Spatial patterns of fish standing biomass across Brazilian reefs

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A large fish-count dataset from the Brazilian province was used to describe spatial patterns in standing biomass and test if total biomass, taxonomic and functional trophic structure vary across nested spatial scales. Taxonomic and functional structure varied more among localities and sites than among regions. Total biomass was generally higher at oceanic islands and remote or protected localities along the coast. Lower level carnivores comprised a large part of the biomass at almost all localities (mean of 44%), zooplanktivores never attained more than 14% and omnivores were more representative of subtropical reefs and oceanic islands (up to 66% of total biomass). Small and large herbivores and detritivores varied greatly in their contribution to total biomass, with no clear geographical patterns. Macrocarnivores comprised less than 12% of the biomass anywhere, except for two remote localities. Top predators, such as sharks and very large groupers, were rare and restricted to a few reefs, suggesting that their ecological function might have already been lost in many Brazilian reefs.

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Key words: Brazilian province; islands; reef fishes; spatial scale; spatial variation; tropical and subtropical.

INTRODUCTION

Reefs are distributed along the western Atlantic coast of South America from *c.* 4° N to 28° S (Floeter *et al.,* 2001), constrained in the north by the Amazon River plume (but see Moura *et al.*, 2016) and in the south by an extensive coastal sedimentary basin. This coast and the four oceanic island groups that occur close by, which have been collectively referred to as the south-western Atlantic (Floeter & Gasparini, 2000; Floeter *et al.*, 2008), have a relatively high ratio of endemic reef species [*c.* 25% for fishes, (Floeter *et al.*, 2008); *c.* 33% for corals (Castro & Pires, 2001)]. Based on this, it has been recognized as a separate biogeographic unit from the Caribbean, the Brazilian province (Briggs, 1974; Floeter & Gasparini, 2000; Floeter *et al.*, 2008). A wide array of environmental and oceanographic conditions shape species distribution within this region, including the contrast of warm oligotrophic surface currents (Stramma &

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England, 1999) and upwelling of cold nutrient-rich deep waters (Campos *et al.*, 2000; Valentin, 2001), substantial river runoff (Leão & Dominguez, 2000; Piola, 2005) and large variability in the width of the continental shelf (Ponte & Asmus, 1978). Reefs are either rocky or biogenic, including the only true coral reef system in the South Atlantic Ocean (Leão *et al.*, 2003).

Knowledge of Brazilian reef fauna is much more recent and incipient than in other regions. Only in the last two decades, have studies on reef-fish taxonomy (Moura, 1994; Sazima & Gasparini, 1998; Sazima *et al.*, 2008; Luiz *et al.*, 2009; Rocha *et al.*, 2010), biogeography (Floeter & Gasparini, 2000; Floeter *et al.*, 2001) and ecology (Ferreira *et al.*, 2001, 2004; Floeter *et al.*, 2004; Krajewski & Floeter, 2011; Pinheiro *et al.*, 2011; Gibran & Moura, 2012) started to unveil the peculiarity of the Brazilian reef-fish fauna. In fact, many species that were supposedly shared with the Caribbean are endemic to the Brazilian province (Moura *et al.*, 2001; Gasparini *et al.*, 2003), with others still being described (Carvalho Filho & Ferreira, 2013; Pinheiro *et al.*, 2013).

Brazil has the fifth largest human population in the world (*c.* 206 million people; IBGE, 2016), with a large proportion concentrated along the coast (IBGE, 2011). This involves considerable variation in human population density: from the remote islands occupied by only a few researchers, to very large cities with 1–12 million people. Nation-wide growing demand for fisheries resources in the past decades (Freire *et al.*, 2015) has been exerting strong pressure on fish populations. Not surprisingly, declining trends in some targeted Brazilian reef-fish species have been described in recent years (Frédou *et al.*, 2009*b*; Bender *et al.*, 2014; Giglio *et al.*, 2015).

A comprehensive understanding of how reef-fish biomass is spatially distributed in this region is still lacking. At community and ecosystem scales, standing biomass is a fundamental ecological variable because individual body size determines energy flux and material cycles (Brown *et al.*, 2004). Therefore, withdrawal of fish biomass above certain levels (*i.e.* maximum sustainable yields) may disrupt some of the key ecosystem processes (*e.g.* herbivory, predation, calcium carbonate recycling; Madin *et al.*, 2010; Bellwood *et al.*, 2012) and result, for example, in trophic cascades (Dulvy *et al.*, 2004; Heithaus *et al.*, 2008; Estes *et al.*, 2011; McClanahan & Muthiga, 2016).

The first comprehensive fish underwater visual survey dataset collected along the whole Brazilian province was used here to examine whether: total fish biomass varies among regions; taxonomic and functional structure, *i.e.* biomass per family and per functional group, vary across nested spatial scales; functional groups and the most representative fish families vary spatially in terms of standing biomass. Fishing removes large individuals from fish assemblages, reducing mean body size (Jennings & Blanchard, 2004; Graham *et al.*, 2005) and potentially standing biomass. Thus, it was hypothesized that remote and protected places have more biomass, especially of functional groups that are more targeted by fisheries, such as large predators (see Williams *et al.*, 2011).

MATERIALS AND METHODS

BIOLOGICAL DATABASE, STUDY AREA AND SAMPLING

Fish assemblages along the Brazilian biogeographic province (*sensu* Floeter *et al.*, 2008) were counted in 4570 transects distributed over 137 sites in 20 localities (Table S1, Supporting information). Sampling ranged from the Brazilian northernmost continental shelf reefs of Parcel de
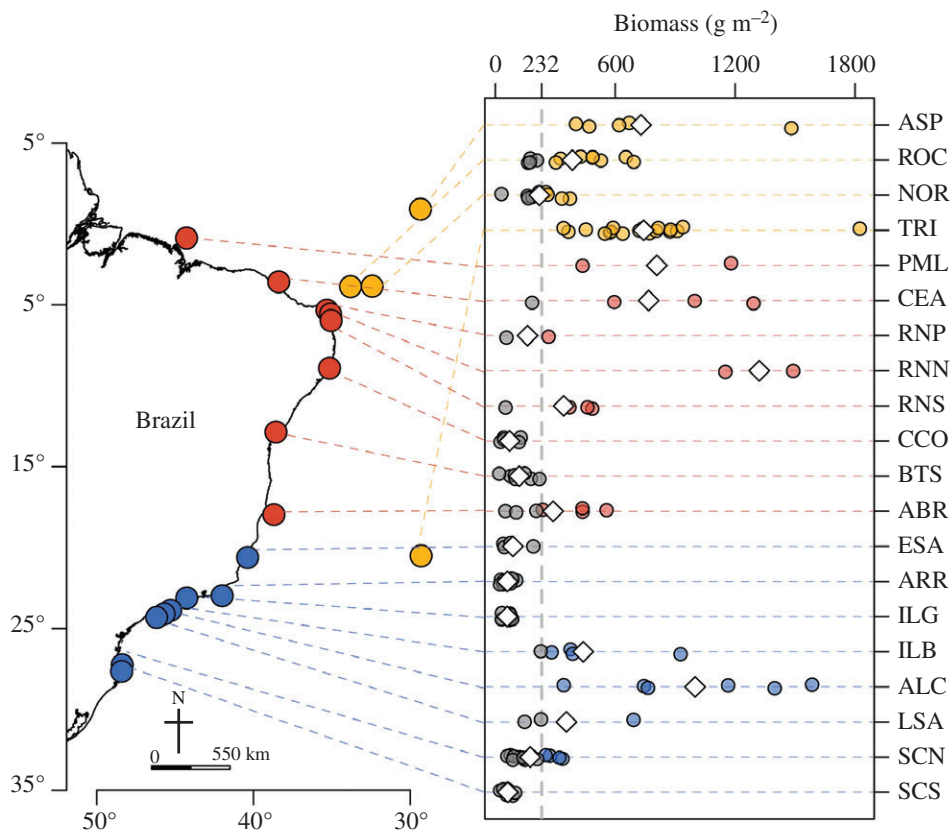
Fig. 1. Twenty localities sampled on Brazilian reefs and estimates of total fish biomass at each. ◇, Mean biomass at each locality; ┆, median biomass for all coastal localities; ◐, sites where fish biomass is lower than coastal mean; ⬤, oceanic island ⬤, tropical reef and ⬤, subtropical reef biomass is greater than coastal mean. ASP, São Pedro e São Paulo; ROC, Atol das Rocas; NOR, Fernando de Noronha; TRI, Ilha da Trindade, PML, Parcel de Manuel Luís; CEA, Ceará – Risca do Meio;, RNP, Rio Grande do Norte – Parrachos; RNN, Rio Grande do Norte – Norte de Natal; RNS, Rio Grande do Norte – Sul de Natal; CCO, Costa dos Corais; BTS, Baía de Todos os Santos; ABR, Arquipélago dos Abrolhos; ESA, Espírito Santo – Guarapari; ARR, Arraial do Cabo; ILG, Ilha Grande; ILB, Ilhabela; ALC, Alcatrazes; LSA, Laje de Santos; SCN, Ilhas de Santa Catarina – Norte; SCS, Ilhas de Santa Catarina – Sul.

Manuel Luís at 0° 52′ S; 44° 15′ W (Castro & Pires, 2001) to the southernmost coastal rocky reefs of Santa Catarina's coastal islands at 27° 50′ S; 48° 26′ W (Anderson *et al.*, 2015; Fig. 1). This also included the four oceanic island groups (Saint Paul's Rocks, 0° 54′ N; 29° 20′ W; Rocas Atoll, 3° 52′ S; 33° 48′ W; Fernando de Noronha Archipelago, 3° 51′ S; 32° 25′ W; and Trindade and Martin Vaz Island group, 20° 29′ S; 29° 19′ W). All samples were obtained in the austral summer from 2007 to 2011. Details of the sampled localities and sites, including number of transects per site are given in Table S1 (Supporting information). Survey localities were selected to give representative cover of the broad environmental features of this region and sites within localities were chosen to cover a representative sample of available reef habitats in each locality. Despite that, logistic constraints probably affected how broad this representativeness was distributed across localities, especially in the northernmost coastal sites. Based on differences in oceanographic features such as mean water temperature, reef type (continental or volcanic rocky, biogenic), distance from the mainland and on previous assessment of reef-fish

assemblage structure along the study area (Floeter *et al.*, 2001; Ferreira *et al.*, 2004), the Brazilian province was divided into three geographic regions: oceanic islands (with four localities) and tropical and subtropical reefs (with eight localities each). Sites or localities with a travel time of ≥3 h by motor boat from the nearest human settlement were considered as remote or isolated.

Underwater visual surveys (UVS) were used to count fish in $20\,m \times 2\,m \times 2\,m$ (length × width × height) strip transects made while free or scuba diving. During a UVS the diver unwound a tape while identifying, counting and estimating the total length (L_T, cm) of non-cryptic fishes >10 cm. Then, while retracting the tape, following the same procedure for benthic-associated non-cryptic fishes <10 cm and cryptic species (Floeter *et al.*, 2007; Krajewski & Floeter, 2011). Size was estimated with a precision of 1 cm for fishes <10 cm L_T, 5 cm for fishes between 10 and 60 cm and 10 cm for fishes >60 cm. Solitary individuals, pairs or small-schools (tens of individuals) were counted; intermediate-sized schools (tens to hundreds of individuals) were estimated with a precision of 10 individuals and large schools (many hundreds) with a precision of 50 individuals. For large schools, the number of individuals in a quarter of the area the school occupied were estimated and multiplied by four. Schools that crossed the sampled area were counted integrally, even if the school was larger than the area occupied by the transect. Since maximum water visibility was usually much lower than the transect length, counts of species were not instantaneous, but rather gradual at 3–6 m ahead of the diver depending on visibility. Some of these procedures overestimate fish abundance and biomass (Ward-Paige *et al.*, 2010; Nadon *et al.*, 2012) and direct comparisons of absolute biomass values with studies with different methods and designs are not recommended. Transects followed the depth availability in each site, with 98·8% in depths shallower than 30 m (range = 1–50 m, mean = 9·3 m).

FUNCTIONAL GROUPS AND STANDING BIOMASS ESTIMATES

Fish were individually assigned to functional groups based on their main diet and individual L_T, as recorded in transects. Information on diet was obtained from previous works on the Brazilian reefs (Ferreira *et al.*, 2004). Assigned groups were: small herbivores and detritivores <30 cm L_T (SHD); large herbivores and detritivores ≥30 cm L_T (LHD); omnivores regardless of their size (OMN); zooplanktivores regardless of their size (ZPK); lower-level carnivores, including both small zoobenthivores and piscivores <50 cm L_T (LLC); macrocarnivores, including large zoobenthivores and piscivores ≥50 cm L_T (MCA). Species recorded, families and assigned functional groups are given in Table S2 (Supporting information).

Body mass (M) was estimated for each individual fish using length–mass relationships, $M = aL_T b$, L_T is total length and the parameters a and b are species-specific constants derived from references in FishBase (Froese & Pauly, 2016). In cases where species coefficients were not available, coefficients of congeneric species that were either phylogenetically or morphologically similar were used. Functional group and total standing biomass, respectively, were calculated by summing the body mass of all individuals within a given functional group and by summing the standing biomass across all functional groups.

DATA ANALYSES

The number of transects varied considerably among sites (*i.e.* from five to 242, mean ± s.d. = 33·4 ± 34·0). To avoid overrepresentation of highly sampled sites, the mean biomass values from all transects of a site were used as the independent observations. The median total fish biomass of coastal localities was used as a reference value with which to contrast individual site values.

Total biomass among regions that differed greatly in sample size (oceanic islands, $n = 1573$ transects; tropical reefs, $n = 769$; subtropical reefs, $n = 2228$) was compared using a three-step hierarchical randomization procedure. Firstly, two sites were drawn randomly from each region (the minimum number of sites for any locality) and 10 transects from each of these sites (the minimum number of transects that at least two sites in each of the localities contained). This resulted in a dataset with 80 transects from oceanic islands, 160 from tropical and 160 from subtropical reefs. Secondly, differences in total biomass of transects among regions (oceanic islands, tropical and subtropical reefs) were modelled using a gamma-distributed generalized

linear mixed model (GLMM) with log as the link function. The gamma-distribution was chosen because it adequately represents biomass data: continuous values with a large frequency of small and small frequency of large values. Random intercepts for each locality and site (nested random effects; Bunnefeld & Phillimore, 2012) were added. This GLMM was employed because of the study's hierarchical sampling design and aimed at assessing and quantifying which spatial scale introduced more variability to biomass (site, locality or residual) and predicting average values of biomass per region, while accounting for these sources of variance. Thirdly, the randomization and the GLMM were repeated 999 times, generating distributions of variances and of predicted biomass values per region. These distributions were visually assessed for differences between categories.

To explore patterns in site segregation according to functional group and taxonomic (family level) biomass structure, non-metric multidimensional scaling (nMDS) over Bray–Curtis dissimilarity matrices were calculated from square-root transformed data. To investigate how much of the variance in functional and family-level biomass structure could be explained by geographic region or locality, permutational multivariate analyses of variance (PERMANOVA) were performed using the adonis function of the R package vegan (www.r-project.org; Oksanen *et al.*, 2017) on the square-root transformed data. Pearson's *r* was used to assess the correlation between each functional group and family to total biomass. Parrotfishes (Scaridae) were treated separately from Labridae (considered as Labridae, Scarini; Westneat & Alfaro, 2005) in all taxonomic analyses due to their very distinctive ecosystem functions (Bellwood & Choat, 1990).

Finally, the possible influence of covariates on both functional and taxonomic patterns of assemblage structure was assessed. To do that, the correlation of the MDS axes with covariates was tested for by using the function envfit of vegan and its permutation test of significance. The covariates used were all measured at the site scale and included environmental (sea-surface temperature and pelagic net primary productivity), habitat (mean depth and depth range), anthropogenic effect (human population density) and biodiversity (mean species richness per transect) variables. Sea-surface temperature was obtained from the Bio-ORACLE online database (Tyberghein *et al.*, 2012). Pelagic primary productivity was modelled from chlorophyll-*a* concentration, photosynthetic active radiation and sea-surface temperature, all obtained from Bio-ORACLE, by using the model in Behrenfeld & Falkowski (1997). Bio-ORACLE data are provided with a resolution of *c*. 9·2 km and are based on mean monthly climatological composites from 1997 to 2009 (photosynthetic active radiation) or from 2002 to 2009 (sea-surface temperature and chlorophyll-*a* concentration). Depth and mean species richness were obtained for each transect and averaged for the site-scale. Depth range was the range in depth encompassed by all transects on a given site. Since the sampling design at each site was intended to maximize depth variation, depth range here is a proxy for topographic slope. Human population density was obtained from the Instituto Brasileiro de Geografia e Estatística (IBGE) and was calculated as the average population density in a circular area of radius 20 km around each sampled site. All Bio-ORACLE variables and human population density were extracted from raster files and handled with the package raster in R (Hijmans *et al.*, 2016).

RESULTS

Total standing reef-fish biomass for all sites ranged from 15 to 1823 g m^{-2}. Median total biomass of all coastal localities was 232 g m^{-2}, while mean biomass of island localities was 557 g m^{-2}. Sites with biomass greater than the overall coastal median occurred in all three geographic regions (Fig. 1). They were, however, more common in oceanic islands (79% of sites at this region) than in tropical (45%) or subtropical coastal reefs (25%).

Observed and predicted fish biomass values for each region are depicted in Fig. 2. Estimated biomass was always higher for oceanic islands (mean ± s.d. = 447 ± 64 g m^{-2}) than for tropical (mean ± s.d. = 245 ± 39 g m^{-2}) and subtropical reefs (mean ± s.d. = 135 ± 20 g m^{-2}; Fig. 2). Random-effect variance was larger for
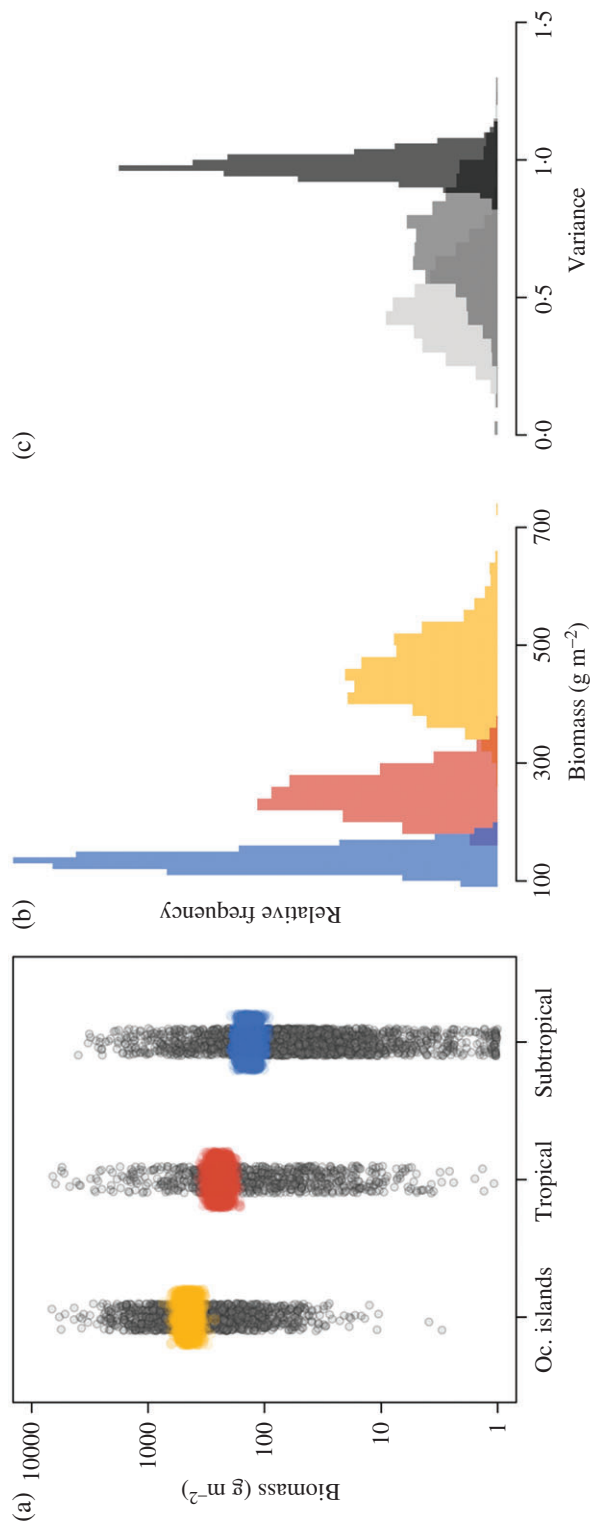
FIG. 2. (a) Gamma-distributed generalized linear mixed-model predictions of biomass and (b) their distributions for oceanic island (□), tropical (■) and subtropical (■) reefs. (c) The distributions of random factors variance for site (□), locality (■) and region (■) scales.
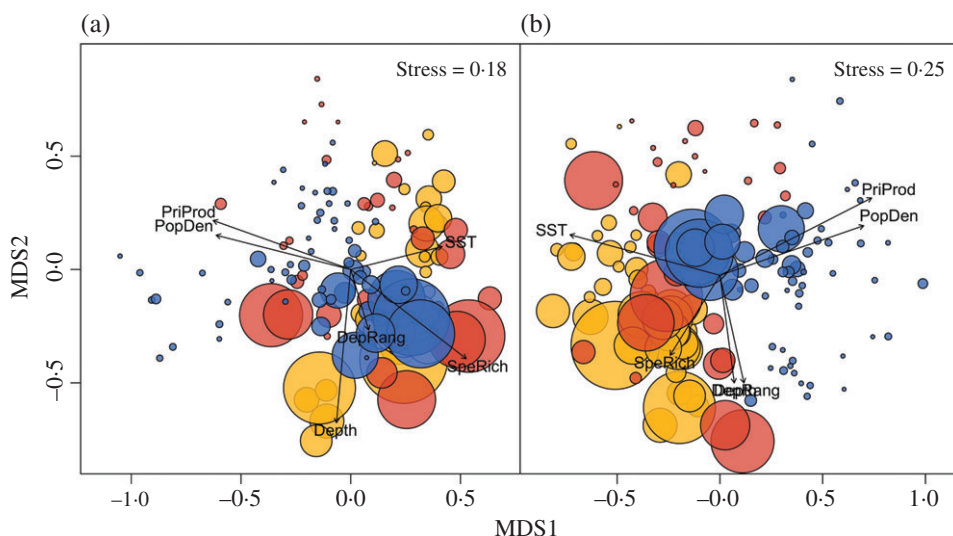
FIG. 3. Non-metric multidimensional scaling of (a) functional and (b) taxonomic (family-level) structure of standing biomass of fishes from Brazilian oceanic (○), tropical (●) and subtropical (●) reefs. Each circle is a sampled site and its size is proportional to its total standing biomass. Vectors depict the correlations of covariates with the MDS axes: PriProd, pelagic net primary productivity; PopDen, human population density; SST, mean sea surface temperature; SpeRich, average species richness per transect; DepRang, depth range.

residuals (mean variance $= 0.96$) and localities (mean variance $= 0.71$) than for sites (mean variance $= 0.49$; Fig. 2).

Biomass size-structure was dominated by fishes of $10-30$ cm in 17 out of 20 localities (Figs S1 and S2, Supporting information). Larger-sized fishes did not comprise more than 50% of the biomass except at four localities, all of which also had most of their sites attaining high biomass (Fig. 1, Figs S1 and S2, Supporting information).

High biomass and low biomass sites tended to occupy opposite areas of both functional and taxonomic nMDS biplots (Fig. 3 and Fig. S3, Supporting information), with secondary concentrations according to geographic region. Both functional and taxonomic structure varied more among localities (PERMANOVA $R^2 = 0.45$ and 0.41, respectively) and sites (PERMANOVA residual $R^2 = 0.39$ and 0.40, respectively) than at geographic regions (PERMANOVA $R^2 = 0.16$ and 0.19, respectively; Table I). Sea-surface temperature, depth, species richness and topography were positively related to high biomass sites, whereas primary productivity and human population density were negatively related to high biomass sites in both functional and taxonomic MDS biplots (Fig. 3 and Fig. S3, Supporting information). All covariates were significantly correlated to the nMDS axes, although the fit varied (Table II). In the functional structure nMDS; fit was smallest for depth range ($R^2 = 0.06$) and sea-surface temperature ($R^2 = 0.14$), whereas species richness, depth, primary productivity and human population density had a similar fit ($R^2 = 0.31-0.36$). In the taxonomic structure nMDS; fit was smallest for species richness ($R^2 = 0.19$), depth ($R^2 = 0.24$) and depth range ($R^2 = 0.25$) and highest for human population density, sea-surface temperature and primary productivity ($R^2 = 0.53-0.66$).

TABLE I. Permutational multivariate analyses of variance (PERMANOVA) of fish assemblages functional and taxonomic (family-level) structure on Brazilian reefs, with region and locality as explanatory variables

	d.f.	Sums of sqs	Mean sq.	F-model	R^2	P
Functional						
Region	2	4·72	2·36	24·69	0·163	<0·001
Locality	17	13·08	0·77	8·05	0·451	<0·001
Residuals	117	11·19			0·386	
Total	136	29·00	0·10		1·000	
Taxonomic						
Region	2	8·06	4·03	28·42	0·193	<0·001
Locality	17	17·14	1·01	7·11	0·410	<0·001
Residuals	117	16·59	0·14		0·397	
Total	136	41·78			1·000	

Examining both absolute and proportional functional structure at the locality scale clarifies why this spatial scale encompassed larger variation in structure than the region scale (Fig. 4). Especially at the oceanic islands and tropical reefs, biomass proportions of functional groups varied considerably. Lower-level carnivores (LLC) were the only group that comprised an important fraction of the standing biomass in almost all localities, with mean relative contribution of 44%. Zooplanktivores (ZPK) and macro-carnivores (MCA) however, comprised only a small part of standing biomass at almost all localities. ZPK were representative only at the oceanic island of ASP and at the mid to outer shelf tropical reefs of CEA and RNN, never attaining more than 14% of total biomass (Fig. 4). MCA were rare in coastal localities and, except for two localities (PML and ROC, where this group comprised 38 and 18% of fish biomass, respectively), never represented more than 12% of total biomass. Omnivores (OMN) were almost absent from tropical reefs such as PML, CEA and RNN (comprising less than 3% of fish biomass; Fig. 4), having greater, though still variable, importance in subtropical localities and oceanic islands (up to 66%). Large herbivores and detritivores (LHD) and small herbivores and detritivores (SHD) varied greatly in their contribution

TABLE II. Environmental and anthropogenic covariates fitted as vectors in an nMDS of fish assemblages functional and taxonomic (family-level) structure on Brazilian reefs. Goodness of fit and significance of the vectors are depicted here

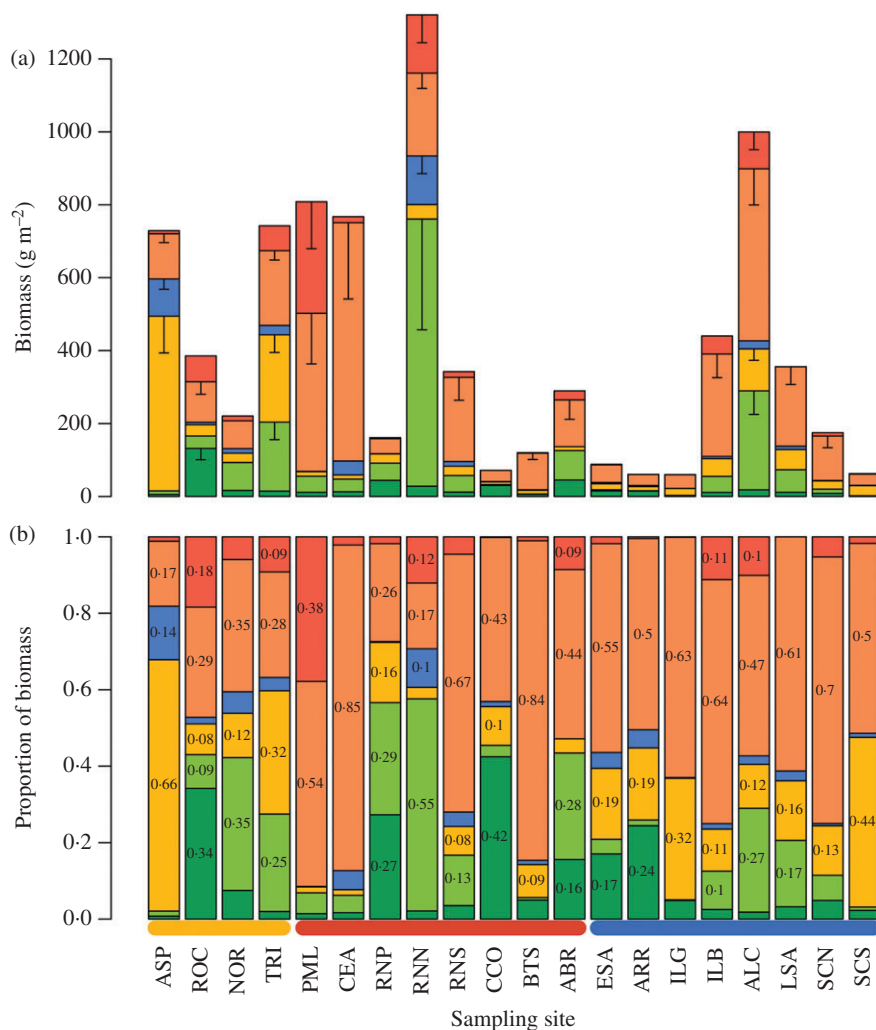| Covariate	Functional		Taxonomic	
	R^2	P	R^2	P
Mean species richness per transect	0·336	<0·001	0·186	<0·001
Depth	0·359	<0·001	0·238	<0·001
Pelagic net primary productivity	0·342	<0·001	0·656	<0·001
Mean sea-surface temperature	0·143	<0·001	0·557	<0·001
Human population density	0·310	<0·001	0·531	<0·001
Depth range	0·061	<0·05	0·246	<0·001

FIG. 4. (a) Absolute (mean − S.E. from the sites at each locality. Since some localities had only two sites, this more accurately shows variability in biomass than standard errors calculated simply from the mean biomass across sites) total standing biomass at each sampled locality on Brazilian reefs: (bars) ■, small herbivores and detritivores; ■, large herbivores and detritivores; ■, zooplanktivores; ■, omnivores; ■, lower-level carnivores; ■, macrocarnivores; (x-axis) ▬, oceanic islands; ▬, tropical; ▬, subtropical reefs.. (b) Proportional contribution of functional groups to total standing biomass at each sampled locality on Brazilian reefs, where the numbers indicate proportions of each functional group at each locality. Only values >0·07 are shown. ■, Oceanic islands; ■, tropical; ■, subtropical reefs. Sampling site abbreviations are as in Fig. 1.

depending on locality (from <1% to 55 and 42% respectively), with no clear geographical patterns.

Most of the variation in functional structure at the site scale was due to variation in the biomass of large herbivores and lower-level carnivores, since these were positively correlated to total biomass (Pearson's $r = 0·74$ for both; Table S3, Supporting information) but weakly correlated to each other (Pearson's $r = 0·31$). Macrocarnivores and

Omnivores were also correlated to total biomass (Pearson's $r = 0.65$ and 0.62, respectively). Small herbivores had their highest biomass in shallow water sites from an oceanic island and a coastal archipelago (ROC and ABR; Figs 3 and 5); large herbivores at specific sites from all three regions (TRI, ALC and RNN); omnivores at oceanic sites mainly from TRI and ASP; zooplanktivores at oceanic islands or coastal sites adjacent to oceanic waters such as TRI, RNN and CEA; lower-level carnivores at a variety of both coastal and oceanic sites; and macrocarnivores at isolated or protected sites from ROC, PML, ALC and RNN. All of these groups however, had a low or moderate correlation (Pearson's $r < 0.50$).

Contrary to the functional structure, taxonomic structure at the site scale could not be explained by a few groups (Table S4, Supporting information). The biomass of Labridae and Kyphosidae correlated with the total biomass with Pearson's r of respectively 0.72 and 0.65, followed by Epinephelidae, Holocentridae, Carangidae, Balistidae, Pomacanthidae and Labridae – Scarini, all with a Pearson's r of between 0.58 and 0.50. Except for Labridae (excluding Scarini) and Pomacanthidae, no high correlations were observed among families (Table S4, Supporting information). Spatial variations in the biomass of the 12 families with the highest values across the study are depicted in Figs 6 and 7; Fig. S3 (Supporting information) depicts the next six families.

Some families were distributed in a consistent geographical pattern relative to their average biomass: Balistidae at sites from the oceanic islands of TRI and ASP (Fig. 6); Haemulidae, Lutjanidae, Pomacanthidae and Sparidae mostly at coastal sites (Figs 6 and 7). From these, Lutjanidae presented high biomass only on tropical reefs, Sparidae only on subtropical reefs and Haemulidae and Pomacanthidae at sites from both regions. Labridae also had highest biomass at specific coastal sites of tropical and subtropical localities (RNN and ALC, respectively). The other families depicted in Figs 6 and 7 had their largest biomass in both oceanic and coastal sites of particular localities: Kyphosidae at sites from TRI and RNN; Epinephelidae at sites from TRI and ALC; Acanthuridae at sites from ROC and ALC; Holocentridae at sites from ROC, TRI, ALC and CEA; Labridae – Scarini at sites from NOR, ABR and ALC; and Carangidae at ASP, ILB, ALC and RNN. Pomacentridae, apart from some high biomass sites at ROC and especially ASP, had a similar biomass almost everywhere.

DISCUSSION

A 120 fold variation in reef-fish biomass was observed across Brazilian reefs, similar to other large spatial scale studies (Newman *et al.*, 2006; Sala *et al.*, 2012; McClanahan *et al.*, 2014; McClanahan, 2015; Williams *et al.*, 2015). This large spatial variability in fish biomass was distributed along almost 30° of latitude and 20° of longitude. This includes tropical and subtropical reefs subject to a wide range of oceanographic features and anthropogenic effects over time (Leão & Dominguez, 2000; Castro & Pires, 2001; Floeter *et al.*, 2001; Leão *et al.*, 2003). For instance, most of the sites with high reef-fish biomass were located in remote places (oceanic islands, Parcel do Manuel Luís) or no-entry marine protected areas (Alcatrazes, Atol das Rocas).

At the regional scale, oceanic islands had larger average fish biomass than coastal reefs. This was not unexpected since high total and apex predatory fish biomasses have repeatedly been observed in remote reefs subject to no or to very restricted human exploitation elsewhere (Sandin *et al.*, 2008; Friedlander *et al.*, 2010, 2012; Williams
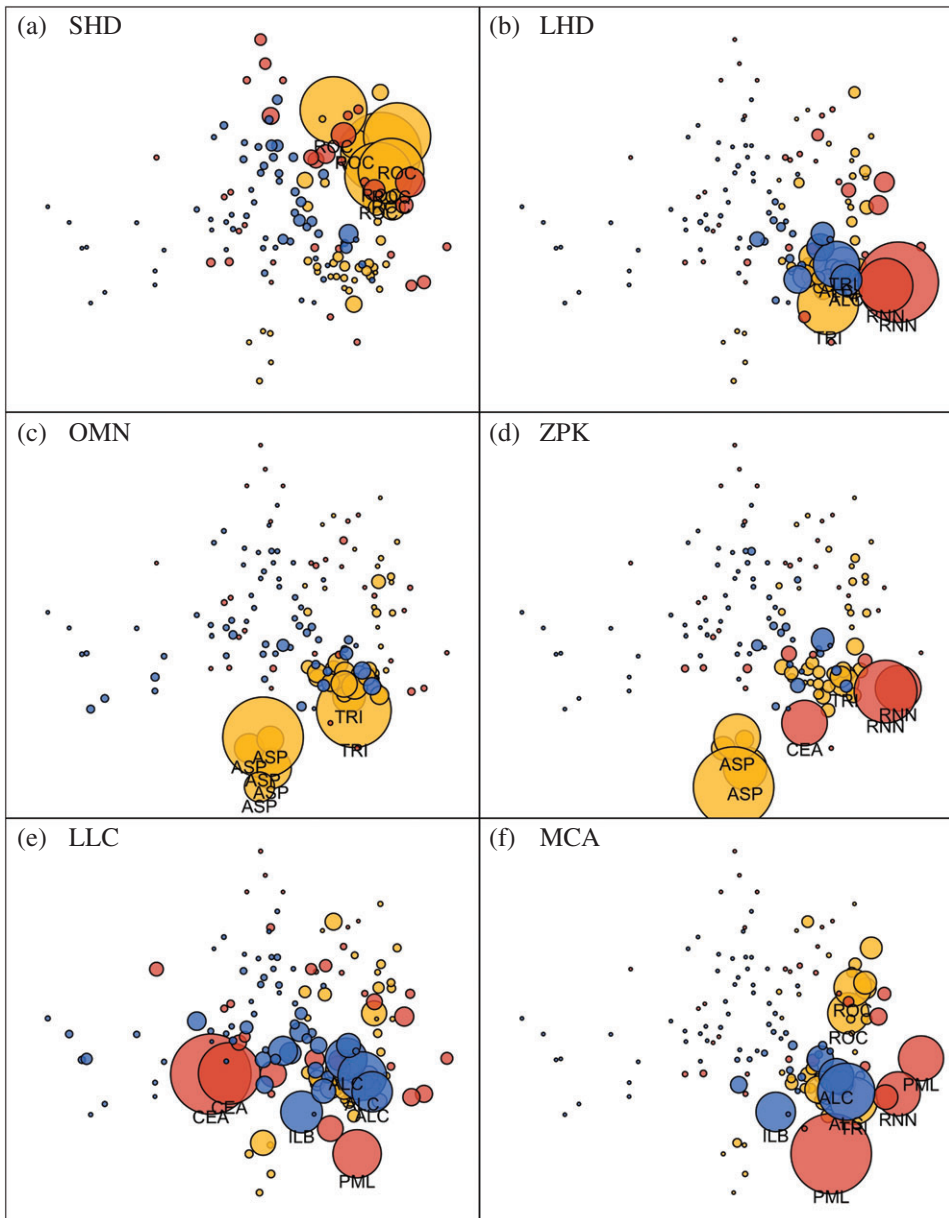
FIG. 5. Non-metric multidimensional scaling of functional structure of standing biomass of fishes from Brazilian oceanic island (■), tropical (■) and subtropical (■) reefs as per Fig. 3, but with circle sizes proportional to the biomass of the respective functional group at each site. (a) small herbivores and detritivores; (b) large herbivores and detritivores; (c) omnivores; (d) zooplanktivores; (e) lower-level carnivores; (f) macrocarnivores. Sampling site abbreviations are as in Fig. 1.
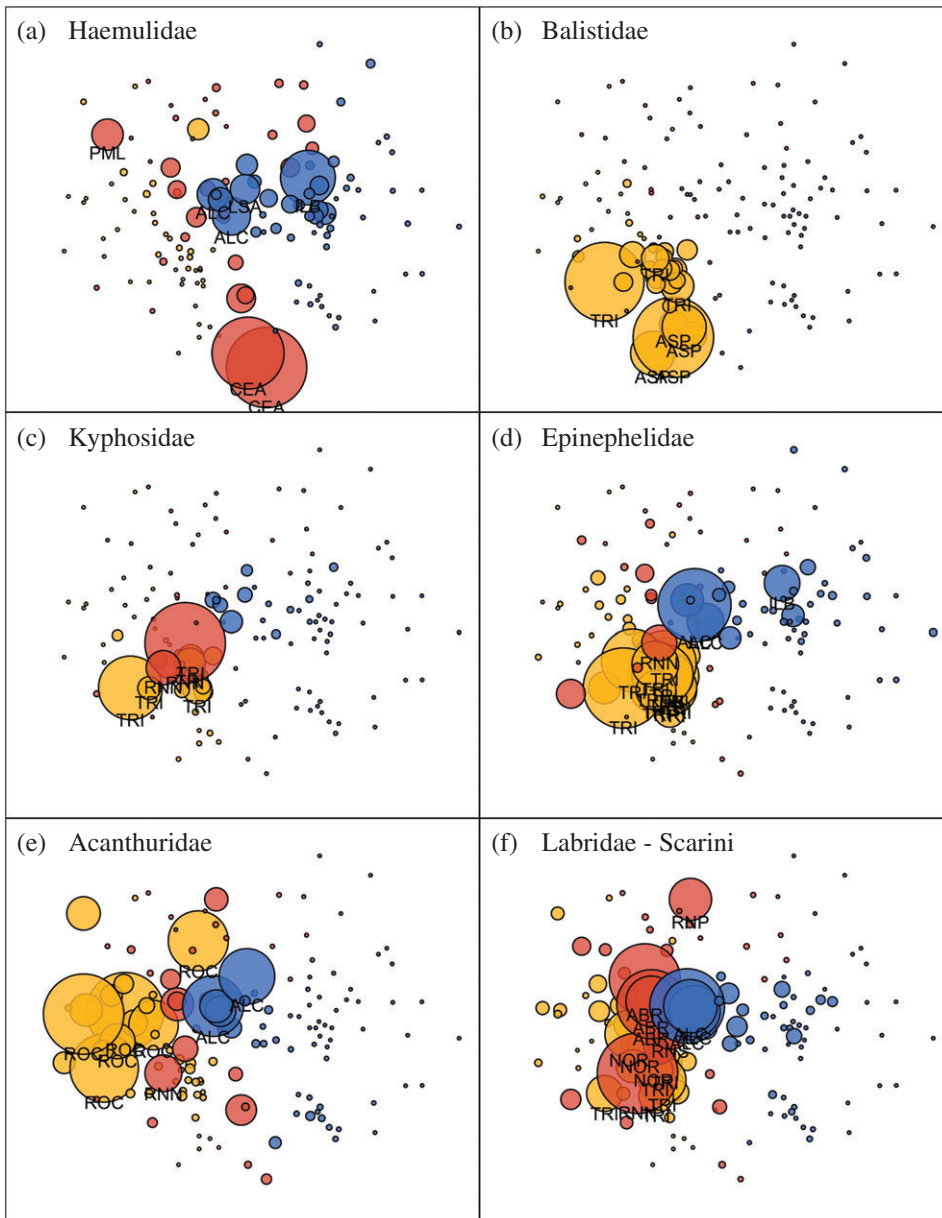
FIG. 6. Non-metric multidimensional scaling of taxonomic (family-level) structure of standing biomass of fishes from Brazilian oceanic island (□), tropical (□) and subtropical (□) reefs as per Fig. 3, but showing the six families with highest fish biomasses across the whole study: (a) Haemulidae, (b) Balistidae, (c) Kyphosidae, (d) Epinephelinae, (e) Acanthuridae and (f) Labridae –Scarinae. Circle size is proportional to the biomass of the respective family at each site. Sampling site abbreviations are as in Fig. 1.
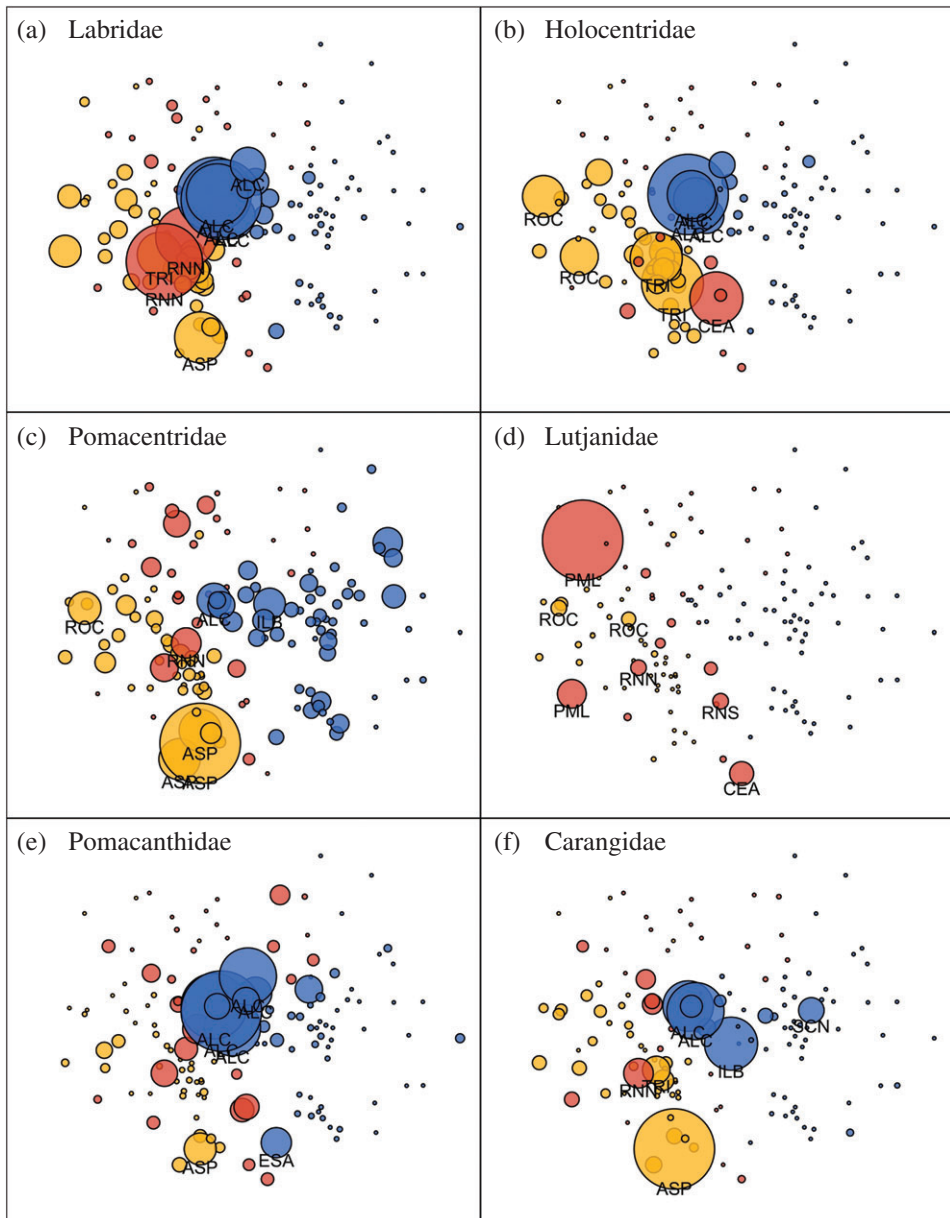
FIG. 7. Non-metric multidimensional scaling of taxonomic (family-level) structure of standing biomass of fishes from Brazilian oceanic island (▢), tropical (▢) and subtropical (▢) reefs as per Fig. 3, but showing the families with the 7th to 12th highest fish biomasses across the whole study: (a) Labridae (b) Holocentridae, (c) Pomacentridae, (d) Lutjanidae, (e) Pomacanthidae and (f) Carangidae. Circle size is proportional to the biomass of the respective family at each site. Sampling site abbreviations are as in Fig. 1.

et al., 2011; Graham & McClanahan, 2013). Moreover, isolated islands enhance phytoplankton biomass and provide larger availability in primary production to consumers, the island mass effect (Gove *et al.*, 2016). It is possible that differences in water visibility might have biased counts favouring higher detection (Bozec *et al.*, 2011) and therefore larger fish biomass in oceanic islands with clear waters. Some coastal sites with poor or modest water visibility (between 4 and 8 m of horizontal transparency, such as Parcel do Manuel Luís and Alcatrazes) however, contained high fish biomass, while some sites with high water transparency (>15 m, particularly in Fernado de Noronha and Atol das Rocas; Fig. 1) had low biomass values. This suggests that the possible bias in detection rates has a smaller influence on fish biomass estimates compared with other environmental or human-related variables. At least one locality with high biomass sites (>1000 g m^{-2}, RNN) stood out for being neither isolated (*c.* 16 km from the coast, close to Natal city, with >1 million people) nor protected. Cinner *et al.* (2016) have drawn attention to 'bright spots'; places that have substantially more biomass than would be predicted from environmental features and human use. The reasons for these deviations are still unclear, but at least for this locality in the present study, the considerable proportion of planktivores (in comparison with other localities in Brazil; Fig. 4) and narrowness of the continental shelf suggest that planktonic energetic inputs could be important.

Both functional and taxonomic biomass structure varied more among localities and sites than among regions in the Brazilian province. The geographic grouping of reefs in oceanic islands, tropical and subtropical reefs has been observed by other large-scale studies using species composition and relative abundance of trophic groups (Floeter *et al.*, 2001, 2008; Ferreira *et al.*, 2004). Biomass is however, an ecological currency that represents energy accumulated over a specific time span (Odum, 1959) and probably reflects other more proximate variables. For example, pelagic primary production and human population were the main drivers of patterns in the biomass of reef-fish trophic groups across different islands in the central Pacific (Williams *et al.*, 2015). Likewise, in the global-scope study by Barneche *et al.* (2014), pelagic primary production was strongly related to planktivorous fish biomass irrespective of the biogeographic realm. In the present study, the main covariates related to both functional and taxonomic biomass structure were also primary productivity and human population density (Table II). Contrary to the studies cited above, these variables were negatively correlated with total biomass (Fig. 4), the biomass of most functional groups (Fig. 5) and most families (except, perhaps, for Haemulidae; Figs 6 and 7). It is possible that human activities are so important in structuring the biomass of fish assemblages that they override the effects of most other variables (Bellwood *et al.*, 2012). Depth was strongly correlated with functional, but not with taxonomic biomass structure; while temperature strongly correlated with taxonomic, but not with functional biomass structure (Table II). This pattern conforms to the expected: depth is a strong driver of the trophic interactions of reef fishes (Hobson, 1991; Friedlander & Parrish, 1998), whereas temperature place heavy constraints to species distributions (Harmelin-Vivien, 2002; Halpern & Floeter, 2008). The cool waters of southern Brazil, for example, are the southern limit of distribution of many tropical reef fishes (Anderson *et al.*, 2015). More detailed inspection of the drivers of fish biomass along the Brazilian coast and islands will hopefully disentangle differences in biomass allocation across functional groups and fish families over multiple spatial scales.

The macrocarnivore category includes targeted fishes like sharks, groupers (Epinephelinae) and jacks (Carangide), which have been depleted from most fished ecosystems (Pauly *et al.*, 1998; Friedlander & DeMartini, 2002; Myers & Worm, 2003; Richards *et al.*, 2012). Sharks are probably the most sensitive to fishing (Robbins *et al.*, 2006; Graham *et al.*, 2010; Nadon *et al.*, 2012), but might be abundant in remote localities (Sandin *et al.*, 2008; Nadon *et al.*, 2012). Trindade and São Pedro e São Paulo (previously known as St. Paul's Rocks; Table S1, Supporting information) are the most remote of Brazilian islands (around 1080 and 960 km from the coast respectively) and were known for high abundance of sharks in the past (Nichols & Murphy, 1914; Lobo, 1919; Edwards & Lubbock, 1982; Luiz & Edwards, 2011). In recent decades, widespread longline fishing has decimated shark populations from these islands (Pinheiro *et al.*, 2010, 2011; Luiz & Edwards, 2011). Although these longlines target mainly pelagic fishes and sharks, they commonly also affect sharks that use reef habitats (Pinheiro *et al.*, 2010) and are probably the main reason for the recent local extinction of the Galapagos shark *Carcharhinus galapagensis* (Snodgrass & Heller 1905) population at São Pedro e São Paulo (Luiz & Edwards, 2011). In contrast, sharks are very common in the inhabited, but protected Fernando de Noronha Archipelago and in the remote, but also protected Atol das Rocas. These islands are nursery grounds for three shark species, the Caribbean reef shark *Carcharhinus perezii* (Poey 1876), the lemon shark *Negaprion brevirostris* (Poey 1868) and the nurse shark *Ginglymostoma cirratum* (Bonnaterre 1788) (Castro & Rosa, 2005; Freitas *et al.*, 2006, 2009, Garla *et al.*, 2006, 2009). Along the coast, only *G. cirratum* were observed in two tropical sites and at most surveyed sites sharks were never recorded.

Other top predators that may be abundant even in shark-depleted places (Friedlander & DeMartini, 2002; Aburto-Oropeza *et al.*, 2011; Friedlander *et al.*, 2014) were also found to dominate predatory-fish assemblages of some isolated or protected sites in the present study. Large groupers (Epinephelinae), for example, were commonly found only in Parcel fo Manuel Luís [the goliath grouper *Epinephelus itajara* (Lichtenstein 1822)] and Alcatrazes [the dusky grouper *Epinephelus marginatus* (Lowe 1834)]. This is remarkable because these iconic species were once very common in coastal Brazilian recreational and subsistence fisheries (Souza, 2000; Gerhardinger *et al.*, 2006; Bender *et al.*, 2014; Ferreira *et al.*, 2014), but are now threatened at the national level (ICM-Bio, 2014). The largest biomass of groupers was found at sites from Trindade Island, mostly due to high densities of the small body-sized and lower-level carnivore coney *Cephalopholis fulva* (L. 1758). In contrast, historical records suggest that in the past larger groupers dominated predatory fish assemblages at Trindade Island (Nichols & Murphy, 1914; Lobo, 1919). Aggregations of tens to hundreds of dog snappers *Lutjanus jocu* (Bloch & Schneider 1801) were also observed dominating predatory fish biomass at Parcel do Manuel Luís and Atol das Rocas. This species is heavily targeted by north-eastern Brazilian fisheries, with a current declining trajectory (Frédou *et al.*, 2009*b*). Its substantial abundance in these two localities, including shallow habitats (1–3 m depth) in the protected Atol das Rocas, suggests that large aggregations of this species could have been common in shallow Brazilian tropical reefs in the past.

Lower-level carnivores are the dominant components of temperate and tropical reefs, both in species richness and biomass (Jones *et al.*, 1991; Wainwright & Bellwood, 2002; Ferreira *et al.*, 2004). These fishes were the main contributors to standing biomass in the present study (Figs 4 and 5). Family-level composition of this group however, varied substantially among regions. This includes low biomass of the genus

Haemulon Cuvier 1829 at oceanic islands (typically <3% of total fish biomass at most sites); and of lutjanids in subtropical sites (<2% of total fish biomass at all sites, Figs 6 and 7). Large schools of *Haemulon* spp. (especially *Haemulon auro-lineatum* Cuvier 1830 and *Haemulon squamipinna* Rocha & Rosa 1999), typically with hundreds to thousands of individuals are one of the main components of fish assemblages in coastal Brazil (Ferreira *et al.*, 2004). Neither of these species occur at the oceanic islands (Ferreira *et al.*, 2004; Krajewski & Floeter, 2011; Longo *et al.*, 2015), although the reason for that remains uninvestigated. The low abundance of snappers (Lutjanidae) in subtropical reefs might be related to their affinity for tropical waters (Ferreira *et al.*, 2004). For instance, this group comprises most catches in north to north-eastern (Frédou *et al.*, 2009*a*), but not in south-eastern to southern Brazilian fisheries (Vasconcellos & Gasalla, 2001).

Zooplanktivorous fishes provide the energetic link between reef and pelagic production, mainly through faeces and predation over them (Hobson, 1991). These visually oriented predators depend on planktonic production, water flux and transparency (Hobson, 1991; Johansen & Jones, 2013) and are expected to increase in importance from coastal to oceanic habitats due to less suspended particles (Ferreira *et al.*, 2004; Wyatt *et al.*, 2012). In the present study, the highest biomass of zooplanktivorous fishes was at oceanic islands (ASP) and coastal sites where the shelf break is located close to shore (CEA and RNN; Fig. 5). Even at these places however, zooplanktivores never attained more than 14% of total fish biomass (Fig. 4). This low representativeness is similar to that commonly found in the Caribbean (Bellwood *et al.*, 2004; Newman *et al.*, 2006) and contrasts greatly with zooplanktivore assemblages in the Indo-Pacific (Williams & Hatcher, 1983; Bellwood *et al.*, 2004), which may attain relatively larger biomasses (Williams *et al.*, 2011).

Omnivorous fishes, capable of feeding on both animal and vegetable matter, comprised more of the biomass at oceanic islands and high-latitude coastal sites (Figs 4 and 5). Increasing relative abundance and feeding pressure of omnivores toward higher latitudes has been observed along the Brazilian coast (Ferreira *et al.*, 2004; Longo *et al.*, 2014). These omnivores change from herbivory to invertivory ontogenetically, seasonally or geographically (Ferreira *et al.*, 2004; Dubiaski-Silva & Masunari, 2006, 2008; Batista *et al.*, 2012). This behavioural and dietary plasticity may allow them to be abundant even at localities where herbivorous-detritivorous fishes (*i.e*. surgeonfishes and parrotfishes) are probably constrained by water temperature (Ferreira *et al.*, 2004; Floeter *et al.*, 2004, 2005; Cordeiro *et al.*, 2016). At oceanic islands, the black triggerfish *Melichthys niger* (Bloch 1786) dominated omnivore biomass, especially at Trindade and São Pedro e São Paulo. This circumtropical feeding generalist reaches swarming abundances of hundreds to thousands of individuals over relatively small areas in some remote islands (Lobo, 1919; Price & John, 1980; Lubbock & Edwards, 1981; Kavanagh & Olney, 2006). Although reasons for this are still unclear, the species may feed in both plankton and benthic sources, potentially being able to adjust its behaviour in response to food availability (Kavanagh & Olney, 2006).

Large detritivores or herbivores such as large parrotfishes (Labridae - Scarini) and chubs (Kyphosidae) had the highest biomass in isolated or protected sites from Trindade, Fernando de Noronha, Alcatrazes and northern Natal reefs (Fig. 5). These fishes are important drivers of ecosystem processes on Indo-Pacific and Caribbean reefs (Mumby, 2009; Bellwood *et al.*, 2012; Bonaldo *et al.*, 2014), with large body sized individuals performing a disproportionately greater role in these processes

(Bruggemann *et al.*, 1996; Bonaldo *et al.*, 2014). Although little is known of these fishes' function on Brazilian reefs (but see Francini-Filho *et al.*, 2008), they are important target species for artisanal fisheries (Floeter *et al.*, 2006; Bender *et al.*, 2014). For example, the largest of Brazilian endemic parrotfishes, the greenback parrotfish *Scarus trispinosus* Valenciennes 1840, has been heavily targeted by fisheries in the eastern and north-eastern regions (Floeter *et al.*, 2006; Padovani-Ferreira *et al.*, 2012; Bender *et al.*, 2014) and was only observed in small groups at a few sites from Maracajaú reef (RNP), Manuel Luís Reefs and, especially, Abrolhos Archipelago. Smaller parrotfishes from the genus *Sparisoma* Swainson 1839 comprised a large part of LHD biomass especially at Fernando de Noronha and Alcatrazes. Unlike parrotfishes, kyphosids are generally avoided by Brazilian fishermen and, therefore, biomass heterogeneity is basically ruled by habitat preferences (such as for more exposed places; Floeter *et al.*, 2007). Contrary to that proposed by Ferreira *et al.* (2004), no trend of latitudinal increase in *Kyphosus* spp. biomass was found. This might be a result of this genus being more influenced by smaller-scale factors (such as wave-energy gradients, Floeter *et al.* 2007) than the large-scale temperature gradient.

Small herbivores and detritivores were especially important in some sites from Atol das Rocas (Fig. 5), where small surgeonfishes *Acanthurus chirurgus* (Bloch 1787) formed schools of hundreds of individuals. These schools grazed actively (Longo *et al.*, 2015) often resembling feeding mobs (Morais *et al.*, 2016). The abundance of adequate substrata for feeding in the protected tidal pools of Rocas Atoll along with a purported safety from predators during the low tide are possible reasons to account for this unusual biomass (Longo *et al.*, 2015). Pomacentrids from the genus *Stegastes* Jenyns 1840 were the most abundant SHD and were present at almost all localities and sites, but contributed little to standing biomass given their small sizes. This abundance patterns were consistent throughout most of Brazilian province and seemed to be constrained only at the edge of distribution of the tropical fish fauna in Brazil, in southern Santa Catarina (SCS; Anderson *et al.*, 2015).

This work represents the first wide scale assessment of how the biomass of reef-fish functional groups varies in the south-western Atlantic Ocean over thousands of kilometres. Large disparities in total standing biomass can be attributed to a combination of human presence and habitat features such as depth, sea-surface temperature and topography (Fig. 3). Taxonomic and functional structure varied more among localities and sites than among regions, which it is believed, was due to the environmental heterogeneity within regions. Even isolated islands with large fish biomass such as Trindade Island and São Pedro e São Paulo Archipelago were almost depleted in terms of large predators, such as sharks and large groupers. This contrasts with historical records of abundant top predators not only at the islands (Lobo, 1919; Luiz & Edwards, 2011), but also along the coast (Souza, 2000) and suggests that their important function (Heithaus *et al.*, 2008) might have already been lost on most Brazilian reefs. Depletion of marine predators is a multi-scale global phenomenon (Pauly *et al.*, 1998; Jackson *et al.*, 2001; Baum *et al.*, 2003; Myers & Worm, 2003; Luiz & Edwards, 2011; Nadon *et al.*, 2012). Fully enforced, no-take marine protected areas are still however, the most propagated management tool to successfully reverse this process (Russ *et al.*, 2005; García-Charton *et al.*, 2008; Russ & Alcala, 2010; Aburto-Oropeza *et al.*, 2011; MacNeil *et al.*, 2015). Currently, marine reserves (no-take marine protected areas) compose only 0·14% of the Brazil's economic

exclusive zone (MMA, 2010) and concerns have been raised about whether many of these are effectively protected (Gerhardinger *et al.*, 2011). The present study may contribute to improving marine resources management in Brazilian reefs by pointing out places where specific fish functional groups or taxa remain abundant and therefore functionality could be maintained; or where these have been depleted and functionality is threatened. Future studies on this topic should address the drivers of these biomass patterns, especially trying to disentangle the relative influences of environmental drivers, such as habitat or temperature, from human-induced drivers, like fisheries activities.

Supporting Information

Supporting Information may be found in the online version of this paper:

TABLE S1. Sampling localities (with abbreviation), site and geographic coordinates for Brazilian oceanic, tropical and subtropical reefs investigated in the present study and the number of fish counts performed per site.

TABLE S2. Functional group and length range of all species, by family, of fish recorded through underwater visual surveys in this study of Brazilian oceanic, tropical and subtropical reefs. SHD, small herbivores and detritivores; LHD, large herbivores and detritivores; ZPK, zooplanktivores; OMN, omnivores; LLC, lower-level carnivores; MCA, macrocarnivores.

TABLE S3. Correlation (Pearson's *r*) among the biomass of fish total and functional groups' biomass in Brazilian oceanic, tropical and subtropical reefs. SHD, small herbivores and detritivores; LHD, large herbivores and detritivores; ZPK, zooplanktivores; OMN, omnivores; LLC, lower-level carnivores; MCA, macrocarnivores.

TABLE S4. Correlation (Pearson's *r*) among the biomass of reef fish total and families' biomass in Brazilian oceanic, tropical and subtropical reefs. Only the 12 families with the highest mean biomass are represented.

FIG. S1. Relative mean (a) abundance and (b) biomass frequency distribution of fish assemblages among localities in Brazilian oceanic island (■), tropical (■) and subtropical (■) reefs. Sampling site abbreviations are as in Fig. 1.

FIG. S2. Relative proportional (a) abundance and (b) biomass frequency distribution of fish assemblages among localities in Brazilian oceanic island (■), tropical (■) and subtropical (■) reefs. Sampling site abbreviations are as in Fig. 1.

FIG. S3. Non-metric multidimensional scaling of taxonomic (family-level) structure of standing biomass of fishes from Brazilian oceanic island (■), tropical (■) and subtropical (■) reefs as per Fig. 3, but showing the families with the 13th to 18th highest fish biomasses across the whole study: (a) Sparidae (b) Ephippidae, (c) Mullidae, (d) Ginglymostomatidae, (e) Murinaenidae and (f) Sphyraenidae. Circle size is proportional to the biomass of the respective family at each site. Sampling site abbreviations are as in Fig. 1.

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