These islands exhibit lower species richness,

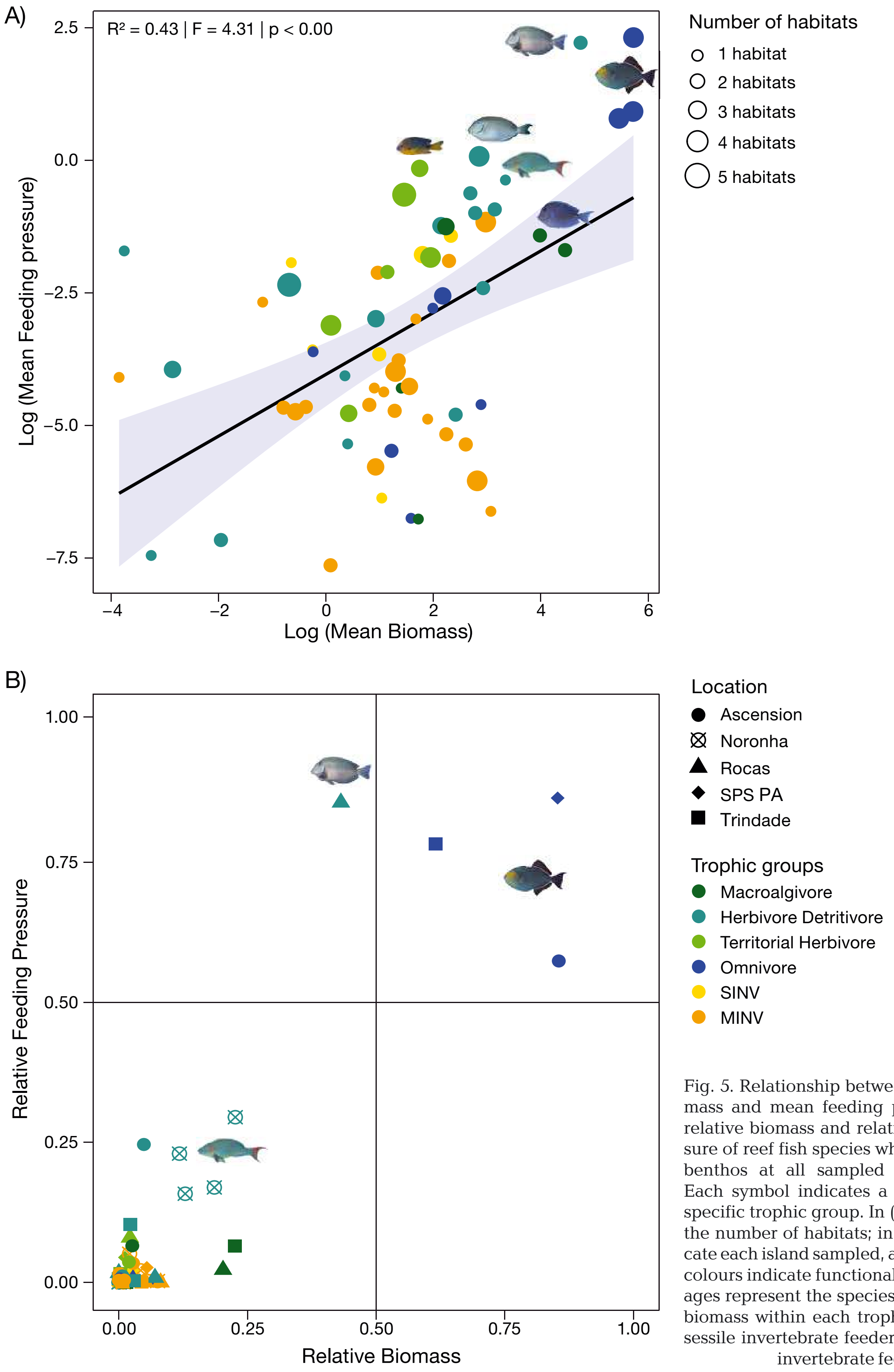

Fig. 5. Relationship between (A) mean biomass and mean feeding pressure and (B) relative biomass and relative feeding pressure of reef fish species which forage in the benthos at all sampled oceanic islands. Each symbol indicates a species within a specific trophic group. In (A), sizes indicate the number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

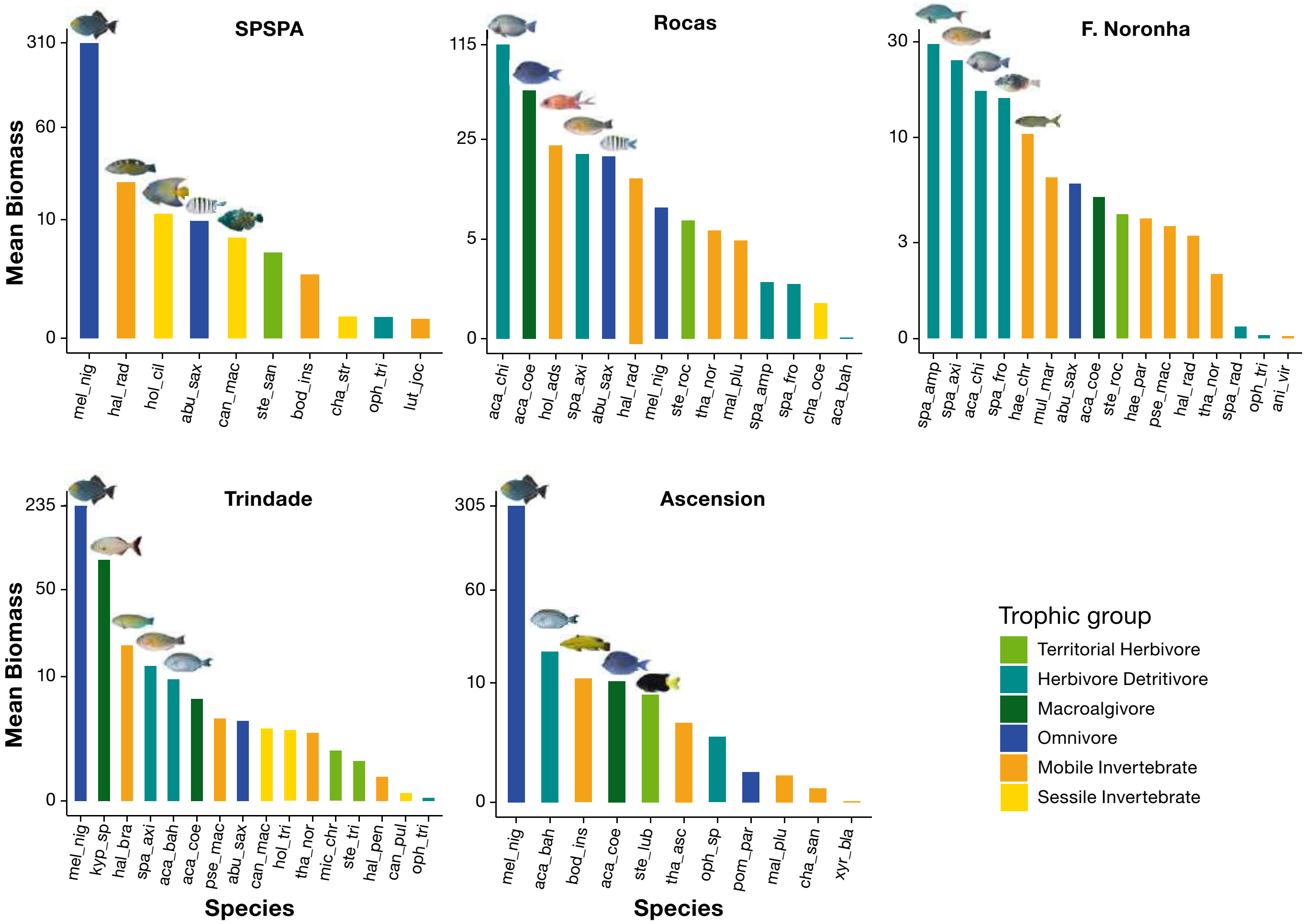

Fig. 6. Mean biomass (g m^{-2}) of reef fish species which forage in the benthos at each sampled oceanic island. SPSPA: St Peter and St Paul's Archipelago. The *y*-axis scale is log$_{10}$ transformed for better visualisation of data dispersion (note different scales among islands). Colours represent fish trophic groups. abu_sax: *Abudefduf saxatilis*; aca_bah: *Acanthurus bahianus*; aca_chi: *Acanthurus chirurgus*; ani_vir: *Anisotremus virginicus*; bod_ins: *Bodianus insularis*; can_mac: *Cantherhines macrocerus*; can_pul: *Cantherhines pullus*; cha_oce: *Chaetodon ocellatus*; cha_san: *Chaetodon sanctaehelenae*; cha_str: *Chaetodon striatus*; hae_chr: *Haemulon chrysargyreum*; hae_par: *Haemulon parra*; hal_bra: *Halichoeres brasiliensis*; hal_pen: *Halichoeres penrosei*; hal_rad: *Halichoeres radiatus*; hal_cil: *Holacanthus ciliaris*; hol_tri: *Holacanthus tricolor*; hol_ads: *Holocentrus adscensionis*; kyp_sp: *Kyphosus* spp.; lut_joc: *Lutjanus jocu*; mal_plu: *Malacanthus plumieri*; mel_nig: *Melichthys niger*; mic_chr: *Microspathodon chrysurus*; mul_mar: *Mulloidichthys martinicus*; oph_sp: *Ophioblennius* spp.; oph_tri: *Ophioblennius trinitatis*; pom_par: *Pomacanthus paru*; pse_mac: *Pseudupeneus maculatus*; spa_amp: *Sparisoma amplum*; spa_axi: *Sparisoma axillare*; spa_fro: *Sparisoma frondosum*; ste_lub: *Stegastes lubbocki*; ste_roc: *Stegastes rocasensis*; ste_san: *Stegastes sanctipauli*; ste_tri: *Stegastes trindadensis*; tha_asc: *Thalassoma ascensionis*; tha_nor: *Thalassoma noronhanum*; xyr_bla: *Xyrichtys blanchardi*

as well as a greater distance from the coast. Conversely, in Rocas Atoll and Fernando de Noronha, where there is higher species richness and closer proximity to the mainland, 2 herbivorous–detritivorous species displayed the highest biomass, but neither can be considered hyperdominant; in Rocas Atoll, the surgeonfish *Acanthurus chirurgus* corresponded to 43.2% of the total fish biomass, whereas in Fernando de Noronha, the biomass of the parrotfish *Sparisoma amplum* represented 22.6% of the total (Fig. 6).

4. DISCUSSION

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

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

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

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

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

As our study shows, the EAM is the most common habitat in 3 of the 5 islands and has a high tolerance under different environmental conditions and pressures. This fast-growing matrix has a great capacity to compete for space, which allows its large distribution (Littler & Littler 1980, Airoldi 1998). It is composed of algae, detritus and small invertebrates, thereby enhancing its nutritional value and significance within the food chain (Wilson et al. 2003). Notably, organic detritus derived from the EAM often contains higher concentrations of protein amino acids compared to filamentous algae (Crossman et al. 2001). However, the relative importance of each food item within the EAM for the nutrition of herbivores in the Atlantic fish fauna is yet to be determined (Mendes et al. 2018).

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

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

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

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

5. CONCLUSIONS

Our study demonstrates that fish feeding pressure is influenced by both habitat features and fish biomass. Specifically, we detected that each trophic group is dominated by only 1 or 2 species in terms of biomass, which aligns with previous findings by Cowburn et al. (2021). Despite the comparatively lower species richness observed on oceanic islands in comparison to coastal environments, the underlying patterns and processes that shape biodiversity are similar. Our study holds important implications for the conservation and management of marine biodiversity, highlighting the necessity of considering both habitat heterogeneity and species dominance in conservation planning. Furthermore, as the study areas comprise various types of MPAs, a recommended approach would involve giving special attention to species that play crucial functional roles in maintaining habitat diversity. This is primarily due to the significant isolation of these islands, which hinders the introduction of new species that could potentially replace functionally important species, like herbivorous fish. Future management and conservation targets should prioritise a controlled management strategy for the fisheries targeting these key species.

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

Acknowledgements. We thank the PELD-ILOC and SISBIOTA-Mar team, especially Marina Sissini, Guilherme Longo, Renato Morais and Renata Mazzei for fieldwork support, and Jaime A. S. Bonilla, Samara L. Danielski, Angela Canterle, Luisa Fontoura, Davi V. Cândido, Anaide W. Aued and Júlia Correia, for help with video and photoquadrat analysis. Funding was provided by CNPq through the grants SISBIOTA–Mar (CNPq 563276/2010-0 and FAPESC 6308/2011-8; PI: S.R.F.), ProspecMar (CNPq 458548/2013-8 to L. Lotufo) and Long Term Ecological Research of Reef Communities at Oceanic Islands – PELD ILOC (CNPq 441327/2020-6; PI: C.E.L.F.). D.S.F. and S.R.F. acknowledge the support received from the European Union's Horizon 2020 Research and Innovation Project MISSION ATLANTIC (grant #862428). L.T.N. and T.C.M. received scholarships from Conselho Nacional de Desenvolvimento Científico e Tecnológico.

LITERATURE CITED

Airoldi L (1998) Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. Ecology 79:2759–2770

Alava JJ, McMullen K, Jones J, Barragán-Paladines MJ and others (2023) Multiple anthropogenic stressors in the Galápagos Islands' complex social–ecological system: interactions of marine pollution, fishing pressure, and climate change with management recommendations. Integr Environ Assess Manag 19:870–895

Aued AW, Smith F, Quimbayo JP, Cândido DV and others (2018) Large-scale patterns of benthic marine communities in the Brazilian province. PLOS ONE 13:e0198452

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429:827–833

Bellwood DR, Streit RP, Brandl SJ, Tebbett SB (2019) The meaning of the term 'function' in ecology: a coral reef perspective. Funct Ecol 33:948–961

Bonaldo RM, Hoey AS, Bellwood DR (2014) The ecosystem roles of parrotfishes on tropical reefs. Oceanogr Mar Biol Annu Rev 52:81–132

Bracewell SA, Clark GF, Johnston EL (2018) Habitat complexity effects on diversity and abundance differ with latitude: an experimental study over 20 degrees. Ecology 99:1964–1974

Brandl SJ, Rasher DB, Côté IM, Casey JM, Darling ES, Lefcheck JS, Duffy JE (2019) Coral reef ecosystem functioning: eight core processes and the role of biodiversity. Front Ecol Environ 17:445–454

Canterle AM, Nunes LT, Fontoura L, Maia HA, Floeter SR (2020) Reef microhabitats mediate fish feeding intensity and agonistic interactions at Príncipe Island Biosphere Reserve, Tropical Eastern Atlantic. Mar Ecol 41:e12609

Cardozo-Ferreira GC, Ferreira CEL, Choat JH, Mendes TC and others (2023) Seasonal variation in diet and isotopic niche of nominally herbivorous fishes in subtropical rocky reefs. Mar Ecol Prog Ser 722:125–143

Ceccarelli DM (2007) Modification of benthic communities by territorial damselfish: a multi-species comparison. Coral Reefs 26:853–866

Clements KD, Choat JH (2018) Nutritional ecology of parrotfishes (Scarinae, Labridae). In: Hoey AS, Bonaldo RM (eds) Biology of parrotfishes. CRC Press, Boca Raton, FL, p 429–68

Cordeiro CMM, Quimbayo JP, Silveira T, Ferreira CEL (2021) Long-term Ecological Monitoring Research Brazilian Oceanic Islands (reef fish). v1.0. Tropical and Subtropical Western South Atlantic OBIS. Dataset/Sampling event. https://doi.org/10.25607/rov4or

Cowburn B, Graham J, Schratzberger M, Brown J and others (2021) Rocky reefs of St Helena and the tropical Atlantic: how the lack of coral and an isolated oceanic location drive unique inshore marine ecology. Mar Ecol Prog Ser 663:31–49

Crossman DJ, Choat JH, Clements KD, Hardy T, McConochie J (2001) Detritus as food for grazing fishes on coral reefs. Limnol Oceanogr 46:1596–1605

De Souza HJ, Miguel EP, Resende RT, Matricardi EAT, Rezende AV, Leal FA, Dos Santos ML (2022) Effects of functional traits on the spatial distribution and hyperdominance of tree species in the Cerrado biome. IForest Biogeosci For 15:339–348

Dietzel A, Bode M, Connolly SR, Hughes TP (2021) The population sizes and global extinction risk of reef-building coral species at biogeographic scales. Nat Ecol Evol 5: 663–669

Elmhagen B, Rushton SP (2007) Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecol Lett 10:197–206

Estes JA, Terborgh J, Brashares JS, Power ME and others (2011) Trophic downgrading of planet Earth. Science 333:301–306

Fauset S, Johnson MO, Gloor M, Baker TR and others (2015) Hyperdominance in Amazonian forest carbon cycling. Nat Commun 6:6857

Ferrari DS, Floeter SR, Leprieur F, Quimbayo JP (2023) A trait-based approach to marine island biogeography. J Biogeogr 50:528–538

Ferreira CEL, Gonçalves JEA (2006) Community structure and diet of roving herbivorous reef fishes in the Abrolhos Archipelago, south-western Atlantic. J Fish Biol 69: 1533–1551

Ferreira CEL, Gonçalves JEA, Coutinho R, Peret AC (1998) Herbivory by the dusky damselfish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. J Exp Mar Biol Ecol 229:241–264

Ferreira CEL, Floeter SR, Gasparini JL, Ferreira BP, Joyeux JC (2004) Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. J Biogeogr 31:1093–1106

Figueiredo MADO, Horta PA, Pedrini ADG, Nunes JMDC (2008) Benthic marine algae of the coral reefs of Brazil: a literature review. Oecol Aust 12:258–269

Fontoura L, Cantor M, Longo GO, Bender MG, Bonaldo RM, Floeter SR (2020) The macroecology of reef fish agonistic behaviour. Ecography 43:1278–1290

Fox RJ, Bellwood DR (2008) Remote video bioassays reveal the potential feeding impact of the rabbitfish *Siganus canaliculatus* (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef. Coral Reefs 27:605–615

Gherardi DFM, Bosence DWJ (2001) Composition and community structure of the coralline algal reefs from Atol das Rocas, South Atlantic, Brazil. Coral Reefs 19:205–219

Giglio VJ, Pinheiro HT, Bender MG, Bonaldo RM and others (2018) Large and remote marine protected areas in the South Atlantic Ocean are flawed and raise concerns: comments on Soares and Lucas (2018). Mar Policy 96:13–17

Graham NA, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32: 315–326

Hachich NF, Bonsall MB, Arraut EM, Barneche DR, Lewinsohn TM, Floeter SR (2015) Island biogeography: patterns of marine shallow-water organisms in the Atlantic Ocean. J Biogeogr 42:1871–1882

Hachich NF, Ferrari DS, Quimbayo JP, Pinheiro HT, Floeter SR (2020) Island biogeography of marine shallow-water organisms. In: Goldstein MI, DellaSala DA (eds) Encyclopedia of the world's biomes. Elsevier Science, Amsterdam, p 61–75

Hay ME (1991) Fish–seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, CA, p 96–119

Hoey AS, Bellwood DR (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? Ecol Lett 14:267–273

Hughes TP, Bellwood DR, Connolly SR (2002) Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. Ecol Lett 5:775–784

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D and others (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 17:360–365

James G, Witten D, Hastie T, Tibshirani R (2021) ISLR: data for an introduction to statistical learning with applications in R. R package version 1.4

Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, Van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28:307–325

Kavanagh KD, Olney JE (2006) Ecological correlates of population density and behavior in the Circumtropical black triggerfish *Melichthys niger* (Balistidae). Environ Biol Fishes 76:387–398

Krajewski JP, Floeter SR (2011) Reef fish community structure of the Fernando de Noronha Archipelago (Equatorial Western Atlantic): the influence of exposure and benthic composition. Environ Biol Fishes 92:25–40

Kramer MJ, Bellwood DR, Bellwood O (2012) Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef. Coral Reefs 31:1007–1015

Kramer MJ, Bellwood O, Bellwood DR (2013) The trophic importance of algal turfs for coral reef fishes: the crustacean link. Coral Reefs 32:575–583

Lefcheck JS, Innes-Gold AA, Brandl SJ, Steneck RS, Torres R, Rasher DB (2019) Tropical fish diversity enhances coral reef functioning across multiple scales. Sci Adv 5: eaav6420

Littler MM, Littler DS (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Am Nat 116:25–44

Lohbeck M, Bongers F, Martinez-Ramos M, Poorter L (2016) The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape. Ecology 97:2772–2779

Longo GO, Ferreira CEL, Floeter SR (2014) Herbivory drives large-scale spatial variation in reef fish trophic interactions. Ecol Evol 4:4553–4566

Longo GO, Morais RA, Martins CDL, Mendes TC and others (2015) Between-habitat variation of benthic cover, reef fish assemblage and feeding pressure on the benthos at the only atoll in South Atlantic: Rocas Atoll, NE Brazil. PLOS ONE 10:e0127176

Longo GO, Hay ME, Ferreira CEL, Floeter SR (2019) Trophic interactions across 61 degrees of latitude in the Western Atlantic. Glob Ecol Biogeogr 28:107–117

Lubbock R (1980) The shore fishes of Ascension Island. J Fish Biol 17:283–303

Lubbock R, Edwards A (1981) The fishes of Saint Paul's rocks. J Fish Biol 18:135–157

Lucena MB, Cordeiro CAMM, Valentin JL, Aguiar AA (2022) Puddingwife wrasse: an important trophic link of an isolated oceanic island in Brazil. Environ Biol Fishes 105: 561–573

Luiz OJ, Mendes TC, Barneche DR, Ferreira CGW and others (2015) Community structure of reef fishes on a remote oceanic island (St Peter and St Paul's Archipelago, equatorial Atlantic): the relative influence of abiotic and biotic variables. Mar Freshw Res 66:739–749

Maia M, Sichel S, Briais A, Brunelli D and others (2016) Extreme mantle uplift and exhumation along a transpressive transform fault. Nat Geosci 9:619–623

Mantyka CS, Bellwood DR (2007) Macroalgal grazing selectivity among herbivorous coral reef fishes. Mar Ecol Prog Ser 352:177–185

Martin TSH, Olds AD, Olalde ABH, Berkström C and others (2018) Habitat proximity exerts opposing effects on key ecological functions. Landsc Ecol 33:1273–1286

McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR (2015) Marine defaunation: animal loss in the global ocean. Science 347:1255641

McQuillen HL, Brewer LW (2000) Methodological considerations for monitoring wild bird nests using video technology. J Field Ornithol 71:167–172

Mendes TC, Cordeiro CAM, Ferreira CEL (2015) An experimental evaluation of macroalgal consumption and selectivity by nominally herbivorous fishes on subtropical rocky reefs. J Exp Mar Biol Ecol 471:146–152

Mendes TC, Ferreira CEL, Clements KD (2018) Discordance between diet analysis and dietary macronutrient content in four nominally herbivorous fishes from the Southwestern Atlantic. Mar Biol 165:180

Mendes TC, Quimbayo JP, Bouth HF, Silva LP, Ferreira CEL (2019) The omnivorous triggerfish *Melichthys niger* is a functional herbivore on an isolated Atlantic oceanic island. J Fish Biol 95:812–819

Michel CJ, Henderson MJ, Loomis CM, Smith JM and others (2020) Fish predation on a landscape scale. Ecosphere 11:e03168

Morais RA, Ferreira CEL, Floeter SR (2017) Spatial patterns of fish standing biomass across Brazilian reefs. J Fish Biol 91:1642–1667

Nicholson GM, Clements KD (2023) Micro-photoautotroph predation as a driver for trophic niche specialization in 12 syntopic Indo-Pacific parrotfish species. Biol J Linn Soc 139:91–114

Nunes LT, Morais RA, Longo GO, Sabino J, Floeter SR (2020) Habitat and community structure modulate fish interactions in a neotropical clearwater river. Neotrop Ichthyol 18:e190127

Oksanen FJ, Blanchet G, Friendly M, Kindt R and others (2020) vegan: community ecology package. R package version 2.5-7

Paine RT (1980) Food webs: linkage, interaction strength and community infrastructure. J Anim Ecol 49:667–685

Pessarrodona A, Tebbett SB, Bosch NE, Bellwood DR, Wernberg T (2022) High herbivory despite high sediment loads on a fringing coral reef. Coral Reefs 41: 161–173

Prat-Varela A, Torres A, Cervantes D, Aquino-Baleytó M, Abril AM, Clua EEG (2023) Improved baited remote underwater video (BRUV) for 24 h real-time monitoring of pelagic and demersal marine species from the epipelagic zone. J Mar Sci Eng 11:1182

Purcell SW, Bellwood DR (1993) A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). Environ Biol Fishes 37:139–159

Quimbayo JP, Dias MS, Kulbicki M, Mendes TC and others (2019) Determinants of reef fish assemblages in tropical oceanic islands. Ecography 42:77–87

Quimbayo JP, Silva FC, Mendes TC, Ferrari DS and others (2021) Life-history traits, geographical range, and conservation aspects of reef fishes from the Atlantic and Eastern Pacific. Ecology 102:e03298

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reaka-Kudla M (1997) The global biodiversity of coral reefs: a comparison with rain forests. In: Reaka-Kudla M, Wilson DE, Wilson EO (eds) Biodiversity II: understanding and protecting our biological resources. Joseph Henry Press, Washington, DC, p 83–108

Rodrigues AC, Villa PM, Neri AV (2019) Fine-scale topography shape richness, community composition, stem and biomass hyperdominant species in Brazilian Atlantic forest. Ecol Indic 102:208–217

Rominger AJ, Goodman KR, Lim JY, Armstrong EE and others (2016) Community assembly on isolated islands: macroecology meets evolution. Glob Ecol Biogeogr 25: 769–780

Sale PF (1991) (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, CA

Schiettekatte NMD, Brandl SJ, Casey JM, Graham NAJ and others (2022) Biological trade-offs underpin coral reef ecosystem functioning. Nat Ecol Evol 6:701−708

Simpfendorfer CA, Heithaus MR, Heupel MR, MacNeil MA and others (2023) Widespread diversity deficits of coral reef sharks and rays. Science 380:1155−1160

Tanedo SA, Hollmen TE (2020) Refining remote observation techniques to estimate productivity of black-legged kittiwakes *Rissa tridactyla* in Resurrection Bay, Gulf of Alaska. Mar Ornithol 48:61−69

Tebbett SB, Hoey AS, Depczynski M, Wismer S, Bellwood DR (2020) Macroalgae removal on coral reefs: realised ecosystem functions transcend biogeographic locations. Coral Reefs 39:203−214

Tebbett SB, Crisp SK, Evans RD, Fulton CJ and others (2023) On the challenges of identifying benthic dominance on Anthropocene coral reefs. BioScience 73:220−228

ter Steege H, Pitman NCA, Sabatier D, Baraloto C and others (2013) Hyperdominance in the Amazonian tree flora. Science 342:1243092

Trygonis V, Sini M (2012) photoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. J Exp Mar Biol Ecol 424-425:99−108

van der Putten WH, Ruiter PC, Bezemer TM, Harvey JA, Wassen M, Wolters V (2004) Trophic interactions in a changing world. Basic Appl Ecol 5:487−494

Vries A, Ripley BD (2020) ggdendro: create dendrograms and tree diagrams using 'ggplot2'. R package version 0.1.22

Whitaker D, Christman M (2014) clustsig: significant cluster analysis. R package version 1.1

Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography: ecology, evolution, and conservation. Oxford University Press, Oxford

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York, NY

Wickham H (2021) tidyr: tidy messy data. R package version 1.1.3

Wickham H, François R, Henry L, Müller K (2021) dplyr: a grammar of data manipulation. R package version 1.0.7

Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanogr Mar Biol Annu Rev 41:279−310

Editorial responsibility: Myron Peck, Den Burg, The Netherlands
Reviewed by: C. H. Stortini and 2 anonymous referees

Submitted: June 21, 2023
Accepted: November 6, 2023
Proofs received from author(s): January 8, 2024