Rocky reefs of St Helena and the Tropical Atlantic: How the lack of coral and an isolated oceanic location drive unique inshore marine ecology

***Running Header* – Tropical Rocky Reefs of St Helena**

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Abstract

This paper presents the first quantitative assessment of the rocky reef ecology of St Helena, a remote island in the central tropical Atlantic. Monitoring data were used to characterise different habitat types found around St Helena. These findings were compared with 9 other locations in the tropical Atlantic, in different biogeographic, oceanic and reef settings, along with the environmental variables known to limit coral reef formation. St Helena's rocky and boulder reefs had ~50% cover dominated by turf and other filamentous algae, with lower levels of sessile invertebrates (15%) and macroalgae (4%). Both coral and rocky reef comparison locations also showed a dominance of turf and filamentous algae, with higher levels of macroalgae and sessile invertebrates in areas with higher nutrient concentrations (e.g. South-East continental Brazil). Coral growth in St Helena appeared to be limited by cool average sea temperatures of 22°C, which is near, but not below accepted lower thresholds for reef formation. The main trophic groups of fish found on rocky reefs in St Helena were comparable to other Atlantic rocky and coral reefs, with a dominance of planktivore, mobile invertivores and roving herbivores, with the major difference in trophic structure being driven by more planktivores in oceanic vs continental versus locations. St Helena's narrow rocky coastal strip varied little in terms of reef geomorphology, resulting in high homogeneity around the island. However, endemic fish were numerous, demonstrating the island's isolation has produced a unique tropical Atlantic marine assemblage.

1. INTRODUCTION

Outside of the Caribbean Sea, much of the tropical Atlantic Ocean lacks coral reefs (Spalding et al. 2001). No biogenic reefs are known from St Helena, the West African coast or nearby islands of Cape Verde or the Gulf of Guinea (Lœuff & Cosel 1998, Maia et al. 2018, Freitas et al. 2019), while marginal coral reef environments are found along the North-Eastern Brazilian coastline (Leão et al. 2003, Dutra et al. 2005, Francini-Filho et al. 2013). Various reasons have been proposed for the lack of reefs in the region including, high sedimentation along the continental Brazilian coast, cold upwelling in Cape Verde and freshwater outflow in the Gulf of Guinea (Lœuff & Cosel 1998, Leão et al. 2003). Globally, biogenic coral reef formation is limited to areas with mean annual sea temperatures between 20-32°C, low turbidity, nutrient poor water and high aragonite saturation (Kleypas et al. 1999, Guan et al. 2015).

Outside of these environmental limits, hard substratum areas in shallow waters have communities of algae, sessile invertebrates with some Scleractinian coral growth, known as rocky or marginal reefs (Perry & Larcombe 2003). These can occur in high latitude settings (e.g. Northern Florida) where cool temperatures are limiting, turbid settings (e.g. inshore Great Barrier Reef) where nutrients and light affect coral growth or in upwelling areas (e.g. Yemen) where temperature and nutrients both reduce coral reef suitability (Perry & Larcombe 2003). Species composition of fish communities on isolated and marginal coral reefs contain representatives from the majority of tropical functional groups (Dominici-Arosemena & Wolff 2006, Krutwa 2014, Mouillot et al. 2014, Quimbayo et al. 2019), suggesting that functioning of fish communities in all shallow tropical hard-substratum habitats may be similar. However, the ecology and biodiversity of coral reefs vary with numerous factors such as wave exposure, depth, currents, nutrients, isolation, and biogeographic region (Hobbs et al. 2012, Kulbicki et al. 2013, Quimbayo et al. 2019, Samoilys et al. 2019). It is therefore reasonable to expect that the fish and benthic communities rocky reefs also vary with local conditions.

The biogeography of the tropical Atlantic based on reef fish comprises four main provinces (Floeter et al. 2008, Kulbicki et al. 2013)(Fig. 1): The Caribbean province is the centre of diversity for the tropical Atlantic but is separated from the Brazilian coast by a dispersion barrier caused by the high sedimentation and low salinity from the Amazon and Orinoco rivers (Floeter et al. 2008, Cowman et al. 2017). The Brazilian province has lower species richness than the Caribbean and shares many species with West Atlantic distributions, but also has many species endemic to the province (Ferreira et al. 2004, Dutra et al. 2005). The East Atlantic is distinct from these two West Atlantic provinces, isolated by wide expanses of open ocean and few islands to act as ‘stepping-stones’ for dispersal (Floeter et al. 2008). The East Atlantic has the lowest marine fish and coral richness of any tropical province globally (Kulbicki et al. 2013, Cowman et al. 2017, Veron et al. 2019), as a result of isolation from other provinces, limited coral reef forming areas and palaeological contractions of the tropical zone during glacial periods, leading to extinctions of wide-spread tropical taxa (Lœuff & Cosel 1998, Vermeij 2012).

St Helena is a highly isolated oceanic island on the Mid-Atlantic Ridge formed by volcanic activity 14 million years ago, located approximately 2000km west of Angola and 3500km east of Brazil (16°00’ S, 5°45’ W). Previous research on shallow water marine life of St Helena has focussed on biodiversity inventories and biogeography (Edwards 1990, Brown 2014a, Brown et al. 2019) noting the importance of isolation for a species composition high in endemics, but with low species richness of 189 inshore fish species and 3 Scleractinian coral species. St Helena and its nearest neighbour Ascension Island (1300km North-West) have biogeographic affinities with both the East and West Atlantic (Floeter et al. 2008, Kulbicki et al. 2013, Wirtz et al. 2014), which could be considered a separate Central Atlantic or Mid-Atlantic Ridge province (Floeter et al. 2008) (Fig. 1). Reef fish on small islands comprise a subset of species from the neighbouring mainland, with richness varying with island size and isolation (Hobbs et al. 2012). Richness is usually lower than in continental areas because the small areas of islands are generally associated with lower habitat diversity, lower species colonisation rates and higher extinction rates (Hobbs et al. 2012, Luiz et al. 2015, Quimbayo et al. 2019). Widespread species with good dispersal abilities and endemics tend to be common (Hobbs et al. 2012, Luiz et al. 2015).

Whilst the biodiversity and biogeographic affinities of St Helena have been discussed in depth, the ecology of its reefs and other marginal Atlantic reef locations are poorly known. What is preventing coral reefs forming in St Helena? Are the rocky reefs fundamentally functioning like coral reefs, but without coral, or are different ecological roles and groups more important? Are differences in reef ecology based on biogeographic patterns or environmental ones? This paper attempts to address these questions by presenting data from an ecological monitoring programme conducted around St Helena since 2013. We compare monitoring data from St Helena with data from 9 locations from around the Tropical Atlantic (Fig. 1) representing both coral reefs and rocky reefs in oceanic and continental contexts. Specifically, we aim to;

- Describe the components of benthic and fish communities in St Helena and how these vary with substrate, wave exposure, depth and season. These factors are important for structuring marine communities in coral reefs and it is expected that they will also drive community structure on St Helena’s rocky reefs (Sandin et al. 2008, Samoilys et al. 2019).

- Define the environmental conditions important for coral reef formation (i.e. temperature, nutrients, aragonite saturation) for each location to investigate why coral reefs are absent in St Helena and 6 of the comparison locations. It is expected that environmental variables at the 3 coral reef locations fall within the global environmental limits for coral reef formation as defined by Kleypas et al. (1999) and Guan et al. (2015), whereas St Helena and the other rocky reef comparison locations fall outside of these. However, it is currently unclear which environmental variables are preventing coral reef formation and growth, and if the same limiting factors are acting in each location.
- Compare the benthic composition and fish communities between coral reef and rocky reef locations to investigate whether reef ecology varies with biogeographic patterns (Kulbicki et al. 2013, Cowman et al. 2017) or other oceanographic factors such as temperature or nutrients (Quimbayo et al. 2019).

2. METHODS

2.1 Field methods in St Helena

The 430,000km^2 Exclusive Economic Zone (EEZ) of St Helena was declared a Sustainable Use (IUCN Category VI) Marine Protected Area (MPA) in St Helena's Environmental Protection Ordinance 2016, protecting a wide range of species and habitats. Almost all of St Helena's 52km coastline consists of steep cliffs with rock and boulder shores, and underwater the slope continues relatively uniformly around the island, with the 50m isobath close (1-3km) to the coast. The rocky reef and other shallow water environments in this narrow strip were investigated by monitoring benthic and fish communities in combined underwater belt transects by members of St Helena Government's Environmental Division (Brown 2014b). In this study, data are presented from 28 sites from both the leeward and windward sides of the island (Fig. 2). Most sites were investigated at two depths between 5-12m (shallow) and 14-25m (deep). All sites were initially surveyed in 2013 during the warmest ocean month (April) and the coolest (October) and 10 sites on the leeward side of the island continued to be monitored on a biannual basis in 2015, 2017 and 2019. Unfortunately, for the other 18 sites, including all the windward sites, this means only one year of monitoring data is available and variability over time remains unknown. Values from different years in the 10 regularly monitored sites were summarised as the mean. One transect was deployed at each site, depth and monitoring period, giving a total of 192 transects.

Fish were surveyed using underwater visual census (UVC). Small cryptic fish were counted in an area of 50 x 2m (100m^2), while large, conspicuous fish were counted on a second pass of the transect in an area 50 x 10m (500m^2). Two divers each counted half of the transect (i.e. 50m x 1m for small transect, 50m x 5m for the large), swimming 1-2m above the seabed, and then combined their counts to give one abundance per species per transect. Each fish was identified to species and assigned a trophic group using classifications commonly used for tropical Atlantic fish (Mouillot et al. 2014, Maia et al. 2018, Freitas et al. 2019). The fish trophic categories used were: ‘Roving herbivores’ feeding on turf and macroalgae and with no fixed abode, ‘Territorial herbivores’ aggressively defending patches of cultivated algae in home patches, ‘Planktivores’ feeding on phytoplankton and zooplankton in the water column, ‘Omnivores’ feeding on a range of benthic organisms and detritus, ‘Sessile invertivores’ targeting sessile invertebrates such as sponges, hydroids and corals, ‘Mobile invertivores’ targeting mobile invertebrate, such as crustaceans and molluscs, ‘Predators’ feeding on other fish, but often still with a component of invertebrate food, depending on the species and age of the predator. Comparisons of fish community used species identity and trophic groups to indicate taxonomic and ecological differences between sites in St Helena and between St Helena and tropical Atlantic comparison locations.

Benthic data were collected using ten 0.5 x 0.5m (0.25m^2) photo-quadrats placed at regular intervals along the transect. Photo-quadrats were classified using Coral Point Count (CPCe) (Kohler & Gill 2006). Each photo was overlaid with 25 points arranged in a regular 5 x 5 grid and every point was double-classified with a living category and substrate category. Categories of living benthic cover were derived from the Collaborative and Annotation Tools for Analysis of Marine Imagery and video (CATAMI) system (Althaus et al. 2013). The term ‘turf algae’ is applied to various epilithic algal communities (Connell et al. 1997), but in the Tropical Atlantic appear to be largely formed of filamentous red algae (Longo et al. 2015), hence these two living categories might be better described as ‘short’ and ‘long’ turf/filamentous red algae. Underlying substrate was classified as being sand (all loose sediment up to gravel), maerl (cobble sized coralline algae lumps), boulder (solid substrate with defined edges) and rock (solid substrate with no defined edges). The category ‘sand’ was used in both substrate and living classifications, as sandy areas had no epifauna or epiflora meaning that ‘living’ category was the same as the ‘substrate’.

2.2 Tropical Atlantic comparisons of benthos, fish and coral reef suitability

Nine previous studies using a similar field method of quantitative transects to record benthic composition and fish community were identified from around the Atlantic (Fig.1, Table 1). Unfortunately, no such studies were available from St Helena’s nearest neighbour, Ascension Island. Each study investigated a range of sites with different depths and wave exposure, representative of that location. Data on benthic cover and fish species abundance were extracted from published articles and supplementary material (Table 1). All studies presented benthic cover as a percentage, but the use of slightly different categories in some studies required some modifications to the original categories to be consistent throughout. For example, in studies that classified red filamentous algae (e.g. St Helena), this category was reclassified as ‘turf’, as filamentous Rhodophytes are the dominant component of Atlantic turf algae (Longo et al. 2015). The difference in cover of living benthic organisms was of primary interest, hence substrates unsuitable for benthic organisms to settle on (i.e. sand and rubble) were removed from benthic cover reported in studies, and the remaining categories were recalculated as a percentage of cover of hard substrate (i.e. total cover – sand + rubble). Fish species were assigned a trophic group as described above, and their geographic range was obtained from FishBase (www.fishbase.com). Fish species ranges were simplified into seven categories; 'Central Atlantic', 'East Atlantic', 'Brazil' and 'Caribbean' refer to species endemic to that biogeographic province, 'West Atlantic' refers to species found both in the Caribbean and Brazil, 'Tropical Atlantic' for species across the entire basin and 'Circumtropical' for species also found in the tropical Indo-Pacific. Fish trophic group was taken from the studies (Table 1). Some papers used the additional category 'piscivore', which was combined with 'predator' in this study. Others did not distinguish between roving herbivores, such as parrotfish (Scarinae) and surgeonfish (Acanthuridae), and territorial herbivores, such as damselfish (Pomacentridae) and blennies (Blenniidae). Any species which lacked an equivalent trophic group in the comparison studies were assigned a group by using trophic information on FishBase's species pages. Absolute abundance data were converted to relative abundance (%) per species, trophic group and biogeographical affinity for each location.

Guan et al. (2015) investigated the limits of coral reef growth using mean sea surface temperature (SST), salinity, nitrate and phosphate concentration and aragonite saturation. The annual mean values for these variables were plotted for the whole tropical Atlantic and values were extracted for St Helena and the nine comparison sites. SSTs were obtained from the Group for High Resolution Sea Surface Temperature (GHRSST) global Level 4 daily analysed SST product at 0.25 degree resolution (https://podaac.jpl.nasa.gov/dataset/). Annual mean SST was calculated over the period 1995-2018. Nitrate, phosphate and salinity climatology for the sites were obtained from *in situ* measurements collated by the World Ocean Atlas 2013 V2 (Garcia et al. 2013, Zweng et al. 2013) spanning the period 1995-2012. As *in situ* nitrate and phosphate data can be sparse in remote regions, these variables were also obtained from the Global Ocean Biogeochemistry Hindcast model provided by E.U. Copernicus Marine Service Information (Copernicus 2020a), for use in spatial analysis. Annual mean values from the hindcast were calculated over 1995-2018. Aragonite saturation was obtained from the GLODAPv2 mapped climatology at a 1 degree resolution (data spanning 1972-2013, 2016b release; Lauvset et al. 2016), but unfortunately no data were available for Cozumel, Mexico. Two additional variables, Chlorophyll-a concentration and visibility measured by Secchi disk depth (as a proxy for turbidity) were obtained from Global Ocean Colour satellite observation products (Copernicus 2020b,c).

2.3 Data Analysis

Living benthic cover and fish trophic structure in St Helena were compared against a range of explanatory variables, including substrate, wave exposure, depth and season, using transect data as replicates. For benthic data, the percentage cover from quadrats was averaged for each transect, which has the benefit of removing spatial correlation between neighbouring quadrats. The dominant substrate type for a transect was defined using photo-quadrat results as; ‘sand’ if the transect contained >75% sand, ‘maerl’ for >25% maerl and <50% rock or boulder, ‘boulder’ for <75% sand when boulder cover was greater than rock and ‘rock’ for <75% sand and rock cover was greater than boulder. Depth was recorded as a numeric value to the nearest metre, however, transects were not deployed regularly across the depth range of 5 – 25m with a bimodal distribution centring around 10m and 20m. A break in the distribution of transect depth occurs at 13m, hence transects <13m deep were classified as ‘Shallow’ and those >13m, as ‘Deep’. Exposure was treated as a two-factor categorical variable ‘Leeward’ and ‘Windward’ based on aspect of the coast to the dominant south-easterly wind and waves. Season was also a two-factor categorical variable: ‘Summer’ and ‘Winter’. Dominant substrate type was highly correlated with depth and exposure (Fig. 2), with sand exclusively found in deep leeward areas, maerl only found on deep transects, and rock only found on windward sites. Statistical analyses of wave exposure, depth and season were therefore only conducted on data from solid boulder and rock substrate transects.

Living benthic categories and fish species, and trophic assemblages in St Helena and Atlantic comparison sites were plotted using Multi-Dimensional Scaling (MDS) using Bray-Curtis similarity distance to identify if there were any distinct groupings of locations. Differences in community structure associated with wave exposure, depth, season and substrate type were investigated using Analysis of Similarity (ANOSIM). These multivariate methods do not perform well if there are species or transects with high proportions of zeros (Henderson & Seaby 2008), hence species and transects with fewer than 10 individuals in total were removed from the analyses. Most of the excluded transects were over sandy substrates, which had very few fish or benthic categories, potentially biasing the findings for this substrate type. The rare species excluded could be described as pelagic vagrants to the reef, including jacks (Carangidae), scads (*Decapterus spp.*) and Chilean devil ray (*Mobula tarapacana*), and it is therefore assumed the removal of these species will not bias the community composition of the demersal fish community. For the benthic analysis, all transects and 15 (of 22) benthic categories were used, while for fish 128 (of 192) transects and 46 (of 58) species were used in the analysis.

The analyses were conducted in the Vegan package for R version 3.5.1 (Oksanen et al. 2019). Differences in the cover of individual benthic categories, fish trophic group and fish species abundance between exposure, depth and season categories were investigated using permutation tests. Permutation tests perform well with non-normal distributions, such as the count data for fish species and percentage data for benthic cover (Whitlock & Schluter 2009). In this approach the chance of Type 1 error increases with multiple tests, hence a Bonferroni conversion was used establish new significance thresholds for the tests; benthic categories p = 0.0055, fish trophic group p = 0.0071, fish species p = 0.0014. Bonferroni conversions were carried out separately for different analyses to reduce the chance of Type 2 errors. Permutations tests were carried out using the Coin package in R (Hothorn et al. 2008), which uses a unified approach and provides independence tests for nominal, ordered, numeric and multivariate data at mixed scales. All mean values are presented along with the standard error.

Unfortunately the sites in St Helena were not well balanced in relation to the explanatory variables of substrate, exposure, depth and season, meaning it was not possible to conduct more complex models (e.g. nested GLMMs) accounting for interaction between explanatory variables. For example, many deep samples on the windward side of the island were rocky or boulder reefs, while on the leeward side most were sand or maerl, meaning that the interaction between depth and exposure are confounded by differences in substrate. Future fieldwork will sample all explanatory variables in a more balanced design to test interactions between them.

3. RESULTS

3.1 Variation in benthic and fish community composition around St Helena

The majority of the benthic cover on rocky and boulder reefs was filamentous algae, with a third (32.1 ± 1.61%) being turf algae and a further 22.2 ± 1.65% was filamentous red algae. The remaining cover consisted of 15.3 ± 0.93% invertebrates, predominately hydroids and the crinoid *Tropiometra carinata* , 9.3 ± 0.70%, encrusting calcareous red algae and 3.9 ± 0.60% of macroalgae from three species (*Asparagopsis taxiformis, Dictyota spp.* & *Caulerpa racemosa*). Two species of hard corals (Scleractinia), *Favia gravida* and *Madracis pharensis*, were observed with a very low cover of 0.1 ± 0.03%. ANOSIM results indicate that wave exposure was the most important explanatory variable for explaining variety in benthic composition of rock and boulder reefs (R = 0.305, p = 0.001) (Fig. 3B), followed by season (R = 0.192, p = 0.001)(Fig. 3C), with no significant differences between shallow and deep transects (R = 0.045, p = 0.146) (Fig. 3D). This variation was primarily driven by the algal community, with significantly higher cover of filamentous algae and macroalgae during the summer and in windward sites (Table S1). In maerl beds, the biogenic substrate created by calcareous red algae covered 68.8 ± 5.79% of the benthos, with turf algae, filamentous red algae, calcareous red algae, sponges and hydroids being the most common living components. Transects on sandy substrate found no epi-fauna or flora with >99% of 'living cover' being classified as 'sand'.

A total of 84,524 fish were counted, and 58 species and 31 families were identified, 19 (33%) of which were endemic to St Helena and Ascension. Individuals were distributed unevenly across species, with 79% of the total abundance comprised of the most common 6 species. Interestingly, 3 of these common species are endemic to the Central Atlantic (*Chaetodon sanctaehelenae*, *Stegastes sanctaehelenae* & *Thalassoma sanctaehelenae*), meaning that endemic species comprised 58.6% of total fish abundance. The rarest 26 species, in contrast, made up just 1% of the overall abundance (Table S2 & S3). The most abundant trophic group were the planktivores with a mean density of 53.2 ± 4.22 individuals per 100m^2, followed by mobile invertivores with 24.1 ± 1.94 ind. per 100m^2 and territorial herbivores with 20.6 ± 1.11 ind. per 100m^2 (Fig. 6, Table S3). The least abundant group were the sessile invertivores with 0.8 ± 0.10 ind. per 100m^2. For fish communities on solid (boulder and rock) substrate, ANOSIM results show that transects from different wave exposure (R = 0.150, p = 0.002), season (R = 0.040, p = 0.001) and depth (R = 0.096, p = 0.003) were significantly different, although the differences in groups were minor, as indicated by the lack of clear separation between groups and low '*R*' values from ANOSIM (Fig. 5B,C,D). There were 3 times more territorial herbivores (z = 5.933, p < 0.001) and ~50% more predators (z = 2.925, p = 0.003) in leeward transects (Fig. 6B) and ~50% higher abundance of territorial herbivores in shallow transects (z = 3.209, p = 0.001) (Fig. 6C). Summer experienced statistically significantly higher abundance of territorial herbivores (z = 2.724, p = 0.006), mobile invertivores (z = 3.086, p = 0.002) and predators (z = 3.293, p < 0.001), although the differences were slight (<25% difference) (Fig. 6D). The fish abundance on sand and maerl substrates was lower (Fig. 6A), but these areas had species not commonly found on solid substrate, such as the endemic St Helena flounder (*Bothus mellissii*) on sand and the endemic marmalade razorfish (*Xyrichthys blanchardi*) on maerl (Table S2).

3.2 Environmental suitability of the Tropical Atlantic for coral reefs

St Helena and six of the comparison sites (see Table 1 for references) did not possess biogenic coral reefs, but did possess hermatypic photosynthetic corals (Table 2). Biogenic coral reefs were also absent at locations in the East Atlantic, but had higher coral cover of ~8% dominated by massive corals *Siderastrea radians* and *Porites astreoides* in Cape Verde and *S. radians* and *Montastraea cavernosa* in São Tomé. On Brazil's continental coast at Arraial do Cabo and Espirito Santo, rocky reefs had hard coral cover of ~5% and were dominated by *Siderastrea stellata* and *Mussismilia hispida*. Just 350 km to the north of Espirito Santo, Abrolhos possesses true coral reefs, with the highest coral cover site of the locations discussed here (12.7%) and a total of 19 coral species, although the majority of cover (>70%) was dominated by the endemic species *Mussismilia braziliensis*. Further north 150 km off the north-east tip of Brazil near the equator, the oceanic atoll, Atol das Rocas, had a lower coral cover (8%) and coral richness (5) compared to Abrolhos, with the dominant hard coral species being *Siderastrea stellata* and the majority of reef building organisms being encrusting calcareous red algae. Cozumel, located in the heart of the Caribbean coral reef-forming region at the northern end of the Meso-American barrier reef, had extensive fringing reefs with a total of 47 scleractinian species recorded, an order of magnitude higher than the rocky reefs and Atol das Rocas. Current coral cover is 11.4%, but this is greatly reduced compared to the 34.9% cover in the 1980s because of hurricane damage and human pressures (Table 2). Four dominant coral species formed 67% of the total coral community in Cozumel, including the foliose *Agaricia agaricites*, and massive *Porites asteroides*, *Siderastrea siderea* and *Montastraea cavernosa*.

The dominant benthic component in all locations were turf, calcareous red and macro-algae, with the highest macro-algae cover (>20%) in Santa Luzia, Trindade and Cozumel (Fig. 7). The MDS does not show any clustering of location-based reef type or oceanic vs. continental location, with the algal categories -located near the centre of the plot indicating these categories varied little between locations. More variation is apparent in the sessile invertebrates (i.e. zoanthid, sponge and other). St Helena had moderate cover (19.6%) of non-coral invertebrates, while nutrient-rich Arraial do Cabo and Espirito Santo had >40% cover with greater importance of the zoanthid *Palythoa caribaeorum* and sponges.

The West Atlantic is warmer than the East Atlantic (Fig. 8A). In the East Atlantic, cool water is advected towards the equator, with the Benguela current from the south and the Canaries current from the north. In contrast, the Caribbean and Brazilian currents advect warm water away from the equator in the West Atlantic, creating a larger area of warm temperatures (Fig. 1). Wind-driven upwelling of cool, sub-surface waters also results in lower temperatures in the East Atlantic as well as the equator. Salinity was highest (~37ppt) in the sub-tropical gyres and was slightly lower at the equator (~36ppt) but was most reduced to ≤29 ppt in the vicinity of the Amazon and Congo river plumes (Fig. 8B). Aragonite saturation appeared relatively uniform across the region between 3.5 – 4.5Ω_A, although no values were available for the Caribbean (Fig. 8C). Nitrate and phosphate concentrations were highest along the coast of the sub-tropical East Atlantic, due to upwelling along the eastern boundary near Cape Verde and Namibia (Fig. 8D,E). Additional input of nitrate is also evident from the Amazon river. These areas of high nutrients coincide with high primary productivity, indicated by the Chlorophyll-A concentrations (Fig. 8F) and, as expected, there is an inverse relationship between Chlorophyll-A and Secchi Depth (Fig. 8G), with values exceeding 40m in the sub-tropical gyres, and less than 10m along some continental coasts.

None of the Atlantic locations selected in this study had environmental variables outside the limits of coral reef growth stated by Guan et al. 2015 (Table 2). St Helena had the coolest average SST (22.4°C) and winter minimum (19.6°C) of any of the sites, but this was still 0.7°C warmer than the coldest limits for coral reef growth (Table 2). Salinity and Aragonite saturation at St Helena were well within the limits of coral reef growth, while low nutrient concentrations resulted in relatively low Chlorophyll-A concentrations of 0.144mg/l and a high Secchi Depth of 27.2m. The seemingly least suitable site for coral reef formation is Arraial do Cabo at the edge of the tropical zone, where the cool Falklands current mixes with the waters of the Brazilian current (Fig. 8A). It had the second lowest average SST (23.5°C) and high nutrient concentrations resulted in the highest Chlorophyll-A concentration (1.424mg/l) and highest turbidity (Secchi Depth - 7.5m) of any location, but nevertheless had more coral (5.7%) than St Helena. Cooler, nutrient-rich environments were also present at Santa Luzia in Cape Verde. Located on the equator, São Tomé had high SST (27.2°C), but appeared to be influenced by riverine inputs from nearby continental Africa, with moderately high Chlorophyll-A concentration (0.321mg/l) and the lowest average salinity of any location (33.8ppt). The location with the most developed coral reefs in Cozumel had highly suitable values for reef growth, with high SST (28°C), low primary productivity (Chl-A: 0.103mg/l) and low turbidity (Secchi Depth - 29.7m). However, Trindade island, although cooler than Cozumel (25.7°C), had lower Chlorophyll-A (0.059mg/l) and lower turbidity (Secchi Depth - 38.9m), suggesting that this site should also be suitable for coral reef formation, but yet has no known biogenic reefs. These variables alone do not appear to satisfactorily explain the presence or absence of coral reefs in the Tropical Atlantic locations considered here.

3.3 Fish ecology and biogeography

Observed fish richness in transects from the different Atlantic comparison sites showed similar patterns to findings from studies comparing total richness from biodiversity inventories (e.g. Floeter et al. 2008), with the Caribbean having relatively high richness and the East Atlantic having lower (Table 3). Additionally, the inshore shelf area (<50m), but not distance to the next reef, appeared to be important for richness with the small (7km^2) near-continent (150km) Atol das Rocas having lower richness than the larger (32km^2), but more isolated Trindade island 1000km from the Brazilian shore. The relative abundance of fish species in each location was highly uneven, with 3-4 common species accounting for >10% of the total abundance each, and rare species (<1% of total abundance) comprising ~80% of all species. This was also evident within trophic groups, where the species richness within most trophic groups increased with overall richness (Table S4); (e.g. 4 species of roving herbivore in St Helena compared to 14 in Cozumel), but where each trophic group was dominated by 1 or 2 species that each made up >25% of that trophic group's total abundance. Evenness showed similar pattern to richness and shelf area, with the least even community was recorded at the tiny (0.03km^2) species poor (33) St Paul's Rocks, while continental Brazilian locations and Cozumel had the highest species evenness (Table 3).

Biogeographically, 20-60% of fish abundance at each site were from species unique to that province, with the MDS plot of range relative abundance clearly separates out locations by biogeographic province (Fig. 9). St Helena had 19 species

(33% of total richness) endemic to the Central Atlantic, which comprised the majority (59%) of the fish abundance observed in transects. Atol das Rocas, Trindade and Cozumel, showed similar patterns where proportionally fewer endemic species comprised >50% of fish abundance. The reverse pattern was observed in São Tomé, where 38 East Atlantic species comprised 58.5% of total richness, but these species only made up 18.0% of the abundance.

Fish trophic structure was not grouped by biogeographic province, with the main differences being between continental and oceanic sites (Fig. 10). On all oceanic islands, planktivores were the most abundant group and comprised between 38.4 – 79.1% of the total abundance, while at continental Brazilian sites, sessile and mobile invertivores were more abundant and there were proportionally fewer planktivores. On average, herbivores made up 24.3% of the total abundance, with very high proportions (61.1%) in Abrolhos and very low proportions of herbivores (>5%) in São Tomé and Santa Luzia. Cozumel had the most balanced community with no trophic group exceeding 40% of the total abundance, whereas São Tomé and Santa Luzia were the least trophically diverse locations with >85% of the fish community comprising planktivores and mobile invertivores. The familial composition of trophic groups was consistent across locations for many groups, but with different families performing for others. For example, all roving herbivores came from 3 families, surgeonfish (Acanthuridae), parrotfish (Scarinae) and chubs (Kyphosidae), while all territorial herbivores were either damselfish (Pomacentridae) or blennies (Blennidae). Conversely, although many planktivores were Pomacentridae or Labridae, but in St Helena the butterflyfish *Chaetodon sanctaehelenae* was a dominant component of this trophic group, while in São Tomé the serranid *Paranthias furcifer* dominated.

Haemulidae, Lutjanidae, Pomacanthidae and Labrisomidae were important families in many Atlantic locations, but were completely absent from St Helena.

4. DISCUSSION

4.1 Why are coral reefs absent at St Helena and other Atlantic locations?

Contrary to our expectation, the rocky reef locations investigated in this study were all within the limits of coral reef formation, *sensu* Guan et al. (2015). St Helena had almost no Scleractinia corals in its nearshore environment despite having an average SST and winter minimum SSTs at which coral growth is sufficient to form reefs in similar conditions of south-east Australia, Japan and the northern Persian/Arabian Gulf (Kleypas et al. 1999). In the Atlantic, coral reefs exist around Bermuda (32°N), which has similar temperatures to St Helena, but was noted as being an exception in the Atlantic by Kleypas et al. (1999). They posited that Atlantic coral reef formation may have narrower thermal tolerance than in the Indo-Pacific. The three biogenic coral reefs investigated here, Abrolhos, Atol das Rocas and Cozumel, had mean SSTs of ≥26°C, while rocky reefs at South-Eastern Brazilian sites and Cape Verde were cooler than this. These rocky reefs also had high nutrient concentrations, primary productivity and turbidity, with Arraial do Cabo representing a transitional tropical environment affected by seasonal cold upwelling (Ferreira et al. 2001) and Cape Verde where upwelling and high dust input from the Sahara further increase nutrient levels and turbidity (Monteiro et al. 2008). These locations also had high cover of sessile invertebrates, most of which feed on plankton. It may be that coral reef formation is limited at different thresholds for a particular variable, such as temperature, when another factor (e.g. nutrients) combines to create less favourable conditions for coral reef growth. Nevertheless, located 1000km from Brazil in the centre of the nutrient poor South-Atlantic sub-tropical gyre, Trindade also did not possess coral reefs despite being only 0.6°C cooler than coral reefs in Abrolhos, and with half the concentration of nitrate.

An alternative hypothesis for the lack of coral reef despite the seemingly suitable environmental conditions in the Central and Eastern Atlantic, is that reef building species cannot reach these locations (Nunes et al. 2011, Peluso et al. 2018). Of the three species of coral listed for St Helena (Brown 2014a), none could be considered dominant framework building species (Laborel 1974, Veron et al. 2019). During glacial periods in the Pleistocene, the tropical zone in the Atlantic was greatly contracted resulting in the extinctions of many previously pan-tropical taxa from the Eastern Atlantic (Laborel 1974, Lœuff & Cosel 1998). The ~10,000 years since the start of the present day inter-glacial, may be too short a time for reef building species from the West Atlantic to arrive, especially considering that dominant equatorial currents pushing the majority of coral larvae westward, away from the East Atlantic (Wood et al. 2014). However, in São Tomé and Cape Verde important West Atlantic reef building species of coral are found (e.g. *Montastraea cavernosa* & *Siderastrea spp.*), but never form true reef structures and exist as isolated colonies or incipient reef pavements in shallow sheltered bays (Laborel 1974, Maia et al. 2018, Freitas et al. 2019). Elsewhere extensive coral reefs can form in highly isolated species poor areas, as demonstrated by Clipperton Atoll in the Eastern Pacific where a fully biogenic atoll has been formed by just 7 species of coral >1000km away from the nearest coral reef

(Glynn et al. 1996), hence isolation and low coral species richness do not appear to explain the lack of East or Central Atlantic reefs.

Yet another alternative hypothesis is that coral reef environmental threshold may not be correctly defined because of lack of resolution in global models. Guan et al. (2015) note that their upper nutrient threshold was determined by the presence of coral reefs in the Galapagos, where average nitrate concentration is 4.51µM and phosphate is 0.63µM. The Galapagos archipelago has a range of rocky and coral reefs at exposed and sheltered sites (Quimbayo et al. 2019). A caging experiment showed that in exposed areas, upwelling nutrient-rich water drives bottom-up processes of benthic communities, with no difference in algal communities between caged and uncaged benthos. Conversely, at sheltered sites, nutrient limitation was evident from the impact of top-down grazing by fish and invertebrates on uncaged surfaces (Krutwa 2014). These sheltered inshore sites were also where the highest coral growth was observed in Galapagos (Krutwa 2014), a trend that was also noted in South-East Brazil (Ferreira et al. 2001, Floeter et al. 2004), Atol das Rocas (Gherardi & Bosence 2001), and Cape Verde, (Monteiro et al. 2008). Isolated oceanic islands often experience locally enhanced nutrient levels as a result of the Island-Mass Effect (Gove et al. 2016), where deeper water can be brought to the surface by upwelling, mixing and internal waves, forcing cooler nutrient rich water into shallow habitats (Lœuff & Cosel 1998, Tkachenko & Soong 2017, Cowburn, Moritz, et al. 2019, Green et al. 2019). In the Gulf of Guinea, the mixed layer depth is shallow (20-50m), with cooler sub-surface waters periodically flushing shallow reef environments (Lœuff & Cosel 1998, Maia et al. 2018). The global datasets used in this analysis and that of Guan et al. (2015) would not detect such local variations in variables around coastlines. The highest spatial resolution used in this study is 4 km, from the ocean colour data products. While such products may resolve the presence (or not) of an Island-Mass Effect (e.g. due to presence of blooms), it is not sufficient to resolve variability around the island, between individual bays or coastlines. Datasets used to produce climatologies (such as WOA) can be very sparse in the open ocean, with a very small number of *in situ* observations contributing to the values for remote locations such as St Helena (not distinguishing between coastal vs open ocean measurements). For this reason, spatial variability in nutrient concentrations were also assessed from an ocean model hindcast. However, as these models lack nutrient run-off information from rivers and other anthropogenic sources, they were not deemed suitable to assess threshold values (hence the reliance on WOA for this purpose).

These factors may mean that St Helena’s reefs experience less favourable coral reef-forming conditions than our data suggest if nearshore upwelling has not been detected by satellite data. Alternatively, coral reefs used to characterise environmental limits defined by Guan et al. (2015) may exist in localised sheltered environments with higher temperatures and lower nutrients than surrounding oceanic conditions, resulting in an overestimation of coral reef growth tolerance limits.

4.2 Are rocky reefs ecologically different from coral reefs?

Corals are not the only benthic component or primary producers of coral reefs, with large proportions of the substrate being covered in encrusting calcareous algae, turf algae, macroalgae and a range of other sessile invertebrates (Francini-Filho et al. 2013, Reyes-Bonilla et al. 2014, Cowburn, Samoilys, et al. 2019). In this study, turf algae and encrusting calcareous algae were the dominant benthic components on all reefs examined, covering >50% of available hard substrate, while (contemporary) coral cover was <15%. Examining the nutritional value of turf algae in Atol das Rocas revealed that turfs contain a range of algal species, often from filamentous Rhodophyte types, and have a variety of invertebrate crypto-fauna (Longo et al. 2015), meaning these turfs are a significant source of energy to the food-web. Corals provide food for some sessile invertivore fish, such as butterflyfish (*Chaetodontidae*) (Motta 1985, Brooker et al. 2016), but this trophic group comprised <4% of fish community in all locations, including coral reefs in Cozumel and Abrolhos. There was no obvious grouping of coral and rocky reef fish assemblages with the majority of the fish community comprised of planktivores, herbivores and mobile invertivores.

Reef fish abundance and diversity is associated with topographic complexity at a local scale (Floeter et al. 2004, Dominici-Arosemena & Wolff 2006, Alvarez-Filip et al. 2011, Francini-Filho et al. 2013) and habitat complexity at the meso-scale (Longo et al. 2015, Luiz et al. 2015, Freitas et al. 2019). Corals provide this complexity to the shallow water environment, both by locally increasing the topographic complexity of underlying rock, and through the creation of habitats in different reef zones such as lagoons, reef flats and slopes (Alvarez-Filip et al. 2011). The most important driver of fish community variation in the Western Indian Ocean was reef geomorphology (Samoilys et al. 2019), which is the product of local topography and wave exposure (Andréfouët et al. 2006). While no statistically significant variation in fish community was detected with the amount of coral cover on reefs in East Africa (Samoilys et al. 2019), in Cozumel, the decline in coral cover due to local stressors and hurricane damage led to a reduction in smaller bodied reef fish and shorter food chains (Alvarez-Filip et al. 2011, Reyes-Bonilla et al. 2014). Some rocky reefs can provide high complexity, such as the South-West of Santa Luzia, where a wide (~1km) shelf of gently shelving rocky reef provided high substrate complexity associated with high fish abundance and diversity (Freitas et al. 2019). However, this is dependent on the underlying geology and weathering processes, rather than biological growth and, consequently, many rocky reefs are less extensive from the shore with lower habitat complexity compared to coral reefs (Ferreira et al. 2001, Perry & Larcombe 2003, Maia et al. 2018).

In St Helena, all the rocky reefs could be described as ‘reef slopes’, as they are ocean facing and often decline steeply away from the coast as in biogenic coral reef slopes. No sheltered bays, sandy beaches, lagoons, reef flats or reef-associated habitats such as seagrass beds or mangroves found around its rocky coastline and the total reef area is limited by the narrow extension (~500m) around the coast, particularly on the leeward side of the island, where sandy substrates are encountered below 15m depth. The only other major habitat type at St Helena was maerl/rhodolith beds, which have a global tropical and temperate distribution, and appear to be an important part of the mesophotic benthic community of Brazil. However, little is known about their ecology other than the calcareous algae nodules provide a semi-solid substrate for life on sediment beds and can be found from the surface to 150m deep (Leão et al. 2003, Amado-Filho et al. 2012, Riosmena-Rodríguez et al. 2017). The lower diversity of habitats on small islands was evident from the species-poor fish community in St Helena, St Paul’s Rocks, Atol das Rocas, as in other oceanic islands globally (Hobbs et al. 2012, Quimbayo et al. 2019).

The most obvious difference in trophic structure of fish in this study was between continental and oceanic settings, with the dominance of planktivores at oceanic locations (also see Quimbayo et al. 2019), supported by local nutrient enrichment from the island mass effect (Gove et al. 2016) and high water clarity (low terrestrial sediment input) that is needed for planktivores to feed (Maia et al. 2018). At continental locations, herbivores and mobile invertivores were more dominant. Wave exposure was an important ecological driver for fish communities along the Brazilian continental coast with more planktivores, omnivores, and macroalgae feeding Kyphosids on exposed coasts and higher proportions of territorial herbivores and sessile invertivores on sheltered reefs (Floeter et al. 2004). In St Helena, São Tomé and St Paul’s Rocks, wave exposure had less effect on fish assemblages (Luiz et al. 2015, Maia et al. 2018), possibly because of lower variation in exposure at those sites (i.e. St Helena has no enclosed bays or lagoons) and wider niche occupancy of species in these low diversity areas. However, fish trophic structure also varies with fishing pressure (Quimbayo et al. 2019), which was not quantified for the locations in this study, and hence the influence of this human pressure on fish trophic structure is not clear.

On both coral reefs and rocky reefs, the dominant primary producers appear to be turf algae and plankton, with the latter being more important around oceanic islands. Living coral’s main function within wider reef ecology is through the creation of topographical complex solid substrate reef habitat. There were few notable ecological differences between the benthic or fish communities of coral reefs and rocky reefs.

4.3 Are there differences in reef ecology based on biogeographic or isolation?

St Helena and the other small isolated locations in this study conform to the expectation that few species can become highly dominant in these conditions (Hobbs et al. 2012, Quimbayo et al. 2019). The benthic community in St Helena had very few species in invertebrate and macroalgal groups, with the crinoid (*Tropiometra carinata*) and harpoon-weed (*Asparagopsis taxiformis*) being the dominant species in each group respectively. Species with wide trophic niches were abundant on the smaller oceanic islands, (St Paul's Rocks, Trindade and Atol das Rocas), with omnivores such as *Melichthys niger* feeding on turf, invertebrates, plankton and detritus, while kyphosid herbivores, with wider dietary capacities that surgeonfish (Acanthuridae) and parrotfish (Scarinae) (Ferreira et al. 2004), were more abundant. A degree of trophic plasticity has been observed within planktivores on oceanic islands, with genera such as *Thalassoma* and *Chaetodon* consuming both benthic invertebrates and plankton (Sazima & Sazima 2001, Luiz et al. 2015). However, why the dominant planktivore in St Helena is a butterflyfish (*Chaetodon sanctaehelenae*) and in Trindade a wrasse (*Thalassoma noronhanum*) is unclear, but is probably the result of founding effects of infrequent colonisation events to oceanic islands (Hobbs et al. 2012, Endo et al. 2019).

Biogeographical province was a key driver of species composition, richness and evenness, with clear division between the four main provinces and higher richness and evenness at Caribbean and continental Brazilian sites, as shown in other studies (Floeter et al. 2008, Kulbicki et al. 2013, Cowman et al. 2017). However, based on relative abundance, each trophic group was dominated by 1 or 2 fish species, indicating that the majority of ecological functioning is performed by a similar number of species (Mouillot et al. 2014). In most trophic groups, the familial identity of species was similar, with the greatest familial diversity in mobile invertivores and predators. Only planktivores had variable dominance at the family levels, (as discussed above), with other groups being dominated by the same families everywhere. There were several families present in locations as a result of biogeography, such as an emperor species (*Lethrinus atlanticus*) in São Tomé, a family common in the Indo-Pacific, but absent in the Atlantic, which must have arrived during a historical break in the cold

Benguela current separating the two African tropical coasts, allowing Indian Ocean species to enter via warm Agulhas waters (Wirtz et al. 2014).

5. Outlook

The Central Atlantic province (i.e. St Helena and Ascension Island) is the smallest and least biodiverse of all marine tropical biogeographic provinces (Floeter et al. 2008, Kulbicki et al. 2013, Cowman et al. 2017), but as a result of its extreme isolation, it possesses a highly unique fauna with species found nowhere else in the world. The inshore area available to these species is limited by both the small coastal area these islands possess and the absence of coral reef. Similar to coral reef systems elsewhere, many of the fish, invertebrates and algae in St Helena rely on the presence of hard substrates for habitat. However, unlike coral reefs, the presence of this hard substrate in St Helena is dependent on underlying geology, not biogenic reef growth. This means that suitable reef habitat in St Helena is limited to a narrow strip around the coast and therefore these unique reef assemblages have extremely limited global distribution.

In this paper, we have presented the first description of the community structure and ecology of the rocky reefs in St Helena using monitoring data of benthos and fish (Brown 2014). We described the quantity and distribution of benthos and fish species and their habitats in terms of “What is there?” and used comparisons with existing data from other reef locations to begin to understand the factors that drive faunal and habitat distribution patterns in terms of “Why is or isn’t it there?”. These data and our findings provide valuable baseline information against which to measure future change resulting from natural environmental dynamics and anthropogenic activities.

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Table 1. Location, reef type, biogeography and key references for St Helena and nine Tropical Atlantic comparison sites.

Location	Abbrev-iation	Country	Coordi-nates	Reef Type	Biogeographic Province	Reference(s)
St Helena	STH	British Overseas Territory	16° 00'S, 5° 45'W	Oceanic Rocky	Central Atlantic	*This study*
São Tomé	STM	São Tomé e Príncipe	00° 00', 6° 35'E	Oceanic Rocky	East Atlantic	*Maia et al. 2018*
Santa Luzia	SLZ	Cape Verde	16° 44'N, 24° 45'W	Oceanic Rocky	East Atlantic	*Freitas et al. 2019*
Trindade	TND	Brazil	20° 30'S, 29° 20'W	Oceanic Rocky	Brazil	*Pinheiro et al. 2011*
St Pauls Rocks	SPL	Brazil	00° 55'N, 29° 20'W	Oceanic Rocky	Brazil	*Luiz et al. 2015*
Atol das Rocas	ADR	Brazil	3° 50'S, 33° 50'W	Oceanic Coral	Brazil	*Longo et al. 2015*
Arraial do Cabo	ADC	Brazil	23° 00'S, 42° 00'W	Continental Rocky	Brazil	*Ferreira et al. 2001*
Espirito Santo	ESP	Brazil	20° 40'S, 40° 20'W	Continental Rocky	Brazil	*Floeter et al. 2004*
Abrolhos	ABL	Brazil	18° 30'S, 39° 00'W	Continental Coral	Brazil	*Francini-Filho & Moura 2008, Francini-Filho et al. 2013*
Cozumel	CZM	Mexico	20° 20'N, 86° 50'W	Continental Coral	Caribbean	*Alvarez-Filip et al. 2011, Reyes-Bonilla et al. 2014*

Table 2. Oceanographic variables that determine the environmental suitability for coral reef formation, showing mean values for St Helena and nine comparison sites from around the Tropical Atlantic. Nitrate and phosphate are here taken from WOA13 v2. *Coral cover for Cozumel is taken from 1980s, prior to reef degradation. '-' indicates no data available.

Site	Reef Type	Coral Cover (%)	Coral Species	Mean SST (°C)	SST Range	Salinity (psu)	Nitrate (µM/l)	Phosphate (µM/l)	Aragonite (Ω_A)	Chlorophyll-A (mg/l)	Turbidity [Seechi Depth] (m)
St Helena	Oceanic Rock	0.1	3	22.4	19.6 – 26.0 (6.1)	36.6	0.316	0.236	3.56	0.144	27.2
São Tomé	Oceanic Rock	8.0	5	27.2	24.2 – 29.6 (5.4)	33.8	0.363	0.146	4.59	0.321	18.4
Santa Luzia	Oceanic Rock	7.5	7	24.5	21.2 – 27.4 (6.2)	36.2	0.336	0.149	3.67	0.541	13.4
Trindade	Oceanic Rock	<1%	3	25.3	22.0 – 29.0 (7.0)	37.1	0.324	0.14	3.95	0.059	38.9
St Pauls Rock	Oceanic Rock	<1%	-	27.5	25.7 -29.3 (3.6)	35.8	0.358	0.084	3.67	0.163	24
Atol das Rocas	Oceanic Coral	8.0	5	27.5	25.9 – 29.5 (3.6)	36.1	0.531	0.143	3.84	0.114	28.5
Arraial do Cabo	Continental Rock	5.7	2	23.5	20.2 – 26.8 (6.6)	35.9	1.354	0.177	4.07	1.424	7.5
Espirito Santo	Continental Rock	4.6	-	24.3	21.5 – 27.2 (5.7)	36.8	1.391	0.125	4.13	0.847	9.9
Abrolhos	Continental Coral	12.7	19	25.9	23.5 – 28.4 (4.9)	36.9	0.625	0.142	4.29	0.203	22.4

Cozumel	Continental Coral	11.4 (34.9*)	47	28	25.7 – 27.4 (1.9)	35.9	0.358	0.197	-	0.103	29.7
Coral Reef Limits (Guan et al. 2015)				***21.7 - 29.6***	***NA***	***28.7 - 40.4***	***< 4.51***	***< 0.63***	***> 2.82***	***NA***	***NA***

Table 3. Fish community comparisons from tropical Atlantic locations, showing the reef type, biogeographic province, sampling effort, inshore shelf area <50m deep (for oceanic locations only), distance to the nearest reef, species richness, Shannon's evenness, number of common species (>10% of total abundance) and number and percentage of rare species (<1% of total). ' – ' Indicates no data available. *Shelf area for Santa Luzia includes other islands in the north-west group of the Cape Verde archipelago, which are connected above the 50m isobath.

Location	Reef Type	Biogeographic Province	Fish Counted	Inshore (<50m) Shelf Area (km^2)	Nearest Reef (km)	Observed Richness	Shannon Evenness (H)	Common species	Rare Species
St Helena	Oceanic Rock	Central Atlantic	84,524	50.83	1300	58	2.41	4	44 (75.9%)
São Tomé	Oceanic Rock	East Atlantic	43,018	277.83	170	65	2.21	3	54 (83.1%)
Santa Luzia	Oceanic Rock	East Atlantic	51,507	512.12*	100	67	1.95	3	58 (86.6%)
Trindade	Oceanic Rock	Brazil	-	32.01	1000	76	2.53	3	64 (82.9%)
St Pauls Rocks	Oceanic Rock	Brazil	50,410	0.03	620	33	1.59	3	24 (72.7%)
Atol das Rocas	Oceanic Coral	Brazil	-	7.04	150	54	2.1	3	44 (81.5%)
Arraial do Cabo	Continental Rock	Brazil	32,135	NA	<10	91	2.98	4	74 (81.3%)
Espirito Santo	Continental Rock	Brazil	12,774	NA	<10	88	2.96	4	73 (83.0%)
Abrolhos	Continental Coral	Brazil	-	NA	50	85	2.95	1	68 (80.0%)
Cozumel	Continental Coral	Caribbean	10,965	NA	20	93	3.18	2	74 (79.6%)

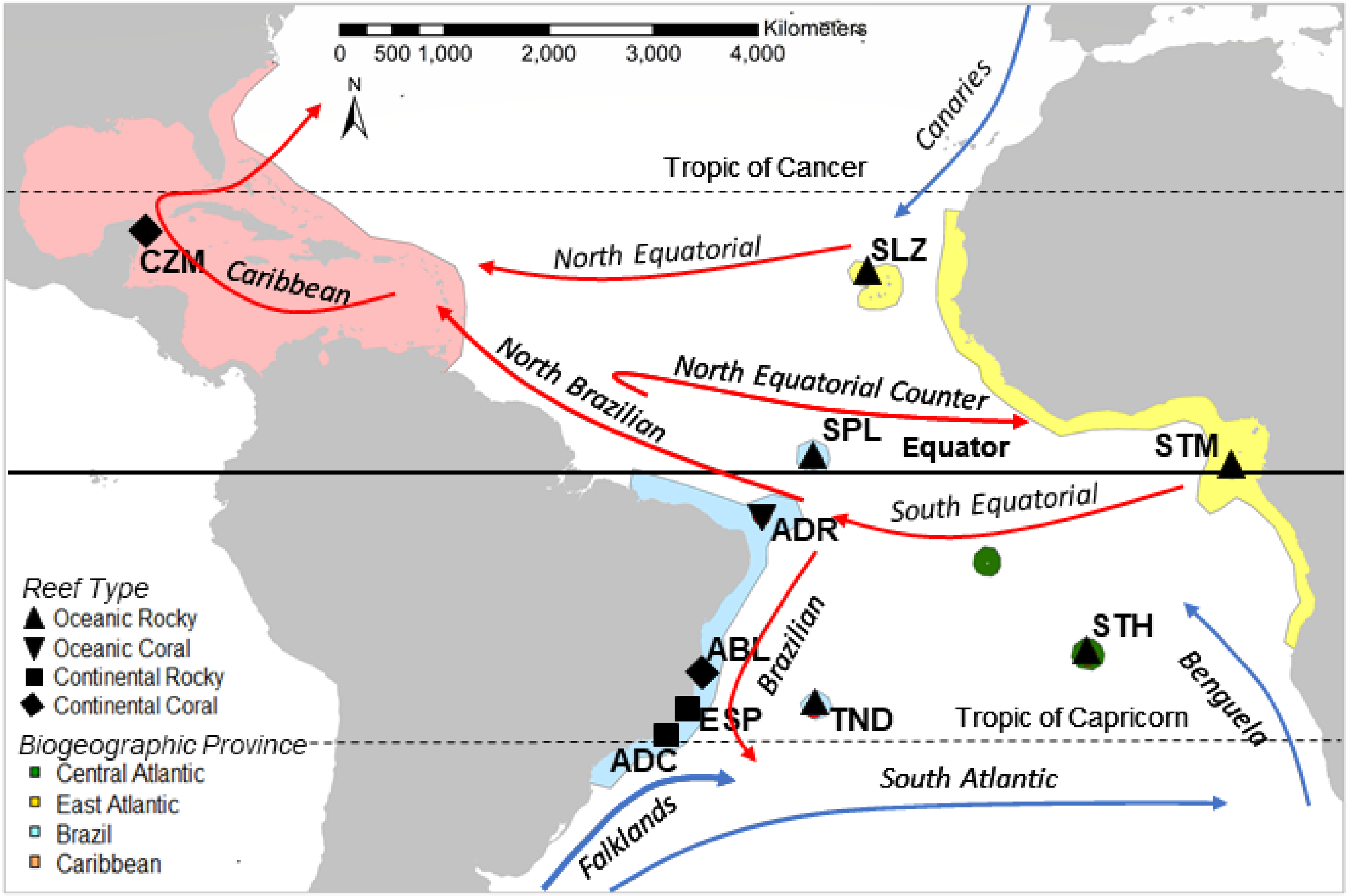


Figure 1. Map of the tropical Atlantic showing biogeographic provinces *censu* Floeter et al. (2008) and main currents, coloured in red for warm currents and blue for cold currents (see Hormann et al. 2012). St Helena (STH) is indicated along with nine comparison sites used in this study; São Tomé (STM), Santa Luzia (SLZ), Trindade (TND), Atol das Rocas (ADR), Arraial do Cabo (ADC), Espirito Santo (ESP), Abrolhos (ABL) and Cozumel (CZM).

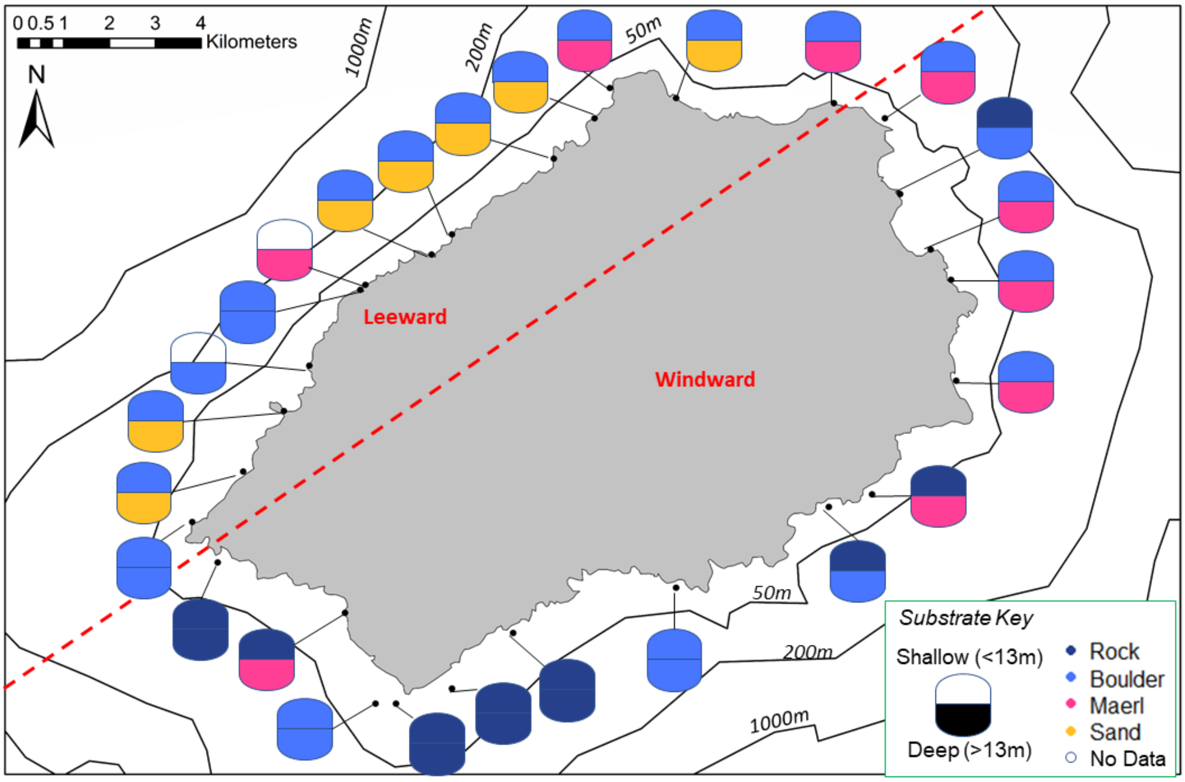


Figure 2. A map of St Helena showing the 28 monitoring sites presented in this study, with the dominant substrate type of shallow and deep transects based on the analysis of photoquadrats. Windward sites are exposed to a dominant south-easterly wind and waves and sheltered north-west facing leeward sites are indicated. Depth contours are derived from GEBCO gridded bathymetry (2019) at 15 arc-second resolution.

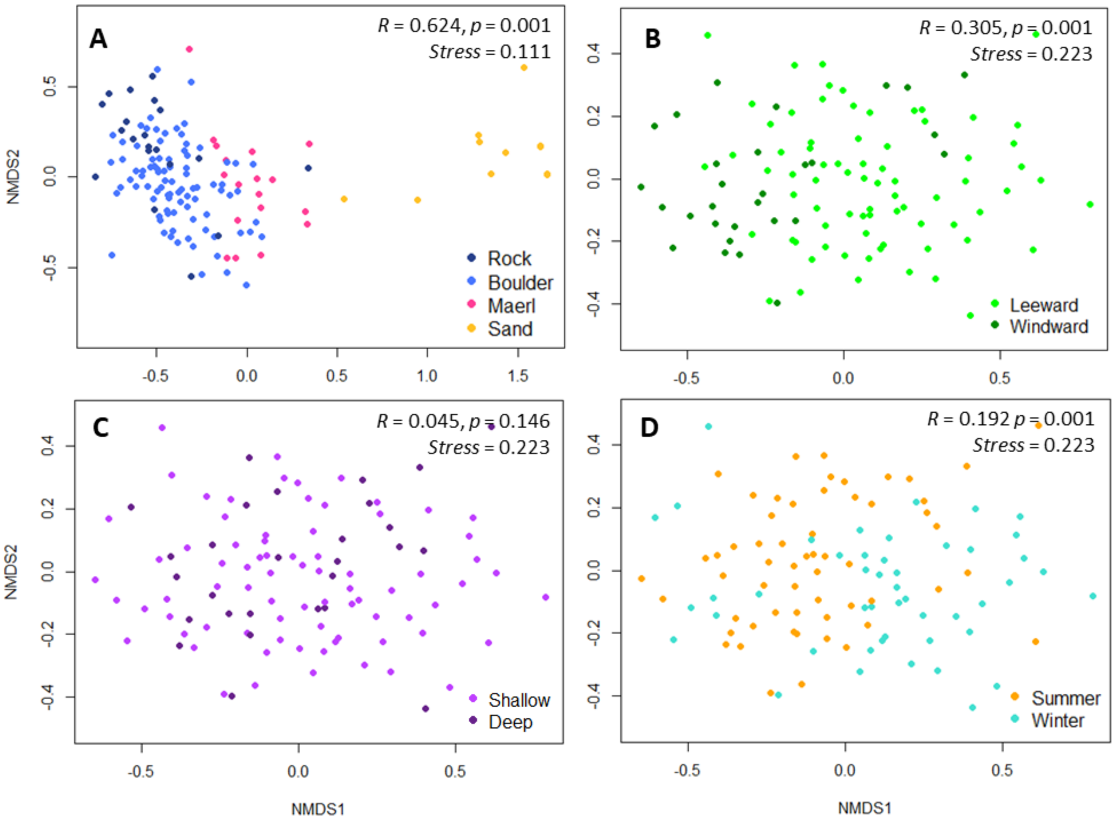


Figure 3 Multi-Dimensional Scaling (MDS) plots of mean living category cover in St Helena on A. all substrate types and rock and boulder substrates for B. wave exposure, C. depth and D. season. The Analysis of Similarity (ANOSIM) results for these groupings are provided, along with the stress of the MDS model.

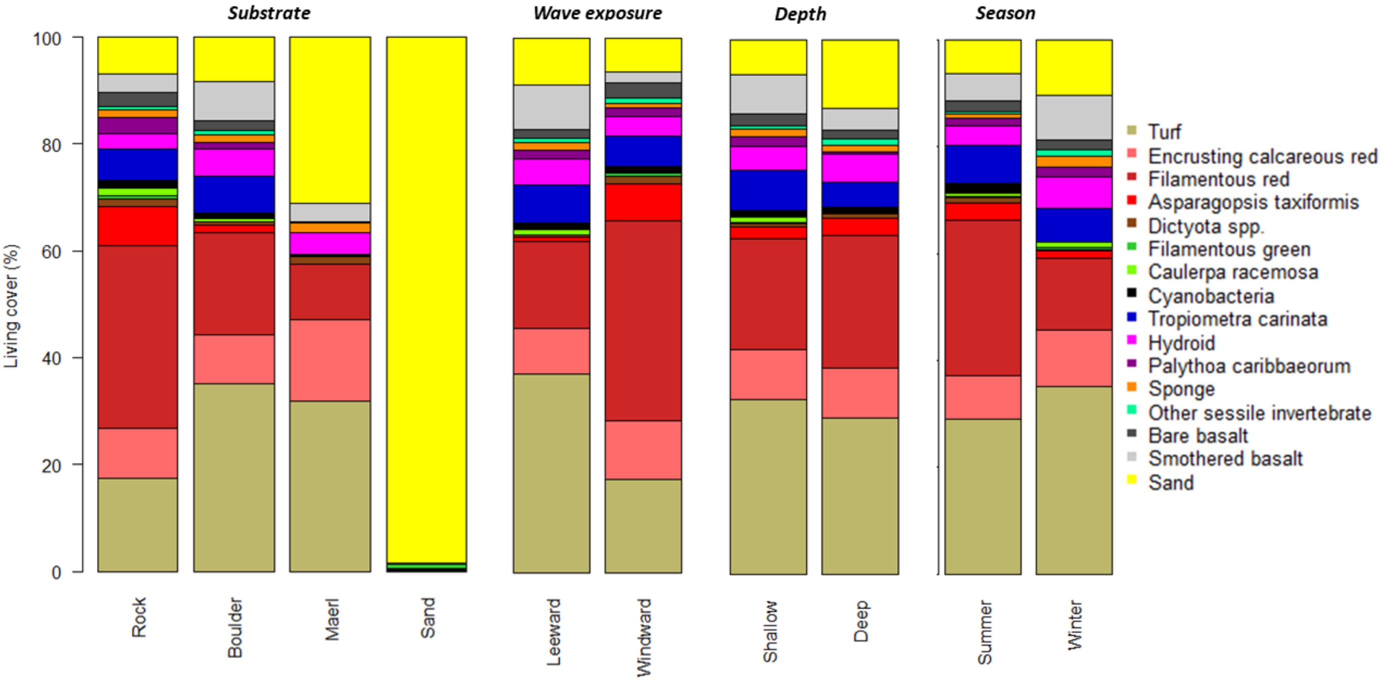


Figure 4. Barplot of mean living category cover in transects from St Helena on all substrate types and rock and boulder substrates for wave exposure, depth and season.

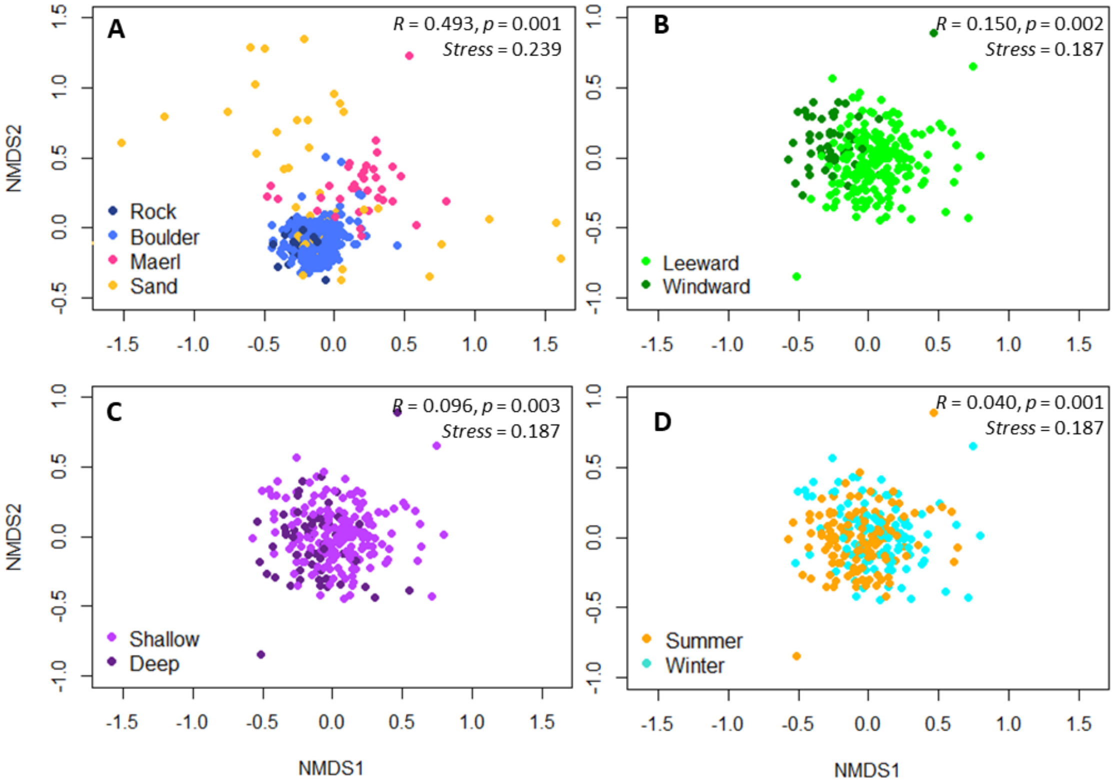


Figure 5. Multi-Dimensional Scaling (MDS) plots of fish species abundance in St Helena in each transect for A. all substrate types and in rock and boulder substrates for B. wave exposure, C. depth and D. season. The Analysis of Similarity (ANOSIM) results for these groupings are provided, along with the stress of the MDS model.

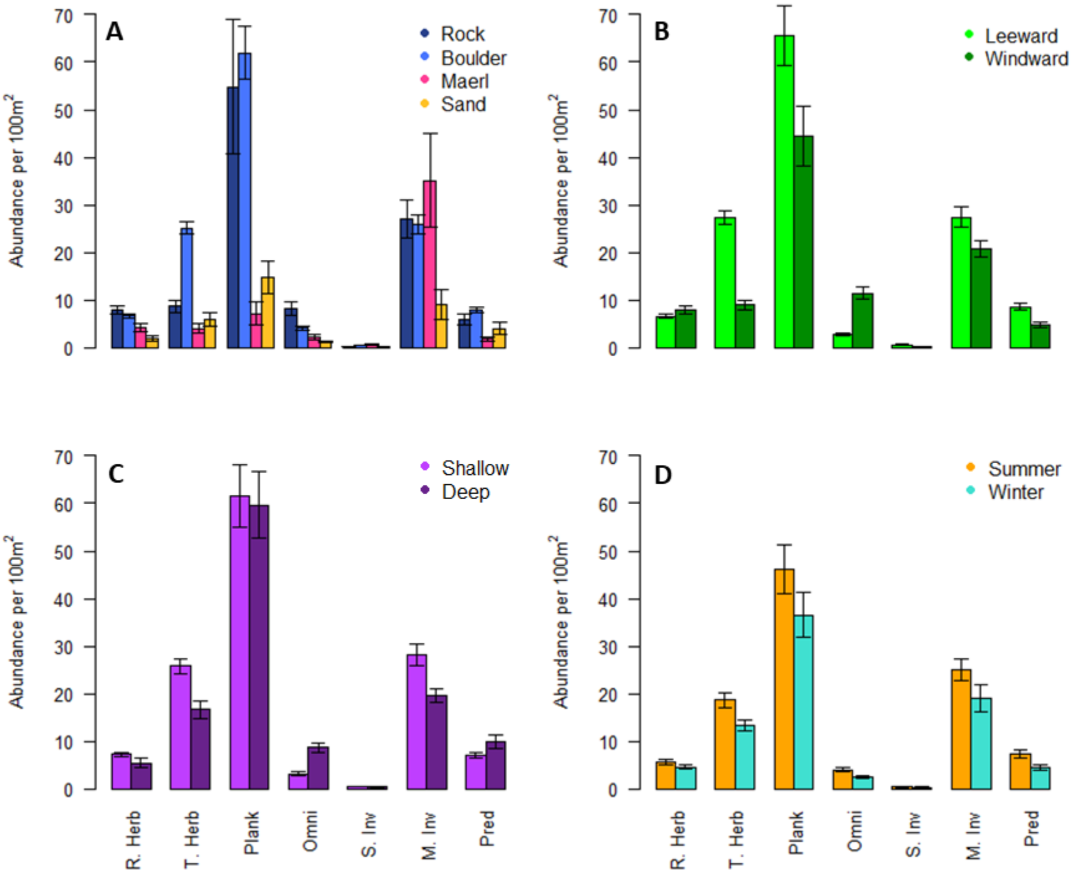


Figure 6. Mean abundance per 100^2 of different fish trophic groups in St Helena in A. all substrate types and in rock and boulder substrates for B. wave exposure, C. depth and D. season. R. Herb = Roving Herbivore, T. Herb = Territorial Herbivore, Plank = Planktivore, Omni = Omnivore, S. Inv = Sessile Invertebrate, M. Inv = Mobile Invertivore, Pred = Predator. Error bars respresent the standard error of the mean.

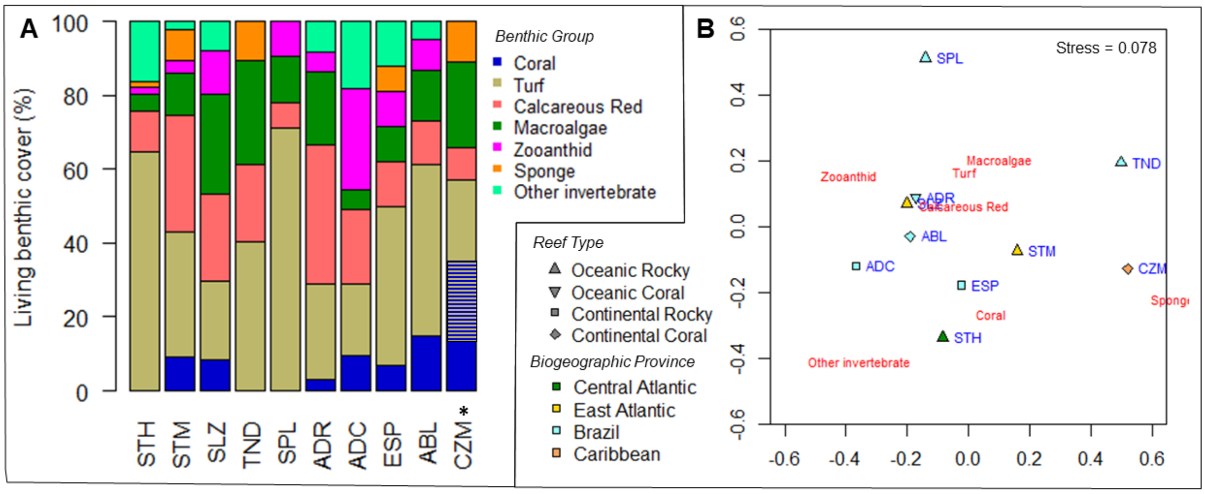


Figure 7. Benthic cover in different Tropical Atlantic locations showing A. barplots of the relative cover of major benthic categories *Note coral cover for Cozumel has a hatched area to show historic coral cover from the 1980s (Reyes-Bonilla et al. 2014). B. an MDS plot based on the contemporary relative cover of categories, with the centroids for the category and stress of the model indicated. St Helena (STH) is indicated along with nine comparison sites used in this study; São Tomé (STM), Santa Luzia (SLZ), Trindade (TND), Atol das Rocas (ADR), Arraial do Cabo (ADC), Espirito Santo (ESP), Abrolhos (ABL) and Cozumel (CZM).

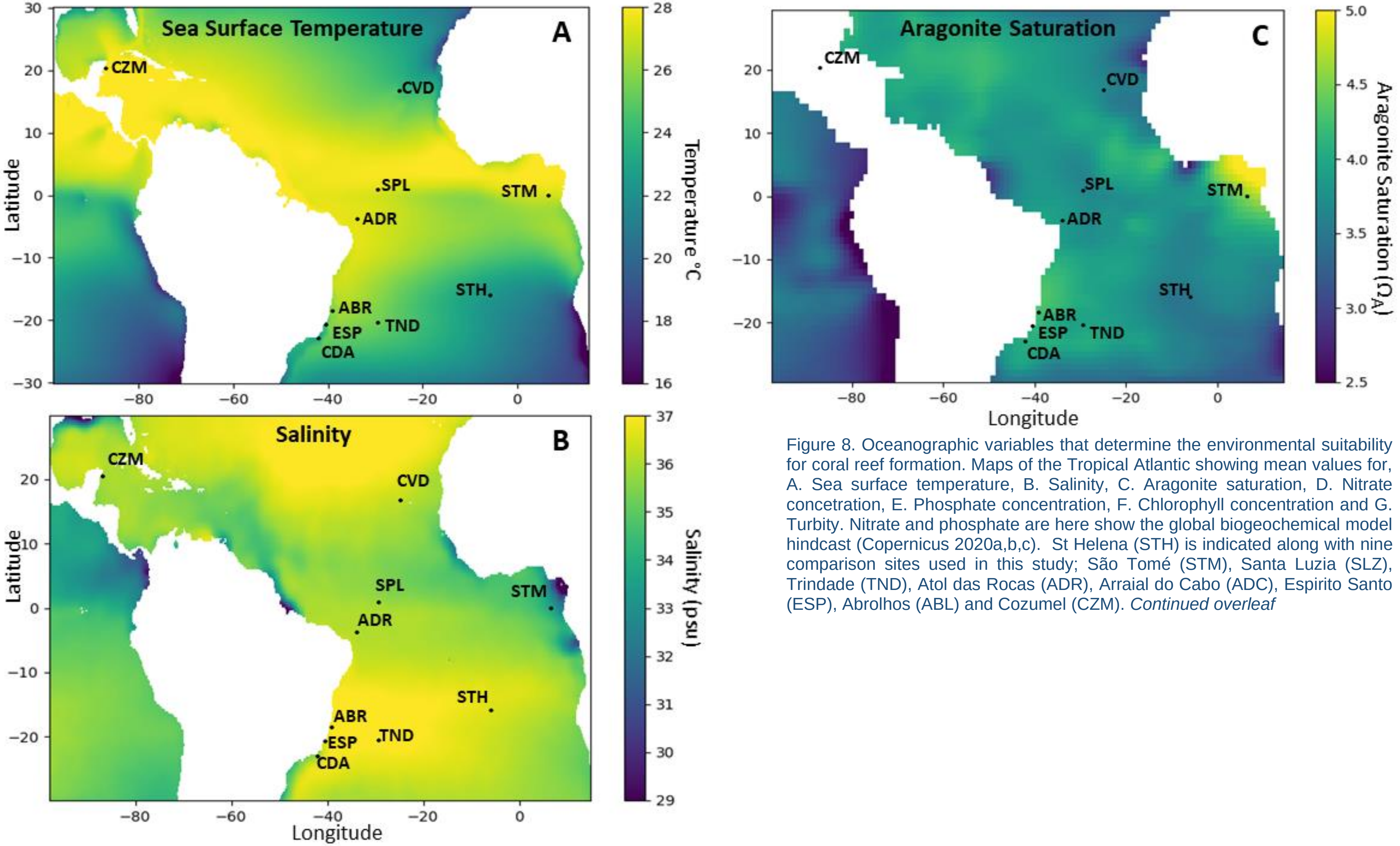
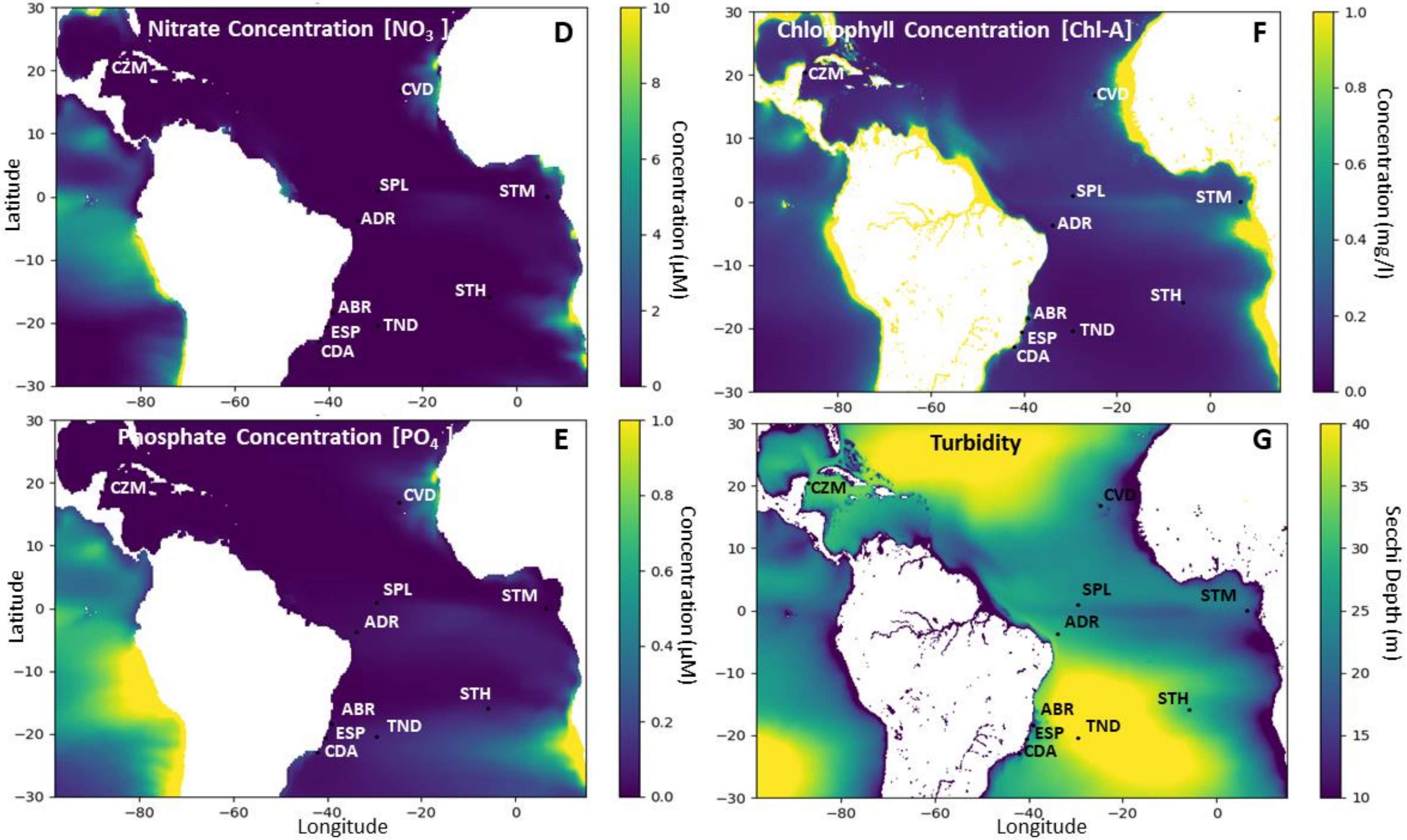


Figure 8. Oceanographic variables that determine the environmental suitability for coral reef formation. Maps of the Tropical Atlantic showing mean values for, A. Sea surface temperature, B. Salinity, C. Aragonite saturation, D. Nitrate concetration, E. Phosphate concentration, F. Chlorophyll concentration and G. Turbity. Nitrate and phosphate are here show the global biogeochemical model hindcast (Copernicus 2020a,b,c). St Helena (STH) is indicated along with nine comparison sites used in this study; São Tomé (STM), Santa Luzia (SLZ), Trindade (TND), Atol das Rocas (ADR), Arraial do Cabo (ADC), Espirito Santo (ESP), Abrolhos (ABL) and Cozumel (CZM). *Continued overleaf*

Figure 8 continued



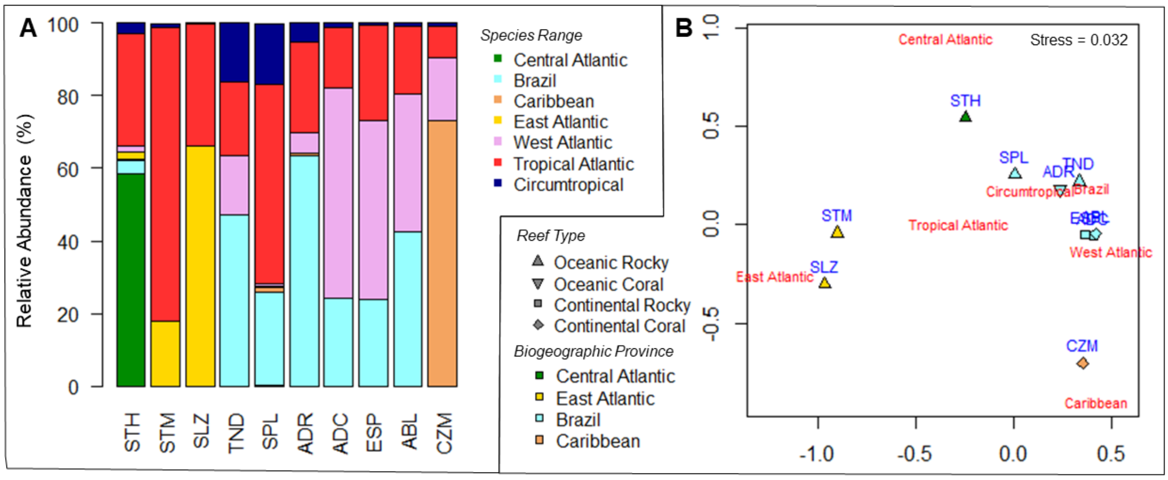


Figure 9. Biogeographic affinity of fish species ranges in different Tropical Atlantic locations showing A. the relative abundance fish counted of different species ranges and B. an MDS plot based on the relative abundance of species ranges, with the centroids for the range categories and stress of the model indicated. St Helena (STH) is indicated along with nine comparison sites used in this study; São Tomé (STM), Santa Luzia (SLZ), Trindade (TND), Atol das Rocas (ADR), Arraial do Cabo (ADC), Espirito Santo (ESP), Abrolhos (ABL) and Cozumel (CZM).

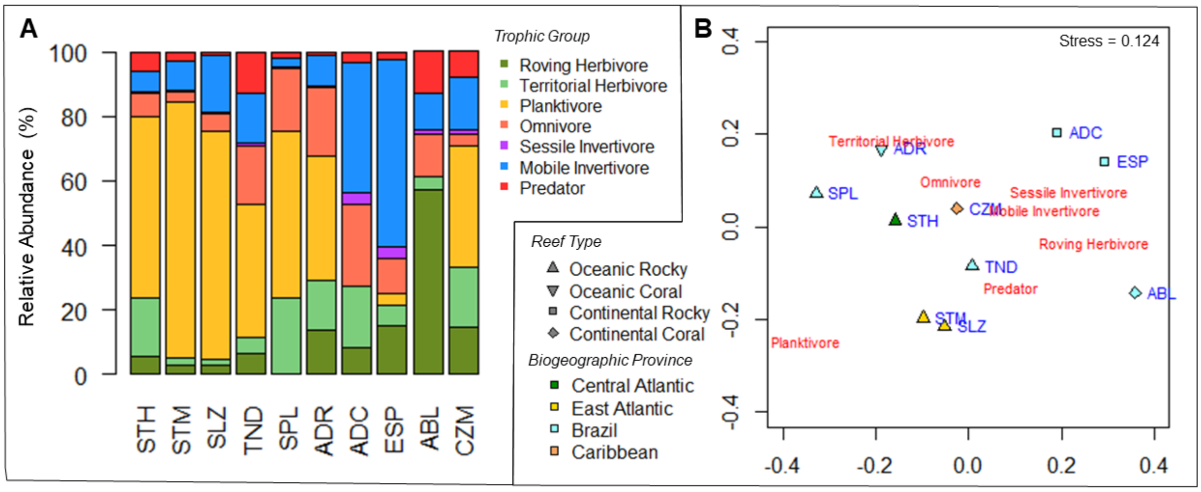


Figure 10. Trophic composition of fish communities in different Tropical Atlantic locations showing A. the relative abundance fish counted from different trophic groups and B. an MDS plot based on the relative abundance of trophic groups, with the centroids for the trophic group and stress of the model indicated. St Helena (STH) is indicated along with nine comparison sites used in this study; São Tomé (STM), Santa Luzia (SLZ), Trindade (TND), Atol das Rocas (ADR), Arraial do Cabo (ADC), Espirito Santo (ESP), Abrolhos (ABL) and Cozumel (CZM).

Supplementary material

Table S1. Differences in benthic categories in St Helena showing test statistics, significant values and trends. ANOSIM results are given at the top to indicate the significance of multi-variate groupings and pairwise permutation results are given below for pairwise comparisons for the main benthic components found in St Helena. Note the Bonferroni conversion of p-values means significant trends are $p < 0.0055$.

	Substrate ***R = Rock*** ***B = Boulder*** ***M = Maerl*** ***S = Sand***			**Exposure** ***W = Windward*** ***L = Leeward***			**Depth** ***S = Shallow*** ***D = Deep***			**Season** ***W = Winter*** ***S = Summer***		
ANOSIM - *R*	0.228			0.296			0.0174			0.169		
ANOSIM - *p*	0.001			0.001			0.217			0.001		
Benthic Categories	*z*	*p*	*trend*	*z*	*p*	*trend*	*z*	*p*	*trend*	*z*	*p*	*trend*
Calcareous red algae	2.764	0.015	=	-0.213	0.831	=	1.867	0.062	=	-2.202	0.028	=
Filamentous red algae	3.906	<0.001	R > B = M	-5.308	<0.001	W > L	-0.139	0.89	=	4.706	<0.001	S > W
Harpoonweed	5.397	<0.001	R > B = M	-5.351	<0.001	W > L	-0.037	0.971	=	2.023	0.043	=
Dictyota	3.23	0.004	R = M > B	-2.908	0.004	W > L	1.811	0.07	=	2.781	0.005	S > W
Cyanobacteria	0.925	0.618	=	-0.074	0.941	=	-0.774	0.439	=	2.95	0.003	S > W
Crinoid	4.858	<0.001	R = B > M	0.899	0.369	=	-4.151	<0.001	S > D	0.827	0.408	=
Hydroid	1.705	0.199	=	1.549	0.121	=	0.568	0.57	=	-2.473	0.013	=
Zoanthid	3.009	0.017	=	-0.219	0.827	=	-1.727	0.084	=	-0.431	0.666	=
Sponge	1.159	0.472	=	2.251	0.024	=	-0.105	0.917	=	-3.924	<0.001	W > S

Table S2. Differences in fish species abundance in St Helena showing test statistics, significant values and trends of pairwise permutation test. Note the Bonferroni conversion of *p*-values means significant trends are $p < 0.0014$

Group	**Species**	**Substrate** ***R = Rock*** ***B = Boulder*** ***M = Maerl*** ***S = Sand***			**Exposure** ***W = Windward*** ***L = Leeward***			**Depth** ***S = Shallow*** ***D = Deep***			**Season** ***W = Winter*** ***S = Summer***			**Abundance**		**Observations**	
		z	*p*	*trend*	*z*	*p*	*trend*	*z*	*p*	*trend*	*z*	*p*		*mean*	*se*	*site*	*survey*
Predator	Rock Hind (*Epinephelus adscensionis*) **[F]**	7.538	<0.001	R > B > M = S	-2.758	0.006	=	-2.258	0.024	=	4.494	<0.001	S > W	0.78	0.047	100	63.6
Predator	Blackbar Soldierfish (*Myripristis jacobus*) **[F]**	4.378	<0.001	R > B | M = S	0.696	0.391	=	-2.612	0.009	=	0.875	0.381	=	1.39	0.196	79.6	36.9
Predator	Squirrelfish (*Holocentrus adscensionis*) **[F]**	7.879	<0.001	R = B > M = S	2.679	0.007	=	0.447	0.655	=	1.138	0.255	=	1.48	0.126	95.9	63.4
Predator	Glasseye Snapper (*Heteropriacanthus cruentatus*) **[F]**	5.005	<0.001	R = B > M = S	2.58	0.01	=	-1.933	0.053	=	2.059	0.039	=	1.75	0.262	81.6	35.1
Predator	Spotted Moray (*Gymnothtorax moringa*) **[F]**	4.436	<0.001	R = B > M = S	0.406	0.685	=	-0.352	0.725	=	1.45	0.147	=	0.19	0.022	63.3	17
Predator	Brown Moray (*Gymnothorax unicolor*)	3.605	0.001	S > B = M | R	-1.804	0.071	=	-0.249	0.804	=	-0.114	0.909	=	0.07	0.014	30.6	7.1
Predator	Trumpetfish (*Aulostomus strigosus*)	8.611	<0.001	B > R > M = S	4.304	<0.001	L > W	2.067	0.039	=	2.561	0.01	=	1	0.069	100	62.3
Predator	Guelly Jack (*Pseudocaranx dentex*)	2.001	0.015	=	NA	NA	NA	0.622	0.534	=	-0.809	0.418	=	0.33	0.224	38.8	6.3
Predator	Soapfish (*Rypticus saponaceus*)	5.8	<0.001	B > M > R = S	3.569	<0.001	L > W	0.237	0.813	=	3.563	<0.001	S > W	0.17	0.015	63.3	31.2
Predator	Red Scorpionfish (*Scorpaena mellissii*) **[E]**	2.996	0.01	=	2.93	0.003	=	2.239	0.025	=	0.333	0.739	=	0.09	0.016	28.6	8.1
Predator	Spotted Scorpionfish (*Scorpaena plumieri*)	2.13	0.113	=	1.107	0.268	=	0.592	0.554	=	-0.335	0.737	=	0.12	0.018	40.8	11.3
Predator	Diamond Lizardfish (*Synodus synodus*)	4.282	<0.001	B = M > R = S	4.0373	<0.001	L > W	0.513	0.608	=	2.46	0.014	=	0.67	0.051	75.5	43.5
Predator	Bluntnose Lizardfish (*Trachinocephalus myops*)	4.921	<0.001	S > B = M | R	NA	NA	NA	0.098	0.922	=	0.409	0.683	=	0.1	0.017	28.6	8.1
Roving Herbivore	Parrotfish (*Sparisoma strigatum*) **[E]**	6.407	<0.001	R = B = M > S	-0.318	0.751	=	3.922	<0.001	S > D	-0.836	0.403	=	1.45	0.095	100	72.5
Roving Herbivore	Sea Chub (*Kyphosus sectacrix*)	5.163	<0.001	R > B = M = S	-4.593	<0.001	W > L	1.877	0.061	=	2.908	0.004	S > W	0.22	0.054	63.3	12

Roving Herbivore	Ocean Surgeonfish (*Acanthurus bahianus*)	4.549	<0.001	R = B > M = S	0.832	0.405	=	1.732	0.083	=	1.419	0.156	=	3.22	0.264	100	73.3
Territorial Herbivore	St Helena Gregory (*Stegastes sanctaehelenae*) **[E]**	10.89	<0.001	B > R = M = S	6.592	<0.001	L > W	3.317	<0.001	S > D	0.873	0.383	=	13.18	0.752	100	74.3
Territorial Herbivore	Redlip Blenny (*Ophioblennus atlanticus*)	2.898	0.014	=	-2.763	0.006	=	1.288	0.198	=	0.957	0.338	=	0.34	0.05	69.4	15.2
Planktivore	St Helena Butterflyfish (*Chaetodon sanctaehelenae*) [E]	3.475	0.002	=	1.138	0.255	=	0.597	0.551	=	1.677	0.094	=	19.66	2.594	100	70.9
Planktivore	St Helena Damselfish (*Chromis sanctaehelenae*) [E]	2.839	0.017	=	1.325	0.185	=	-4.107	<0.001	D > S	0.718	0.473	=	0.62	0.129	53.1	14.9
Planktivore	Brown Chromis (*Chromis multilineata*)	7.395	<0.001	R = B > M = S	1.503	0.133	=	0.631	0.528	=	-1.411	0.158	=	17.8	1.348	95.9	60.7
Omnivore	Sergeant Major (*Abudefduf saxatilis*)	2.903	0.014	=	-4.944	<0.001	W > L	-3.586	<0.001	D > S	0.865	0.387	=	1	0.16	85.7	28
Omnivore	St Helena Sea Bream (*Diplodus sargus helenae*) [E]	4.4	<0.001	R > B = M > S	-9.039	<0.001	W > L	-4.875	<0.001	D > S	3.09	0.002	=	1.55	0.163	98	51.8
Omnivore	St Helena Pufferfish (*Canthigaster sanctaehelenae*) [E]	7.715	<0.001	R = B = M > S	3.675	<0.001	L > W	-0.119	0.905	=	0.941	0.347	=	0.66	0.034	96	67.8
Omnivore	Black Triggerfish (*Melichtys niger*)	7.579	<0.001	R > B | M = S	-5.337	<0.001	W > L	0.604	0.544	=	1.951	0.051	=	0.12	0.027	53.1	9.9
Invertivore	St Helena Wrasse (*Thalassoma sanctaehelenae*) [E]	6.879	<0.001	R > B > M = S	-4.07	<0.001	W > L	2.15	0.032	S > D	3.63	<0.001	S > W	2.8	0.164	100	67.3
Invertivore	Marmalade Razorfish (*Xyrichthys blanchardi*) [E]	12.634	<0.001	M > R = B = S	-0.176	0.861	=	NA	NA	NA	0.243	0.808	=	0.18	0.028	63.3	15.7
Invertivore	Island Hogfish (*Bodianus insularis*) [E]	9.067	<0.001	R = B > M > S	1.584	0.113	=	-2.376	0.018	=	1.342	0.18	=	0.99	0.055	100	72
Invertivore	St Helena Flounder (*Bothus mellissi*) [E]	5.578	<0.001	S > R = B = M	NA	NA	NA	1.621	0.105	=	0.928	0.353	=	0.25	0.028	36.7	20.7
Invertivore	Auxillary Spot Cardinalfish (*Apogon axillaris*) [E]	3.112	0.007	=	1.75	0.08	=	-0.247	0.805	=	1.623	0.105	=	0.84	0.215	51	27.5
Invertivore	Hedgehog Butterflyfish (*Prognathodes dichrous*) [E]	1.754	0.248	=	1.613	0.107	=	-0.194	0.846	=	1.322	0.186	=	0.19	0.048	49	20.9
Invertivore	Cowfish (*Acanthostracion notacanthus*)	5.683	<0.001	M > R = B > S	4.461	<0.001	L > W	NA	NA	NA	-1.697	0.09	=	0.2	0.017	51	33.5
Invertivore	Hawkfish (*Amblycirrhitus pinos*)	7.356	<0.001	R = B > M = S	-1.406	0.16	=	2.074	0.038	=	2.585	0.01	=	1.01	0.076	89.8	45.8
Invertivore	Dragonet (*Helcogramma ascensionis*)	2.637	0.031	=	1.041	0.298	=	0.416	0.678	=	1.992	0.046	=	0.5	0.15	49	8.6

Invertivore	Goldspot goby (*Gnatholepis thompsoni*)	5.587	<0.001	M > R = B = S	2.071	0.039	=	-0.638	0.523	NA	-1.135	0.256	=	6.86	1.606	63.3	29.6
Invertivore	Goatfish (*Mulloidichthys martinicus*)	2.342	0.0482	=	-1.347	0.178	=	-1.573	0.116	=	3.7	<0.001	S > W	0.2	0.043	65.3	14.4

Table S3. Fish species abundance observed in St Helena, showing the family, trophic group and biogeographical range. The mean abundance per 100m^2 is shown for all transects, different substrates and wave exposure, depth and season on rock and boulder transects.

Family	Species	Trophic Group	Range	All Transects	Substrate				Wave Exposure		Depth		Season	
					Rock	***Boulder***	***Maerl***	***Sand***	***Leeward***	***Windward***	***Shallow***	***Deep***	***Summer***	***Winte***
Acanthuridae	*Acanthurus bahianus*	Roving Herbivore	Brazil	3.33	3.88	4.44	2.08	1.43	4.43	4.21	4.64	3.65	3.69	2.88
Acanthuridae	*Acanthurus coeruleus*	Roving Herbivore	Caribbean	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00
Antennariidae	*Antennarius striatus*	Predator	Circumtropical	0.00	0.00	0.00	0.00	0.01	1.61	0.17	1.22	1.59	0.00	0.01
Apogonidae	*Apogon axillaris*	Mobile Invertivore	Central Atlantic	0.86	0.09	1.45	0.00	0.17	1.71	0.70	1.59	1.25	1.18	0.47
Aulostomidae	*Aulostomus strigosus*	Predator	East Atlantic	1.03	0.87	1.57	0.21	0.28	2.29	1.47	1.76	3.15	1.19	0.83
Balistidae	*Canthidermis sufflamen*	Planktivore	Tropical Atlantic	0.04	0.00	0.06	0.05	0.02	0.94	0.61	0.85	0.93	0.06	0.03
Balistidae	*Melichthys niger*	Omnivore	Circumtropical	0.12	0.90	0.11	0.00	0.00	0.26	0.49	0.25	0.48	0.17	0.06
Belonidae	*Platybelone argalus trachura*	Predator	Central Atlantic	0.02	0.00	0.01	0.00	0.05	0.29	0.04	0.23	0.26	0.03	0.00
Blenniidae	*Entomacrodus textilis*	Territorial Herbivore	Central Atlantic	0.01	0.00	0.01	0.00	0.01	4.72	0.15	4.35	2.10	0.01	0.01
Blenniidae	*Ophioblennius atlanticus*	Territorial Herbivore	Tropical Atlantic	0.34	0.91	0.48	0.00	0.07	0.03	0.02	0.04	0.00	0.40	0.28
Bothidae	*Bothus mellissi*	Mobile Invertivore	Central Atlantic	0.26	0.04	0.15	0.24	0.54	0.94	0.36	0.88	0.66	0.28	0.23
Callionymidae	*Callionymus bairdi*	Mobile Invertivore	Caribbean	0.51	2.04	0.68	0.00	0.01	0.06	0.03	0.05	0.08	0.79	0.17
Carangidae	*Caranx crysos*	Predator	Tropical Atlantic	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.01	0.04	0.00	0.00
Carangidae	*Caranx lugubris*	Predator	Circumtropical	0.01	0.07	0.01	0.00	0.00	29.03	19.65	27.45	26.00	0.02	0.00
Carangidae	*Caranx ruber*	Predator	West Atlantic	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carangidae	*Decapterus muroadsi*	Planktivore	Circumtropical	0.36	0.00	0.25	0.38	0.67	0.92	5.89	1.18	4.20	0.63	0.03
Carangidae	*Decapterus tabl*	Planktivore	Circumtropical	0.00	0.00	0.00	0.00	0.00	0.01	0.09	0.01	0.07	0.00	0.00
Carangidae	*Elagatis bipinnulata*	Predator	Circumtropical	0.04	0.00	0.03	0.00	0.09	0.01	0.00	0.01	0.00	0.07	0.01
Carangidae	*Pseudocaranx dentex*	Predator	Circumtropical	0.34	0.10	0.05	0.08	1.09	0.15	0.00	0.14	0.05	0.17	0.54
Carangidae	*Seriola rivoliana*	Predator	Circumtropical	0.04	0.03	0.04	0.03	0.06	26.88	7.91	25.23	16.28	0.06	0.02
Carangidae	*Trachinotus ovatus*	Predator	East Atlantic	0.65	1.29	0.27	0.00	1.54	0.01	0.00	0.00	0.01	1.00	0.22
Chaetodontidae	*Chaetodon sanctaehelenae*	Planktivore	Central Atlantic	20.14	19.34	27.96	4.16	10.93	32.82	22.26	31.76	27.33	24.11	15.36
Chaetodontidae	*Prognathodes dichrous*	Sessile Invertivore	Central Atlantic	0.19	0.03	0.26	0.25	0.06	0.27	0.09	0.23	0.26	0.25	0.12
Cirrhitidae	*Amblycirrhitus pinos*	Mobile Invertivore	West Atlantic	1.04	1.74	1.53	0.10	0.25	1.45	1.91	1.64	1.28	1.22	0.82
Diodontidae	*Chilomycterus reticulatus*	Mobile Invertivore	Circumtropical	0.00	0.00	0.00	0.00	0.00	1.02	0.44	0.38	2.39	0.00	0.00
Gobiidae	*Gnatholepis thompsoni*	Omnivore	Tropical Atlantic	7.02	0.09	4.19	33.34	3.56	0.27	0.26	0.25	0.33	5.29	9.11
Gobiidae	*Priolepis ascensionis*	Omnivore	Central Atlantic	0.06	0.00	0.03	0.07	0.12	0.03	0.16	0.03	0.13	0.09	0.02
Holocentridae	*Holocentrus adscensionis*	Mobile Invertivore	Tropical Atlantic	1.52	1.43	2.43	0.18	0.23	0.06	0.67	0.20	0.15	1.65	1.36
Holocentridae	*Myripristis jacobus*	Mobile Invertivore	West Atlantic	1.42	2.57	2.21	0.21	0.04	0.01	0.00	0.01	0.00	1.58	1.23

Kyphosidae	*Kyphosus sectatrix*	Roving Herbivore	Tropical Atlantic	0.23	1.34	0.23	0.01	0.06	0.01	0.00	0.00	0.03	0.38	0.05
Labridae	*Bodianus insularis*	Mobile Invertivore	Central Atlantic	1.45	1.65	2.17	0.55	0.30	0.16	0.06	0.17	0.03	1.60	1.27
Labridae	*Thalassoma sanctaehelenae*	Planktivore	Central Atlantic	9.55	19.15	12.85	1.07	4.08	0.34	0.51	0.34	0.48	12.66	5.81
Labridae	*Xyrichtys blanchardi*	Mobile Invertivore	Central Atlantic	0.19	0.02	0.08	1.21	0.02	0.00	0.00	0.00	0.00	0.19	0.19
Labridae	*Xyrichtys sanctaehelenae*	Mobile Invertivore	Central Atlantic	0.12	0.00	0.01	0.00	0.44	0.00	0.00	0.00	0.00	0.14	0.10
Monacanthidae	*Aluterus monoceros*	Omnivore	Circumtropical	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00
Monacanthidae	*Aluterus scriptus*	Omnivore	Circumtropical	0.03	0.05	0.04	0.00	0.00	0.04	0.04	0.04	0.05	0.03	0.01
Mullidae	*Mulloidichthys martinicus*	Mobile Invertivore	West Atlantic	0.21	0.52	0.28	0.05	0.04	0.38	1.09	0.58	0.36	0.36	0.03
Muraenidae	*Enchelycore anatina*	Predator	East Atlantic	0.01	0.00	0.02	0.00	0.00	1.12	1.69	1.10	1.62	0.02	0.01
Muraenidae	*Gymnothorax miliaris*	Predator	West Atlantic	0.01	0.00	0.02	0.00	0.01	0.13	0.04	0.11	0.14	0.02	0.01
Muraenidae	*Gymnothorax moringa*	Predator	West Atlantic	0.19	0.22	0.28	0.07	0.06	0.01	0.02	0.01	0.00	0.22	0.16
Muraenidae	*Gymnothorax unicolor*	Predator	East Atlantic	0.08	0.04	0.12	0.00	0.02	3.36	0.71	2.26	4.40	0.08	0.08
Myliobatidae	*Mobula tarapacana*	Planktivore	Circumtropical	0.01	0.00	0.01	0.01	0.00	2.31	2.02	1.72	3.79	0.01	0.00
Ostraciidae	*Acanthostracion notacanthus*	Sessile Invertivore	East Atlantic	0.20	0.14	0.23	0.46	0.04	0.26	0.08	0.24	0.17	0.17	0.24
Pomacentridae	*Abudefduf saxatilis*	Omnivore	Tropical Atlantic	1.03	2.30	1.43	0.03	0.32	0.82	4.15	0.89	3.34	1.15	0.87
Pomacentridae	*Chromis multilineata*	Planktivore	West Atlantic	20.24	32.45	30.41	2.44	3.92	0.27	0.04	0.27	0.07	20.04	20.48
Pomacentridae	*Chromis sanctaehelenae*	Planktivore	Central Atlantic	0.63	0.43	0.95	0.19	0.20	0.00	0.00	0.00	0.00	0.71	0.53
Pomacentridae	*Stegastes sanctaehelenae*	Territorial Herbivore	Central Atlantic	16.34	7.79	24.65	4.23	6.28	13.22	14.49	15.41	7.90	18.72	13.47
Priacanthidae	*Heteropriacanthus cruentatus*	Predator	Circumtropical	1.79	1.20	2.99	0.16	0.14	0.12	1.17	0.43	0.09	2.29	1.19
Scarinae	*Sparisoma strigatum*	Roving Herbivore	Central Atlantic	1.74	2.77	2.04	2.36	0.62	0.93	0.40	0.82	0.84	1.71	1.77
Scorpaenidae	*Scorpaena mellissii*	Predator	Central Atlantic	0.09	0.00	0.13	0.00	0.06	0.04	0.03	0.03	0.06	0.10	0.08
Scorpaenidae	*Scorpaena plumieri*	Predator	West Atlantic	0.13	0.09	0.15	0.17	0.06	1.98	2.62	2.27	1.66	0.12	0.13
Serranidae	*Epinephelus adscensionis*	Predator	West Atlantic	0.85	1.81	1.17	0.24	0.21	0.02	0.00	0.01	0.03	1.03	0.63
Serranidae	*Rypticus saponaceus*	Predator	Tropical Atlantic	0.17	0.05	0.25	0.14	0.05	0.16	0.11	0.13	0.19	0.22	0.11
Sparidae	*Diplodus sargus helenae*	Omnivore	Central Atlantic	1.59	4.35	1.68	1.74	0.69	0.02	0.00	0.01	0.03	2.05	1.03
Synodontidae	*Synodus synodus*	Predator	Tropical Atlantic	0.69	0.35	0.88	0.83	0.32	0.06	0.00	0.05	0.03	0.81	0.55
Synodontidae	*Trachinocephalus myops*	Predator	Tropical Atlantic	0.10	0.00	0.05	0.02	0.24	0.07	0.09	0.04	0.18	0.11	0.09
Tetraodontidae	*Canthigaster sanctaehelenae*	Omnivore	Central Atlantic	0.68	0.66	0.90	0.57	0.27	0.00	0.01	0.00	0.01	0.70	0.64
Tripterygiidae	*Helcogramma ascensionis*	Omnivore	Central Atlantic	0.01	0.00	0.01	0.00	0.00	2.57	1.40	2.36	2.23	0.00	0.01

Table S4. Fish trophic group composition in different Tropical Atlantic locations. For each location and trophic group the total species richness, the number of common species (>25% of total trophic group abundance), and the families found in this trophic group ordered by abundance from most abundant to least. Common families (>25% of total trophic group abundance), are shown in **bold.**

Site	***Roving Herbivores***		
	Richness	Common	Families
St Helena	4	2	**Acanthuridae, Scarinae,** Kyphosidae
Sao Tome	5	2	**Acanthuridae,** Scarinae, Kyphosidae
Santa Luzia	6	1	**Scarinae,** Kyphosidae, Acanthuridae
Trindade	6	2	**Kyphosidae, Acanthuridae,** Scarinae
St Pauls Rocks	1	1	**Kyphosidae**
Atol das Rocas	9	1	**Acanthuridae,** Scarinae, Kyphosidae
Arraial do Cabo	11	2	**Acanthuridae, Scarinae,** Kyphosidae
Espirito Santo	10	1	**Acanthuridae,** Scarinae, Kyphosidae
Abrolhos	9	1	**Scarinae,** Acanthuridae
Cozumel	14	1	**Acanthuridae, Scarinae,** Kyphosidae
	Territorial Herbivores		
	Richness	Common	Families
St Helena	3	1	**Pomacentridae,** Blennidae
Sao Tome	3	1	**Pomacentridae, Blennidae**
Santa Luzia	5	2	**Pomacentridae, Blennidae**
Trindade	5	2	**Pomacentridae, Blennidae**
St Pauls Rocks	2	1	**Pomacentridae,** Blennidae
Atol das Rocas	3	1	**Pomacentridae,** Blennidae

Arraial do Cabo	5	1	**Pomacentridae,** Blennidae
Espirito Santo	4	1	**Pomacentridae,** Blennidae
Abrolhos	5	1	**Pomacentridae,** Blennidae
Cozumel	7	2	**Pomacentridae**
	Planktivores		
	Richness	Common	Families
St Helena	8	2	**Pomacentridae, Chaetodontidae,** Holocentridae, Labridae, Carangidae, Balistidae, Myliobatidae
Sao Tome	7	2	**Serranidae, Pomacentridae,** Holocentridae, Sparidae, Labridae, Gobiidae
Santa Luzia	4	2	**Pomacentridae,** Holocentridae, Balistidae,
Trindade	6	1	**Labridae,** Pomacentridae, Holocentridae, Serranidae, Balistidae, Clupeidae
St Pauls Rocks	5	1	**Pomacentridae,** Holocentridae, Balistidae, Serranidae, Labridae
Atol das Rocas	6	1	**Labridae,** Pomacentridae, Pempheridae, Holocentridae, Serranidae, Apogonidae
Arraial do Cabo	2	1	**Pomacentridae,** Carangidae
Espirito Santo	8	1	**Pomacentridae,** Holocentridae, Labridae, Grammatidae, Serranidae
Abrolhos	5	0	Pomacentidae, Labridae, Grammatidae
Cozumel	7	2	**Pomacentridae, Labridae,** Serranidae, Haemulidae, Balistidae
	Omnivores		
	Richness	Common	Families
St Helena	9	1	**Gobiidae,** Sparidae, Pomacentridae, Tetraodontidae, Monacanthidae, Tripterygiidae
Sao Tome	10	1	**Gobiidae, Tetraodontidae,** Monacanthidae, Pomacentridae
Santa Luzia	10	1	**Gobiidae, Sparidae,** Blenniidae, Pomacentridae, Tetraodontidae, Monacanthidae, Mugilidae
Trindade	13	1	**Balistidae,** Pomacentridae, Gobiidae, Monacanthidae, Sparidae, Tetraodontidae
St Pauls Rocks	5	1	**Balistidae,** Pomacentridae, Monacanthidae

Atol das Rocas	5	2	**Gobiidae, Pomcentridae,** Balistidae,Pomacanthidae, Monacanthidae
Arraial do Cabo	10	2	**Sparidae, Pomacentridae,** Gobiidae, Tetraodontidae, Pomacanthidae. Monacanthidae, Mugilidae
Espirito Santo	9	2	**Sparidae, Pomcacentridae,** Monacanthidae, Gobiidae, Tetraodontidae, Pomacanthidae
Abrolhos	9	2	**Pomacanthidae,** Pomacentidae, Moncanthidae, Gobiidae, Tetraodontidae
Cozumel	7	1	**Pomacentridae,** Tetraodontidae, Pomacanthidae, Monacanthidae
	Sessile Invertivores		
	Richness	Common	Families
St Helena	2	2	**Ostraciidae, Chaetodontidae**
Sao Tome	4	1	**Pomacanthidae**, Chaetodontidae, Ostraciidae
Santa Luzia	2	2	**Chaetodontidae, Pomacanthidae**
Trindade	5	2	**Chaetodontidae, Pomacanthidae,** Ostraciidae
St Pauls Rocks	3	1	**Pomacanthidae,** Chaetodontidae
Atol das Rocas	3	1	**Chaetodontidae,** Ostraciidae
Arraial do Cabo	8	1	**Chaetodontidae,** Ostraciidae, Pomacanthidae, Syngnathidae
Espirito Santo	6	1	**Chaetodontidae,** Pomacanthidae, Ostraciidae
Abrolhos	3	2	**Pomacanthidae, Chaetodontidae**
Cozumel	10	2	**Chaetodontidae, Pomacanthidae,** Ostraciidae
	Mobile Invertivores		
	Richness	Common	Families
St Helena	11	3	**Holocentridae, Labridae,** Cirrhitidae, Apogonidae, Mullidae, Callionymidae, Bothidae, Diodontidae
Sao Tome	19	0	**Apogonidae, Holocentridae,** Mullidae, Serranidae, Haemulidae, Balistidae, Cirrhitidae, Bothidae, Diodontidae, Lethrinidae
Santa Luzia	15	1	**Labridae,** Haemulidae, Serranidae, Mullidae, Sparidae, Labrisomidae, Apogonidae, Holocentridae, Balistidae, Diodontidae, Tetraodontidae

Trindade	21	1	**Labridae, Labriosomidae,** Holocentridae, Mullidae, Malacanthidae, Balistidae, Haemulidae, Diodontidae, Tetraodontidae, Blennidae, Callionymidae, Cirrhitidae, Dactylopteridae
St Pauls Rocks	6	2	**Labridae, Labriosomidae,** Chaenopsidae, Holocentridae, Dactylopteridae
Atol das Rocas	10	2	**Albulidae, Haemulidae,** Labridae, Mullidae, Balistidae, Bothidae, Diodontidae
Arraial do Cabo	32	1	**Haemulidae,** Labridae, Mullidae, Sciaenidae, Serranidae, Labrisomidae, Monacanthidae, Bothidae, Tetraodontidae, Dactylopteridae, Sparidae, Diodontidae, Balistidae, Chaenopsidae, Callionymidae, Gerreidae
Espirito Santo	31	2	**Holocentridae, Haemulidae, Labridae,** Labrisomidae, Mullidae, Sciaenidae, Tetraodontidae, Serranidae, Cirrhitidae, Chaenopsidae, Bothidae, Dactylopteridae, Diodontidae
Abrolhos	28	1	**Haemulidae, Labridae,** Balistidae, Mullidae, Labrisomidae, Serranidae, Sparidae, Holocentridae, Diodontidae, Ephippidae, Cirrhitidae, Tetraodontidae
Cozumel	25	1	**Haemulidae, Labridae,** Holocentridae, Mullidae, Balistidae, Grammatidae, Diodontidae, Sparidae
	Predators		
	Richness	Common	Families
St Helena	21	1	**Priacanthidae,** Carangidae, Aulostomidae, Serranidae, Synodontidae, Muraenidae, Scorpaenidae, Belonidae, Antennariidae
Sao Tome	16	0	**Muraenidae,** Aulostomidae, Lutjanidae, Carangidae, Serranidae, Priacanthidae, Synodontidae, Ophichthidae
Santa Luzia	25	0	Serranidae, Lutjanidae, Priacanthidae, Sparidae, Muraenidae, Scorpaenidae, Aulostomidae, Synodontidae, Carangidae, Fistulariidae, Ginglymostomatidae, Dasytidae, Sciaenidae
Trindade	21	1	**Serranidae,** Carangidae, Priacanthidae, Muraenidae, Belonidae, Sphyraenidae, Synodontidae, Ophichthidae, Scorpaenidae, Ginglymostomatidae
St Pauls Rocks	11	1	**Muraenidae,** Carangidae, Aulostomidae, Serranidae, Sphyraenidae, Lutjanidae
Atol das Rocas	16	1	**Serranidae,** Carangidae, Lutjanidae, Malacanthidae, Belonidae, Ginglymostomatidae, Carcharhinidae, Muraenidae, Sphyraenidae
Arraial do Cabo	23	0	**Carangidae, Serranidae,** Muraenidae, Scorpaenidae, Synodontidae, Ophichthidae, Ogcocephalidae, Torpediniae, Fistulariidae, Antennariidae
Espirito Santo	20	1	**Sciaenidae, Serranidae,** Lutjanidae, Synodontidae, Aulostomidae, Scorpaenidae, Muraenidae, Carangidae, Ogcocephalidae, Priacanthidae, Ophichthidae
Abrolhos	26	0	**Lutjanidae,** Carangidae, Serranidae, Sphyraenidae, Synodontidae, Muraenidae, Scorpaenidae, Sciaenidae, Ogcocephalidae
Cozumel	22	2	**Lutjanidae,** Carangidae, Serranidae, Muraenidae, Syphraenidae, Scorpaenidae