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REPORT

Conservation status of the southernmost reef of the Amazon Reef System: the Parcel de Manuel Luís

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Abstract The Parcel de Manuel Luís (PML) is located at the southern end of the Amazon Reef System, which comprises the northernmost reef formations of the Brazilian biogeographical province. Its unique position and singular seascape make the PML an important stepping-stone for marine organisms between the Brazilian and Caribbean provinces. Yet, due to its distance from the shore, high tidal amplitude, and strong currents associated with a series of pinnacles exposed during low spring tides, the PML is one of the least studied reefs in the Western South Atlantic. Here, we integrated sessile benthic community data, fish assemblage surveys, and remote filming of fish interactions to establish the most complete community assessment of the PML reefs to date. In our surveys, we documented 78 sessile benthic taxa, with a taxonomic dominance of macroalgae (54 taxa), including two new occurrences of sponges for the North Brazilian Shelf, as well as four endemic species, such as the fire coral *Millepora laboreli*. The fish assemblage comprised 59 reef fish species, with biomass dominated mainly by large carnivorous species (e.g., groupers and snappers). Intra- and interspecific interactions were dominated by herbivorous fishes, particularly underpinned by grazing behavior and chasing by

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territorial species. The considerably high biomass and large-bodied species found in our surveys is rarely seen elsewhere in the Western South Atlantic, suggesting a low level of fishing compared to most other places, and only a few changes were observed in the fish assemblages since the first assessment made in 1998. We also highlight the usefulness of an integrated approach for continued assessment of Western South Atlantic reefs, particularly given emerging threats from mining and oil exploration, and the heavy traffic of commercial vessels in the region. Our findings support the PML as an area of critical conservation interest for reef systems, emphasizing the need for continued enforcement of this marine protected area and its integration in long-term plans of offshore oil and gas development projects.

Keywords Atlantic Ocean · Brazil · Marine protected area · Low human impacts · Shallow reefs · RAMSAR site

Introduction

Marine habitats have been profoundly affected by human population expansion, but some areas subject to relatively low human impacts remain (Jackson and Sala 2001; Friedlander and Demartini 2002; Sandin et al. 2008). These potential refuges can provide reference points that hypothetically approximate the original conditions of marine ecosystems before high impact activities (Friedlander et al. 2010; Sala et al. 2012; Graham and McClanahan 2013). Features traditionally associated with near pristine reef ecosystems include substantial contribution of high trophic level and large-bodied species to community structure (León et al. 2016; Robinson et al. 2017), as well as high taxonomic, phylogenetic or functional diversity (Mouillot et al. 2014; D'Agata et al. 2016) due to lower direct anthropogenic pressures such as overfishing and habitat degradation. The Parcel de Manuel Luís (PML) was declared a no-take marine protected area (Parcel de Manuel Luís Marine State Park) in 1991 due to its singular reef formations, composed of pinnacles rising abruptly from soft bottom in an otherwise featureless continental shelf, and also its diverse benthic communities dominated by coralline algae, sponges, hard corals and ascidians (Rocha and Rosa 2001). Its relative isolation (∼ 84 km from the coast), perilous surrounding waters with strong tidal currents (tidal amplitude ∼ 6 m), and the traditional favoring of non-reef fishes for marketing purposes in the region have helped to keep the PML reefs under relatively low anthropogenic pressure (Coura 2016). However, the same difficulties of access have kept scientific information about the PML scarce (Rocha and Rosa 2001; Amaral et al. 2006, 2007). These conditions make the PML one of the few places along the Brazilian coast that could fulfill some of the expectations of a near-pristine reef, and potentially provide insights on what coastal ecosystems used to be like. This is particularly critical at present because the area surrounding the PML has been increasingly surveyed for mineral resources, with recent expansion of permits for oil drilling and the exploitation of carbonate grounds (IBAMA 2018). Some of these permits are located immediately adjacent to the PML state park boundaries, highlighting the need for enhancing our knowledge about the region's marine ecosystems.

Efforts to map and understand reefs off the mouth of the Amazon River reinforced the importance for conservation of their unique formations, ecological and economic features (Moura et al. 2016; Francini-Filho et al. 2018; Mahiques et al. 2019). These northern reef formations also provide connectivity between the Caribbean and the Brazilian province (Collette and Rutzler 1974; Rocha 2003). Although broad conservation strategies have been recently developed aiming to protect coastal reefs in Brazil (such as *The National Plan of Action for the Conservation of Coral Environments*—PAN Corais; MMA 2016), many areas lack biodiversity data to support management actions, including the PML. Despite being included as a priority area among Brazilian MPAs and having a management plan under construction, there is no actual plan to insert the PML within a network of protected areas at the national level, with the closest reef MPA located over 700 km to the south east (the Pedra da Risca do Meio Marine State Park—DOE 1997).

Knowledge about the composition and community structure of a conservation area is considered essential to biodiversity evaluations (Noss 1990; Tucker et al. 2017) and implementation of management plans and monitoring programs (Green et al. 2014). Integrated assessment of different components of reef communities (e.g., benthos, fishes) have the potential to help understand the relative contribution of anthropogenic and natural disturbances to community patterns (Friedlander et al. 2014; Meirelles et al. 2015). Previous studies on the PML focused on corals (Moura et al. 1999), reef fishes (Rocha and Rosa 2001), and hydroids (Amaral et al. 2007). Other large-scale studies have included data on reef fish assemblages, benthic communities and ecological interactions from the PML (e.g., Rocha et al. 2002; Ferreira et al. 2004; Morais et al. 2017; Aued et al. 2018; Longo et al. 2019). However, a detailed analysis integrating these different datasets with the addition of other important functional components, such as macroalgae and sponges (Bruno et al. 2009; de Goeij et al. 2017) and considering local-scale habitat heterogeneity is still lacking. Here, we integrate benthic community and fish assemblage surveys, with remote filming of species interactions, to establish the most comprehensive ecological assessment of the Parcel de Manuel Luís reefs to date. This multi-taxon approach is timely considering the emerging threats to Brazilian coral reefs, such as mining (Vilar et al. 2020), oil exploration (Moura et al. 2013; Santos et al. 2016; Vilar et al. 2020), and overfishing (Dutra et al. 2005; Floeter et al. 2006; Frédou et al. 2006).

Based on the few previous reports of its fauna and flora, its isolation and difficulty of access, we expected to find near pristine conditions of the PML's marine ecosystem. The information obtained can help identify effective conservation measures for the north Brazilian coastal region. First, we expected to find a fish community with a high proportion of large predators and species with commercial value, since these reefs are exposed to low fishing pressure. Second, because of strong tidal currents and high sedimentation, we expected to observe a larger contribution of benthic taxa resistant to burial events, fast-growing species and hydrodynamic resistant species. Third, we expected herbivorous fishes, either territorial or roving, to be the main group interacting with the substrate on those reefs because they are the main grazing group of tropical subtidal consolidate substrates (Harborne and Mumby 2018; Longo et al. 2019). We expected that herbivorous fishes presented a higher number of agonistic interactions since these represent an important component of the fish assemblage reported in PML (Morais et al. 2017). Finally, strong interactions dependent on the abundance of species (Vázques et al. 2007) and, as herbivores are abundant in the PML (Morais et al. 2017), large part of agonistic interactions are expected to be played between herbivorous species (Fontoura et al. 2020).

Material and methods

Study region

The Parcel de Manuel Luís State Park, located ~ 84 km offshore from the coast of the state of Maranhão (northeast Brazil), is a RAMSAR site since 2000 (Coura 2016). The PML reefs are located in the continental shelf of Maranhão state, in the southern border of the Amazon Reef System. This reef system was first discovered in the 1970s (Collette and Rützler 1977) but was only recently mapped in detail (Moura et al. 2016; Francini-Filho et al. 2018). Although located closer to the coast compared to the four groups of oceanic islands in Brazil, its inaccessibility and complex logistics for surveying make the PML the least known of all Brazilian shallow reefs. This 5-km-long formation has hundreds of pinnacles rising up from the 30 m deep sea floor to the surface but there are still limited geological and physical–chemical data for the region despite its shallow and relatively clear waters. For example, although the current hypothesis is that the Manuel Luís reefs sit on a rocky base (Coura 2016), there is no currently available geological data (seismic or probe) testing this. The local geology of the Maranhão shelf indicates a predominantly sedimentary geomorphology influenced by sea level transgressions, tides and rivers that existed during the Holocene (Gualberto and El-Robrini 2005). Most of the sediment in the shelf is lithoclast, pointing to a possible igneous origin of the Maranhão sedimentary basin (Klein and Moura 2003). The only exposed parts of the Parcel are the tips of the pinnacles during spring low tides, making local navigation particularly dangerous. Those factors combined with a high tidal range (up to 6 m) and strong currents (up to 2.5 knots), have kept both researchers and fishers relatively away from the area. According to Coura (2016), 13 shipwrecks have been located from the estimated 200 that may lie within the PML (Maida and Ferreira 1997).

We conducted two field expeditions to the Parcel de Manuel Luís, one in April of 2012 and another in April 2013. As navigation charts for the PML region lack details of the reef formations, two known shipwrecks (Basil, and Ana Cristina) were used as reference points (Fig. 1). Surveys were stratified according to habitat and depth profile, aiming to obtain a representative snapshot of the PML's reef communities (Fig. 2). Based on the general habitat availability throughout the local seascape, we chose to survey four habitat types: (1) shipwreck—two sunken vessels with 30 and over 100 yrs, mostly covered by sponges, epilithic algae and sparse coral colonies, depth from 5 to 28 m; (2) pinnacles—tall pillars and walls formations covered by macroalgae and sponges, associated with coral and hydrocoral colonies, depth from 6 to 27 m; (3) patch reefs—sparse groups of congregated coral and rhodoliths, sponges and hydrocorals, depth between 24 and 27 m; and, (4) interface—the borders of the other three habitats, mainly composed by rhodoliths with attached macroalgae, carbonate gravel and encrusting sponges, depth from 19 to 28 m.

Benthic surveys

We quantitatively estimated the cover of benthic reef organisms at the PML using digital images (25 × 25 cm) randomly distributed along two depth strata (5–8 m, and 25–27 m) because of logistical restrictions imposed by wave action (shallow pinnacle tops), currents (walls with channeled currents), and excessive suspended sediments in other habitats. Pinnacles were the predominant component of the local seascape and representative of PML reefs despite their heterogeneity in size. Images were analyzed for relative cover using the software *photoQuad* (Trygonis

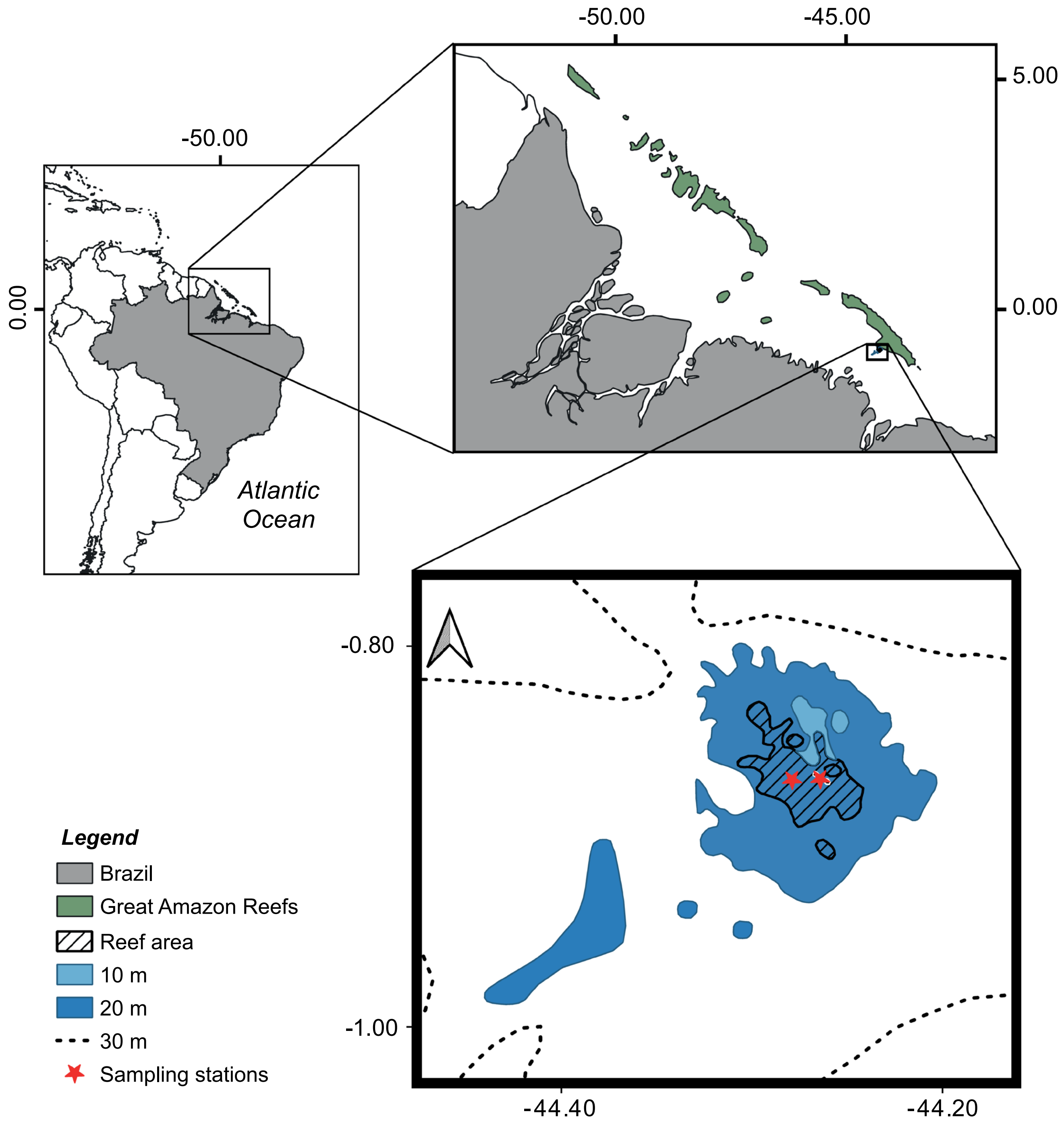

Fig. 1 Map indicating sampled stations in the Parcel de Manuel Luís and its relative position to the Great Amazon reefs

and Sini 2012) by overlaying 50 random points on each image. A total of 202 images were analyzed for the two sites investigated (Ana Cristina, $n = 190$; and Basil, $n = 12$), but only images from the Ana Cristina were tested for statistical differences due to the low number of replicates obtained for the second site (Basil) and poor quality due to suspended sediments. Benthic organisms were visually identified at the lowest taxonomic level, then the following morpho-functional categories (Aued et al. 2018) were assigned for analysis purposes: turf algae, macroalgae, coral (including fire corals), zoanthid, crustose coralline algae (CCA), suspension/filter feeders (sponges), cyanobacteria and other invertebrates (see Table 1 for details). Information lost due to edges, shade or undefined features comprised less than 0.5% of total cover and were not included in the analysis. A qualitative sampling routine

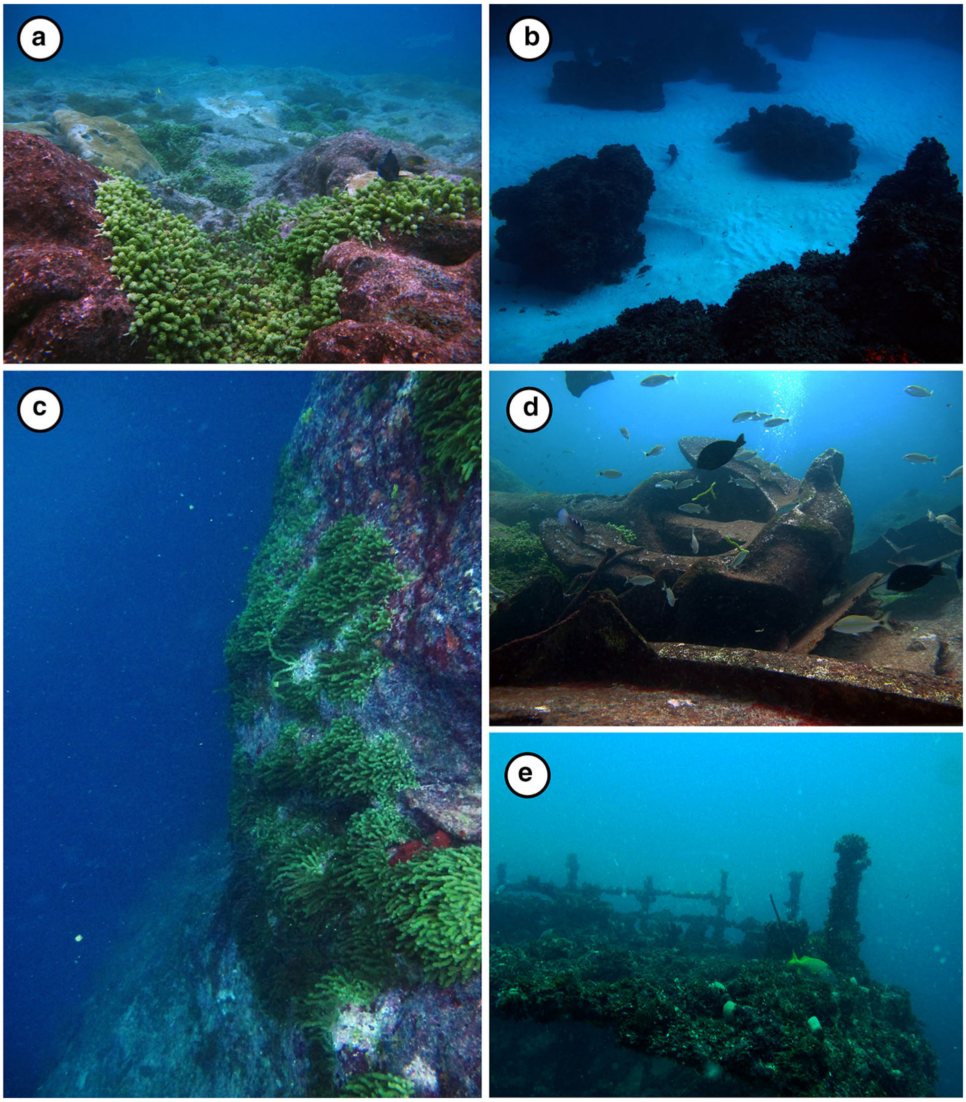

Fig. 2 Main habitats found at Parcel do Manuel Luís State Park (Brazil). **a** pinnacle top, **b** interface, **c** pinnacle wall, **d** shallow shipwreck, and **e** deep shipwreck

using active search was done by two divers along all habitats to search for new species occurrences and to collect voucher specimens of macroalgae, sponges and corals. The collected specimens were used to help identify and to complete the list of benthic taxa. Cnidaria and Porifera material sampled were deposited at the Museu Nacional—UFRJ (Rio de Janeiro, Brazil) and the macroalgae were deposited at Flor Herbarium at Federal University of Santa Catarina (Florianópolis, Brazil).

Reef fish assemblages

Species richness, abundance, and biomass of fishes were estimated from 83 underwater visual surveys (UVSs) along belt transects of 40 m^2 (20 × 2 m) following the method described by Morais et al. (2017). Transects were placed randomly within depth intervals (5 m, when possible) at both sites (Basil $n = 21$; and Ana Cristina $n = 62$) in four habitat types (i.e., shipwreck, pinnacles, patch reef and interface) according to habitat availability (See Table 1s in supplementary material for details). During the surveys, we identified and estimated the size (total length in cm) of each individual fish within the transect boundaries. The body mass of each fish was calculated using the length–weight conversions with species-specific regression parameters (a and b) obtained from *FishBase* (Froese and Pauly 2019). All fishes recorded within the UVSs were classified into trophic groups (HD—herbivores–detritivores, HM—macroalgal feeders, SI—sessile invertebrate feeders, MI—mobile invertebrate feeders, PK—planktivores, CP—carnivores-piscivores, OM—omnivores) based on diet, size and feeding behavior following the categories listed by Longo et al. (2014).

Table 1 Taxa and morpho-functional groups of benthic cover found quantitative surveys in reefs at the Parcel do Manuel Luis Marine State Park. Brazil

Group	Organism	Ana Cristina				Basil	
		5–8 m		25–27 m		25–27 m	
		Mean	s.d	Mean	s.d	mean	s.d
Macroalgae	*Dictyota* sp.	36.3	34.8	22.6	30.3	11.2	12.0
	Halimeda sp.	1.6	4.4	15.7	23.7	26.8	15.0
	Caulerpa racemosa	12.7	28.4	1.5	8.7	–	–
	Unidentified articulated calcareous algae	0.3	1.4	4.4	11.8	–	–
	Ceramium nitens	1.2	9.0	–	–	–	–
	Unidentified filamentous algae	–	–	–	–	4.2	7.9
	Champia parvula	–	–	0.1	1.4	–	–
	Unidentified foliaceous algae	–	–	0.1	1.0	–	–
	Unidentified corticated algae	0.1	1.3	–	–	0.2	0.6
	Unidentified crustose coralline algae	0.1	1.3	–	–	–	–
	Amphiroa sp.	–	–	0.1	0.7	–	–
	Caulerpa sp.	–	–	0.0	0.2	–	–
	Caulerpa verticillata	< 0.1	0.2	–	–	–	–
	Codium spp.	–	–	–	–	0.2	0.6
Turf algae	Turf calcareous algae	24.7	31.6	8.1	13.6	22.7	8.8
	Turf filamentous algae	2.3	9.6	3.1	9.1	0.3	0.8
Cyanobacteria	Cyanobacteria	5.6	13.8	13.8	18.9	5.2	4.8
CCA	Crustose coralline algae	4.3	13.2	0.6	2.7	3.8	11.0
Filter Feeders	Incrusting sponge	0.9	3.0	0.7	2.4	2.0	4.7
	Massive sponge	0.1	0.7	1.1	5.1	0.5	1.7
Coral	*Siderastrea stellata*	< 0.1	0.4	0.8	3.8	0.2	0.6
	Montastraea cavernosa	–	–	0.2	0.9	1.0	2.9
	Porites astreoides	–	–	0.2	2.5	–	–
	Favia gravida	0.1	0.6	–	–	0.2	0.6
	Meandrina brasiliensis	–	–	–	–	0.5	1.7
Zoanthid	*Palythoa caribaeorum*	6.3	20.1	–	–	–	–
Other invertebrates	Polychaeta *Bispira* sp.	–	–	1.1	5.2	18.7	16.7

s.d., standard deviation. '–', absent

Reef fish ecological interactions

We assessed fish ecological interactions (agonistic and benthic feeding interactions) using remote underwater video recordings, following Longo and Floeter (2012). For each video, an area of 2 × 1 m was filmed for 15 min with a digital video camera (GoPRO) focusing on the reef substratum. We placed the cameras at the same depth strata used for benthic surveys, except for high sloping areas and walls, and also avoided artificial habitats that could bias the associated community because of the different ages and composition of the two wrecks (Perkol-Finkel et al. 2006, Simon et al. 2011). In total, we obtained 22 video plots, all recorded during daylight hours (from 0900 to 1600 h). From the footages, we counted the number of bites delivered on the substratum and estimated the total length of each fish to calculate the feeding pressure of an individual fish. We then aggregated this across all individuals from the same species and averaged among videos to obtain species-level mean and variance of the feeding pressure. Agonistic interactions within and among fish species were defined as events when one fish chased another without any obvious feature associated with predation. These interactions were quantified by counting the number of interactions observed per individual and aggregated at the species level (Fontoura et al. 2020). The expected contribution of species based on relative abundance, both for feeding pressure and interactions (i.e., chases) was investigated using the Ivlev index of electivity, using the Chi-square distribution to estimate the 95%

confidence intervals (Byers et al. 1984). The relative abundance of fish species in the same habitat of videos (i.e., pinnacles) was applied as observed availability, and the relative grazing pressure and relative number of chases were used as observed utilization on each case.

Statistical analysis

We used permutational multivariate analyses of variance (PERMANOVA—Anderson 2001) to test for differences in the structure of benthic communities between depth strata and in the structure of fish assemblages between depth strata and habitats. We used a principal coordinate analysis (PCoA) to visualize differences in the feeding pressure of all species and trophic groups between depth strata. The PERMANOVA analysis were performed using a Euclidean dissimilarity matrix for benthic communities and Bray-Curtis dissimilarity for fishes, with statistical significance tested by 999 permutations under a reduced model, and type II (conditional) sums of squares (Anderson et al. 2008). PERMANOVA analyses were done using the *adonis* function within the *vegan* package (Oksanen et al. 2015) from R software.

To assess whether fish species richness (number of species per 40 m^2), abundance (number of individuals per 40 m^2) and biomass (grams per 40 m^2) varied among habitats (shipwreck, pinnacles, patch reef, and interface) and depth, we applied generalized linear mixed models (GLMM) with a negative binomial error distribution for richness and abundance, and gamma error distribution (link log) for biomass data. We considered habitat and depth as fixed factors, and site as a random factor. Tukey tests were used post hoc to determine the differences between groups and performed using the function *glht* from the *multicomp* package (Hothorn et al. 2008).

Results

Benthic communities

A total of 54 taxa of macroalgae were identified: 34 from the phylum Rhodophyta, 10 from the phylum Chlorophyta, eight from the class Phaeophyceae (phylum Heterokontophyta), and two Cyanobacteria (Table 2). We found a relatively low diversity of sponges (Porifera), with only 11 species identified from the qualitative and quantitative surveys (Table 2). However, two of these were new records for the North Brazilian Shelf: *Chelonaplysilla erecta* and *Scopalina ruetzleri* (Fig. 2s Online Resource). *Clathria nicoleae* was the only species endemic to the Brazilian province. We also identified 10 species of Anthozoa (phylum Cnidaria), one only at genus level, belonging to eight families (Table 2). Three out of nine scleractinian species identified are endemic to Brazil: *Favia gravida*, *Mussismilia hispida* and *Siderastrea stellata*.

Overall, benthic community cover was dominated by macroalgae (47.8%), with *Dictyota* spp. and *Halimeda* spp. as major components at both investigated depth strata (Fig. 4). Algal turfs were the second most abundant group (18.6%), followed by cyanobacteria (9.9%, Fig. 3). Coral cover was low (0.8%) and mainly consisting of *Siderastrea stellata*, *Montastraea cavernosa* and *Porites astreoides*. Benthic communities differed between depth strata (PERMANOVA: *F-value* depth = 27.21, $p < 0.001$), with the shallow stratum dominated by macroalgae and turf algae and the deep stratum with relatively higher cover of cyanobacteria and other invertebrates (mainly sessile polychaetes) (Fig. 3).

Reef fish assemblages

A total of 59 species in 19 families were recorded during the quantitative surveys (Table 3) with species richness ranging from three to 18 species per transect (median = 8, $Q_{25\%} = 6.5$, $Q_{75\%} = 10$). We found no evidence for depth or habitat effects on fish species richness ($F_{3,\ 82}$-*value* = 1.89, $p > 0.05$). There was marginal evidence for an effect of habitat on fish abundance ($F_{3,\ 82}$-*value* = 4.92, $p < 0.046$; shipwreck = pinnacle, shipwreck > patch reef = interface), but not for depth ($F_{1,\ 82}$-*value* = 0.02, $p > 0.05$). Fish biomass was highest at shipwrecks, followed by patch reefs, interface and pinnacles (Fig. 4; $F_{3,\ 82}$-*value* = 7.59, $p < 0.01$; shipwreck > patch reef = interface = pinnacle), but values were similar between depths ($F_{1,\ 82}$-*value* = 0.01, $p > 0.05$).

Mobile invertebrate feeders (MI), herbivores–detritivores (HD), and carnivores–piscivores (CP; > 30 cm) were the most abundant and had the higher biomass (Fig. 5). Carnivores–piscivores attained the largest sizes (range = 12–200 cm, median = 50, $Q_{25\%} = 40$, $Q_{75\%} = 80$), followed by macroalgae feeders (HM-range = 35–60 cm, median = 50, $Q_{25\%} = 45$, $Q_{75\%} = 50$) and MI (range = 4–100 cm, median = 18, $Q_{25\%} = 12$, $Q_{75\%} = 35$). Mobile invertebrate feeders accounted for 87.6% of total biomass and 56.2% of total abundance, while carnivores–piscivores summed 7.3% of biomass and 3.7% of abundance. The relative frequency of occurrence of macroalgae feeders was the highest (31.1%), followed by omnivores (16.3%) and carnivores–piscivores (10.6%). Species composition was similar among habitats and depth (PERMANOVA: $F_{1,\ 82}$-*value* depth = 1.18, $p = 0.26$; $F_{1,\ 82}$-*value* habitat = 0.80, $p = 0.79$). No effect of depth or type of habitat was observed on patterns of biomass by trophic group (PERMANOVA: $F_{1,\ 82}$-*value* depth = 0.39, $p = 0.86$; $F_{1,\ 82}$-*value* habitat = 0.98, $p = 0.46$) or size

Table 2 Taxa observed or sampled at Parcel de Manuel Luis State Park (Brazil)

Higher order classification	Family	Species
Phylum Rhodophyta		
Class Florideophyceae	Acrochaetiaceae	*Acrochaetium microscopicum*
	Callithamniaceae	*Aglaothamnion felliponei*
	Lithophyllaceae	*Amphiroa anastomosans*[a]
	Ceramiaceae	*Antithamnionella graeffei*
	Bonnemaisoniaceae	*Asparagopsis taxiformis*
	Hymenocladiaceae	*Asteromenia peltata*
	Delesseriaceae	*Branchioglossum* sp.
	Callithanmiaceae	*Callithamnion corymbosum*
		Crouania attenuate
	Ceramiaceae	*Ceramium comptum*
		Ceramium nitens[a]
		Ceramium tenuicorne
		Ceramium virgatum
		Ceramium sp.1
	Champiaceae	*Champia parvula*[a]
	Derbesiaceae	*Derbesia marina*
	Erythrotrichiaceae	*Erythrotrichia carnea*
	Gelidiaceae	*Gelidium pusillum*
	Wrangeliaceae	*Haloplegma duperreyi*
		Griffithsia globulifera
		Griffithsia schousboei
	Hydrolithaceae	*Hydrolithon farinosum*
	Hypneaceae	*Hypnea cf. spinella*
		Hypnea sp.
	Delesseriaceae	*Hypoglossum hypoglossoides*
	Corallinaceae	*Jania* cf. *adhaerens*
		Jania cubensis
		Jania sp. 1
	Rhodomelaceae	*Laurencia* cf. *filiformis*
		Laurencia oliveirana
		Laurencia sp.1
	Lithothamniaceae	*Lithothamnion crispatum*
	Peyssonneliaceae	*Peyssonnelia* sp.*
	Porolithaceae	*Porolithon antillarum*
	Rhizophyllidaceae	*Ochtodes secundiramea*
	Wrangeliaceae	*Wrangelia argus*
Class Phaeophyceae	Dictyotaceae	*Canistrocarpus cervicornis*[a]
		Dictyopteris cf. *delicatula*
		Dictyota ciliolate
		Dictyota crenulata
		Dictyota hamifera
		Dictyota humifusa
		Dictyota menstrualis
		Dictyota pinnatifida
Phylum Chlorophyta		
Class Ulvophyceae	Bryopsidaceae	*Bryopsis hypnoides*
		Bryopsis pennata

Table 2 continued

Higher order classification	Family	Species
	Caulerpaceae	*Caulerpa racemosa*[a]
		Caulerpa verticillata[a]
	Halimedaceae	*Halimeda* sp.1
		Halimeda sp.2
		Halimeda tuna[a]
	Udoteaceae	*Udotea abbottiorum*
		Udotea dixonii
	Valoniaceae	*Valonia ventricosa*
Phylum Cyanobacteria		
Class Cyanophyceae	Oscillatoriaceae	*Lyngbya* sp.
Phylum Porifera		
Class Demospongidae	Agelasidae	*Agelas* sp.
	Aplysinidae	*Aplysina cauliformis*
	Microcionidae	*Clathria (Clahtria) nicoleae*
	Clionaidae	*Cliona schmidtii*
	Darwinellidae	*Chelonaplysilla erecta* [c]
	Geodiidae	*Geodia* sp.
	Irciniidae	*Ircinia* sp.
	Crambeidae	*Monanchora* sp.
	Niphatidae	*Niphates alba*
	Scopalinidae	*Scopalina ruetzleri* [c]
	Spongiidae	*Spongia* sp.
Phylum Cnidaria		
Class Hydrozoa	Milleporidae	*Millepora laboreli*[b]
Class Anthozoa	Agariciidae	*Agaricia* sp.
	Faviidae	*Favia gravida*[ab]
		Mussismilia hispida[b]
		Scolymia wellsii
	Meandrinidae	*Meandrina brasiliensis*[a]
	Montastraeidae	*Montastraea cavernosa*[a]
	Pocilloporidae	*Madracis decactis*
	Poritidae	*Porites astreoides*[a]
	Siderastreidae	*Siderastrea stellata*[ab]
	Sphenopidae	*Palythoa caribaeorum*[a]

[a] Species found in the photoquadrats sampling,

[b] Species endemic to Brazil,

[c] New record for the North Brazilian shelf

class (PERMANOVA: $F_{1,\ 82}$-*value* depth = 0.46, p = 0.81; $F_{1,\ 82}$-*value* habitat = 1.16, p = 0.28). *Lutjanus jocu, Sparisoma frondosum* and *Acanthurus chirurgus* were the most abundant species (Table 3). The dog snapper (*L. jocu*) showed the highest mean biomass values (11.2 ± 3.1 kg.40 m^{-2}), followed by *Chaetodipterus faber* (2.1 ± 1.3 kg.40 m^{-2}) and *Haemulon parra* (2.1 ± 1.5 kg.40 m^{-2}). Other large carnivorous species, besides *L. jocu*, with high mean biomass were *Sphyraena barracuda* (1.1 ± 0.4 kg.40 m^{-2}) and *Mycteroperca*

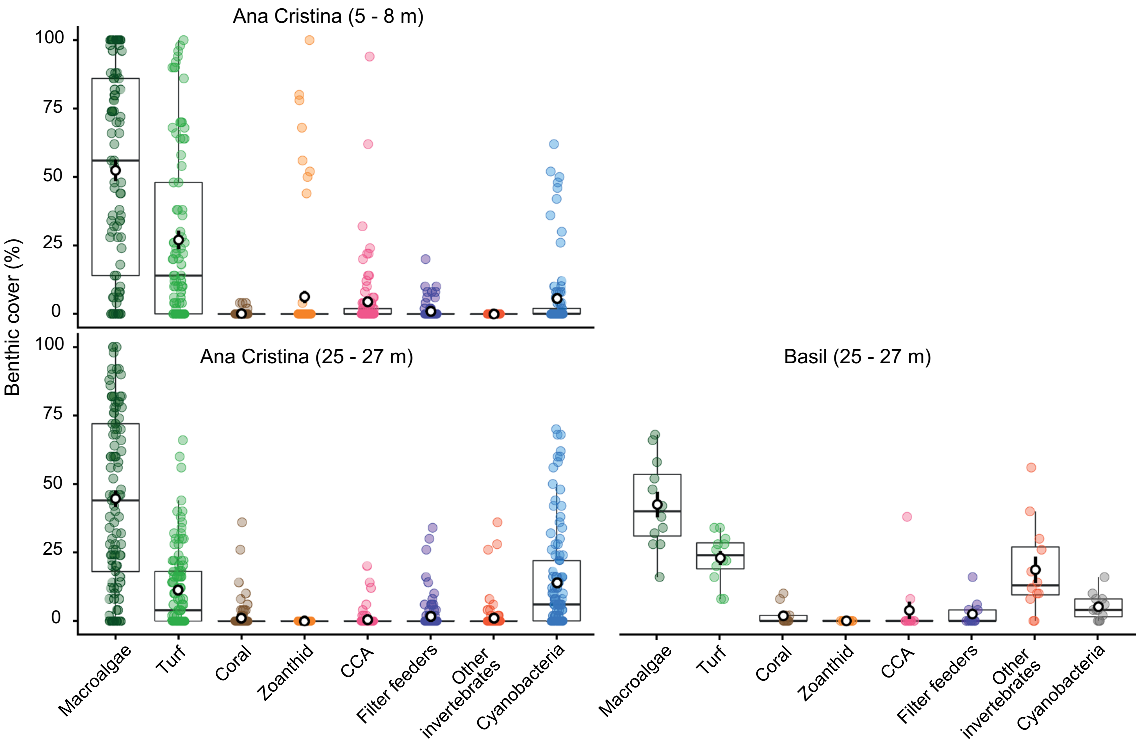

Fig. 3 Benthic cover from pinnacles according to site and depth stratum in the Parcel de Manuel Luís Marine State Park, Brazil. Red dots are mean values. Boxes define the interquartile range, with whiskers limiting the 95% quantile interval. Hollow dots and black lines represent, respectively, the mean and standard error of the mean

bonaci (0.3 ± 0.1 kg.40 m^{-2}). Endangered ($n = 1$), near threatened ($n = 1$) and vulnerable species ($n = 1$) contributed with 2.1% of total abundance (Table 1) and 1% of total biomass. Highly ($n = 14$) and very highly ($n = 15$) targeted species accounted for 48.9% and 10.5% of total abundance (Table 1), and 16.2% and 5.5% of total biomass, respectively.

Reef fish interactions

We recorded a total of 2041 ecological interactions, both inter and intraspecific, during the 220 min of video. Feeding interactions were exclusively recorded with benthic components ($n = 2029$), performed by 20 fish species distributed in three out of the seven trophic groups (Fig. 6). Agonistic interactions were much less common, and exclusively performed by six species from two trophic groups (Fig. 7). The herbivore–detritivore group exerted most of the feeding pressure (97.1%), followed by mobile invertebrate feeders (2.7%) and macroalgal feeders (0.3%; Fig. 6). The grazer surgeonfish *Acanthurus chirurgus* alone accounted for about 62% of the total feeding pressure ($n = 18$, median = 3.3, $Q_{25\%} = 2.3$, $Q_{75\%} = 5.8$), followed by the excavator parrotfish *Scarus trispinosus*, with ~ 14% ($n = 4$, median = 5.7, $Q_{25\%} = 4.5$, $Q_{75\%} = 9.3$). The feeding pressure was largely influenced by the abundance and individual biomass, which is demonstrated by the contribution of *A. chirurgus* (9.44% of total abundance; individual estimated weight = 0.14 ± 0.16 kg) and *S. trispinosus* (1.76% of total abundance; individual estimated weight = 2.3 ± 1.9 kg). The relative contribution of species to total feeding pressure was not different from the expected exclusively based species relative on abundance, as evidenced by the electivity index (Fig. 6s). No significant differences were observed on feeding pressure between depth strata for all fish species ($F_{1,\ 20}$-*value* = 1.53, $p = 0.10$) or trophic groups ($F_{1,\ 20}$-*value* = 2.03, $p = 0.09$).

The few agonistic interactions detected (14 events in 220 min of videos) were mostly interspecific and performed exclusively by the territorial herbivore *Stegastes variabilis*, mainly towards roving herbivores such as the abundant *A. chirurgus* (67%), the small territorial herbivore–detritivore *Ophioblennius trinitatis* (16.5%) and the small parrotfish *Sparisoma radians* (16.5%). All other five species chased exclusively conspecifics, although these interactions were rare (Fig. 7), and there was no difference from the expected contribution based on relative abundance of chased species in the electivity index (Fig. 6s).

Table 3 Fish species observed in belt transects at Parcel do Manuel Luis Marine State Park reefs (Brazil) in 2012 and 2013. Commercial importance and conservation status were compiled from FishBase (Froese and Pauly 2019)

Family	Species	*n*	Abundance (%)	Mean size in cm (mean ± sd)	Diet	Commercial importance	Conservation status
Acanthuridae	*Acanthurus chirurgus*	274	9.44	14.7 ± 5.6	HD	Medium	LC
	Acanthurus coeruleus	14	0.48	24.6 ± 10.3	HD	Medium	LC
	Acanthurus bahianus	7	0.24	10.0 ± 4.1	HD	Not targeted	LC
Batrachoididae	*Amphichthys cryptocentrus*	1	0.03	35.0 ± 0.0	MI	Not targeted	LC
Carangidae	*Carangoides bartholomaei*	67	2.31	43.4 ± 10.1	CP	Medium	LC
	Caranx crysos	2	0.07	42.5 ± 3.5	CP	Low	LC
	Caranx ruber	2	0.07	45.0 ± 0.0	CP	Medium	LC
	Trachinotus falcatus	2	0.07	95.0 ± 7.1	MI	Medium	LC
Chaetodontidae	*Chaetodon ocellatus*	15	0.52	11.8 ± 1.9	MI	Not targeted	LC
	Chaetodon sedentarius	6	0.21	10.4 ± 0.9	MI	Not targeted	LC
	Chaetodon striatus	1	0.03	10.0 ± 0.0	SI	Not targeted	LC
Epinephelidae	*Mycteroperca bonaci*	10	0.34	43.0 ± 23.9	CP	Very high	NT
	Epinephelus itajara	2	0.07	170.0 ± 42.4	CP	Very high	VU
	Dermatolepis inermis	1	0.03	30.0 ± 0.0	CP	Very high	DD
	Epinephelus adscensionis[b]	1	0.03	40.0 ± 0.0	CP	Very high	LC
Grammatidae	*Gramma brasiliensis*	12	0.41	6.3 ± 1.7	MI	Not targeted	NE
Haemulidae	*Haemulon plumierii*	181	6.23	28.0 ± 8.5	MI	Medium	LC
	Haemulon parra	144	4.96	35.5 ± 9.0	MI	Medium	LC
	Anisotremus virginicus	130	4.48	18.9 ± 7.1	MI	Medium	LC
	Haemulon aurolineatum	51	1.76	17.5 ± 6.5	MI	Medium	LC
	Haemulon melanurum	2	0.07	17.5 ± 3.5	MI	Medium	LC
Holocentridae	*Holocentrus adscensionis*	50	1.72	16.7 ± 4.5	MI	Medium	LC
	Myripristis Jacobus	4	0.14	14.3 ± 1.5	PK	Medium	LC
Kyphosidae	*Kyphosus sectatrix*	25	0.86	47.1 ± 8.1	HM	High	LC
	Kyphosus vaigiensis	5	0.17	52.5 ± 10.6	HM	High	LC
Labridae	*Sparisoma frondosum*[a]	369	12.71	13.3 ± 8.8	HD	High	DD
	Halichoeres bivittatus	146	5.03	13.0 ± 3.9	MI	Very high	LC
	Sparisoma radians	130	4.48	6.5 ± 2.3	HD	High	LC
	Halichoeres dimidiatus[a]	52	1.79	18.2 ± 7.7	MI	Very high	LC
	Scarus trispinosus[a]	51	1.76	32.5 ± 10.1	HD	High	EN
	Sparisoma axillare[a]	50	1.72	13.7 ± 10.3	HD	High	DD
	Sparisoma amplum[a]	29	1.00	32.1 ± 18.1	HD	High	LC
	Halichoeres poeyi	22	0.76	12.5 ± 4.9	MI	Very high	LC
	Cryptotomus roseus	21	0.72	8.9 ± 3.3	HD	High	LC
	Bodianus rufus	20	0.69	15.1 ± 4.9	MI	Very high	LC
	Clepticus brasiliensis[a]	17	0.59	15.0 ± 0.0	PK	Very high	LC
	Thalassoma noronhanum	8	0.28	12.8 ± 2.2	PK	Very high	LC
	Halichoeres penrosei[a]	5	0.17	15.0 ± 2.4	MI	Very high	LC
	Scarus zelindae[a]	5	0.17	33.8 ± 13.1	HD	High	DD
	Bodianus pulchellus	3	0.10	13.3 ± 6.1	MI	Very high	LC
	Halichoeres brasiliensis[a]	2	0.07	12.5 ± 3.5	MI	Very high	DD
Lutjanidae	*Lutjanus jocu*	640	22.04	45.7 ± 13.5	MI	High	DD
	Ocyurus chrysurus[a]	40	1.38	19.7 ± 11.0	HD	Medium	DD
Mullidae	*Mulloidichthys martinicus*	12	0.41	13.1 ± 3.9	MI	Medium	LC
	Pseudupeneus maculatus	7	0.24	16.4 ± 7.0	MI	Medium	LC

Table 3 continued

Family	Species	*n*	Abundance (%)	Mean size in cm (mean ± sd)	Diet	Commercial importance	Conservation status
Ogcocephalidae	*Ogcocephalus vespertilio*[b]	1	0.03	35.0 ± 0.0	MI	Not targeted	NE
Ostraciidae	*Acanthostracion polygonius*	1	0.03	40.0 ± 0.0	SI	High	LC
Pomacentridae	*Abudefduf saxatilis*	1	0.03	10.0 ± 0.0	OM	Not targeted	LC
	Chromis multilineata	5	0.17	9.0 ± 1.4	PK	Not targeted	LC
	Chromis scotti	5	0.17	5.5 ± 0.6	PK	Not targeted	LC
	Stegastes variabilis	55	1.89	7.7 ± 1.8	HD	Not targeted	NE
	Stegastes pictus	19	0.65	6.1 ± 1.8	OM	Not targeted	NE
Pomacanthidae	*Pomacanthus arcuatus*	2	0.07	17.5 ± 3.5	OM	High	LC
	Pomacanthus paru	47	1.62	23.5 ± 10.2	OM	High	LC
	Holacanthus ciliaris	11	0.38	12.8 ± 3.2	SI	High	LC
Serranidae	*Serranus baldwini*	18	0.62	6.5 ± 1.6	MI	Medium	LC
	Rypticus saponaceus	1	0.03	30.0 ± 0.0	MI	Very high	LC
Sphyraenidae	*Sphyraena barracuda*	22	0.76	87.5 ± 14.8	CP	Medium	LC
Tetraodontidae	*Canthigaster figueiredoi*[a]	6	0.21	7.0 ± 1.1	MI	Very high	LC

HD, herbivore–detritivore, HM, macroalgal feeder, SI, sessile invertebrate feeder, MI, mobile invertebrate feeder, PK, planktivore. CP, carnivore-piscivore. OM, omnivorous; *Synonym in Rocha and Rosa (2001); ** not observed by Rocha and Rosa (2001);†new observation for the region and extension on species previous range. Not evaluated (NE); Data deficient (DD); Least concern (LC); Near threatened (NT); Vulnerable (VU); Endangered (EN)

Discussion

General aspects

The PML reefs have formations that are unique in the Western South Atlantic and make up the northernmost shallow reef formations in the Brazilian province, at the southernmost limit and only explored shallow water representative of the Amazon Reef System. Reefs at the Parcel de Manuel Luís are dominated by macroalgae and have high biomass of mid to high-trophic level fishes. Our approach revealed fish assemblage characterized by large abundance of commercial species and bearing similarities with a previous survey conducted over 20 yrs ago (Rocha and Rosa, 2001). The simultaneous dominance of macroalgae and abundant herbivorous fish species contradicts assumptions that healthy tropical reefs have to be coral dominated, and also supports the literature suggesting low herbivore-mediated control of benthic communities (Russ et al. 2015; Donovan et al. 2018; Bruno et al. 2019). Indeed, coral cover is typically low and macroalgae cover typically high in other reefs along the Brazilian coast (Castro and Pires 2001; Aued et al. 2018).

A remarkable aspect of the PML is the considerable abundance and large size of the commercially valuable and highly targeted species *Lutjanus jocu* (7.7 ± 1.6 ind.40 m^{-2}) (Frédou et al. 2009) and *Sparisoma frondosum* (4.5 ± 0.5 ind.40 m^{-2}), and the common occurrence of large specimens of carnivorous-piscivorous fish species (e.g., groupers), unlike most other Brazilian locations (Morais et al. 2017). Thus, the region may be a hope spot (Earle 2016) for populations of large carnivores such as the endangered species (e.g., the goliath grouper, *Epinephelus itajara*), species of high commercial value as, groupers, snappers and Brazilian endemic parrotfishes (*S. trispinosus* and *S. frondosum*). Indeed, in a large-scale survey effort, Morais et al. (2017) highlighted the fact that the abundance of these species at the PML was exceptional for shallow reefs of the Brazilian Province.

Benthic cover

The benthic communities of the PML were characterized by a high contribution of macroalgae, whereas algal turfs and corals had a relatively low cover. Although the PML reefs are likely to have a rocky basis (Coura 2016), the gains in complexity might be due to secondary contribution of several groups of organisms. As corals had low contribution to cover, we hypothesize that *Halimeda* spp and coralline alga, together with sponges may have contributed to this secondary framework, stabilizing the substrate and contributing to reef accretion, as described by Wood

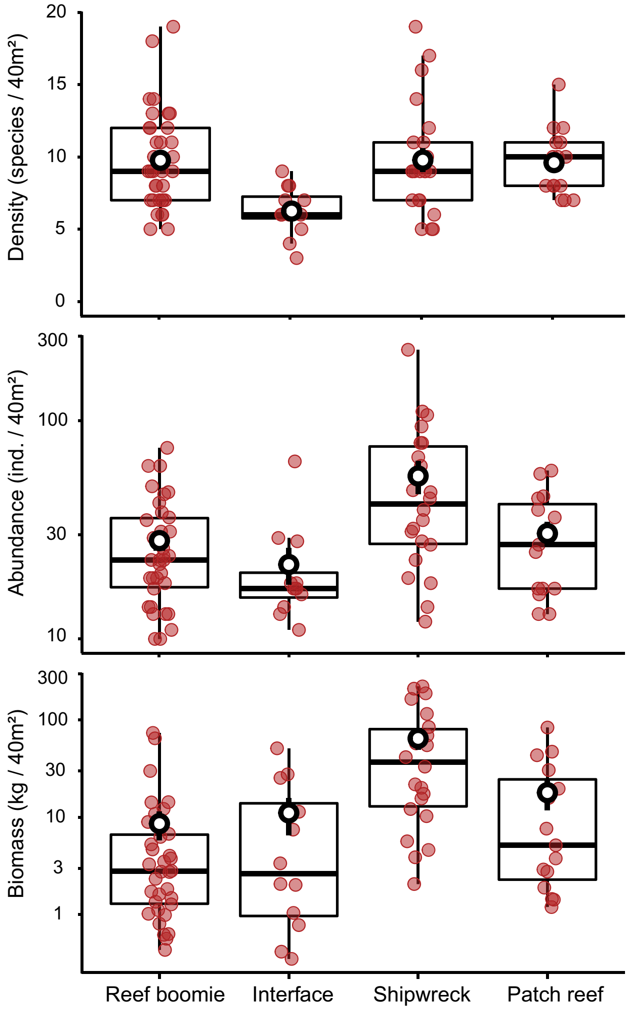

Fig. 4 Species richness, abundance and biomass of reef fish species according to habitat type at Parcel de Manuel Luís Marine State Park, Brazil. Boxes define the interquartile range, with whiskers limiting the 95% quantile interval. Hollow dots and black lines represent, respectively, the mean and standard error of the mean

(2003), but core drilling studies must be done to solve this question. Macroalgae cover was almost threefold larger than other Brazilian and Caribbean formations (Williams and Polunin 2001; Schutter et al. 2010; Vermeij et al. 2010; Aued et al. 2018). Traditionally, the balance between coral and macroalgae cover has been an important proxy of coral reef health with a higher proportion of corals expected for healthy tropical coral reefs (Bellwood et al. 2004, 2019; Hughes et al. 2010). Despite the scarcity of comparative baselines of benthic communities at the PML, available evidence suggests that the dominance of macroalgae is not a recent phenomenon for this reef system. The PML is located in the only part of the Amazon Reef System with water transparency to allow the penetration of enough light to support reef building species (Omachi et al. 2019). At the same time, this part of the Amazon Reef is exposed to substantial inputs of dissolved organic nitrogen and phosphorus from the Amazon River plume (Gouveia et al. 2019), favoring high planktonic productivity (Stuckel et al. 2014) and, potentially, also macroalgae and sponges that could outcompete scleractinian corals under such conditions. Waters around the PML are also exposed to an abundance of suspended particles, especially during spring tide currents (authors pers. obs.). Although coral species endemic to the Brazilian province tolerate high sediment deposition (Leão et al. 2003; Loiola et al. 2019) and productive waters (Costa et al. 2008), sedimentation rates can also negatively affect those scleractinian corals (Dutra et al. 2006; Segal and Castro 2011; Freitas et al. 2019). Finally, the isolation and the strong currents at the PML may be an additional obstacle to connectivity, self-recruitment and larval settlement, precluding the establishment of large coral populations, a topic which warrants further investigation.

The phytobenthic structure of the PML presents clear affinity with the tropical Atlantic flora, but the absence of common and abundant taxa also draws attention. The red algae *Ceramium nitens* is very common on the Caribbean reefs, and was often found on PML reefs, despite being only found elsewhere in Pernambuco State along the Brazilian coast (Fujii et al. 2001). This highlights the importance of the PML reefs as corridors between the Caribbean and Brazilian flora. The absence of *Sargassum*, *Gracilaria* and the order Halymeniales in our survey as well as in the bibliographical review for the region is noteworthy. These groups tend to be highly palatable for fishes (McCook, 1996) and often reported as important dietary items for herbivores abundant in the PML, such as kyphosids (Ferreira and Gonçalves 2006). Although kyphosids were not observed feeding on the benthos in the filming survey, these macroalgal-feeding specialists comprised a significant proportion of fish biomass. Thus, the possibility remains that kyphosids together with other nominally herbivores exert a potential impact over macroalgae through feeding pressure that could preclude the establishment or keep the undetected macroalgae species cited above in a state of low abundance with low probability of detection. In contrast, other less palatable macroalgae species, such as *Dictyota* sp., *Halimeda* sp. and *Caulerpa racemosa*, were locally abundant.

Although sponges did not comprise a high cover in the benthic surveys, they often contribute disproportionately to ecosystem processes on reefs compared to their perceived abundance (Richter et al. 2001; de Goeij et al. 2014). Our study is the first comprehensive assessment of sponges for the PML and first sampling effort for Porifera at shallow depths (5–20 m) using SCUBA diving in the Maranhão state coast. We added four species and two genera records to the Amazon ecoregion (Soest et al., 2017). Still, with the

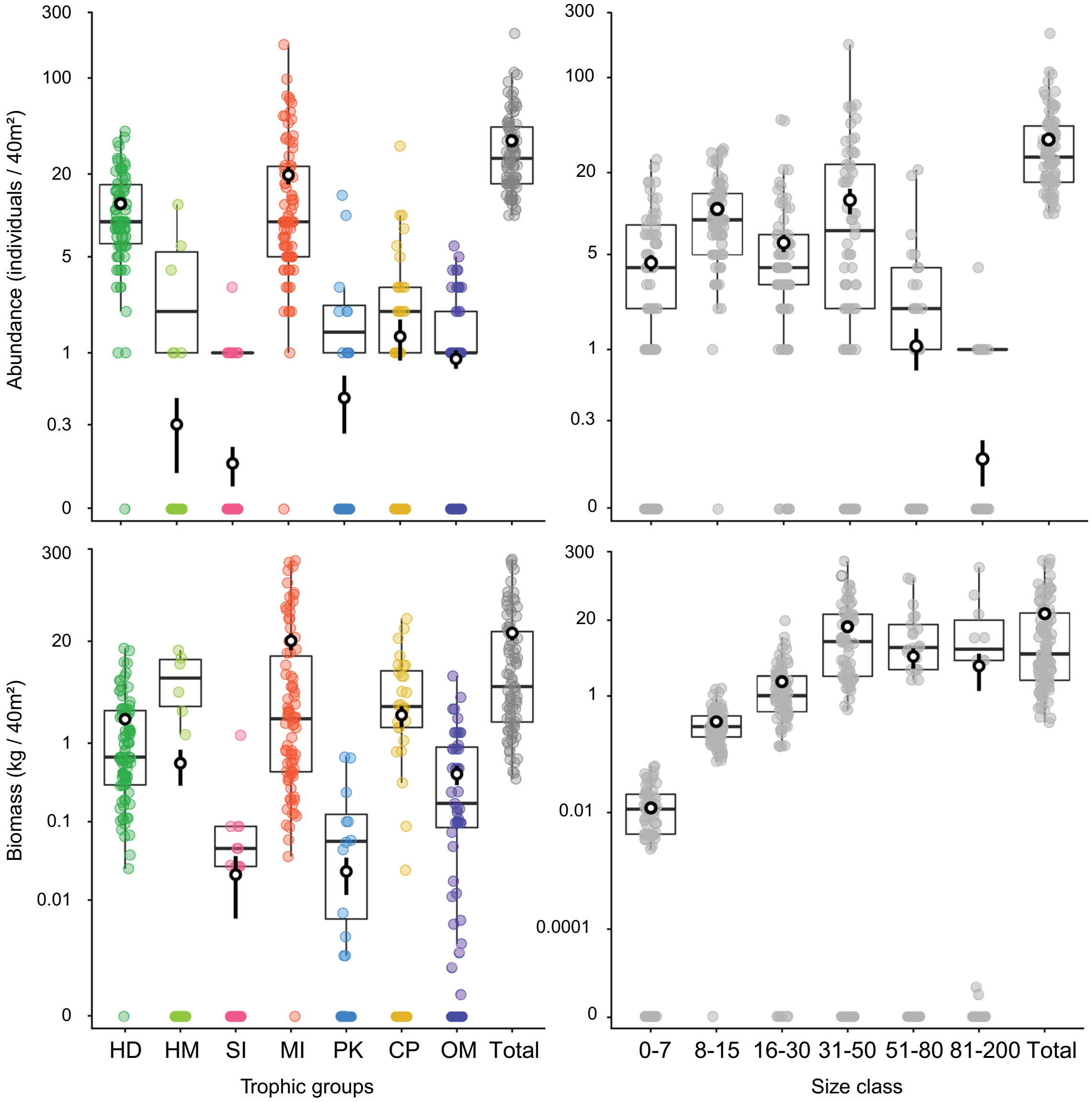

Fig. 5 Abundance and biomass of reef fish species according to trophic group and size class at Parcel de Manuel Luís Marine State Park, Brazil. HD—herbivore–detritivore, HM—macroalgal feeder, SI—sessile invertebrate feeder, MI—mobile invertebrate feeder, PK—planktivore, CP—carnivore-piscivore, OM—omnivore. Boxes define the interquartile range, with whiskers limiting the 95% quantile interval. Hollow dots and black lines represent, respectively, the mean and standard error of the mean

exception of the Brazilian endemic *Clathria nicoleae*, most of identified species present wide distribution, usually from the Caribbean to the southern Brazilian coast (*e.g., Amphimedon* and *Monanchora*).

According to Amaral et al. (2007), 12 species of scleractinian corals are recorded for the PML region. In our surveys, we recorded only 10 species, all of them previously reported for the PML. Four of these species are endemic to Brazilian waters, with the majority of this impoverished coral assemblage broadly distributed in Brazil and the Caribbean. Shallow-water species, such as Brazilian-endemic corals *Mussismilia* spp., cannot use the Amazon Reef System as a stepping-stone system to cross the Amazon River plume barrier because these reef structures are overwhelmingly concentrated in deeper waters (Collette and Rützler 1977; Rocha et al. 2002).

Reef fish assemblages

Although the richness of species is relatively low in comparison to other localities along the coast (Floeter et al. 2001; Pinheiro et al. 2018), the PML harbors species both at their northern and southern limits of distribution, considering the Brazilian and Caribbean provinces, respectively. Here, we expanded the list of reef fish species provided in Rocha and Rosa (2001) adding two species

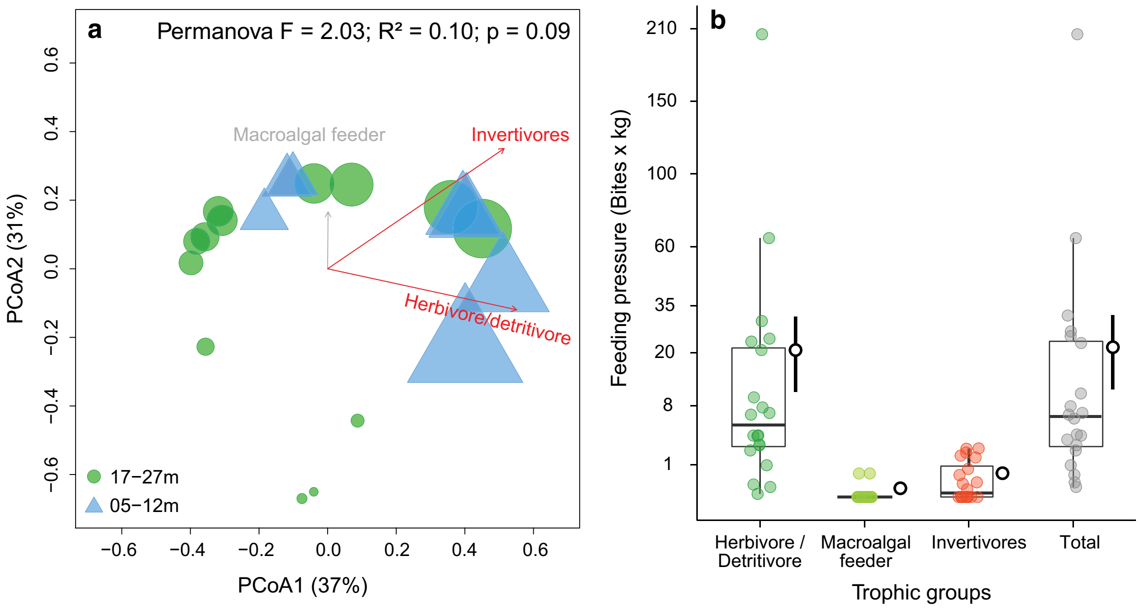

Fig. 6 Fish feeding pressure ordination (**a**) and average values per habitat type (**b**) at Parcel de Manuel Luís Marine State Park, Brazil

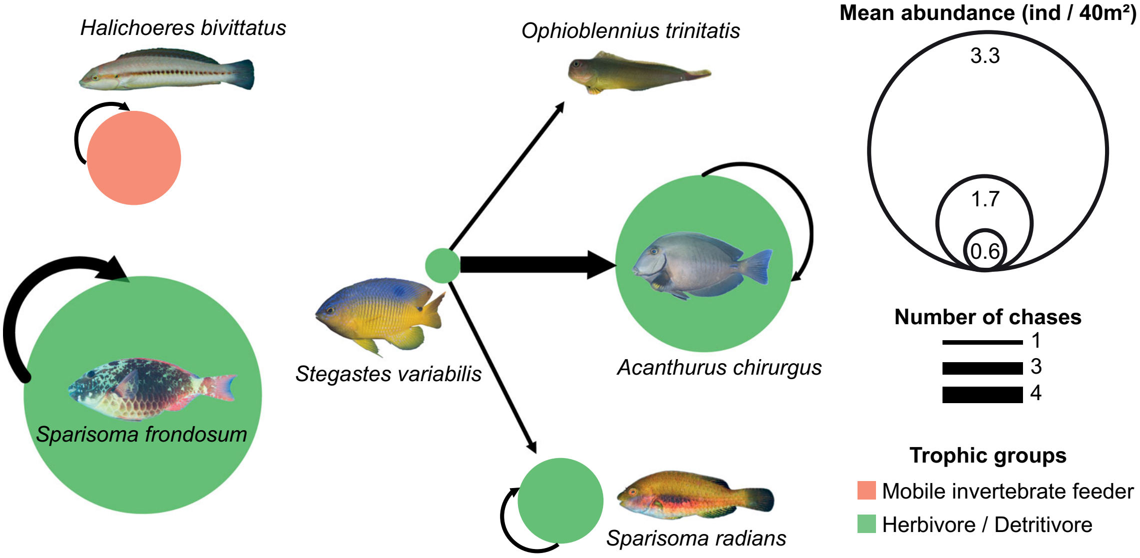

Fig. 7 Interaction network of reef fish species at Parcel de Manuel Luís Marine State Park, Brazil, based on chasing attempts, functional group and abundance

(*Epinephelus adscensionis* and *Ogcocephalus vespertilio*) for the PML, and including 10 taxonomic updates ranging from recent nomenclatural changes to newly described species (Table 3). Compared to previous surveys by Rocha and Rosa (2001), the family level contribution, trophic structure and mean size of species appears to have changed little. There was a small decrease in the relative abundance of carnivores and piscivores from 1998 to 2012, and an increase of herbivores–detritivores (Fig. 7s in supplementary material). That inversion on representativeness of these two groups was especially evident in their frequency of occurrence (Fig. 7s), but that could be an effect of distinct sampling efforts applied in both studies (15 stationary counts in 1998 versus 83 belt-transects in 2012), and the more scattered sampling study from 2001 study. Large predators such as jacks, groupers, snappers and barracudas were also frequently observed by Rocha and Rosa (2001), although, with the exception of *Lutjanus jocu*, they were not particularly abundant in their counts, which again might be attributed to differences in the counting methodology. The average size reported for *L. jocu* and *S. frondosum* by Rocha and Rosa (2001) indicated smaller specimens but similar sizes for *S. trispinosus* and other species (Table 2s in supplementary material).

Here, herbivores–detritivores and large mobile invertebrate feeders (> 30 cm) were the dominant groups in both abundance and biomass. In many reefs on the Brazilian coast, these groups tend to be relatively rare, particularly large specimens that are heavily targeted (Bender et al. 2014; Chaves et al. 2010; Ferreira et al. 2015a, b; Morais et al. 2017). The largest Brazilian parrotfish, the endemic greenback parrotfish *Scarus trispinosus* Valenciennes 1840*,* was often observed in small groups (< 15 individuals), although it appears to be less abundant than in other locations in the northeastern coast of Brazil, such as in Rio Grande do Norte and Abrolhos (Morais et al. 2017; Roos et al. 2019, 2020). This species has been historically targeted by fisheries in the eastern and northeastern regions in Brazil (Floeter et al. 2006; Bender et al. 2014; Roos et al. 2019, 2020), but there is no strong reason to believe that fishing activities would have recently caused abundance declines that could explain the relatively low densities observed at the PML. *Scarus trispinosus* was more abundant on Brazilian reefs with a large contribution of reef building corals and calcareous algae (Roos et al. 2019), which may be more favorable for a species that relies on excavating the substratum. In this sense, the relatively low abundance of calcareous substrate (e.g., calcareous algae) may be unfavorable for the species. Supporting this likely environmental constraint, Rocha and Rosa (2001) also reported low abundance of *S. trispinosus* at the PML almost two decades before our study. This contrasts with other fish species with high market value and often targeted elsewhere, such as the black grouper *Mycteroperca bonaci,* the dog snapper *Lutjanus jocu*, and the goliath grouper *Epinephelus itajara* which are often seen in dives on the PML. Most large carnivores had low frequency of occurrence, which could also be attributed to the low detectability by short belt transects (Ward-Paige et al. 2010) as those applied here. Still, the dominance of mesopredator species even with often seen large-bodied species raises a red flag about possible illegal fishing targeting large predators such as sharks and groupers. The globally vulnerable goliath grouper (Bertoncini et al. 2018) is protected by specific national legislation (ICMBio 2018) and was once very common in coastal Brazilian recreational and subsistence fisheries (Gerhardinger et al. 2006; Bender et al. 2014), but rare elsewhere in Brazil (Morais et al. 2017). Furthermore, contrasting to Rocha and Rosa (2001) and as noted by Morais et al. (2017), no sharks were seen in the PML. The PML Marine State Park has been suggested as a nursery and feeding area for endangered species of shark and rays (Motta et al. 2009), but their absence on our expeditions suggests fishing nearby or illegal fishing within the PML boundaries (Feitosa et al. 2018; Martins et al. 2018).

We found higher fish abundance and biomass in shipwrecks compared to other habitats, but similar species richness and composition. The main biological feature influencing this high biomass was the conspicuous presence of schooling species (i.e., *Chaetodipterus faber*, *Haemulon parra*, *Haemulon plumieri* and *Lutjanus jocu*) at the shipwrecks. Several studies have compared fish communities between artificial and natural reefs concerning their fish assemblage composition (e.g., Rilov and Benayahu 2000; Terashima et al. 2007; Simon et al. 2011) and trophic structure (e.g., Honório et al. 2010; Fowler and Booth 2012). In general, differences between artificial and natural reefs are associated with the benthic cover and substrate characteristics affecting attractiveness besides age of the shipwrecks (Simon et al. 2013), involves mainly large schooling species feeding in the unconsolidated substrate (Honório et al. 2010) or benefitting from prey associated with the wreck structure.

Reef fish interactions

Reef fish feeding pressure on the substrate is considered as a proxy of their functional impact on the benthic community (Longo and Floeter 2012; Longo 2019), and grazing pressure is considered crucial on benthic dynamics (Green et al. 2014). Feeding pressure at the PML was concentrated in the key group of scrapers that represent a large part of fish biomass and indicate the potential local importance of this group. The abundance of Acanthuridae is also reflected in the high chasing rates the species received from their territorial competitor (*Stegastes variabilis*). The total feeding pressure observed at the PML is considered high even when compared to other higher latitude reefs both in the Brazilian coast and the Caribbean (Longo et al. 2019). Most parrotfish and surgeonfish species observed in the PML feed on large amounts of detritus (Ferreira and Gonçalves 2006; Mendes et al. 2018), while some scrappers (*Sparisoma axillare* and *S. frondosum*) may also be fleshy algae consumers. Although the majority of the feeding pressure was exerted by scrapers, the excavator species (*Scarus trispinosus*, and large individuals of *Scarus zelindae* and *Sparisoma amplum*—Lellys et al. 2019) were also abundant locally and suggest an important contribution of those bioeroding species. Bioeroders usually have lower bite rates than scraper species (Bellwood and Choat 1990) and focus on coralline substrate. Thus, because of the low coral cover observed and their more specific diet, their function role may not be adequately quantified by static filming, as applied in this study. Animal focal approaches would possibly provide more precise estimates of the grazing pressure by excavating parrotfish and kyphosid species. However, even with the dominant cover in the PML being macroalgae, the diet plasticity of the nominally herbivorous fishes ensures their potentially high influence over benthic dynamics. Lastly, the low frequency of chasing events could be a reflex of the high predation risk affecting the aggressive behavior of territorial herbivores, but may be biased by the technique applied as indicated previously, thus further investigation should be carried out for clarification. Despite the lack of previous quantification of interactions between fishes and the benthos and agonistic interactions, these first records will be a basis for further monitoring of basic features of reef systems that may act as ecosystem functioning indicators.

Unfolding conservation issues

The Parcel de Manuel Luís represents the northernmost shallow reef formations of the Brazilian coast (Rocha 2003; Floeter et al. 2006), even with the recently updated recently and extensive scientific efforts to map the extension of the Amazon River reef complex (Moura et al. 2016; Francini-Filho et al. 2018). Now, the Parcel de Manuel Luís and the Banco do Álvaro are also considered the southernmost and shallowest part of the Amazon reef system (Francini-Filho et al. 2018) but still represent the northernmost shallow reefs of the Brazilian Province. The Amazon Reef System is not easily accessible throughout their extension because its central and northern portions are deep and largely under the influence of murky waters from the Amazon river plume (Omachi et al. 2019). However, the southern region suffers only limited and seasonal influence of the Amazon plume, hardly affecting the water transparency in the PML (Collette and Rützler 1977; Moura et al. 2016; Omachi et al. 2019). Therefore, reefs of the PML are unique in that they represent the only part of the Amazon Reef System with water conditions consistently within the limits required for significant growth of shallow reef building scleractinian corals.

As indicated here, the PML fish assemblage showed larger biomass of mesopredators and presence of large-bodied species, especially groupers (> 60 cm on total length, see Fig. 5s in supplementary material) and abundant target species when compared to other shallow reefs in Brazil (Morais et al. 2017). The distance from the coast, strong tidal currents, and lack of demand for reef fishes in the area's markets may buffer this reef system against some coastal anthropogenic pressures (e.g., artisanal fishing fleets and recreational diving). Fishing is prohibited and tourism is rare to nonexistent, mainly due to the difficult access. Nevertheless, illegal fishing has been previously reported in the MPA area (Coura 2016) and patrolling efforts are still inexistent. The absence of sharks and the low level of enforcement suggests that illegal fishing may occur. Furthermore, other threats, such as those arising from mining in the PML vicinities (e.g., carbonate extraction and oil, Francini-Filho et al. 2018) are also of concern. Plans for oil exploration in the area include two blocks licensed in the shelf edge about 120 km north of the PML (Francini-Filho et al. 2018). As dominant currents flow northward (Omachi et al. 2019), the potential impacts from oil spills from extraction activities may be lower in comparison to potential risk of oil spills from ships transporting the production and in the route of the PML. Such concerns are timely after the tragic oil spill registered in September 2019, which affected more than 2000 km of Brazilian coast (Duncombe 2019), including the Maranhão coast, and, possibly, even the PML. Finally, invasive species are likely to arrive at the PML due to the intense traffic and potential future oil platforms to be established in the area. Oil platforms are notorious vectors for the sun coral *Tubastraea tagusensis* and *T. coccinea* in the southwestern Atlantic coast (Capel et al. 2019), aggressive competitors often displacing native species (Guilhem et al. 2020). Also, the lionfish *Pterois volitans*, an aggressive invasive species widespread in the Caribbean is expected to expand its range by crossing the Amazon barrier, with the PML as one of the potential first sites to be colonized (Ferreira et al. 2015a, b; Luiz et al. 2013).

Rhodolith exploration for calcium carbonate and limestone extraction has increased globally (Colleti et al. 2017), and Brazil has a vast extension of rhodolith beds in its north and northeastern coasts (Amado-Filho et al. 2012) that has been targeted for mining. Currently, only one company has a functional permission to explore rhodolith banks in the shelf of the Maranhão state, but another has applied to start dragging in areas south of the PML (IBAMA 2018). Direct effects of rhodolith mining include habitat removal, changes in local carbonate availability and increase in water turbidity, which can affect all taxa associated with this habitat and adjacent areas. Rhodolith beds found in the shallow shelf south of the Amazon have a high diversity of coralline algae and other builders (Vale et al. 2018), consisting of a rich ecosystem that is already going to suffer changes in next the decades because of ocean acidification (Amado-Filho et al. 2012). Finally, Brazil is the second biggest iron ore exporter in the world (UNCTAD 2018), and > 60% of Brazilian iron exports flows through the Itaqui port complex (ANTAQ 2019), located only 100 km from the PML. A regular traffic of > 800,000 tons (ANTAQ 2019) flows out of Itaqui terminals yearly. Since ship traffic is a real risk for oil and other spills (see recent accident of the Stellar Banner 300,000 ton ore carrier 40 km from the PML, Hancock 2020), transport of alien species, and habitat destruction through groundings (Burke et al. 2011; Magris et al. 2018), a risk management policy including potential accidents involving large vessels in the region would be a welcome addition to the State Park management plan.

The difficulty of access that protects the PML from many human impacts is also a problem for enforcement and monitoring. The PML is the only part of the Amazon Reef that is legally protected, but the MPA is still in the initial phase of a management plan (FUNBIO 2019), with the general lack of funds and infrastructure, including vessels. Gerhardinger et al. 2006) indicated that several flaws in the Brazilian National System of Protected areas make it difficult to successfully produce an integrated management action plan. These authors showed that the lack of a solid plan for a marine network of protected areas is also a reflection of the poor inter-institutional coordination of coastal and ocean governance. Alongside the national politics that exacerbates an historical institutional crisis faced by the national conservation agency, the PML faces a pessimist scenario where financial shortages and bureaucracy hold back progresses in the conservation of marine ecosystems in Brazil.

Even though our surveys add novel information, ecosystems at the PML are very different from most other Brazilian reefs and far from being well studied. Results presented here rigorously described of one portion of the PML and are possibly representative of sampled habitats which are conspicuous to the PML, but we acknowledge that an extensive investigation of the PML is needed to account for local heterogeneity among unrepresented habitats. For example, some groups (e.g., Bryozoa; Soares et al. 2016) have never been surveyed in the area and the other major reef system within the PML Marine State Park, the Banco do Álvaro reef system, were only observed by scientists once, in 1998 (Rocha and Rosa 2001). Therefore, strengthening enforcement and governance is needed, and ideally long-term monitoring should start as soon as possible and consist of regular visits, including a formal evaluation of possible effects of the recent oil spill from the Stellar Banner vessel (Hancock 2020).

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

Aued AW, Smith F, Quimbayo JP, Candido DV, Longo GO, Ferreira CEL, Witman JD, Floeter SR, Segal B (2018) Large-scale patterns of benthic marine communities in the Brazilian Province. PLoS ONE 13(6):e0198452

Amaral FMD, Hudson MM, Steiner AQ (2006) Note on the widespread bleaching observed at the Manuel Luiz State Park. Maranhão, Brazil Arq Ciên Mar, pp 138–141

Amaral FMD, Hudson MM, Steiner AQ, Ramos CAC (2007) Corals and calcified hydroids of the Manuel Luiz Marine State Park (State of Maranhão, Northeast Brazil). Biota Neotrop 7(3):73–81

Amado-Filho GM, Moura RL, Bastos AC, Salgado LT, Sumida PY, Guth AZ, Francini-Filho RB, Pereira-Filho GH, Abrantes DP, Brasileiro PS, Bahia RG, Leal RN, Kaufman L, Kleypas JA, Farina M, Thompson FL (2012) Rhodolith beds are major $CaCO_3$ bio-factories in the tropical South West Atlantic. PLoS ONE 7(4):e35171

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymounth

ANTAQ (2019) National Waterway Transportation Agency. https://web.antaq.gov.br/Anuario/ (accessed 01 July 2019).

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environ Biol Fish 28:189–214

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429(6994):827

Bellwood DR, Pratchett MS, Morrison TH, Gurney GG, Hughes TP, Álvarez-Romero JG, Day JC, Grantham R, Grech A, Hoey AS, Jones GP, Pandolfi JM, Tebbett SB, Techera E, Weeks R, Cumming GS (2019) Coral reef conservation in the Anthropocene: Confronting spatial mismatches and prioritizing functions. Biol Conserv 236:604–615

Bender MG, Machado GR, Silva PJDA, Floeter SR, Monteiro-Netto C, Luiz OJ, Ferreira CEL (2014) Local ecological knowledge and scientific data reveal overexploitation by multigear artisanal fisheries in the Southwestern Atlantic. PLoS ONE 9(10):e110332

Bertoncini AA, Aguilar-Perera, Barreiros J, Craig MT, Ferreira B, Koenig C (2018) *Epinephelus itajara* (errata version published in 2019). The IUCN Red List of Threatened Species 2018: e.T195409A145206345. Downloaded on 28 June 2019

Bruno JF, Sweatman H, Precht WF, Selig ER, Shutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90(6):1478–1484

Bruno JF, Côté IM, Toth LT (2019) Climate change, coral loss, and the curious case of the parrotfish paradigm: why don’t marine protected areas improve reef resilience? Annu Rev Mar Sci 11:307–334

Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk - revisited. World Resources Institute, Washington, 130pp

Byers CR, Steinhorst RK, Krausman PR (1984) Clarification of the technique for analysis of utilization-availability data. J Wildlife Manage 48(3):1050–1053

Capel KCC, Creed J, Kitahara MV, Chen CA, Zilberberg C (2019) Multiple introductions and secondary dispersion of *Tubastraea* spp. in the Southwestern Atlantic. Sci Rep 9:13978

Castro CB, Pires DO (2001) Brazilian coral reefs: what we already know and what is still missing. Bull Mar Sci 69(2):357–371

Chaves LCT, Nunes JACC, Sampaio CLS (2010) Shallow reef fish communities of south Bahia coast, Brazil. Braz J Oceanogr 58:33–46

Collette BB, Rützler K (1977) Reef fishes over sponge bottoms off the mouth of the Amazon River. Proceedings of the Third International Coral Reef Symposium: 305–310

Colleti G, Basso D, Frixa A (2017). Economic Importance of Coralline Carbonates. https://doi.org/10.1007/978-3-319-29315-8_4

Costa OS Jr, Nimmo M, Attrill MJ (2008) Coastal nutrification in Brazil: A review of the role of nutrient excess on coral reef demise. J S Am Earth Sci 25(2):257–270

Coura MF (2016) Contribuição ao plano de manejo do Parque Estadual Marinho do Parcel de Manuel Luís/MA: atualização e avanços da unidade após 25 anos. Dissertation. Fundación Universitaria Iberoamericana, Brasília, Brazil. 73pp.

D'Agata S, Mouillot D, Wantiez L, Friedlander AM, Kulbicki M, Vigliola L (2016) Marine reserves lag behind wilderness in the conservation of key functional roles. Nat Commun 7:12000

de Goeij JM, van Oevelen D, Vermeij MJA, Osinga R, Middelburg JJ, de Goiej AFPM, Admiraal W (2014) Surviving in a marine desert: the sponge loop retains resources within coral reefs. Science 342(6154):108–110

de Goeij JM, Lesser MP, Pawlik JR (2017) Nutrient fluxes and ecological functions of coral reef sponges in a changing ocean. In Climate Change, Ocean Acidification and Sponges. Springer, Cham, pp 373–410. https://doi.org/10.1007/978-3-319-59008-0_8

DOE – Diário Oficial do Estado do Ceará (1997) Law N° 12.717 of 5th of September 1997 on the creation of the Parque Estadual Marinho da Pedra da Risca do Meio.

Donovan MK, Friedlander AL, Lecky J, Jouffray J-B, Williams GJ, Wedding LM, Crowder LB, Erickson AL, Graham NAJ, Gove JM, Kappel CV, Karr KK, Kittinger JN, Norström AC, Nyström M, Oleson KLL, Stamoulis KA, White C, Williams ID, Selkoe KA (2018) Combining fish and benthic communities into multiple regimes reveals complex reef dynamics. Sci Rep 8:16943

Duncombe J (2019) Brazil's oil spill is a mystery, so scientists try oil forensics. Eos 100:2019. https://doi.org/10.1029/2019EO136177 (Published on 24 October)

Dutra LXC, Kikuchi RKP, Leão ZMAN (2006) Effects of sediment accumulation on reef corals from Abrolhos, Bahia, Brazil. J Coast Res 39:633–638

Dutra GF, Allen GR, Werner T, McKenna SA (eds) (2005) A Rapid Marine Biodiversity Assessment of the Abrolhos Bank, Bahia. Brazil. RAP Bulletin of Biological Assessment, Conservation International, Washington, DC, USA

Earle S (2016) Protect the Ocean, Protect Ourselves. In: Johnson M, Bayley A (eds) Coastal Change. Springer International Publishing Switzerland, Ocean Conservation and Resilient Communities, p 168

Feitosa LM, Martins AP, Giarrizzo T, Macedo W, Monteiro IL, Gemaque R, Nunes JLS, Schneider H, Sampaio I, Souza R, Sales JB, Rodrigues-Filho LF, Tchaika L, Carvalho-Costa LF (2018) DNA-based identification reveals illegal trade of threatened shark species in a global elasmobranch conservation hotspot. Sci Rep 8:3347

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

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

Ferreira CM, Coni EOC, Medeiros DV, Sampaio CLS, Reis-Filho JA, Barros F, Loiola M, Costa Nunes JACC (2015) Community structure of shallow rocky shore fish in a tropical bay of the southwestern Atlantic. Braz J Oceanogr 63(4):379–396

Ferreira CEL, Luiz OJ, Floeter SR, Lucena MB, Barbosa MC, Rocha RC, Rocha LA (2015) First record of invasive lionfish (*Pterois volitans*) for the Brazilian coast. PLoS ONE 10(4):e0123002

Floeter SR, Guimarães RZP, Rocha LA, Ferreira CEL, Rangel CA, Gasparini JL (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. Glob Ecol Biogeogr 10:423–433

Floeter SR, Halpern BS, Ferreira CEL (2006) Effects of fishing protection on Brazilian reef fishes. Biol Conserv 128:391–402

Floeter SR, Krohling W, Gasparini JL, Ferreira CEL, Zalmon IR (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. Environ Biol Fishes 78:147–160

Fontoura L, Cantor M, Longo GO, Bender MG, Bonaldo RM, Floeter SR (2020) The macroecology of reef fish agonistic behaviour. Ecography 43:1278–1290. https://doi.org/10.1111/ecog.05079

Fowler AM, Booth DJ (2012) Evidence of sustained populations of a small reef fish on artificial structures. Does depth affect production on artificial reefs? J Fish Biol 80(3):613–629

Francini-Filho RB, Asp NE, Siegle E, Hocevar J, Lowyck K, D'Avila N, Vasconcelos AA, Baitelo R, Rezende CE, Omachi CY, Thompson CC, Thompson FL (2018) Perspectives on the Great Amazon Reef: Extension, Biodiversity, and Threats. Front Mar Sci 5:142

Frédou T, Ferreira BP, Letourneur Y (2006) A univariate and multivariate study of reef fisheries off northeastern Brazil. ICES J Mar Sci 63:883e896

Frédou T, Ferreira BP, Letourneur Y (2009) Assessing the stocks of the primary snappers caught in Northeastern Brazilian Reef Systems. 2-A multi-fleet age-structured approach. Fish Res 99:97–105

Freitas LM, Oliveira MDM, Leão ZMAN, Kikuchi RKP (2019) Effects of turbidity and depth on the bioconstruction of the Abrolhos reefs. Coral Reefs 38:241–253

Froese R, Pauly D (ed) (2019) FishBase. World Wide Web electronic publication. www.fishbase.org, accessed in April 2019

Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. Mar Ecol Prog Ser 230:253–264

Friedlander A, Sandin S, DeMartini EE, Sala E (2010) Spatial patterns of the structure of reef fish assemblages at a pristine atoll in the central Pacific. Mar Ecol Prog Ser 410:219–231

Friedlander AM, Caselle JE, Ballesteros E, Brown EK, Turchik A, Sala E (2014) The real bounty: marine biodiversity in the Pitcairn Islands. PLoS ONE 9(6):e100142

Fujii MT, Cocentino ALM, Pereira SMB (2001) Ceramium nitens (Ceramiaceae, Rhodophyta), an uncommon species from Brazil. Revista Brasileira de Botânica 24(3):359–363. https://doi.org/10.1590/s0100-84042001000300014

FUNBIO (2019) Termo de referência para contratação de consultoria pessoa jurídica especializada para elaborar o plano de manejo da unidade deconservação "Parque Estadual Marinho do Parcel de Manuel Luís", no estado do Maranhão (termo de referência no. 2018.0822.00057-5). Available only inportuguese at https://www.funbio.org.br/wp-content/uploads/2020/01/TdR-2018.0822.00057-5.pdf. Accessed 10 June 2020

Gerhardinger LC, Bertoncini AA, Hostin-Silva, (2006) Local ecological knowledge and Goliath grouper spawning aggregations in the South Atlantic Ocean: Goliath grouper spawning aggregations in Brazil. Traditional Marine Resource Management and Knowledge Information Bulletin 20:33–34

Gouveia NA, Gherardi DFM, Wagner FH, Paes ET, Coles VJ, Aragão LEOC (2019) The salinity structure of the Amazon river plume drives spatiotemporal variation of oceanic primary productivity. J Geophys Res Biogeosci 124:147–165

Graham NAJ, McClanaham TR (2013) The last call to wilderness? Bioscience 63(5):397–402

Green AL, Fernandes L, Almany G, Abesamis R, McLeod E, Aliño PM, White AT, Salm R, Tanzer J, Pressey RL (2014) Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. Coast Manage 42:143–159

Gualberto LPS, El-Robrini M (2005) Faciologia da cobertura sedimentar superficial da plataforma continental do Maranhão. Estudos Geológicos 15:234–243

Guilhem I, Mais B, Creed J (2020) Impact of invasive *Tubastraea* spp. (Cnidaria: Anthozoa) on the growth of the space dominating tropical rocky-shore zoantharian *Palythoa caribaeorum* (Duchassaing and Michelotti, 1860). Aquat Invasions 15:98–113

Hancock P (2020) Stellar Banner. Accessed on 18th of June 2020. Available at https://shipwrecklog.com/log/2020/02/stellar-banner/

Harborne AR, Mumby PJ (2018) FAQs about Caribbean parrotfish management and their role in reef resilience. In: Bonaldo RM (ed) Hoey AS. Biology of parrotfishes. CRC Press Taylor & Francis Group, Florida, USA

Honório PPF, Ramos RTC, Feitoza BM (2010) Composition and structure of reef fish communities in Paraiba State, north-eastern Brazil. J Fish Biol 77(4):907–926

Hothorn T, Bretz F, Peter W (2008) Simultaneous inference in general parametric models. Biometrical J 20:346–363

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 25(11):633–642

ICMBio (2018) Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Vols I - 6. Brasília, DF: ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade)/MMA (Ministério do Meio Ambiente), 492 pp

IBAMA – Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais (2018) Online permit documentation. Available at: https://servicos.ibama.gov.br/licenciamento/consulta_empreendimentos.php. Accessed 26 Feb 2018

Jackson JBC, Sala E (2001) Unnatural oceans. Sci Mar 65:273–281

Klein EL, Moura CAV (2003) Síntese geológica e geocronológica do Cráton São Luís e do Cinturão Gurupi na região do Rio Gurupi (NE-Pará / NW-Maranhão). Geol USP Sér Cient 3:97–112

Leão ZMAN, Kikuchi PKP, Testa V (2003) Corals and coral reefs of Brazil. In: Cortés J (ed) Latin American Coral Reefs. Elsevier Science B. p 9–52. https://doi.org/10.1016/B978-044451388-5/50003-5

León PSD, Acuña-Marrero D, Rastoin E, Friedlander AM, Donovan MK, Sala E (2016) Largest global shark biomass found in the northern Galápagos Islands of Darwin and Wolf. PeerJ, 4

Lellys NT, De Moura RL, Bonaldo RM, Francini-Filho RB, Gibran FZ (2019) Parrotfish functional morphology and bioerosion on SW Atlantic reefs. Marine Ecol Prog Ser 629:149–163. https://doi.org/10.3354/meps13102

Loiola M, Cruz ICS, Lisboa DS, Mariano-Neto E, Leão ZMAN, Oliveira MDM, Kikuchi RKP (2019) Structure of marginal coral reef assemblages under different turbidity regime. Mar Environ Res 147:138–148

Longo GO, Floeter SR (2012) Comparison of remote video and diver's direct observations to quantify reef fishes feeding on benthos in coral and rocky reefs. J Fish Biol 81:1773–1780

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

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

Luiz OJ, Allen AP, Robertson DR, Floeter SR, Kulbicki M, Vigliola L, Becheler R, Madin JS (2013) Adult and larval traits as determinants of geographic range size among tropical reef fishes. P Natl Acad Sci USA 110(41):16498–16502

Magris RA, Grech A, Pressey RL (2018) Cumulative human impacts on coral reefs: assessing risk and management implications for Brazilian coral reefs. Diversity 10(2):26

Mahiques MM, Siegle E, Francini-filho RB, Thompson FL, Rezende CE, Gomes JD, Asp NE (2019) Insights on the evolution of the living Great Amazon Reef System, equatorial West Atlantic. Sci Rep 9:13699

Maida M, Ferreira BP (1997) Coral reefs of Brazil overview and field guide. Proceedings 8th International Coral Reef Symposium 1:263–274

Martins APB, Feitosa LM, Lessa RP, Almeida ZS, Heupel M, Silva WM, Tchaicka L, Nunes JLS (2018) Analysis of the supply chain and conservation status of sharks (Elasmobranchii: Superorder Selachimorpha) based on fisher knowledge. PLoS ONE 13(3):e0193969

McCook LJ (1996) Effects of herbivores and water quality on *Sargassum* distribution on the central Great Barrier Reef: cross-shelf transplants. Mar Ecol Prog Ser 139:179–192

Meirelles PM, Amado-Filho GM, Pereira-Filho GH, Pinheiro HT, de Moura RL, Joyeux J-C et al (2015) Baseline assessment of mesophotic reefs of the Vitória-Trindade seamount chain based on water quality, microbial diversity, benthic cover and fish biomass data. PLoS ONE 10(6):e0130084. https://doi.org/10.1371/journal.pone.0130084

MMA – Ministério do Meio Ambiente (2016) Portaria N°19 - Plano de Ação Nacional para a Conservação dos Ambientes Coralíneos – PAN Corais (Processo n° 02070.001393/2013–01).

Morais RA, Ferreira CEL, Floeter SR (2017) Spatial patterns of fish standing biomass across Brazilian reefs. J Fish Biol 91(6):1642–1667

Motta FS, Moura RL, Francini-Filho RB, Namora RC (2009) Notas sobre a biologia reprodutiva e alimentar de elasmobrânquios no Parque Estadual Marinho Parcel Manoel Luís, Maranhão, Brasil. Pan-Am J Aquat Sci 4:593–598

Mouillot D, Villeger S, Parravicini V, Kulbicki M, Arias-Gonzalez JE, Bender M, Chabanet P, Floeter SR, Friedlander A, Vigliola L, Bellwood DR (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc Natl Acad Sci 111(38):13757–13762

Moura RL, Rodrigues-Martins MC, Francini-Filho RB, Sazima I (1999) Unexpected richness of reef corals near the southern Amazon river mouth. Coral Reefs 18:170

Moura RL, Secchin NA, Amado-Filho GM, Francini-Filho RB, Freitas MO, Minte-Veta CV, Teixeira JB, Thompson FL, Dutra GF, Sumida PYG, Guth AZ, Lopes RM, Bastos AC (2013) Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. Cont Shelf Res 70(1):109–117

Moura RL, Amado-Filho GM, Moraes FC, Brasileiro PS, Salomon PS, Mahiques MM, Bastos AC, Almeida MG, Silva JM Jr, Araujo BF, Brito FP, Rangel TP, Oliveira BCV, Bahia RG, Paranhos RP, Dias RJS, Siegle E, Figueiredo AG Jr, Pereira RC, Leal CV, Hajdu E, Asp NE, Gregoracci GB, Neumann-Leitão S, Yager PL, Francini-Filho RB, Fróes A, Campeão M, Silva BS, Moreira APB, Oliveira L, Soares AC, Araujo L, Oliveira NL, Teixeira JB, Valle RAB, Thompson CC, Rezende CE, Thompson FL (2016) An extensive reef system at the Amazon River mouth. Sci Adv 2:e1501252

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Conserv Biol 4(4):355–364

Oksanen J, Blanchet FG, Kindt R et al (2015) vegan: Community Ecology Package. R package version 2:3–4

Omachi CY, Aspa NE, Siegleb E, Couceiro MAA, Francini-Filho RB, Thompson FL (2019) Light availability for reef-building organisms in a plume-influenced shelf. Cont Shelf Res 181:25–33

Perkol-Finkel S, Shashar N, Benayahu Y (2006) Can artificial reefs mimic natural reef communities? The roles of structural features and age. Marine Environ Res 61(2):121–135. https://doi.org/10.1016/j.marenvres.2005.08.001

Pinheiro HT, Rocha LA, Macieira RM, Carvalho-Filho A, Anderson AB, Bender MG, Di Dario F, Ferreira CEL, Francini-Filho RB, Gasparini JL et al (2018) Southwestern Atlantic reef fishes: zoogeographic patterns and ecological drivers reveal a secondary biodiversity center in the Atlantic Ocean. Divers Distrib 24:951–965

Richter C, Wunsch M, Rasheed M, Kötter I, Badran MI (2001) Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. Nature 413:726–730

Rilov G, Benayahu Y (2000) Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. Mar Biol 136(5):931–952

Robinson JPW, Williams ID, Edwards AM, McPherson J, Yeager L, Vigliola L, Baum JK (2017) Fishing degrades size structure ofcoral reef fish communities. Global Change Biol 23(3):1009–1022. https://doi.org/10.1111/gcb.13482

Rocha LA (2003) Patterns of distribution and processes of speciation in Brazilian reef fishes. J Biogeogr 30(8):1161–1171

Rocha LA, Rosa IL (2001) Baseline assessment of reef fish assemblages of Parcel Manuel Luiz Marine State Park, Maranhão, north-east Brazil. J Fish Biol 58(4):985–998

Rocha LA, Bass AL, Robertson DR, Bowen BW (2002) Adult habitat preferences, larval dispersal and the comparative phylogeography of three Atlantic Acanthurus (Teleostei: Acanthuridae). Mol Ecol 11(2):243–252

Roos NC, Pennino MG, Carvalho AR, Longo GO (2019) Drivers of abundance and biomass of Brazilian parrotfishes. Mar Ecol Prog Ser 623:117–130

Roos NC, Taylor BM, Carvalho AR, Longo GO (2020) Demography of the largest and most endangered Brazilian parrotfish, *Scarus trispinosus*, reveals overfishing. Endang Species Res 41:319–327

Russ GR, Questel SA, Rizzari JR, Alcala AC (2015) The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. Mar Biol 162:2029–2045

Sala E, Ballesteros E, Dendrinos P, Di Franco A, Ferretti F, Foley D, Simonetta F, Friedlander A, Garrabou J, Güçlüsoy H, Guidetti P, Halpern BS, Hereu B, Karamanlidis AA, Kizilkaya Z, Macpherson E, Mangialajo L, Mariani S, Micheli F, Pais A, Riser K, Rosenberg AA, Sales M, Selkoe KA, Starr R, Tomas F, Zabala M (2012) The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. PLoS ONE 7(2):e32742

Sandin S, Smith J, Demartini E, Dinsdale E, Donner S et al (2008) Baselines and degradation of coral reefs in the northern Line Islands. PLoS ONE 3:e1548

Santos CSG, Lino JB, Veras PC, Amado-Filho GM, Francini-Filho RB, Motta FS, Moura RL, Pereira-Filho GH (2016) Environmental licensing on rhodolith beds: insights from a worm. Nat Conserv 14(2):137–141

Schutter VGW, Selig ER, Bruno JF (2010) Regional spatio-temporal trends in Caribbean coral reef benthic communities. Mar Ecol Prog Ser 402:115–122

Segal B, Castro CB (2011) Coral community structure and sedimentation at different distances from the coast of the Abrolhos Bank. Brazil Braz J Oceanogr 59(2):119–129

Simon T, Pinheiro HT, Joyeux J-C (2011) Target fishes on artificial reefs: evidences of impacts over nearby natural environments. Sci Total Environ 409(21):4579–4584

Simon T, Joyeux J-C, Pinheiro HT (2013) Fish assemblages on shipwrecks and natural rocky reefs strongly differ in trophic structure. Mar Environ Res 90:55–65

Soares MO, Lotufo TMC, Vieira ML, Salani S, Hadju E, Matthews-Cascon, H, Leão ZMAN, Kikuchi RKP (2016) Brazilian marine animal forests: a new world to discover in the Southwestern Atlantic. p.1–38 In: Rossi S, Bramanti L, Gori A, del Valle COS (Org.) Marine Animal Forests. 1ed. Springer, Cham

Stukel MR, Coles VJ, Brooks MT, Hood RR (2014) Top-down, bottom-up and physical controls on diatom-diazotroph assemblage growth in the Amazon River plume. Biogeosciences 11:3259–3278

Terashima H, Sato M, Kawasaki H, Thiam D (2007) Quantitative biological assessment of a newly installed artificial reef in Yenne. Senegal Zool Stud 46(1):69–82

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

Tucker CM, Cadotte MW, Carvalho SB, Davies TJ, Ferrier S, Fritz SA, Grenyer R, Helmus MR, Jin LS, Mooers AO, Pavoine S, Purschke O, Redding DW, Rosauer DF, Winter M, Mazel F (2017) A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biol Rev 92:698–715

UNCTAD - United Nations Conference on Trade and Development (2018) Review of maritime transport. Geneva, Switzerland, 162p

Vale NF, Amado-Filho GM, Braga JC, Brasileiro PS, Karez CS, Moraes FC, Bahia RG, Bastos AC, Moura RL (2018) Structure and composition of rhodoliths from the Amazon River mouth, Brazil. A S Am Earth Sci 84:149–159

Van Soest RWM, Boury-Esnault N, Hooper JNA, Rützler K, de Voogd NJ, Alvarez B, Hajdu E, Pisera AB, Manconi R, Schönberg C, Klautau M, Picton B, Kelly M, Vacelet J, Dohrmann M, Díaz M-C, Cárdenas P, Carballo JL, Rios P, Downey R (2017) World Porifera database. Accessed at https://www.marinespecies.org/porifera on 2019–10–20

Vázquez DP, Melián CJ, Williams NM, Blüthgen N, Krasnov BR, Poulin R (2007) Species abundance and asymmetric interaction strength in ecological networks. Oikos 116(7):1120–1127

Vermeij MJA, Moorselaar IV, Engelhard S, Hörnlein C, Vonk SM, Visser PM (2010) The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrowth coral in the Caribbean. PLoS ONE 5(12):e14312

Vilar CC, Magris RA, Loyola R, Joyeux J-C (2020) Strengthening the synergies among global biodiversity targets to reconcile conservation and socio-economic demands. Aquat Conserv 30(3):497–513

Ward-Paige C, Flemming JM, Lotze HK (2010) Overestimating fish counts by non-instantaneous visual censuses: Consequences for population and community descriptions. PLoS ONE 5(7):1–9. https://doi.org/10.1371/journal.pone.0011722

Williams ID, Polunin NVC (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19:358–366