



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

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## ABSTRACT

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

## 1. Introduction

The structure of biological communities is influenced by diverse ecological processes occurring at different spatial scales (Ovaskainen et al., 2017). At the local level, the interplay of biotic and abiotic factors fosters the establishment and abundance patterns of species in natural communities. Meanwhile, at the regional scale, dispersal mechanisms and environmental gradients play a crucial role in shaping species distributions and community composition. In the marine ecosystem, most shallow-water organisms, such as fish, algae, corals, and other invertebrates, have a planktotrophic larval stage in their life cycle. This ability to float, feed, or photosynthesize at the water's surface enhances their dispersal through ocean currents. Thus, the dispersal capacity of marine species, which can range from a few meters to hundreds of kilometres, influences the colonisation of new areas (Luiz et al., 2013, 2015). For reef fish, local community structure is shaped by various mechanisms, including habitat availability and complexity (Pinheiro et al., 2011; Canterle et al., 2020; Ferrari et al., 2024), interspecific interactions (Canterle et al., 2020) and environmental drivers like depth, wave exposure and temperature (Krajewski and Floeter, 2011; Maia

et al., 2018; Silva et al., 2023). However, for the successful colonisation of isolated areas, fish species engaged in these dispersal processes are commonly those with generalist or opportunistic habits, exhibiting adaptable physiological and behavioural traits that enable them to thrive in diverse environmental conditions (Luiz et al., 2013; Hachich et al., 2020). In isolated areas, reef fish are selected by a unique set of features that allows the colonisation of these systems, resulting in a community composed only of a subset of the mainland species pool (Bender et al., 2017).

Oceanic islands are a good example of isolated areas, being surrounded by the open ocean and lacking any connection to the continental shelf (Dawson, 2015). These unique characteristics contribute to the prevalence of endemic species (Whittaker and Fernandez-Palacios, 2007; Hachich et al., 2015, 2020), although accompanied by relatively low species diversity and functional redundancy (Ferrari et al., 2023). Oceanic islands have been important models for testing Island Biogeography Theory (Hachich et al., 2015; Ávila et al., 2018; Ferrari et al., 2023) and investigating species evolution (Rominger et al., 2016). The high isolation and distinct dynamics of dispersal, colonisation, speciation, and extinction observed in oceanic islands provide valuable

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insights into biogeographical hypotheses and community assembly (Hachich et al., 2020), especially self-recruitment which plays a significant role in sustaining populations (Robertson, 2001). The self-recruitment phenomena can potentially result from greater isolation and limited connectivity within reef communities on oceanic islands, in contrast to the mainland (Robertson, 2001).

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

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

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

2017).

## 2. Methods

### 2.1. Study area

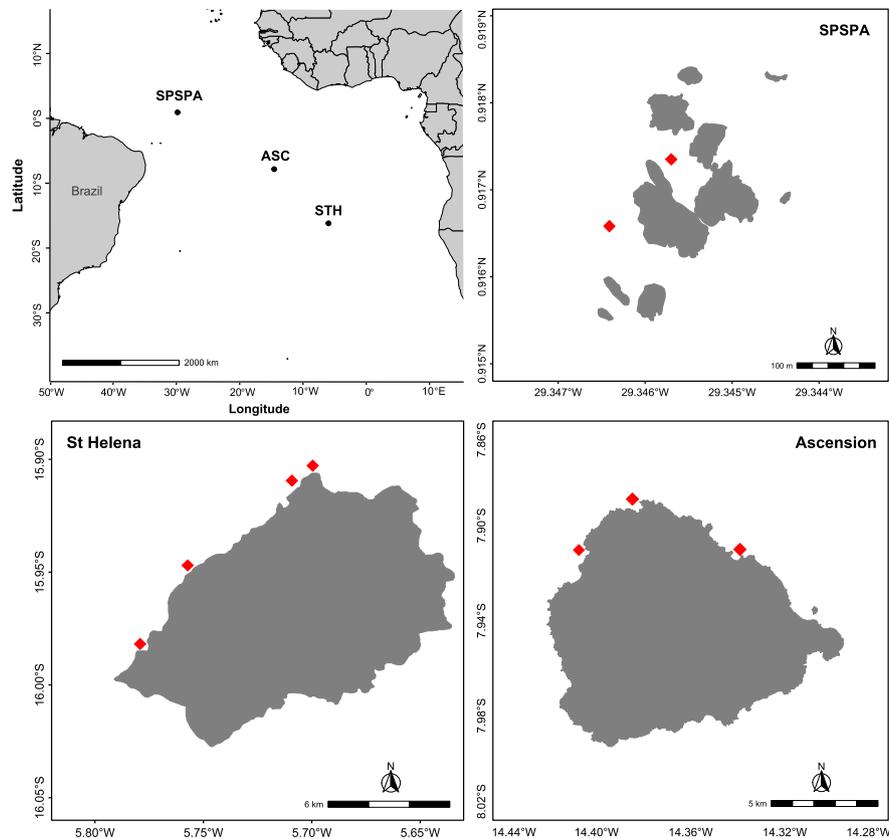
We sampled three oceanic islands located on the Mid-Atlantic Ridge (Fig. 1): St. Peter and St. Paul's Archipelago (SPSPA, 0°55'1"N | 29°20'44" W), approximately 1010 km away from the Brazilian northeast coast; Ascension Island (7°56'26"S | 14°22'25" W) located ~1600 km from the western coast of Africa;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

### 2.2. Data collection

#### 2.2.1. Reef fish communities

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

The fish species recorded in the surveys were categorised into distinct trophic groups based on their feeding habits, including



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

macrocarivores, mobile invertebrate feeders, omnivores, planktivores, herbivores-detritivores, sessile invertebrate feeders, and territorial herbivores (Ferreira et al., 2004; Cowburn et al., 2021; Nunes et al., 2023). To estimate fish biomass, we employed length–weight transformations and allometric conversions using the equation  $W = a * LT^b$ , where the parameters  $a$  and  $b$  represent constants in the allometric growth equation. In cases where coefficient values were unavailable for a particular species, we substituted coefficients derived from closely related species (congeners).

### 2.2.2. Biogeographic and environmental data

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

We also estimate the thermal niche breadth of species. This metric indicates the extent of temperature range that a species can endure, thereby serving as a gauge of its response to fluctuations in temperature (Schuster et al., 2022). To estimate the thermal niche breadth of each species, we gathered data on the maximum and minimum preferred

temperatures (i.e. the lower and upper percentiles, specifically the 10th and 90th percentile) within the distribution range of each recorded species. This data was sourced from FishBase (Froese and Pauly 2023) and Aquamaps (Kaschner et al., 2023). For species without recorded values, we used the maximum and minimum sea surface temperature (SST) values from the distribution range.

### 2.2.3. Data analysis

We first performed a species accumulation curve to indicate the adequacy of the survey in representing the fish richness at each oceanic island. Species accumulation curves approached an asymptote with 50 samples indicating additional sampling effort yields very few species (Fig. 1S). We then employed descriptive analyses to illustrate reef fish trophic structure. A scatterplot was generated to understand the abundance and biomass patterns of different fish trophic groups per island. A scatterplot was also generated to understand fish abundance and biomass across different size classes. To understand similarities among islands we performed a principal coordinate analysis (PCoA) by using the UVS transects as samples and applying the Bray-Curtis dissimilarity to the abundance data (individuals/m<sup>2</sup>). We also performed a permutational multivariate analysis of variance (PERMANOVA) to test for significant differences in the abundance and biomass of species, trophic groups, and size classes among islands. To validate the PERMANOVA results and test for heterogeneity among groups, we used the Betadisper function ( $p < 0.05$ ) along with the ANOVA function for all PERMANOVAs performed. To assess the significance of species on each island, we calculate  $R^2$  and  $p$ -values for each species, applying a threshold of  $R^2 \geq 0.2$  and  $p$ -values  $\leq 0.05$ . A Co-inertia analysis was carried out to visualise the correlation between fish abundance and habitat/island variables. Additionally, we calculated two components of the Beta-diversity: nestedness, i.e. species-poor sites are subsets of those found

in more diverse species-rich sites and turnover, i.e. replacement of some species by others, by using a species presence-absence matrix of the three islands and the Jaccard similarity coefficient. To assess whether there were differences in the mean thermal niche breadth of species among the islands, we applied a Kruskal-Wallis test. All analyses and graphics were performed using the “betapart” (Baselga et al., 2020), “tidyr” (Wickham, 2021), “vegan” (Oksanen et al., 2020), “ggplot2” (Wickham 2016), “ISLR” (James et al., 2021) and “dplyr” (Wickham et al., 2023) packages of R software (R Core Team, 2021).

### 3. Results

We recorded a total of 30,792 fish individuals belonging to 75 species in the three islands. Only 14 species accounted for 90% of the overall abundance in all islands. Ascension Island exhibited higher species richness in contrast to SPSPA and St. Helena which exhibited a similar pattern of species accumulation (Fig. 1S). The reef fish communities displayed significant variations across the islands. The mean density of individuals per m<sup>2</sup> recorded in SPSPA was  $4.67 \pm 0.34$  ind/m<sup>2</sup> (mean  $\pm$  SE). Ascension held the highest value, with a mean density of  $4.80 \pm 0.20$ , whereas St. Helena had the lowest mean  $1.91 \pm 0.08$ . The mean density of endemics in SPSPA took third place with  $1.28 \pm 0.09$  ind/m<sup>2</sup>, while Ascension exhibited the highest density at  $2.01 \pm 0.10$ , followed by St. Helena with  $1.33 \pm 0.05$  ind/m<sup>2</sup> (Table 1). These endemic densities represented 27% of the total density in SPSPA, 42% in Ascension, and an impressive 70% of the total fish density in St. Helena. The total mean biomass per m<sup>2</sup> followed a distinct pattern, with Ascension showing the higher biomass ( $0.86 \pm 0.07$  g/m<sup>2</sup>), SPSPA ranking second with  $0.38 \pm 0.04$  g/m<sup>2</sup>, and St. Helena with the lowest value ( $0.30 \pm 0.03$  g/m<sup>2</sup>). However, when considering only the endemic fishes' biomass, a reverse pattern emerged. SPSPA showed the lowest value ( $0.003 \pm 0.001$  g/m<sup>2</sup>), followed by Ascension ( $0.02 \pm 0.001$  g/m<sup>2</sup>), and St. Helena displayed the highest value ( $0.06 \pm 0.004$  g/m<sup>2</sup>) (Table 1). In terms of mean species richness, SPSPA recorded  $0.25 \pm 0.01$ , with Ascension displaying the highest mean ( $0.37 \pm 0.01$ ), and St. Helena mirroring SPSPA with  $0.25 \pm 0.01$ . However, when considering only endemic species richness, SPSPA had the lowest value ( $0.03 \pm 0.001$ ), while Ascension and St. Helena shared the same mean ( $0.12 \pm 0.004$ ) (Table 1).

#### 3.1. Abundance and biomass of trophic groups

The abundance and biomass of trophic groups displayed significant variations across the islands ( $p < 0.001$ ). Planktivores comprised the most abundant trophic group in SPSPA, ranking second in Ascension and St. Helena (Fig. 2A). Among the islands, planktivores exhibited  $1.90 \pm 0.29$  ind/m<sup>2</sup> in SPSPA, then Ascension ( $1.39 \pm 0.16$  ind/m<sup>2</sup>), and finally

**Table 1**

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

	SPSPA	Ascension	St. Helena
<b>Mean <math>\pm</math> SE density (Abundance/m<sup>2</sup>)</b>	$4.67 \pm 0.34$	$4.80 \pm 0.20$	$1.91 \pm 0.08$
<b>Mean <math>\pm</math> SE density of endemics (Abundance/m<sup>2</sup>)</b>	$1.28 \pm 0.09$	$2.01 \pm 0.10$	$1.33 \pm 0.05$
<b>Mean <math>\pm</math> SE biomass (kg/m<sup>2</sup>)</b>	$0.38 \pm 0.04$	$0.86 \pm 0.07$	$0.30 \pm 0.03$
<b>Mean <math>\pm</math> SE biomass of endemics (kg/m<sup>2</sup>)</b>	$0.003 \pm 0.001$	$0.02 \pm 0.001$	$0.06 \pm 0.004$
<b>Mean <math>\pm</math> SE richness (spp/m<sup>2</sup>)</b>	$0.25 \pm 0.01$	$0.37 \pm 0.01$	$0.25 \pm 0.01$
<b>Mean richness of endemics (spp/m<sup>2</sup>)</b>	$0.03 \pm 0.001$	$0.12 \pm 0.004$	$0.12 \pm 0.004$
<b>Total richness based on censuses (spp)</b>	32	47	34

St. Helena with  $0.54 \pm 0.07$  ind/m<sup>2</sup> (Fig. 2A). Herbivore-detritivores was the most abundant group in Ascension, and ranking second in SPSPA (Fig. 2A). SPSPA had an average of  $1.31 \pm 0.09$  ind/m<sup>2</sup>, Ascension displayed the highest abundance of them with an average of  $1.51 \pm 0.07$  ind/m<sup>2</sup>, and lastly, in St. Helena herbivores accounted for  $0.75 \pm 0.03$  ind/m<sup>2</sup> (Fig. 2A). Omnivores exhibited a substantial mean abundance in SPSPA ( $1.03 \pm 0.10$  ind/m<sup>2</sup>) and Ascension ( $0.81 \pm 0.05$  ind/m<sup>2</sup>). In St. Helena, omnivores accounted for only a modest abundance of this trophic group ( $0.08 \pm 0.01$  ind/m<sup>2</sup>) (Fig. 2A).

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

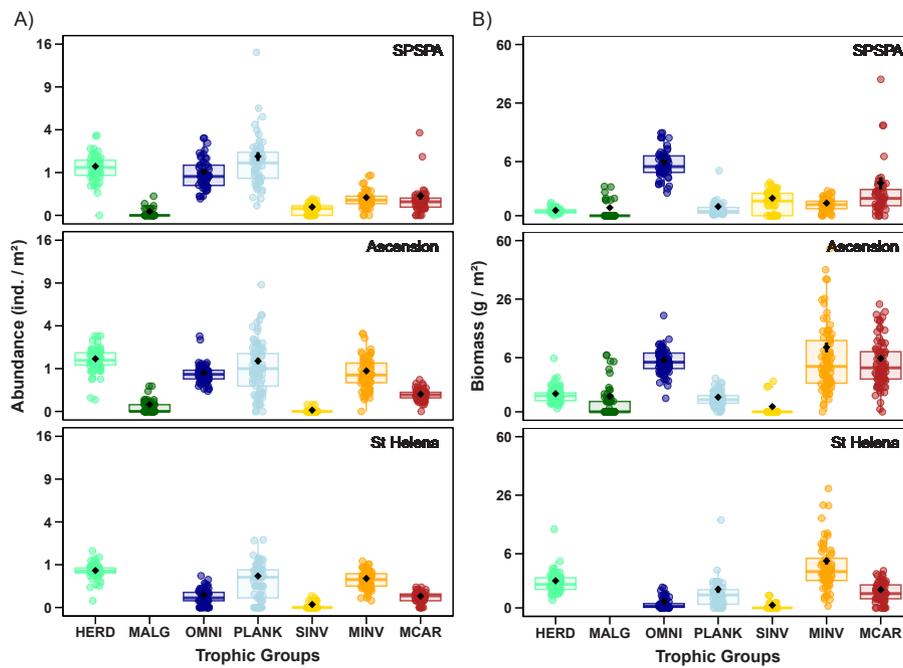
#### 3.2. Body size structure

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

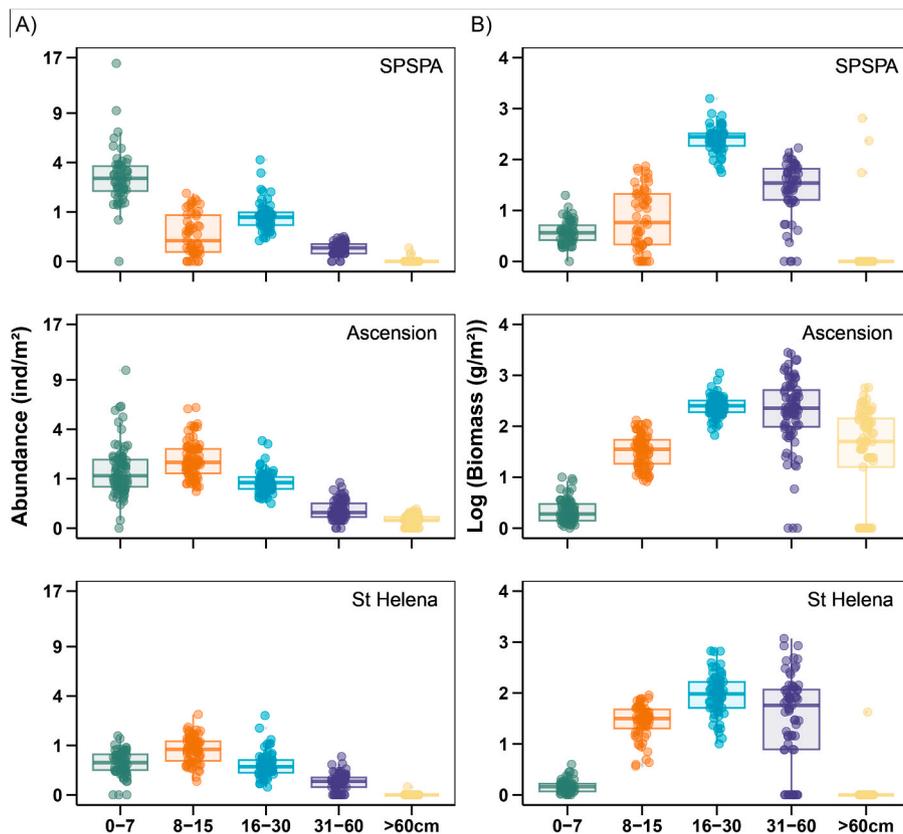
#### 3.3. Fish communities and environmental correlations

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

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



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

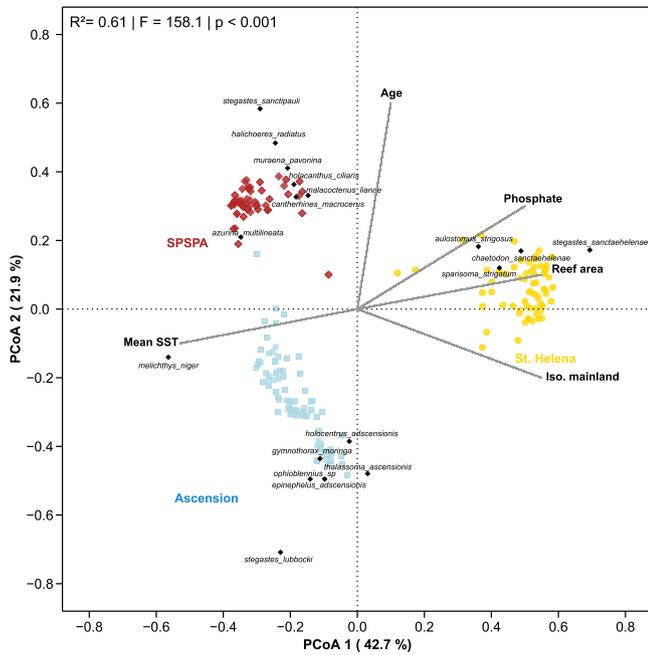


**Fig. 3.** Comparative boxplot and scatterplot showing the abundance and biomass of reef fishes on each island according to body size class.

### 3.4. Thermal niche

There were marginally significant differences in thermal niche breadth between SPSPA and St. Helena ( $p$ -value = 0.056), however, this

difference was not observed between Ascension and St. Helena. SPSPA exhibited a lower thermal niche breadth average, whereas St. Helena showed a higher average (Fig. 5A). In St. Helena, the species with the highest abundance also possess a wider thermal range, such as



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

*Chaetodon sanctaehelena* and *Stegastes sanctaehelena* (Fig. 5A). Distinct temperature patterns were evident in the monthly variations across the three islands. St. Helena experiences the highest seasonal variation, with temperatures varying up to 4.9 °C between months (Fig. 5B). SPSPA had the highest monthly average, reaching a maximum of 27.8 °C and a minimum of 26 °C. Ascension followed, with a maximum of 27.5 °C and a minimum of 24 °C. In contrast, St. Helena has a comparatively lower monthly average, ranging between 24.9 °C and 20.2 °C.

**4. Discussion**

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

seasonal temperature variation.

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

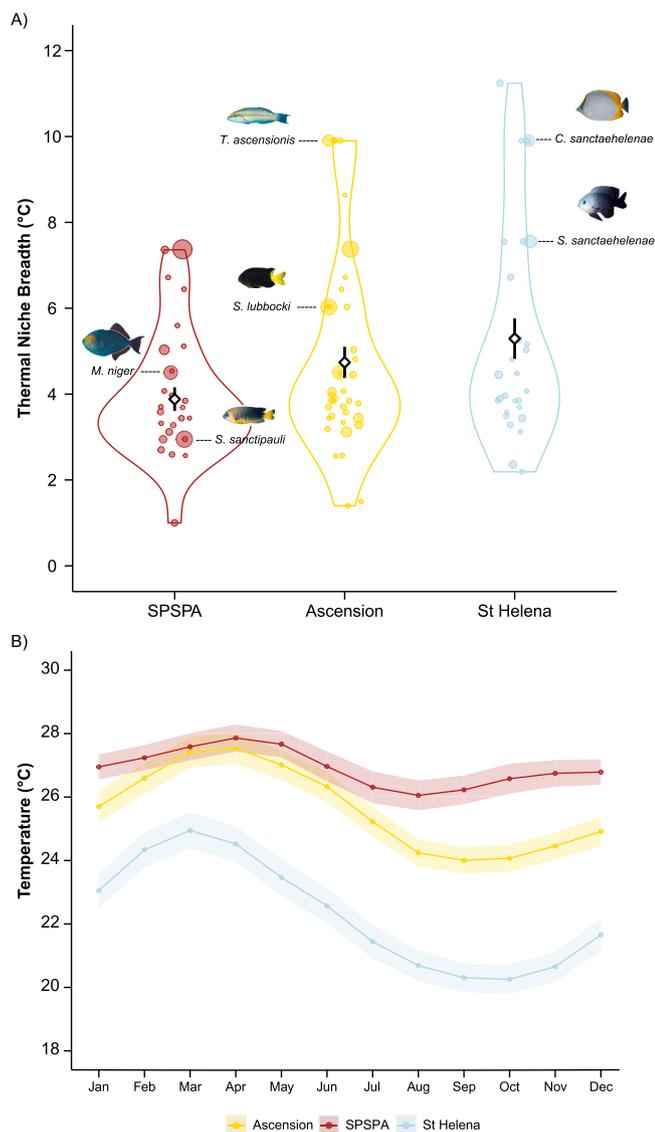
The highest temperature found in SPSPA, followed by Ascension, leads to the establishment and reproduction of tropical reef fishes, particularly herbivores and planktivores. There is a consensus that the warmer temperatures found in low latitudes (i.e. tropical regions) influence the richness, abundance,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

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

**Table 2**

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

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



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

plankton, thereby supporting the feeding activity of planktivorous fish species (Johansen and Jones, 2013).

Although Ascension and St. Helena share many species (including some shared endemics), there are differences in terms of abundance and biomass. We can observe this pattern within trophic groups, where Ascension shows more than double the abundance in almost all trophic groups, except for sessile invertebrate feeders, although their populations are relatively low on both islands. However, the 12-fold discrepancy in the number of individuals within omnivores on Ascension is partly due to the high abundance of the species *Melichthys niger*, which is very low in abundance in St. Helena. *M. niger* is highly abundant on tropical oceanic islands around the world, with a circumtropical distribution, plastic feeding capabilities and being a successful coloniser (Kavanagh and Olney, 2006). However, there is still no consensus regarding variations in body size and abundance on specific oceanic islands. A hypothesis is that, locations with higher reef fish diversity, especially within the families Balistidae and Monacanthidae, could lead to higher competition and a lower abundance in a local scale (Kavanagh and Olney, 2006). Nevertheless, when we observe the number of species

from Balistidae and Monacanthidae families ( $n = 6$ ), as well as species diversity, on St. Helena (Kavanagh and Olney, 2006), it is lower compared to Trindade Island, where there is a high abundance of *M. niger*. This hypothesis does not seem to explain the low abundance of this species on St. Helena. However, given that the thermal tolerance of this species ranges between 24.4 to 28.9 °C, with a thermal niche breadth of 4.5 °C, we hypothesise that temperature could be the primary limiting factor for the population expansion of this species on St. Helena. While the species thrives in the annual thermal variation of SPSPA and Ascension, it lacks sufficient thermal amplitude to withstand the variations in St. Helena (~20.2–24.9 °C), especially during the cold season.

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

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

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

Historical and contemporary factors also shape the patterns of beta diversity (Maxwell et al., 2022). Although the three islands share some endemic species suggesting a faunal link between these places (Wirtz et al., 2017; Brown et al., 2019), the high turnover among the studied islands indicates low species connectivity. The greater dissimilarity found for SPSPA can be explained by its stronger affinity with the Brazilian province and the Fernando de Noronha Ridge (Floeter et al., 2008). On the other hand, Ascension and St. Helena share trans-Atlantic species and also endemic species (Kulbicki et al., 2013). Despite the similarities between these two islands, there is a higher turnover than

nestedness in their species composition. Ascension exhibits a stronger affinity with the Western Atlantic compared to St. Helena, whereas St. Helena shows a similar affinity with both the Western and the Eastern Atlantic (Briggs and Bowen, 2012).

## 5. Conclusion

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

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## CRediT authorship contribution statement

**Débora S. Ferrari:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Lucas T. Nunes:** Investigation, Formal analysis, Conceptualization. **Kirsty L. Jones:** Writing – review & editing. **Carlos E.L. Ferreira:** Writing – review & editing, Project administration, Conceptualization. **Sergio R. Floeter:** Writing – review & editing, Supervision, Project administration, Conceptualization.

## Declaration of competing interest

The authors, declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data supporting this research are available on <https://marineinfo.org/id/dataset/8462>.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2024.106611>.

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