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Spatial patterns and drivers of fish and benthic reef communities at São Tomé Island, Tropical Eastern Atlantic

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Abstract

Marine communities vary across spatial scales due to changes in habitat structure, wave exposure, depth and anthropogenic activities. Here, we quantitatively characterized, for the first time, the reef fish assemblages and benthic communities in six sites around São Tomé Island, in the Tropical Eastern Atlantic region. We performed 139 underwater visual census and 112 photo-quadrats across six sites around the island to explore the relative importance of exposure, depth and topographic complexity as drivers of fish and benthic reef communities. Planktivores were the most important trophic group, in terms of both fish abundance and biomass. Small fishes (0–7 cm) dominated the abundance, whereas biomass was mainly concentrated in 8–15 and 16–30 cm body size classes. About 30% of the total benthic cover was composed of turf algae and circa of 28% of calcareous coralline algae, whereas corals were comparably less abundant (only 8%). Among these, *Montastraea cavernosa* was the most abundant coral (46% of the coral cover and 4% of total benthic cover). Wave exposure was the most important driver of the reef fish assemblages and was also important for benthic communities. Also, fish species composition seemed to respond, although weakly, to benthic composition. Topographic complexity had little effect on the indicators of fish assemblages but seemed to drive some changes in benthic cover. Overall, our results evidence the dominance of small planktivorous reef fish assemblages and of turf algal communities in São Tomé. Taken together,

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they support the idea of benthic communities shaped by wave action, with minor importance of corals, and of important energetic contribution from planktonic material. We also suggest that the relatively low biomass of medium and large fish species reflects the long-term fishing pressure in São Tomé Island.

KEYWORDS
abiotic factors, abundance, biomass, Gulf of Guinea, species density

1 | INTRODUCTION

Several studies have evaluated the role of environmental variables in shaping tropical reef fish assemblages (e.g., Jones & Syms, 1998; Luckhurst & Luckhurst, 1978). Important drivers highlighted so far include wave exposure (e.g., Friedlander, Brown, Jokiel, Smith, & Rodgers, 2003; Fulton & Bellwood, 2004; Fulton, Bellwood, & Wainwright, 2005), water temperature (e.g., Floeter, Behrens, Ferreira, Paddack, & Horn, 2005; Parravicini et al., 2013), depth (e.g., Brokovich, Einbinder, Shashar, Kiflawi, & Kark, 2008; Friedlander & Parrish, 1998), habitat topography and complexity (e.g., García-Charton et al., 2004; Pinheiro et al., 2013; Wilson, Graham, & Polunin, 2007), benthic community cover (Ferreira, Gonçalves, & Coutinho, 2001; Friedlander & Parrish, 1998; García-Charton et al., 2004) and interactions among species (Wisz et al., 2013). For example, it is generally acknowledged that shallow, sheltered and highly complex coral habitats host large abundances and high diversity of reef fishes (Dustan, Doherty, & Pardede, 2013; Gratwicke & Speight, 2005), whereas deeper areas in isolated places often contain high fish biomass (Friedlander, Sandin, DeMartini, & Sala, 2010; Khalil, Bouwmeester, & Berumen, 2017; Luiz et al., 2015). Moreover, the interplay between hydrodynamics and fish swimming ability (with its associated feeding performance) enables certain functional groups, like planktivores, to be more abundant in high-wave exposure areas (Bellwood, Wainwright, Fulton, & Hoey, 2002; Floeter, Krohling, Gasparini, Ferreira, & Zalmon, 2007; McGehee, 1994; Wainwright, Bellwood, & Westneat, 2002).

In the last 15 years, studies focused on oceanic islands have revealed remarkable features, such as unusual high fish biomass and peculiar benthic communities (e.g., Sandin et al., 2008; Stevenson et al., 2007; Williams et al., 2013; Quimbayo et al., 2018). The high abundance and biomass of large predators and herbivorous species in these isolated systems contrasts with more accessible reef systems (Friedlander et al., 2003, 2010 ; Graham & McClanahan, 2013; Morais, Ferreira, & Floeter, 2017; Williams et al., 2015). These observations have provided the basis for posterior large-scale studies showing that human-related variables explain reef fish assemblage biomass around the world (Bellwood, Hoey, & Hughes, 2012; Cinner, Graham, Huchery, & Macneil, 2013; Mora et al., 2011; Williams et al., 2015). However, most studies addressing the structure of fish (and benthic) assemblages in tropical oceanic islands have been performed in the Indo-Pacific (Sandin et al., 2008; Williams et al., 2013), in the southwestern Atlantic (Krajewski & Floeter, 2011; Longo et al., 2015; Luiz et al., 2015; Pinheiro, Ferreira, Joyeux, Santos, & Horta, 2011) or in the Tropical Eastern Pacific (e.g., Edgar et al., 2011; Friedlander et al., 2012; Quimbayo, Mendes, Kulbicki, Floeter, & Zapata, 2017; Quimbayo et al., 2018). In comparison, fish assemblages from the Tropical Eastern Atlantic (TEA) remain poorly explored apart from species checklists (Afonso et al., 1999; Wirtz et al., 2013, 2007). So far, ecological aspects of TEA reef fish assemblages have been described by one study in oil platforms (Friedlander, Ballesteros, Fay, & Sala, 2014) and another one at the oceanic island of Príncipe in the Gulf of Guinea (Tuya, Bosch, Abreu, & Haroun, 2017). The study of Tuya and collaborators (2017) specifically addressed the influence of depth on the distribution and structure of reef fish assemblages. Much more remains to be understood in terms of how TEA fish assemblages respond to other environmental gradients, and how benthic communities vary locally and regionally.

Oceanic island ecosystems in the Tropical Eastern Atlantic (TEA) include the Cape Verde Archipelago and the islands from the Gulf of Guinea: Annobón, São Tomé and Príncipe (Floeter et al., 2008). Despite of its relatively old age, São Tomé has low marine endemism levels (e.g., 3% for fishes; Hachich et al., 2015) due to high oceanographic connectivity between the Gulf of Guinea islands and the African coast (Floeter et al., 2008; Wirtz, 2003). The islands form a chain that is relatively close to the mainland, thus maintaining connectivity. On the other hand, the regional endemism level of the TEA is high (30%; Floeter et al., 2008), a phenomenon presumably linked to the geographic isolation of the TEA from the other Atlantic reef areas (e.g., ~3,500 km from the Brazil and ~8,696 km from the Caribbean; Floeter et al., 2008), as well as a history of isolation and reconnection with the Indo-Pacific in the evolutionary timescale (Cowman, Parravicini, Kulbicki, & Floeter, 2017). In addition to the Benguela Current that limits the movements of tropical species from the Indian Ocean, cold waters from the northeastern Atlantic also limit the geographic range of tropical species (Almada et al., 2013; Floeter et al., 2008). As a result of this compression, the relatively small tropical area of the TEA harbours a small species richness of key benthic organisms, like hard corals (Laborel, 1974; Morri, Cattaneo, Sartoni, & Bianchi, 2000; Polidoro et al., 2017). A growing human population (Belhabib, 2015), with high levels of local dependence on fisheries for food (Carneiro, 2011), and the emergence of foreign industrial fisheries vessels (Belhabib, 2015), contribute to the Gulf of Guinea being listed as one of the most threatened marine hotspots of the world (Roberts et al., 2002). There is a gap of knowledge on how reef organisms are locally distributed relative to habitat features and oceanographic conditions, precluding progress towards marine conservation. Simultaneously, no Marine Protected Areas or effective fisheries management exist in the Gulf of Guinea.

Our objective here was to quantify for the first time the reef fish assemblages and benthic composition of the São Tomé Island (hence STI), the largest oceanic island in the Gulf of Guinea. We specifically aim to answer the questions: (a) What is the influence of wave exposure (WE), topographic complexity (TC) and depth (DP) on the species density (i.e., the mean number of species per unit area), abundance and biomass of reef fishes among sites in STI? (b) What are the effects of WE, TC and DP in the trophic and body size structure of the fish assemblages across sites in STI? (c) What are the dominant benthic components in STI reefs (with a focus on corals)? (d) How do WE, TC and DP influence the composition of benthic communities among sites in STI? (e) Do the structure of fish assemblages change as a function of changes in coral cover? To address these questions, we combined underwater visual surveys of reef fishes and benthic communities in different sites and depth strata of STI.

2 | MATERIAL AND METHODS

2.1 | Study area description

São Tomé Island is located along the Cameroon Volcanic Line in the Gulf of Guinea, Western Africa (0°20'94"N; 6°62'10"E; Figure 1a,b). It was formed by volcanic activity around 13 million years ago (Caldeira, 2002; Lee, Halliday, Fitton, & Poli, 1994). São Tomé Island has a land area of 857 km^2, but its steep underwater relief results in a relatively small shallow platform (see Figure 1c). Underwater, São Tomé seascape is mainly dominated by volcanic rocky reefs with limited coral growth (Laborel, 1974; Quimbayo et al., 2012). The area is influenced by the Benguela Current (coming from South) and Gulf of Guinea Current (coming from North), which converge in São Tomé to form the South Equatorial current (Measey et al., 2007). The sea surface temperature in São Tomé

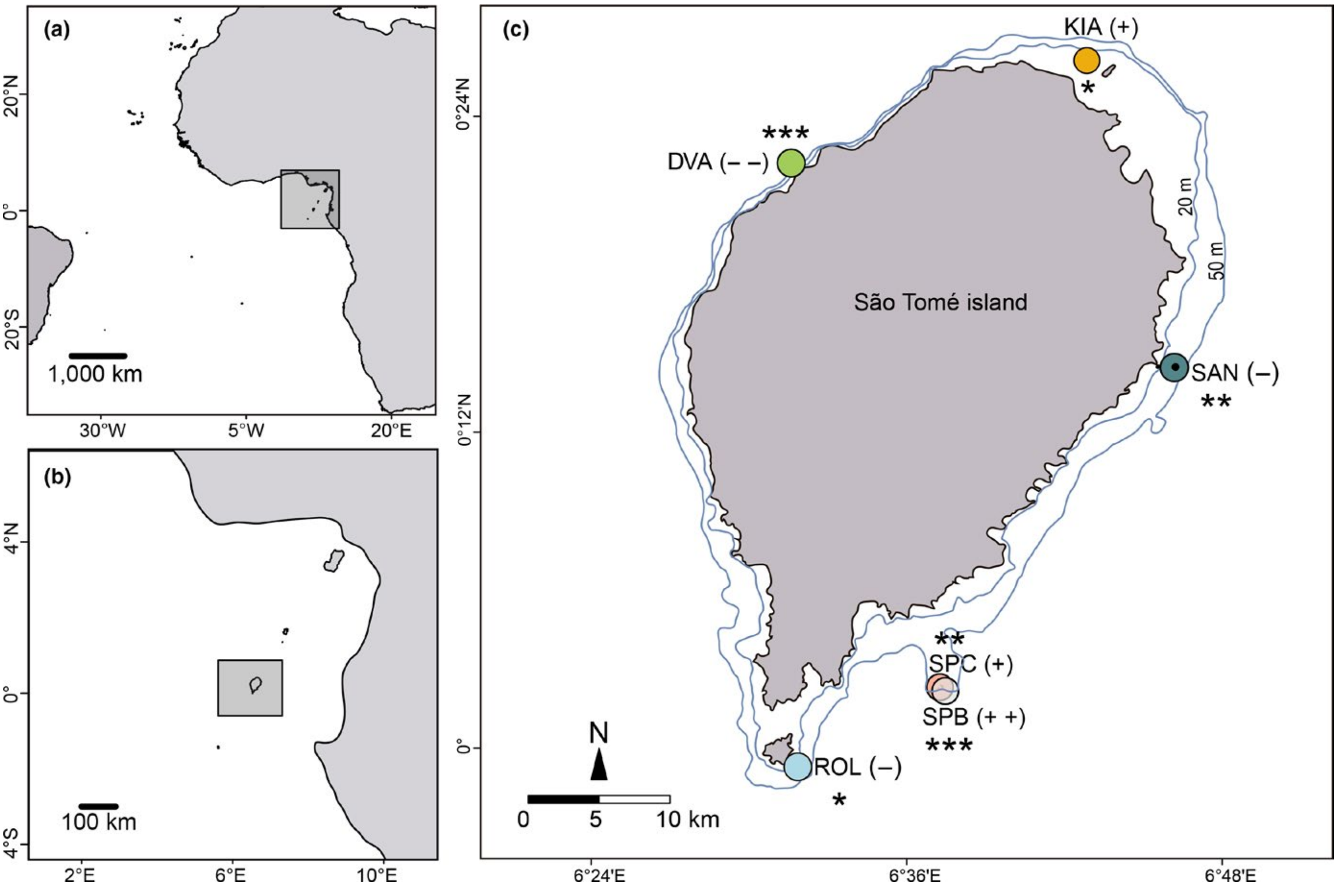

FIGURE 1 The location of the São Tomé Island in the Atlantic Ocean: (a) the Gulf of Guinea represented by a grey square; (b) the São Tomé Island; and (c) the distribution of sampling sites across the island. Sites: Diogo Vaz (DVA—light green), Ilhéu das Cabras (KIA—orange), Ilhéu Santana (SAN—dark green), Sete Pedras—Catedral (SPC—dark orange), Sete Pedras—Pedra Branca (SPB—light pink) and Ilhéu das Rolas (ROL—blue). Blue lines represented the isobaths between 20 and 50 m. Level of wave exposure of sites: (- -) = low; (-) low-medium; (+) medium-high; and (+ +) high. * = level of topographic complexity of sites: * = high; ** = medium; and *** = low

ranges between 26 and 29°C during September to May and decreases to approximately 25°C during June to August (Horemans, Gallène, & Njock, 1994). Cool waters from the Benguela Current are normally restricted to layers below 20–30 m and can reach temperatures of 20°C (Laborel, 1974).

We collected underwater data on reef fish and benthic communities in six sites around the island (Figure 1c). These sites were (a) "Diogo Vaz" (DVA), which presents a small terrace with underdeveloped coral formations above sand and high concentration of gorgonians; (b) "Cabras Kia" (KIA), which encompasses a sandy bottom with some sparse hard coral growth and high density of sea urchins; (c) "Ilhéu Santana" (SAN), which is composed by rocky slopes and large boulders with some level of coral overgrowth; (d) "Sete Pedras—Catedral" (SPC), a boulder field with hard coral and gorgonian growth; (e) "Sete Pedras—Pedra Branca" (SPB), a submerged rocky outcrop rising steeply from sand and dominated by *Tubastrea* sp. growing on the vertical walls; and (f) "Ilhéu das Rolas" (ROL), presenting a small terrace with sparse coral colonies and the bottom dominated by a rhodolith bank. Among all sites, SPC and SPB are the only ones located <10 km from a river discharge.

2.2 | Reef fish assemblages

Underwater visual surveys (UVSs) along transects of 40 m^2 (20 x 2 m) were used to estimate reef fish richness (i.e., species per unit area), numerical abundance of individuals and biomass. This method consists on identifying, counting and estimating the size (total length in cm) of all fish individuals observed both in the water column (in the layout phase) and on the bottom (in the returning phase; Morais et al., 2017). We performed 139 UVSs between 5 and 30 m of depth. We used total length to estimate the weight of each fish using length–weight equations of the form $W = a * \mathrm{TL}^b$, where parameters a and b are species-specific constant and W is the weight in grams. Length–weight parameters were gathered for each species from FishBase (Froese & Pauly, 2016). In cases where species coefficients were not available, we used coefficients of congeneric species that are presumably phylogenetically close and morphologically similar.

Assemblage structure was evaluated in terms of trophic and body size groups. These are highly relevant and commonly assessed fish functional traits that reflect physiological and energetic processes. We classified all observed reef fish species according to their trophic group (seven classes) following Mouillot et al. (2014), and to body size (five classes) following Kulbicki, Parravicini, and Mouillot (2015). The fish trophic groups considered were herbivores–detritivores (HD: feed upon turf and filamentous algae and/or detritus), macroalgae-feeders (HM: feed upon large fleshy algae and/or seagrass), omnivores (OM: feed on both vegetal and animal material), sessile invertebrate feeders (IS: feed mainly on corals, sponges or ascidians), mobile invertebrate feeders (IM: feed on mobile benthic prey, such as crabs, snails and polychaetes), planktivores (PK: feed on zooplankton in the water column) and piscivores (PS: feed on fish or cephalopods). The body size classes used were <7 cm, between 8 and 15 cm, between 16 and 30 cm, between 31 and 50 cm, and larger than 50 cm.

2.3 | Reef benthic communities

We estimated the cover (%) of each component of reef benthic communities using photo-quadrats. We distributed a mean of 19 (from seven to 35) photo-quadrats uniformly along the same depth contours and at the same sites where the visual censuses were conducted, for a total of 112 photo-quadrats. Photographs were taken at ~80 cm from the substratum, and each photo-quadrat corresponded to an area of 40 × 60 cm (e.g., Krajewski & Floeter, 2011). Each photo-quadrat was analysed using the software Coral Point Count v3.6 (CPCe) with Excel extensions (Kohler & Gill, 2006). Thirty points were randomly positioned over each image and the organism below each point was identified as the "turf" (the epilithic algal matrix), calcareous algae, sponges, macroalgae, sand, coral, zoanthids, gorgonians and other organisms (e.g., Echinoidea and Crustacea; Bell & Barnes, 2001; Littler & Littler, 1984; Steneck & Dethier, 1994). All corals observed were identified according to Laborel (1974) to the lowest taxonomic level possible.

2.4 | Environmental drivers of fish assemblages

We investigated the effect of depth (DP), topographic complexity (TC) and wave exposure (WE) on reef fish assemblages in São Tomé Island. We classified DP in three levels: shallow (4–8 m), medium (9–16 m) and deep (17–30 m). We classified TC in three categories according to Ferreira et al. (2001) and Pinheiro et al. (2013): high (large boulders and holes >1 m in size and depth), medium (predominance of small boulders and holes <1 m in size and depth) and low (few and small benthic organisms and predominance of epilithic algae). Finally, we classified WE in four levels (similarly to Pinheiro et al. 2013): high (unsheltered site, unprotected from currents and dominant waves); medium-high (unsheltered site, unprotected from currents, but protected from dominant waves); low-medium (site sheltered by physical barriers such as islets, or protected against the main current or dominant waves); and low (site sheltered by physical barriers, protected against current and wave dominant waves).

2.5 | Data analysis

To assess whether species richness (number of species per 40 m^2), abundance and biomass of reef fishes varied with wave exposure levels (high, medium-high, low-medium and low), topographic complexity levels (high, medium and low) and depth strata (shallow, medium and deep), we used generalized linear models (GLMs) with Gamma distribution in R (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Tukey tests were used as post hoc tests to determine the differences between groups. We carried out this analysis using the function glht within of the package multcomp (Hothorn, Bretz, & Peter, 2008).

To test the importance of the drivers of reef fish species richness, abundance and total biomass, we employed three generalized linear mixed model (GLMMs) using wave exposure, topographic complexity and depth as covariates (fixed factors), and sites as random variables (i.e., random-intercept model). For all these models, we used a Gamma distribution. We considered this distribution because all variables are positive and have continuous values (Zuur et al., 2009). Additionally, we evaluated whether fish abundance and biomass structure in terms of trophic groups and size classes were affected by wave exposure, topographic complexity, depth and site. To do so, we used a permutational multivariate analysis of variance (PERMANOVA; with 999 permutations) based on a Bray–Curtis dissimilarity matrix. We used another PERMANOVA based on a Bray–Curtis dissimilarity matrix to explore variations of the different group of benthic assemblages and the abiotic factors considered above. We used a redundancy analysis (RDA) to graphically display the influence of the abiotic factors (detected by PERMANOVA) on fish abundance and biomass in São Tomé.

To test the influence of benthic cover on São Tomé Island reef fish assemblages—that is, sites with highest fish affinities would have highest benthic affinities—we used the Mantel analysis with 999 permutations. Benthic cover data represent a relative abundance index (%) and did not need to be standardized. Two dissimilarity matrices were built with the Bray–Curtis index: one using reef fish abundance and biomass per species and another one with benthic cover. All statistical analyses were performed in R software version 3.2.4 (R Core Team, 2016).

3 | RESULTS

3.1 | Reef fish assemblages

We recorded 43,018 individuals belonging to 66 species from 30 families in the 139 UVSs (Supporting Information Table S1). The

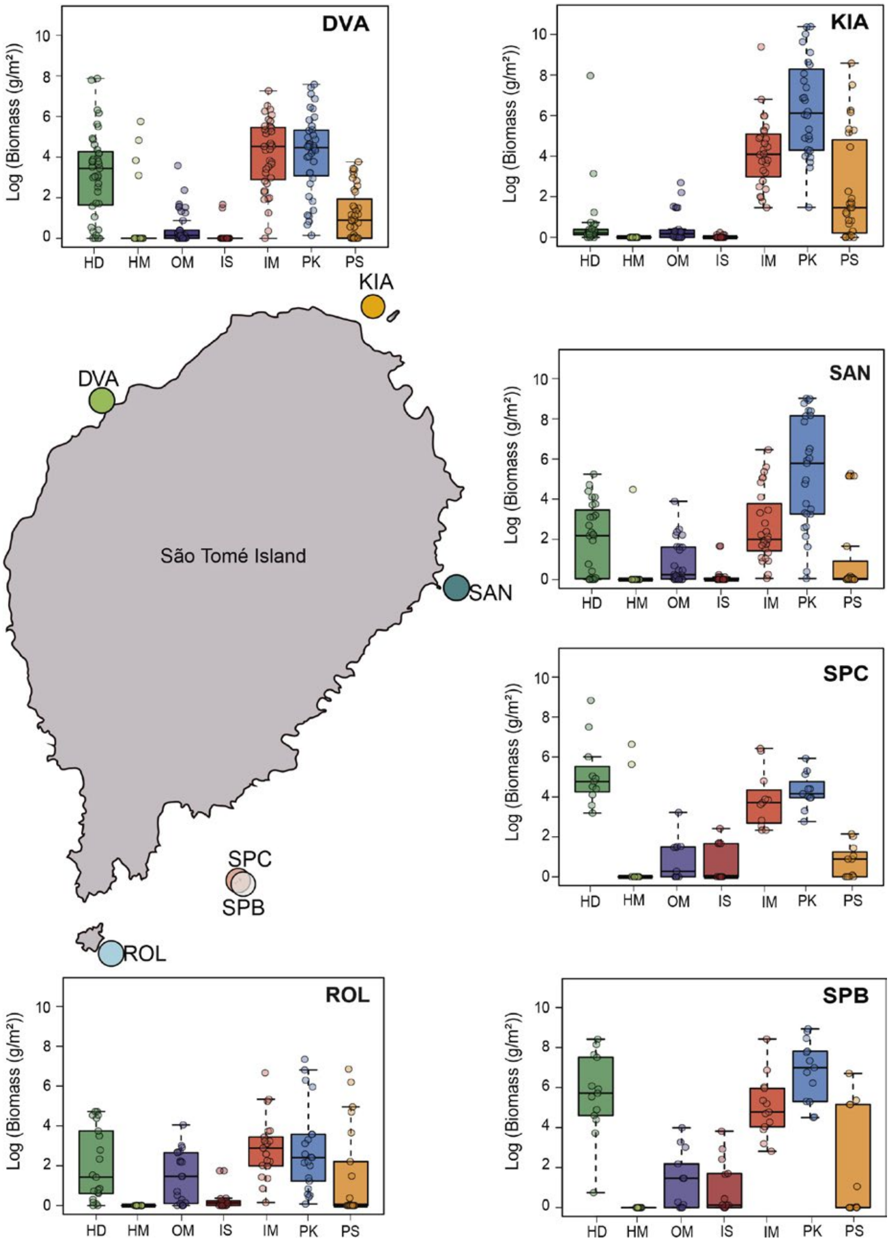

FIGURE 2 Variation in total biomass of reef fish assemblages per trophic groups at São Tomé Island. Boxplots denote medians (black line), upper and lower quartiles and 95% confidence intervals. Each circle represents an underwater visual census. See Figure 1 for the acronym and colour of the sites. Trophic groups: herbivores–detritivores (HD), macroalgae-feeders (HM), omnivores (OM), sessile invertebrate feeders (IS), mobile invertebrate feeders (IM), planktivores (PK) and piscivores (PS)

most representative families were Labridae (including parrotfishes; seven species), followed by Gobiidae and Serranidae (including Epinephelidae) with six species each, Muraenidae and Pomacentridae (five species each) and Balistidae, Holocentridae and Lutjanidae (three species each; Supporting Information Table S1). Fifteen species represented 95% of the total abundance, whereas only seven species represented 95% of total biomass. The most important species in terms of abundance and biomass were *Paranthias furcifer*, *Chromis multilineata*, *Myripristis jacobus*, *Holocentrus adscensionis* and *Heteropriacanthus cruentatus* (Supporting Information Table S1).

The reef fish assemblages varied spatially among the studied sites in STI (Supporting Information Figure S1). For example, the mean species density (species richness per transect of 40 m^2) was highest at KIA 16.35 ± 0.64 (mean ± *SE* spp/40 m^2), followed by SPC, SPB and ROL (~12.36 ± 0.57, each site), whereas DVA and SAN had the lowest species richness: 10.54 ± 0.26 (Supporting Information Figure S1a). Fish abundance was highest at KIA (14.26 ± 0.78 ind/m^2), followed by SPB (12.34 ± 0.51 ind/m^2), SAN (7.32 ± 0.55 ind/m^2), DVA (5.21 ± 0.37 ind/m^2), SPC (3.56 ± 0.25 ind/m^2) and ROL (3.57 ± 0.20 ind/m^2; Supporting Information

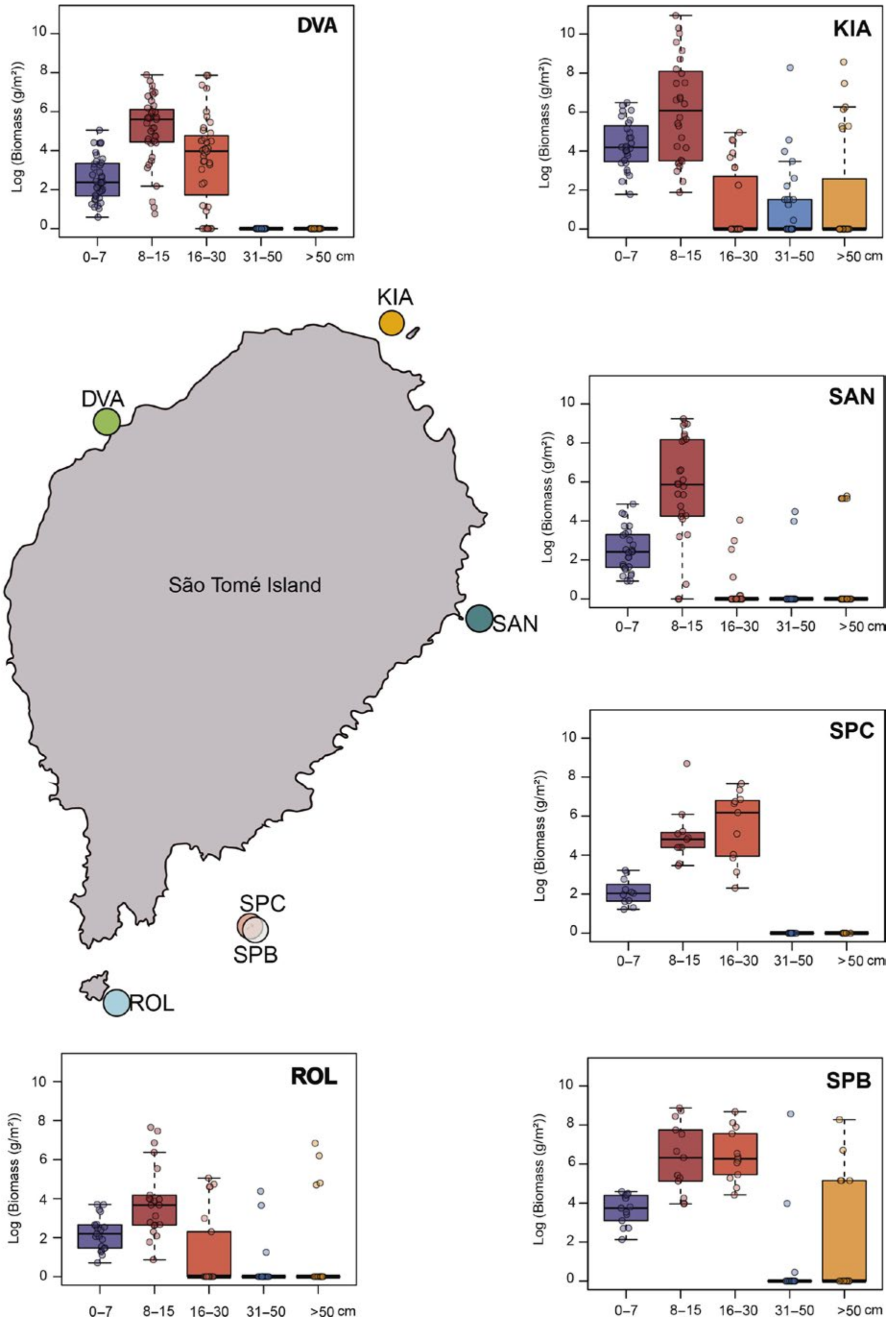

FIGURE 3 Comparative variation in total biomass of fish assemblages per size classes at São Tomé Island. Trophic groups: herbivores–detritivores (HD), macroalgae-feeders (HM), omnivores (OM), sessile invertebrate feeders (IS), mobile invertebrate feeders (IM), planktivores (PK) and piscivores (PS). Fish images represent the most abundant species of each trophic or size group

Figure S1b). Fish biomass was highest at SPB (359.86 ± 15.66 g/m^2), followed by KIA (344.23 ± 39.42 g/m^2), SAN (173.73 ± 16.30 g/m^2), SPC (141.37 ± 13.62 g/m^2), DVA (96.75 ± 6.94 g/m^2) and ROL (58.85 ± 5.29 g/m^2; Supporting Information Figure S1c).

Planktivores were the most abundant trophic group, summing 84% of all individuals and an average abundance of 6.52 ± 0.57 ind/m^2 (Supporting Information Figure S2a). Each of the other trophic groups contributed less than 15% of the total abundance. This pattern of abundance per trophic group was observed across all sites (Supporting Information Figure S3). Similarly, biomass was concentrated in planktivores, summing 60% of the total biomass and with an average biomass of 111.71 ± 18.52 g/m^2 (Figure 2 and Supporting Information Figure S2b), followed by mobile invertebrate feeders (29.71 ± 5.69 g/m^2) and herbivores/detritivores (27.05 ± 5.68 g/m^2). The contribution of planktivores and mobile invertebrate feeders to total biomass was high across all sites, whereas herbivores/detritivores and the other trophic groups varied considerably (Figure 2). The smallest size class (0–7 cm) encompassed the highest abundance, totalling 71% of all individuals (5.50 ± 0.45 ind/m^2; Supporting Information Figure S2c), followed by fishes 8–15 cm that totalled 27% of all individuals (mean: 2.08 ± 0.31 ind/m^2), whereas other classes included less than 10% of the total abundance. Biomass, however, was concentrated in the 8–15 cm size class that totalled 68% of total biomass (125.40 ± 21.04 g/m^2; Figure 3 and Supporting Information Figure S2d), followed by the 16–30 cm size class (16%) and by the 0–7 cm size class (6%). The overall pattern of biomass per size classes was similar across sites, although larger size classes (16–30 cm or larger) were more variable than smaller ones (Figure 3 and Supporting Information Figure S4).

3.2 | The influence of wave exposure, depth and topographic complexity on fish assemblages

Wave exposure and depth were the most important factors structuring reef fish assemblages in São Tomé Island (Table 1). Species density, abundance and biomass increased with wave exposure level (Tukey test: $p < 0.001$; Figure 4a,d,g) and also with depth (Tukey test: $p < 0.001$; Figure 4c,f,i). Topographic complexity affected only reef fish abundance of individuals, but not species density or biomass (Table 1; Figure 4e). High topographic complexity areas had the lowest fish abundances.

Overall, we detected significant effects of all predictors on reef fish abundance and biomass per trophic group and size class, but wave exposure generally explained more variation than depth and topographic complexity (Table 2). For instance, 18% of the variation in abundance and 8% in biomass between trophic groups were explained by wave exposure (Table 2). In contrast, much less variance was explained by topographic complexity and depth. In terms of abundance per size class, wave exposure explained 15% of the variation observed. No single variable explained more than 18% of total variance and residual variance was overall very high (69% to 74%, respectively for trophic groups and size classes, Table 2).

The abundance of planktivorous was positively correlated with wave exposure, whereas mobile invertebrate feeders, omnivores and piscivores were negatively correlated with exposure. Herbivores–detritivores and macroalgae-feeders were positively correlated with topographic complexity and negatively with depth. On the other hand, sessile invertebrate feeders exhibited a positive effect associated with depth (Figure 5a). In terms of biomass, wave exposure was positively correlated with piscivores and negatively with mobile invertebrate feeders, omnivores and macroalgae-feeders. The herbivores–detritivores were positively associated with topographic complexity (Figure 5b). Species with small and medium size (8–30 cm) presented high abundance in sites with high wave exposure, whereas the medium–large size (31–50 cm) were negatively associated with depth (i.e., were associated with shallow sites; Figure 5c). In terms of biomass, very small (0–7 cm) and medium (16–30 cm) species were negatively associated with depth, very large species (> 50 cm) were positively associated with topographic complexity and small species (8–15 cm) occupied mainly shallow areas with low wave exposure (Figure 5d).

TABLE 1 Output of GLMM evaluating the influence of wave exposure (WE), topographic complexity (TC) and depth (DP) on the fish assemblage metrics (species density, abundance and biomass). Bold values indicate $p < 0.05$

Fish assemblages	*df*	*F*	*p*-Value
Species density			
DP	2	6.384	**0.041**
TC	2	0.01	0.920
WE	3	37.82	**<0.001**
Total abundance			
DP	2	42.54	**<0.001**
TC	2	57.72	**<0.001**
WE	3	50.00	**<0.001**
Total biomass			
DP	2	9.00	**0.011**
TC	2	5.40	0.067
WE	3	10.04	**0.018**

3.3 | Benthic cover

São Tomé Island's reef benthic communities were dominated by turf algae (epilithic algal matrix), with an average cover of 30% (± 2.42), followed by calcareous algae (28% ± 2.28%), sand (14% ± 2.41%), macroalgae (10% ± 1.50%), corals (8% ± 1.21%), sponges (7% ± 1.05%), zoanthids (3% ± 0.68%), gorgonians (0.36% ± 0.12%) and others (1.88% ± 0.51%). However, this order varied among sites (Figure 6). About one third of the total variation on the benthic composition was associated with topographic complexity (nested within site; Table 2). Wave exposure (18%) and depth (8%) were less important factors influencing changes on the benthic community (Table 2). *Montastraea cavernosa* was the most abundant hard coral, being particularly abundant in areas below 17 m of depth, although in Diogo Vaz this species was also abundant between 9 and 16 m (3% to 12% cover). The cup coral

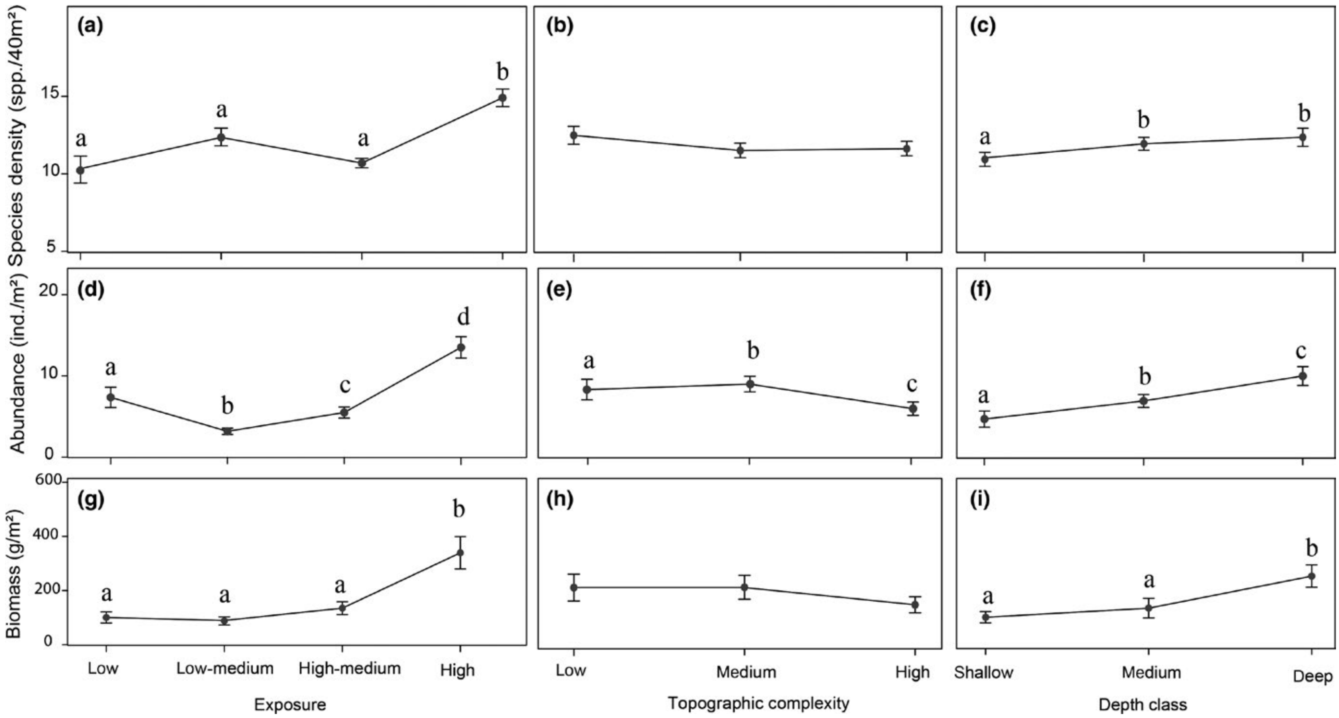

FIGURE 4 Mean (± SE) values of fish assemblages metrics per exposure levels (a, d and g), topographic complexity level (b, e and h) and depth stratum (c, f and i) at São Tomé Island. Different lowercase letters indicate significantly different values identified by Tukey post hoc tests; if letters are absent, no differences have been found between categories

TABLE 2 Outputs of PERMANOVAs evaluating the influence of wave exposure (WE), topographic complexity (TC) and depth (DP) on the fish abundance and biomass between different trophic groups and size classes and benthic community. Bold values indicate $p < 0.05$

Fish	Abundance				Biomass				Benthic community	Benthic cover			
Source	*df*	*F*	R^2	*p*-Value	*df*	*F*	R^2	*p*-Value	Source	*df*	*F*	R^2	*p*-Value
Trophic group													
WE	3	10.98	0.18	**0.001**	3	4.65	0.08	**0.001**	WE	3	8.97	0.18	**0.001**
TC	2	2.77	0.03	**0.018**	2	3.80	0.04	**0.001**	TC	2	4.00	0.27	**0.005**
DP	2	2.46	0.02	**0.040**	2	3.69	0.04	**0.001**	DP	2	6.00	0.08	**0.001**
Residual	131		0.75		131		0.81		Residual	104		0.70	
Size classes													
WE	3	8.88	0.15	**0.001**	3	3.75	0.07	**0.001**					
TC	2	1.75	0.02	0.078	3	2.27	0.02	**0.011**					
DP	2	2.77	0.03	**0.015**	2	4.13	0.05	**0.001**					
Residual	131		0.78		131		0.84						

Tubastraea sp. dominated shallow depths in SPC and SAN, varying in cover from six to 12%. Other relatively common coral species were *Porites branneri*, attaining up to 16% of the coral cover at SPB; *Siderastrea radians*, which varied from 0.2% and 3% of cover in all depths of DVA and KIA; and finally, *Schizoculina fissipara* and *Porites porites*, which had very small cover and were restricted to ROL, one in mid-depths and the other in the deeper depth stratum (Figure 7).

3.4 | Influence of benthic community on fish assemblage

We observed only a weak relationship between benthic communities and the composition of fish species. Benthic composition correlated slightly more strongly with fish species biomass (Mantel R = 0.102, $p = 0.001$) than with abundance (Mantel R = 0.061, $p = 0.019$).

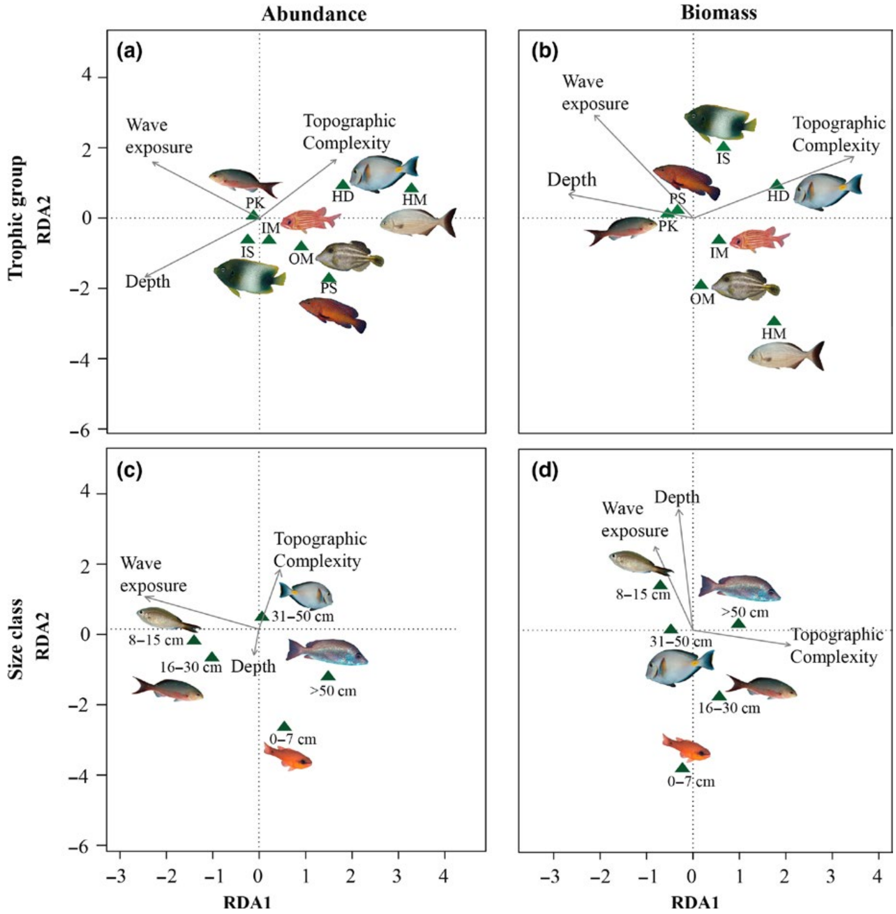

FIGURE 5 Biplots from redundancy analysis representing the influence of abiotic factors by trophic group (a and b) and size class (c and d). Each fish figure represents the most common species observed in each level. Trophic groups: herbivores–detritivores (HD), macroalgae-feeders (HM), omnivores (OM), sessile invertebrate feeders (IS), mobile invertebrate feeders (IM), planktivores (PK) and piscivores (PS)

4 | DISCUSSION

The main findings of this study were that 1) planktivores and small individuals dominated reef fish assemblages at São Tomé Island in both biomass and abundance; 2) benthic communities were dominated by the epilithic algal matrix and calcareous encrusting algae, with hard corals having a secondary importance only; and 3) wave exposure was the main variable affecting benthic communities and fish assemblages, regardless of the indicator variable investigated (total, per trophic group or per size class abundance or biomass). Depth was also important to explain variability in total fish species density, abundance and biomass. Interestingly, species density depicted an unexpected pattern; *that is*, it increased with depth. Topographic complexity, on the other hand, was mainly correlated with patterns in benthic cover and less related to fish assemblages. These findings are consistent with a scenario of a highly hydrodynamic and isolated oceanic reef system, likely reliant on plankton as an important energy source, and where benthic communities are constrained in their development both by wave energy and the general impoverished regional pool.

4.1 | Reef fish assemblages

Wind, waves and currents clash with oceanic island masses, bringing allochthonous oceanic productivity in the form of plankton and allowing the rise of cold deeper waters rich in nutrients (Gove et al., 2016). Such a highly hydrodynamic environment favours high availability of plankton (Hamner, Jones, Carleton, Hauri, & Williams, 1988) and, thus, of planktivorous fishes (Hobson, 1991). Additionally, oceanic systems receive very little sediment input from continental landmasses and, as such, conserve clear waters that are adequate for the feeding activity of these planktivores fishes (Johansen & Jones, 2013). As a result, most oceanic islands are dominated by reef planktivores, despite differences in fishing pressure (e.g., Friedlander et al., 2010; Krajewski & Floeter, 2011; Luiz et al., 2015; Quimbayo et al., 2017; Quimbayo et al., 2018). Our results, showing both a pivotal role of wave exposure in shaping reef fish assemblages and a numerical and biomass dominance of planktivores at São Tomé Island are consistent with this scenario. Altogether, they suggest an important role of plankton in São Tomé's reef food webs, such as has been reported for temperate rocky reefs (Truong, Suthers, Cruz, & Smith, 2017). Circumstantial evidence also suggests it might be the case of some marginal tropical isolated reef systems (e.g., Luiz et al., 2015; Quimbayo et al., 2017).

The effects of topographic complexity on reef fish species richness, abundance and biomass have been demonstrated in a range of ecosystems, including coral reefs (e.g., Friedlander et al., 2003), seagrass (e.g., Heck & Wetstone, 1977) and kelp beds (e.g., Russell, 1977). Even in the South Atlantic oceanic islands there is evidence for topographic complexity as a driver of reef

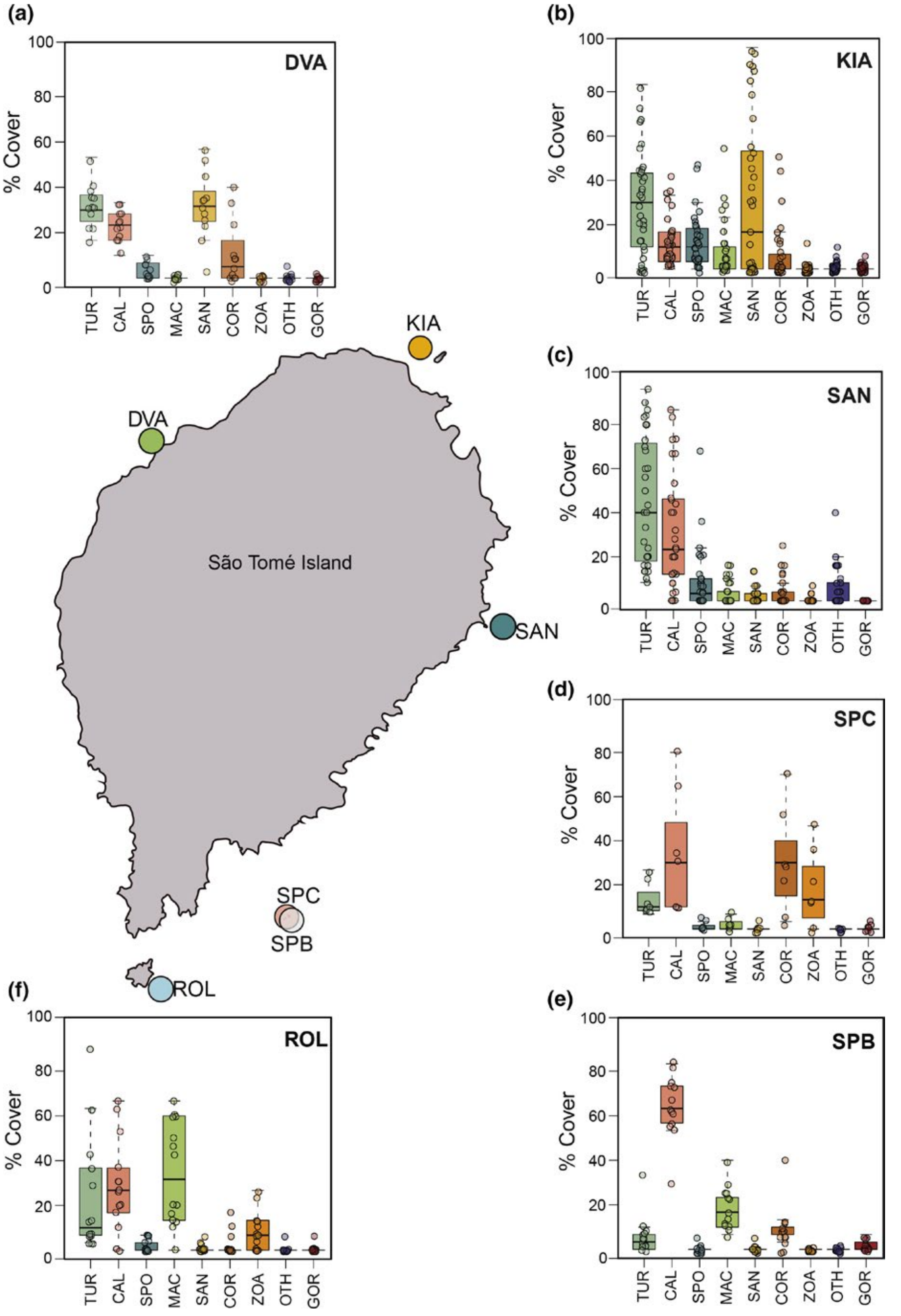

FIGURE 6 Variation of benthic cover sampled at São Tomé Island. Each point represents a photo-quadrat. Benthic categories: turf (TUR), coralline algae (CAL), sponges (SPO), macroalgae (MAC), sand (SAN), coral (COR), zoanthids (ZOA), other life (OTH) and gorgonians (GOR). See Figure 1 for the acronym of the sites

fish assemblages (e.g., Krajewski & Floeter, 2011, Luiz et al., 2015, Pinheiro et al., 2011). These islands are predominantly volcanic, with rocky reefs often dominating the underwater seascape. Biogenic reefs in these islands are limited in extent and do not harbour branching growth forms of hydrocorals as is the case of coastal coral reef systems in Brazil (e.g., Leão, Kikuchi, & Testa, 2003; Francini-Filho & Moura, 2008). Therefore, reefs in these islands frequently do not attain the same level of structural complexity as other coral reef systems (e.g., from the Caribbean, Indo-Pacific or coastal Brazil). Furthermore, reef fish assemblages of these islands seem to strongly respond only to the upper range of topographic complexity values (e.g., as in deep areas with high coral cover, Krajewski & Floeter, 2011). In São Tomé Island, we also observed very little response of traditional assemblage metrics, like species density, abundance or biomass to topographic complexity, although we noticed some level of correlation between reef fish assemblages and benthic communities. Thus, it is possible that the level of topographic complexity attained by São Tomé's reefs could be also insufficient to trigger strong responses from fish assemblages.

It is a common feature of reef fish assemblages to decrease in richness and abundance with depth (e.g., Brokovich et al., 2008; MacDonald, Bridge, & Jones, 2016; Tuya et al., 2017). In some cases, peak values might occur at a mid-depth below which there is a steep decrease in fish abundance and richness (Garcia-Sais, 2010). At Príncipe Island, an island close to São Tomé, Tuya and collaborators

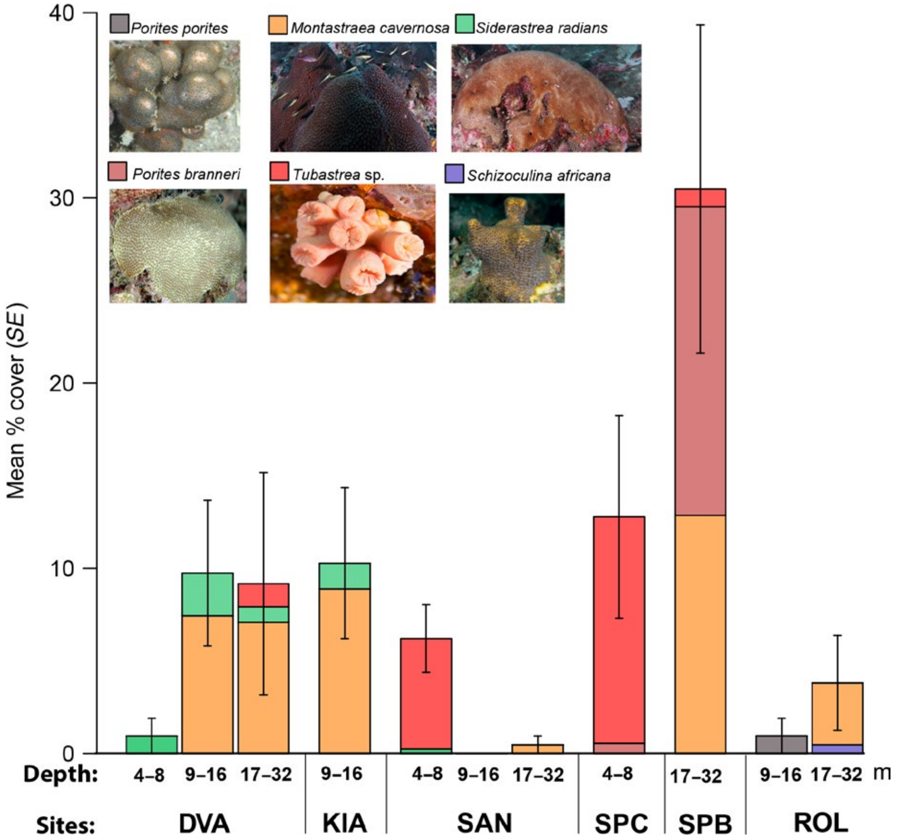

FIGURE 7 Mean coral cover per species along of a depth gradient of sites in São Tomé Island

(2017) found that the taxonomic and functional diversity of reef fishes decreased linearly with depth. We found results that are opposite to many studies (e.g., Brokovich et al., 2008; Tuya et al., 2017): species richness, abundance and biomass all increased with depth in the range investigated (Figure 4). This is similar to what was observed for the very isolated and impoverished St. Peter and St. Paul's Archipelago, in the Mid-Atlantic (Luiz et al., 2015). One possible explanation for this pattern would be that deeper areas suffer less influence of human activities. Reef fisheries in São Tomé, for instance, are mainly artisanal, characterized by low-technology fishing gear and predominantly small boats (Maia et al., 2018). Thus, most fishermen do not have access to deeper fishing grounds. Thus, it seems natural that deeper reefs would be protected from many of the anthropogenic disturbances that affect shallower regions. However, these activities are expected to affect more directly fish biomass than abundance or species richness (McClanahan, Graham, Calnan, & Macneil, 2007) and this hypothesis does little to explain why these descriptors are also maximized in deeper areas. Moreover, there is evidence that even deeper reefs in São Tomé are also affected by fishing activities (Morais & Maia, 2017). An alternative hypothesis is that deeper sites in São Tomé are under more direct influence of a constant thermocline resulting from intrusion of cold waters from the Benguela current (Laborel, 1974; Morais & Maia, 2017). This would allow the coexistence, in the local scale, of species with tropical and subtropical affinity. Evidence of species zonation due to this thermocline has been provided by Wirtz and D'Udekem D'Acoz (2008) and Morais and Maia (2017). Additionally, more abundant fish assemblages could result from steeper bottom relief promoting zooplankton concentration, and increased habitat complexity due to, among other features, larger abundance of gorgonians.

As expected on the basis of São Tomé's human population density and reliance on fishing activities for provision of animal protein (Maia et al., 2018), the biomass of large fish, especially predators, was low and patchy. The low contribution of large predators, such as groupers, sharks, snappers and jacks, to the fish biomass is consistent to what has been observed in populated islands around the world (e.g., Sandin et al., 2008; Williams et al., 2015; Robinson et al., 2017). Particularly, no sharks have been observed during the sampling or on following successive dives (E. L. C. Ferreira, C. L. S. Sampaio, S. R. FLoeter, pers. obs.). Sharks have been threatened globally and are the first to decline in abundance or disappear after being fished (e.g., Ferretti, Worm, Britten, Heithaus, & Lotze, 2010; Graham, Spalding, & Sheppard, 2010; Myers, Baum, Shepherd, Powers, & Peterson, 2007). Shark fishing has been invoked as a likely cause of regional extirpation elsewhere in the Atlantic (Morais et al., 2017; Ward-Paige et al., 2010), and even local extinction of a shark population in an isolated Mid-Atlantic island has been likely caused by fishing (Luiz & Edwards, 2011).

4.2 | Benthic communities

Turf and calcareous coralline algae were the overall dominant benthic component of São Tomé Island's reefs, with 30% and 28% of total cover, respectively. This pattern is similar to the observed in other South Atlantic oceanic islands such as Trindade Island (turf: 30%–40%; calcareous algae: 16%–25%; Pinheiro et al., 2011), Rocas Atoll (turf: 51%; calcareous algae: 33%; Longo et al., 2015) and St. Peter and St. Paul's Archipelago (turf: 20%–70%; calcareous algae: 10%–25%; Luiz et al., 2015). Overall, turf algae (the main component of the epilithic algal matrix) are the dominant primary producers on most tropical and many temperate coasts, playing key roles in the ecology of subtidal shores (Adey & Goertemiller, 1987; Aued et al., 2018; Hatcher, 1988). They occupy substantial areas of rock substrate, both on surface cover and biomass basis (Copertino, Connell, & Cheshire, 2005). Coralline algae are also important bulk producers and consolidators of the reef in most tropical and subtropical areas. They are particularly important in coral reef ecosystems where they play a major role in the carbonate budget (Littler & Littler, 1988; Payri, 1995; Steneck, 1997).

Coral cover was generally low in our samples, although there are some localized areas of high cover. This pattern is similar to what is observed in the Brazilian southeastern coast (e.g., Floeter et al., 2007) and oceanic islands (e.g., Longo et al., 2015; Pinheiro et al., 2011). Laborel (1974) noted that the species poor and homogeneous coral assemblages of the Eastern Atlantic are generally unable to fuse and form large reef structures. Although isolation from more biodiverse regions (i.e., Indo-Pacific and Caribbean) could be invoked to explain this pattern, the existence of coral reefs along the Brazilian coast (e.g., Castro & Pires, 2001; Leão et al., 2003) make evident that this might not be the complete picture. It is interesting to note that some of the main reef builders in Brazil are from the genus *Mussismillia*, which is absent from the Eastern Atlantic (Laborel, 1974).

We found abundant cover of the cup coral (cf. *Tubastrea* sp.) in shallow reefs of Santana and Sete Pedras. Species from this genus are alien both in the Caribbean and in Brazil (Creed et al., 2017) and have become particularly invasive in Brazilian reefs (Capel et al., 2017; De Paula & Creed, 2004; Sampaio, Miranda, Maia-Nogueira, & Nunes, 2012). *Tubastrea* spp. display biological traits that enhance their potential of population growth, such as aggressiveness in competition for space (Capel, Migotto, Zilberberg, & Kitahara, 2014). Considering the biogeographical context of the coral fauna of West Africa, Laborel (1974) concluded that *Tubastraea* spp. must be a relatively recent invader, maybe coming from the Indo-Pacific. In addition, Friedlander et al. (2014) reported a mean of 47% of *Tubastraea* cover in oil rigs investigated off Gabon, where it was the most abundant taxon. They also considered it likely a relatively recent invader of the Gulf of Guinea. More recently, an endemic species of the genus has been described from Cape Verde (*Tubastraea caboverdiana* Ocaña & Brito, 2015), raising the possibility that cup corals could indeed be a native feature of West African reefs. However, the absence of older records of this highly conspicuous, but taxonomically poorly known coral, and the current uncertainties regarding its identification suggest that *Tubastraea* spp. should be considered at least as cryptogenic in the island of São Tomé.

Gorgonians had one of the lowest benthic cover around São Tomé's reefs. This is likely a bias of using bidimensional photo-quadrats to estimate the abundance of an organism with verticalized growth and body plan. Gorgonians indeed appear to be common in deeper areas (not sampled in this study). Wirtz and D'Udekem D'Acoz (2008) reported large gorgonians forming forests below 30 m deep in Príncipe and São Tomé islands. Morais and Maia (2017) noted that these forests, mainly formed with gorgonians but also with a substantial number of black corals, extended to mesophotic reefs down to at least 50 m depth, but certainly much deeper (E. L. C. Ferreira, C. L. S. Sampaio, S. R. FLoeter, pers. obs.).

Depth and wave exposure are all important drivers of change in the cover of reef benthic communities (e.g., Friedlander et al., 2013). Topographic complexity is normally evaluated as either correlated or as a property of benthic communities and not a potential causal agent to them (e.g., Wilson et al., 2007). Nevertheless, in our study, most of variation on species composition was explained by wave exposure and topographic complexity, with depth being a minor driver. Wave exposure brings, at the same time, both physical and nutritional consequences to marine organisms. From one perspective, wave-swept habitats preclude the colonization by organisms that do not hold adequate morphology to withstand the energetic water movements (Denny, Daniel, & Koehl, 1985). On the other hand, organisms with some level of morphologic plasticity can develop in different growth forms in response to water movements (e.g., massive instead of branching milleporine corals; see Morri & Bianchi, 1995 and Souza et al., 2017). From a nutritional perspective, water currents bring food for many sessile benthic organisms in the form of plankton and dissolved organic matter (Gili & Coma, 1998).

4.3 | Influence of benthic community on fish assemblage

Overall, benthic communities correlated only weakly with fish assemblages, in terms of either abundance or biomass. This suggests some level of decoupling of these compartments of reef communities and reinforces what has been observed in other studies in South Atlantic oceanic islands: that benthic communities seem less important in shaping fish assemblages than in coral reefs (e.g., Krajewski & Floeter, 2011; Luiz et al., 2015).

Besides testing the importance of exposure, depth and topographic complexity as drivers of reef community structuring in a marginal tropical reef, this work provides information about some of the least known tropical reefs of the world. We concluded that (a) reef fish assemblage, in terms of richness, abundance and biomass, vary significantly along sites even on small spatial scales. Small fishes peaked in abundance, whereas the biomass was mainly concentrated in medium (8–15 and 16–30 cm) body size classes. The biomass of top predators is relatively low; (b) the wave exposure level was the most important abiotic factor in structuring of the reef fish assemblages in STI; (c) the benthic cover varies among sites, and the turf (epilithic algal matrix) was the most important benthic group; (d) the hard coral *Montastraea cavernosa* was the most important coral species, comprising 46% of the coral cover; (e) wave exposure and depth influenced the benthic cover; and (f) the reef fish assemblage changed, although weakly, as a function of benthic cover. Taken together, these results provide baseline information and can inform conservation efforts aimed at protecting reef environments of this poorly known marine hotspot in the Gulf of Guinea.

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REFERENCES

Adey, W. H., & Goertemiller, T. (1987). Coral reef algal turfs: Master producers in nutrient poor seas. *Phycologia*, *26*, 374–386. https://doi.org/10.2216/i0031-8884-26-3-374.1

Afonso, P., Porteiro, F. M., Santos, R. S., Barreiros, J. P., Worms, J., & Wirtz, P. (1999). Coastal Marine fishes of São Tomé Island (Gulf of Guinea). *Arquipélago Life and Marine Sciences*, *17*, 65–92.

Almada, V. C., Toledo, J. S., Brito, A., Levy, A., Floeter, S. R., Robalo, J. I., … Almada, F. (2013). Complex origins of the Lusitania biogeographic province and northeastern Atlantic fishes. *Frontiers of Biogeography*, *5*, 3–11.

Aued, A. W., Smith, F., Quimbayo, J. P., Cândido, D. V., Longo, G. O., Ferreira, C. E. L., … Segal, B. (2018). Large-scale patterns of benthic marine communities in the Brazilian Province. *Plos ONE*, *13*, e0198452. https://doi.org/10.1371/journal.pone.0198452

Belhabib, D. (2015). *Fisheries of Sao Tome and Principe, a catch reconstruction (1950–2010)*. Fisheries Centre Working Paper. Working Paper #2015-6786. University of British Columbia, Vancouver, BC, Canada.

Bell, J. J., & Barnes, D. K. A. (2001). Sponge morphological diversity: A qualitative predictor of species diversity? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *11*, 109–121. https://doi.org/10.1002/aqc.436

Bellwood, D. R., Hoey, A. S., & Hughes, T. P. (2012). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1621–1629. https://doi.org/10.1098/rspb.2011.1906

Bellwood, D. R., Wainwright, P. C., Fulton, C. J., & Hoey, A. (2002). Assembly rules and functional groups at global biogeographical scales. *Functional Ecology*, *16*, 557–562. https://doi.org/10.1046/j.1365-2435.2002.00655.x

Brokovich, E., Einbinder, S., Shashar, N., Kiflawi, M., & Kark, S. (2008). Descending to the twilight zone: Changes in coral reef fish assemblages along a depth gradient down to 65 m. *Marine Ecology Progress Series*, *371*, 253–262. https://doi.org/10.3354/meps07591

Caldeira, R. J. M. M. (2002). Petrology of ultramafic nodules from São Tomé Island, Cameroon Volcanic Line (oceanic sector). *Journal of African Earth Sciences*, *34*, 231–246. https://doi.org/10.1016/S0899-5362(02)00022-2

Capel, K. C. C., Migotto, A. E., Zilberberg, C., & Kitahara, M. V. (2014). Another tool towards invasion? Polyp "bail-out" in *Tubastraea coccinea*. *Coral Reefs*, *33*, 1165–1165. https://doi.org/10.1007/s00338-014-1200-z

Capel, K. C. C., Toonen, R. J., Rachid, C. T. C. C., Creed, J. C., Kitahara, M. V., Forsman, Z., & Zilberberg, C. (2017). Clone wars: Asexual reproduction dominates in the invasive range of *Tubastraea* spp. (Anthozoa: Scleractinia) in the South-Atlantic Ocean. *PeerJ*, *5*, e3873.

Carneiro, G. (2011). They come, they fish, and they go: Fisheries agreements with Cape Verde and São Tomé e Príncipe. *Marine Fisheries Review*, *73*, 1–25.

Castro, C. B., & Pires, D. O. (2001). Brazilian coral reefs: What we already know and what is still missing. *Bulletin of Marine Science*, *69*, 357–371.

Cinner, J. E., Graham, N. J., Huchery, C., & Macneil, M. A. (2013). Global effects of local human population density and distance to markets on the condition of coral reef fisheries. *Conservation Biology*, *27*, 453–458. https://doi.org/10.1111/j.1523-1739.2012.01933.x

Copertino, M. S., Connell, S. D., & Cheshire, A. (2005). Prevalence and production of turf-forming algae on a temperate subtidal coast. *Phycologia*, *43*, 241–248.

Cowman, P. F., Parravicini, V., Kulbicki, M., & Floeter, S. R. (2017). The biogeography of tropical reef fishes: Endemism and provinciality through time. *Biological Reviews*, *92*, 2112–2130. https://doi.org/10.1111/brv.12323

Creed, J. C., Fenner, D., Sammarco, P., Cairns, S., Junqueira, A. O. R., Cruz, I., … Oigman-pszczol, S. (2017). The invasion of the azooxanthellate coral *Tubastraea* (Scleractinia: Dendrophylliidae) throughout the world: History, pathways and vectors. *Biological Invasions*, *19*, 283–305. https://doi.org/10.1007/s10530-016-1279-y

De Paula, A. F., & Creed, J. C. (2004). Two species of the coral *Tubastraea* (Cnidaria, Scleractinia) in Brazil: A case of accidental introduction. *Bulletin of Marine Science*, *74*, 175–183.

Denny, M. W., Daniel, T. L., & Koehl, M. A. R. (1985). Mechanical limits to size in wave-swept organisms. *Ecological Society of America*, *55*, 69–102. https://doi.org/10.2307/1942526

Dustan, P., Doherty, O., & Pardede, S. (2013). Digital reef rugosity estimates coral reef habitat complexity. *PLoS ONE*, *8*(2), e57386. https://doi.org/10.1371/journal.pone.0057386

Edgar, G. J., Banks, S. A., Bessudo, S., Cortés, J., Guzmán, H. M., Henderson, S., … Zapata, F. A. (2011). Variation in reef fish and invertebrate communities with level of protection from fishing across the Eastern Tropical. *Global Ecology and Biogeography*, *20*, 730–743.

Ferreira, C. E. L., Gonçalves, J. E. A., & Coutinho, R. (2001). Community structure of fishes and habitat complexity on a tropical rocky shore. *Environmental Biology of Fishes*, *61*, 353–369.

Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, *13*, 1055–1071. https://doi.org/10.1111/j.1461-0248.2010.01489.x

Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddack, M. J., & Horn, M. H. (2005). Geographical gradients of marine herbivorous fishes: Patterns and processes. *Marine Biology*, *147*, 1435–1447. https://doi.org/10.1007/s00227-005-0027-0

Floeter, S. R., Krohling, W., Gasparini, J. L., Ferreira, C. E. L., & Zalmon, I. R. (2007). Reef fish community structure on coastal islands of the southeastern Brazil: The influence of exposure and benthic cover. *Environmental Biology of Fishes*, *78*, 147–160. https://doi.org/10.1007/s10641-006-9084-6

Floeter, S. R., Rocha, L. A., Robertson, D. R., Joyeux, J. C., Smith-Vaniz, W. F., Wirtz, P., … Bernardi, G. (2008). Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, *35*, 22–47.

Francini-Filho, R. B., & Moura, R. L. (2008). Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil. *Aquatic Conservation Marine Freshwater Ecosystems*, *18*, 1166–1179. https://doi.org/10.1002/aqc.966

Friedlander, A. M., Ballesteros, E., Beets, J., Berkenpas, E., Gaymer, C. F., Gorny, M., & Sala, E. (2013). Effects of isolation and fishing on the marine ecosystems of Easter Island and Salas y Gómez, Chile. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *531*, 515–531. https://doi.org/10.1002/aqc.2333

Friedlander, A. M., Ballesteros, E., Fay, M., & Sala, E. (2014). Marine communities on oil platforms in Gabon, West Africa: High biodiversity oases in a low biodiversity environment. *PLoS ONE*, *9*, e103709. https://doi.org/10.1371/journal.pone.0103709

Friedlander, A. M., Brown, E. K., Jokiel, P. L., Smith, W. R., & Rodgers, K. S. (2003). Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs*, *22*, 291–305. https://doi.org/10.1007/s00338-003-0317-2

Friedlander, A. M., & Parrish, J. D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, *224*, 1–30. https://doi.org/10.1016/S0022-0981(97)00164-0

Friedlander, A. M., Sandin, S. A., DeMartini, E. E., & Sala, E. (2010). Spatial patterns of the structure of reef fish assemblages at a pristine atoll in the central Pacific. *Marine Ecology Progress Series*, *410*, 219–231. https://doi.org/10.3354/meps08634

Friedlander, A., Zgliczynski, B. J., Ballesteros, E., Aburto-Oropeza, O., Bolaños, A., & Sala, E. (2012). The shallow-water fish assemblage of Isla del Coco National Park, Costa Rica: Structure and patterns in an isolated, predator-dominated ecosystem. *Revista De Biología Tropical*, *60*, 321–338.

Froese, R., & Pauly, D. (2016). *FishBase*. World Wide Web electronic publication. Retrieved from https://www.fishbase.org

Fulton, C. J., & Bellwood, D. R. (2004). Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. *Marine Biology*, *144*, 429–437. https://doi.org/10.1007/s00227-003-1216-3

Fulton, C. J., Bellwood, D. R., & Wainwright, P. C. (2005). Wave energy and swimming performance shape coral reef fish assemblages. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 827–832. https://doi.org/10.1098/rspb.2004.3029

García-Charton, J. A., Pérez-Ruzafa, Á., Sánchez-Jerez, P., Bayle-Sempere, J. T., Reñones, O., & Moreno, D. (2004). Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Marine Biology*, *144*, 161–182. https://doi.org/10.1007/s00227-003-1170-0

Garcia-Sais, J. R. (2010). Reef habitats and associated sessile-benthic and fish assemblages across a euphotic–mesophotic depth gradient in Isla Desecheo, Puerto Rico. *Coral Reefs*, *29*, 277–288. https://doi.org/10.1007/s00338-009-0582-9

Gili, J. M., & Coma, R. (1998). Benthic suspension feeders: Their paramount role in littoral marine food webs. *Trends in Ecology & Evolution*, *13*, 316–321. https://doi.org/10.1016/S0169-5347(98)01365-2

Gove, J. M., McManus, M. A., Neuheimer, A. B., Polovina, J. J., Drazen, J. C., Smith, C. R., … Williams, G. (2016). Near-island biological hotspots in barren ocean basins. *Nature Communications*, *7*, 1–34. https://doi.org/10.1038/ncomms10581

Graham, N. A. J., & McClanahan, T. R. (2013). The last call for marine wilderness? *BioScience*, *63*, 397–402. https://doi.org/10.1525/bio.2013.63.5.13

Graham, N. A. J., Spalding, M. D., & Sheppard, C. R. C. (2010). Reef shark declines in remote atolls highlight the need for multi-faceted conservation action. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *548*, 543–548. https://doi.org/10.1002/aqc.1116

Gratwicke, B., & Speight, M. R. (2005). The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, *66*, 650–667. https://doi.org/10.1111/j.0022-1112.2005.00629.x

Hachich, N. F., Bonsall, M. B., Arraut, E. M., Barneche, D. R., Lewinsohn, T. M., & Floeter, S. R. (2015). Island biogeography: Patterns of marine shallow-water organisms in the Atlantic Ocean. *Journal Biogeography*, *45*, 1871–1882. https://doi.org/10.1111/jbi.12560

Hamner, W. M., Jones, M. S., Carleton, J. H., Hauri, I. R., & Williams, D. M. B. (1988). Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bulletin of Marine Science*, *42*, 459–479.

Hatcher, B. G. (1988). Coral reef primary productivity: A beggar's banquet. *Trends in Ecology & Evolution*, *3*, 106–111. https://doi.org/10.1016/0169-5347(88)90117-6

Heck, K. L. J., & Wetstone, G. S. (1977). Habitat complexity and invertebrate species richness and abundance in tropical seagrass. *Journal of Biogeography*, *4*, 135–142.

Hobson, E. S. (1991). Trophic relationships of fishes specialized to feed on Zooplankters above coral reefs. In P. F. Sale (Ed.), *The ecology of fishes on coral reefs* (pp. 69–95). New York, NY: Academic Press.

Horemans, B., Gallène, J., & Njock, J. (1994). *Revista setorial da pesca artesanal a São Tomé e Príncipe. Programa de desenvolvimento integrado das pescas artesanais na África Ocidental (DIPA)*. Retrieved from https://www.fao.org/docrep/015/an097PT/an097PT.pdf

Hothorn, T., Bretz, F., & Peter, W. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *20*, 346–363. https://doi.org/10.1002/bimj.200810425

Johansen, J. L., & Jones, G. P. (2013). Sediment-induced turbidity impairs foraging performance and prey choice of planktivorous coral reef fishes. *Ecological Applications*, *23*, 1504–1517. https://doi.org/10.1890/12-0704.1

Jones, G. P., & Syms, C. (1998). Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology*, *23*, 287–297. https://doi.org/10.1111/j.1442-9993.1998.tb00733.x

Khalil, M. T., Bouwmeester, J., & Berumen, M. L. (2017). Spatial variation in coral reef fish and benthic communities in the central Saudi Arabian Red Sea. *PeerJ*, *5*, e3410. https://doi.org/10.7717/peerj.3410

Kohler, K. E., & Gill, S. M. (2006). Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences*, *32*, 1259–1269. https://doi.org/10.1016/j.cageo.2005.11.009

Krajewski, J. P., & Floeter, S. R. (2011). Reef fish community structure of the Fernando de Noronha Archipelago (Equatorial Western Atlantic): The influence of exposure and benthic composition. *Environmental Biology of Fishes*, *92*, 25–40. https://doi.org/10.1007/s10641-011-9813-3

Kulbicki, M., Parravicini, V., & Mouillot, D. (2015). Patterns and processes in reef fish body size. In C. Mora (Ed.), *Ecology of fishes on coral reefs* (pp. 104–115). Cambridge, UK: Cambridge University Press.

Laborel, J. (1974). West African reefs corals: An hypothesis on their origin. *Proceedings of the 2nd International Coral Reef Symposium*, *1*, 425–443.

Leão, Z. M., Kikuchi, R., & Testa, V. (2003). Corals and coral reefs of Brazil. In J. Cortés (Ed.), *Latin American coral reefs* (pp. 9–52). Amsterdam, the Netherlands: Elsevier.

Lee, D. C., Halliday, A. N., Fitton, J. G., & Poli, G. (1994). Isotopic variations with distance and time in the volcanic islands of the Cameroon line: Evidence for a mantle plume origin. *Earth and Planetary Science Letters*, *123*, 119–138. https://doi.org/10.1016/0012-821X(94)90262-3

Littler, M. M., & Littler, D. S. (1984). Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. *Journal of Experimental Marine Biology and Ecology*, *74*, 13–34. https://doi.org/10.1016/0022-0981(84)90035-2

Littler, M. M., & Littler, D. S. (1988). Structure and role of algae in tropical reef communities. In C. A. Lembi, & J. R. Waaland (Eds.), *Algae and human affairs* (Vol. 28, pp. 29–56). Cambridge, UK: Cambridge University Press.

Longo, G. O., Morais, R. A., Martins, C. D. L., Mendes, T. C., Aued, A. W., Cândido, D. V., … Floeter, S. R. (2015). Between habitat variation of benthic cover, reef fish assemblage and feeding pressure on the benthos at the only atoll in south Atlantic: Rocas atoll, NE Brazil. *PLoS ONE*, *10*(6), e0127176. https://doi.org/10.1371/journal.pone.0127176

Luckhurst, E., & Luckhurst, K. (1978). Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology*, *323*, 317–323. https://doi.org/10.1007/BF00455026

Luiz, O. J., & Edwards, A. J. (2011). Extinction of a shark population in the Archipelago of Saint Paul's Rocks (equatorial Atlantic) inferred from the historical record. *Biology Conservation*, *144*, 2873–2881. https://doi.org/10.1016/j.biocon.2011.08.004

Luiz, O. J., Mendes, T. C., Barneche, D. R., Ferreira, C. G. W., Noguchi, R., Villaça, R. C., … Ferreira, C. E. L. (2015). Community structure of reef fishes on a remote oceanic island (St Peter and St Paul's Archipelago, equatorial. Atlantic): The relative influence of abiotic and biotic variables. *Marine and Freshwater Research*, *66*, 739–749. https://doi.org/10.1071/MF14150

MacDonald, C., Bridge, T. C. L., & Jones, G. P. (2016). Depth, bay position and habitat structure as determinants of coral reef fish distributions: Are deep reefs a potential refuge? *Marine Ecology Progress Series*, *561*, 217–231. https://doi.org/10.3354/meps11953

Maia, H. A., Morais, R. A., Siqueira, A. C., Hanazaki, N., Floeter, S. R., & Bender, M. G. (2018). Shifting baselines among traditional fishers in São Tomé and Príncipe islands, Gulf of Guinea. *Ocean and Coastal Management*, *154*, 133–142. https://doi.org/10.1016/j.ocecoaman.2018.01.006

McClanahan, T. R., Graham, N. J., Calnan, J. M., & Macneil, M. A. (2007). Toward pristine biomass: Reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Society of America*, *17*, 1055–1067. https://doi.org/10.1890/06-1450

McGehee, M. A. (1994). Correspondence between assemblages of coral reef fishes and gradients of water motion, depth and substrate size off Puerto Rico. *Marine Ecology Progress Series*, *105*, 243–255. https://doi.org/10.3354/meps105243

Measey, J. G., Vences, M., Drewes, R. C., Chiari, Y., Melo, M., & Bourles, B. (2007). Freshwater paths across the ocean: Molecular phylogeny of the frog *Ptychadena newtoni* gives insights into amphibian colonization of oceanic islands. *Journal Biogeography*, *34*, 7–20.

Mora, C., Aburto-Oropeza, O., Ayala, B. A., Ayotte, P. M., Banks, S., Bauman, A. G., … Zapata, F. A. (2011). Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. *PLoS Biology*, *9*(4), e1000606. https://doi.org/10.1371/journal.pbio.1000606

Morais, R. A., Ferreira, C. E. L., & Floeter, S. R. (2017). Spatial patterns of fish standing biomass across Brazilian reefs. *Journal of Fish Biology*, *91*, 1642–1667. https://doi.org/10.1111/jfb.13482

Morais, R. A., & Maia, H. A. (2017). Lush underwater forests in mesophotic reefs of the Gulf of Guinea. *Coral Reefs*, *36*, 95. https://doi.org/10.1007/s00338-016-1523-z

Morri, C., Cattaneo, V. R., Sartoni, G., & Bianchi, C. N. (2000). Shallow epibenthic communities of Ilha do Sal (Cape Verde Archipelago, Eastern Atlantic). *Arquipélago, Life and Marine Sciences*, *2*(Part A), 157–165.

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-Gonzales, J. E., Bender, M. G., … Bellwood, D. R. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas of tropical reefs. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 13757–13762.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, *315*, 1846–1850. https://doi.org/10.1126/science.1138657

Parravicini, V., Kulbicki, M., Bellwood, D. R., Friedlander, A. M., Chabanet, P., Floeter, S. R., … Mouillot, D. (2013). Global patterns and predictors of tropical reef fish species richness. *Ecography*, *37*, 1254–1262. https://doi.org/10.1111/j.1600-0587.2013.00291.x

Payri, C. E. (1995). Production carbonatée de quelques algues calcifiées sur un récif corallien en Polynésie Française. *Bulletin De La Société Géologique De France*, *166*, 74–84.

Pinheiro, H. T., Ferreira, C. E. L., Joyeux, J. C., Santos, R. G., & Horta, P. A. (2011). Reef fish structure and distribution in a south western Atlantic Ocean tropical island. *Journal Fish Biology*, *79*, 1984–2006. https://doi.org/10.1111/j.1095-8649.2011.03138.x

Polidoro, B. A., Carpenter, K. E., Ralph, G. M., Strongin, K., Harvey, M., Arnold, R., … Christophe, J. (2017). The status of marine biodiversity in the Eastern Central Atlantic (West and Central Africa). *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*, 1021–1034. https://doi.org/10.1002/aqc.2744

Quimbayo, J. P., Dias, M. S., Kulbicki, M., Mendes, T. C., Lamb, R. W., Johnson, A. F., … Floeter, S. R. (2018). Determinants of reef fish assemblages in tropical oceanic islands. *Ecography*, *41*, 1–11. https://doi.org/10.1111/ecog.03506

Quimbayo, J. P., Floeter, S. R., Noguchi, R., Rangel, C. A., Gasparini, J. L., Sampaio, C. L. S., … Rocha, L. A. (2012). Cleaning mutualism in Santa Luzia (Cape Verde Archipelago) and São Tomé islands, Tropical Eastern Atlantic. *Marine Biodiversity Records*, *5*, 1–7. https://doi.org/10.1017/S175526721200108X

Quimbayo, J. P., Mendes, T. C., Kulbicki, M., Floeter, S. R., & Zapata, F. A. (2017). Unusual reef fish biomass and functional richness in a remote island in the Tropical Eastern Pacific. *Environmental Biology of Fishes*, *100*, 149–162.

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Roberts, C. M., McClean, C. J., Veron, J. E. N., Hawkins, J. P., Allen, G. R., McAllister, D. E., … Werner, T. B. (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, *295*, 1280–1284. https://doi.org/10.1126/science.1067728

Robinson, J. P. W., Williams, I. D., Edwards, A. M., McPherson, J., Yeager, L., Vigliola, L., … Baum, J. K. (2017). Fishing degrades size structure of coral reef fish communities. *Global Change Biology*, *23*, 1009–1022. https://doi.org/10.1111/gcb.13482

Russell, B. C. (1977). Population and standing crop estimates for rocky reef fishes of North-Eastern New Zealand, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *11*, 23–36. https://doi.org/10.1080/00288330.1977.9515659

Sampaio, C. L. S., Miranda, R. J., Maia-Nogueira, R., & Nunes, J. C. C. A. (2012). New occurrences of the nonindigenous orange cup corals *Tubastraea coccinea* and *T. tagusensis* (Scleractinia: Dendrophylliidae) in Southwestern Atlantic. *Check List*, *8*, 528–530.

Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Friedlander, A. M., … Sala, E. (2008). Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE*, *3*(2), e1548. https://doi.org/10.1371/journal.pone.0001548

Souza, J. N., Nunes, F. L. D., Zilberberg, C., Sanchez, J. A., Migotto, A. E., Hoeksema, B. W., … Lindner, A. (2017). Contrasting patterns of connectivity among endemic and widespread fire coral species (*Millepora* spp.) in the tropical Southwestern Atlantic. *Coral Reefs*, *36*, 701–716. https://doi.org/10.1007/s00338-017-1562-0

Steneck, R. S. (1997). Crustose corallines, other algal functional groups and sediments: complex interactions along reef productivity gradients. *Proceedings of the 8th International Coral Reef Symposium*, *1*, 695–700.

Steneck, R. S., & Dethier, M. N. (1994). A functional group approach to the structure of algal dominated communities. *Oikos*, *69*, 476–498. https://doi.org/10.2307/3545860

Stevenson, C., Katz, L., Micheli, F., Block, B., Heiman, K. W., Perle, C., … Witting, J. (2007). High apex predator biomass on remote Pacific islands. *Coral Reefs*, *26*, 47–51. https://doi.org/10.1007/s00338-006-0158-x

Truong, L., Suthers, I. M., Cruz, D. O., & Smith, J. A. (2017). Plankton supports the majority of fish biomass on temperate rocky reefs. *Marine Biology*, *73*, 1–12. https://doi.org/10.1007/s00227-017-3101-5

Tuya, F. A., Bosch, N. E. A., Abreu, A. D. B., & Haroun, R. A. (2017). Reef fish at a remote tropical island (Principe Island, Gulf of Guinea): Disentangling taxonomic, functional and phylogenetic diversity patterns with depth. *Marine and Freshwater Research*, *69*, 395–402. https://doi.org/10.1071/MF17233

Wainwright, P. C., Bellwood, D. R., & Westneat, M. W. (2002). Ecomorphology of locomotion in labrid fishes. *Environmental Biology of Fishes*, *65*, 47–62.

Ward-Paige, C. A., Mora, C., Lotze, H. K., Pattengill-Semmens, C., McClenachan, L., Arias-Castro, E., & Myers, R. A. (2010). Large-scale absence of sharks on reefs in the greater-Caribbean: A footprint of human pressures. *PLoS ONE*, *5*(8), e11968. https://doi.org/10.1371/journal.pone.0011968

Williams, I. D., Baum, J. K., Heenan, A., Hanson, K. M., Nadon, M. O., & Brainard, R. E. (2015). Human, oceanographic and habitat drivers of central and Western Pacific coral reef fish assemblages. *PLoS ONE*, *10*(4), e0120516. https://doi.org/10.1371/journal.pone.0120516

Williams, G. J., Smith, J. E., Conklin, E. J., Gove, J. M., Sala, E., & Sandin, S. A. (2013). Benthic communities at two remote Pacific coral reefs: Effects of reef habitat, depth, and wave energy gradients on spatial patterns. *PeerJ*, *1*, e81. https://doi.org/10.7717/peerj.81

Wilson, S. K., Graham, N. A. J., & Polunin, N. V. C. (2007). Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*, *151*, 1069–1076. https://doi.org/10.1007/s00227-006-0538-3

Wirtz, P. (2003). New records of marine invertebrates from São Tomé island (Gulf of Guinea). *Journal of the Marine Biological Association of the United Kingdom*, *83*, 735–736.

Wirtz, P., Brito, A., Falcón, J. M., Freitas, R., Fricke, R., Monteiro, V., … Tariche, O. (2013). The coastal fishes of the Cape Verde Islands – new records and an annotated check-list. *Spixiana*, *36*, 113–142.

Wirtz, O., & D'Udekem D'Acoz, C. (2008). Crustaceans associated with Cnidaria, Bivalvia, Echinoidea and pisces at São Tomé and Príncipe islands. *Arquipélago: Life and Marine Sciences*, *25*, 63–69.

Wirtz, P., Ferreira, C. E. L., Floeter, S. R., Fricke, R., Gasparini, J. L., Iwamoto, T., … Sampaio, C. L. S. (2007). Coastal fishes of São Tomé and Principe islands, Gulf of Guinea (Eastern Atlantic Ocean)—An update. *Zootaxa*, *1523*, 1–48.

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., … Svenning, J. C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, *88*, 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R. Statistics for biology and health*. Dordrecht, the Netherlands: Springer.

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