



Turbidity shapes shallow Southwestern Atlantic benthic reef communities

Erika F.C. Santana^a, Miguel Mies^{b,c}, Guilherme O. Longo^d, Rafael Menezes^a, Anaide W. Aued^e, André Luís Luza^f, Mariana G. Bender^f, Barbara Segal^g, Sergio R. Floeter^e, Ronaldo B. Francini-Filho^{h,*}

^a Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Universidade Federal da Paraíba, Cidade Universitária, 58059-900, JP, PB, Brazil

^b Instituto Oceanográfico, Universidade de São Paulo, SP, Brazil

^c Instituto Coral Vivo, Santa Cruz Cabralia, BA, Brazil

^d Laboratório de Ecologia Marinha, Departamento de Oceanografia e Limnologia, Universidade Federal do Rio Grande do Norte, Natal, RN, 59014-002, Brazil

^e Laboratório de Biogeografia e Macroecologia Marinha, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, 88040-970, SC, Brazil

^f Laboratório de Macroecologia e Conservação Marinha, Universidade Federal de Santa Maria, Santa Maria, RS, Brazil

^g Laboratório de Ecologia de Ambientes Recifais, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, 88040-970, SC, Brazil

^h Laboratório de Ecologia e Conservação Marinha, Centro de Biologia Marinha, Universidade de São Paulo, 11612-109, São Sebastião, SP, Brazil

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ABSTRACT

Southwestern Atlantic reefs (Brazilian Province) occur along a broad latitudinal range (~5°N–27°S) and under varied environmental conditions. We combined large-scale benthic cover and environmental data into uni- and multivariate regression tree analyses to identify unique shallow (<30 m) benthic reef communities and their environmental drivers along the Brazilian Province. Turbidity was the leading environmental driver of benthic reef communities, with the occurrence of two main groups: clear-water (dominated by fleshy macroalgae) and turbid (dominated by turf algae). Seven out of 14 scleractinian coral species were more abundant in the turbid group, thus corroborating the photophobic nature of some Brazilian corals. The most abundant scleractinian in Brazil (*Montastraea cavernosa*), largely dominated (71–93% of total coral cover) both, the shallow turbid and deeper clear-water reefs. Because these habitat types are widely recognized as potential climate refuges, local threats (e.g. pollution, overfishing) should be averted.

1. Introduction

Benthic reef communities are highly diverse and shaped by a set of biotic interactions and environmental conditions. At small spatial scales (tens of meters to a few kilometers) biotic interactions, disturbance regimes and variables such as water motion and bottom complexity, determine the cover and composition of benthic communities (Longo et al., 2015; Williams et al., 2015). In contrast, over larger spatial scales (tens to hundreds of kilometers) physical/climatic limits imposed by depth and temperature regimes prevail (Gove et al., 2015; Williams et al., 2015). Variations in background (historical) physical conditions are more pronounced over broad depth, cross-shelf and latitudinal gradients (Wismer et al., 2009; Matheus et al., 2019), and thus lead to adaptive responses of organisms and differentiation of benthic communities at geographical scales (Aued et al., 2018; Williams et al., 2015). Most studies testing the effects of environmental drivers have

focused on coral communities – and their species richness - over small spatial scales, with only a few multi-taxa broad spatial scale studies based on abundance data available to date (e.g. Jouffray et al., 2015; Williams et al., 2015).

Because depth is often negatively correlated with temperature and light irradiance, it is generally identified as the most influential variable affecting benthic reef communities (Francini-Filho et al., 2013; Williams et al., 2013). Differences in light availability are more important for photosynthetic organisms, particularly corals and algae, which generally dominate in shallow well-lit habitats (Vermeij and Bak 2002). Inshore reefs are influenced by nutrients and sediment input from land, while deeper reefs closer to the shelf break are usually affected by cold and nutrient-rich waters from upwelling (Andrews and Gentien 1982; Rovira et al., 2019). Such influences may explain, for example, the dominance of sediment-resistant coral species on nearshore reefs (Loiola et al., 2019; Morgan et al., 2016), as well as increased sponge abundance

* Corresponding author.

E-mail address: francinifilho@usp.br (R.B. Francini-Filho).

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(Lesser 2006; Rovira et al., 2019) and the occurrence of unique benthic communities (Matheus et al., 2019) in deeper reefs closer to the shelf break.

Increased turbidity, as often found in coastal reefs, may decrease the availability of photosynthetically active radiation and bury reef corals, thus compromising coral recruitment, growth and reproductive output (Rogers 1990; Browne et al., 2014; Junjie et al., 2014). However, some coral taxa can cope with and even thrive under naturally high turbidity levels through adaptations such as a massive colony morphology and large polyps (Logan 1988; Loiola et al., 2013), efficient sediment removal (Lasker 1980), enhanced heterotrophy (Anthony 2006; Mies et al., 2018) and the preferential association with different phylotypes of symbiodiniaceans (Cooper et al., 2011; Rowan and Knowlton 1995). In fact, rich and extensive coral communities under natural high turbidity regimes were recently discovered worldwide (Zweifler et al., 2021) and there is geological evidence for extensive reef development on turbid waters over millennial time scales (Smithers and Larcombe 2003; Palmer et al., 2010; Perry and Smithers 2011).

Southwestern Atlantic reefs are within the Brazilian Province (Briggs 1974; Castro and Pires 2001; Pinheiro et al., 2018). Brazilian corals are adapted to high turbidity levels caused by the influx and resuspension of terrigenous sediments, a condition particularly prevalent on shallow inshore reefs influenced by the discharge of several large rivers along the coast (Leão et al., 2003; Mies et al., 2020). Turbidity is believed to have shaped the composition and evolution of coral communities in the Brazilian Province (Leão et al., 2003) and may function as a buffer against coral bleaching in the face of global warming by attenuating light intensity (Mies et al., 2020). Brazilian reefs host a depauperate coral fauna in comparison with the Caribbean and Indo-Pacific regions, but with a relatively high endemism rate for scleractinians (about 30%) (Leão et al., 2003). The absence of branching scleractinians (Coni et al., 2013; Luza et al., 2022) and the dominance of algae and zoanthids (Reverter et al., 2021; Aued et al., 2018) are other peculiar features of Brazilian reefs. In addition, reefs are mostly continental, with only four oceanic sites (Rocas Atoll and the archipelagos of Fernando de Noronha, Trindade/Martim Vaz and St. Peter and St. Paul's) that are impoverished outposts of the continental reef biodiversity (Leão et al., 2003; Aued et al., 2018; Pinheiro et al., 2018).

Brazilian reefs are spread along a broad latitudinal range ($\sim 5^{\circ}\text{N}$ - 27°S) and subjected to varied environmental conditions (Spalding et al., 2007), thus providing a unique opportunity to evaluate possible adaptive responses of benthic reef communities to background environmental conditions. Although several local-scale studies about benthic reef communities were published in the last decade (e.g. Villaçã and Pitombo, 1997; Oigman-Pszczol et al., 2004; Ghilardi et al., 2008; Francini-Filho et al., 2013; Magalhães et al., 2015), as well as a recent broad-scale assessment for the region (Aued et al., 2018), a comprehensive study evaluating the environmental drivers of benthic reef communities at the province scale is still missing.

We aimed to assess how environmental variables shape shallow (<30 m depth) benthic reef communities along the Brazilian Province. We used multivariate and univariate machine learning techniques (regression trees) to identify possible non-linear relationships and thresholds of benthic communities along environmental gradients. We hypothesize that turbidity is the most important variable affecting not only coral assemblages, but the structure of the entire benthic reef communities. Our integrative analyses were performed using the most comprehensive dataset for Brazilian benthic reef communities available to date and large-scale climatological data obtained through remote sensing.

2. Material and methods

2.1. Study system

Different types of reefs were sampled along the Brazilian coast

between 2008 and 2018. Temporal data for Brazilian reefs indicate that major spatial patterns in benthic community structure are consistent through time (e.g. Francini-Filho et al., 2013; Zamoner et al., 2021). The north/northeastern and central coasts are dominated by sandstone (beach rock) and biogenic reefs, while rocky reefs prevail from the central coast (Espírito Santo State, 20°S) to southern Brazil (Santa Catarina State, 27°S). Three out of the four Brazilian oceanic sites (the archipelagos of Fernando de Noronha, Trindade/Martim Vaz and St. Peter and St. Paul's) comprise rocky reefs with sparse coral formations, while the Rocas Atoll is a biogenic reef mostly built by calcareous algae (Gherardi and Bosence 2001). Shelf width varies from ~ 10 to 300 km along the coast and from ~ 0.5 to 5 km in oceanic islands. In the southeastern coast, reefs are seasonally subjected to cold ($\sim 15^{\circ}\text{C}$) and enriched waters from upwelling and the South Atlantic Central Waters (SACW) (Ekau and Knoppers 1999; Valentim 2001; Castro 2014). Upwelling is also a common feature in the oceanic St. Peter and St. Paul's Archipelago (SPSPA) (Moreira et al., 2015).

We used primary data for the four Brazilian oceanic islands and the coast (139 sites distributed between $0^{\circ}55'\text{N}$ - $27^{\circ}00'\text{S}$) (see Fig. 2). Sites were composed by a combination of location and depth strata (Table S1). Part of this database is already available through published work focused on specific locations (Pereira-Filho et al., 2011; Francini-Filho et al., 2013; Longo et al., 2015; Magalhães et al., 2015; Aued et al., 2018; Matheus et al., 2019). Benthic cover was estimated using two different methodologies based on photo-quadrats (cf. Francini-Filho et al., 2013; Aued et al., 2018). In total, 1547 samples (photo-quadrats) were obtained between 0 and 30 m depth. Unpublished data and those provided by Pereira-Filho et al. (2011), Francini-Filho et al. (2013), Magalhães et al. (2015) and Matheus et al. (2019) were obtained using 66×75 cm quadrats, with 5–33 haphazardly allocated replicates obtained per site (i.e. total area surveyed of 2.5–16.3 m^2). Data from Aued et al. (2018) were obtained with 25×25 cm quadrats and with 40–150 haphazardly distributed replicates obtained per site (i.e. total area surveyed of 20–75 m^2). Images obtained with the 66×75 cm quadrats were analyzed through the identification of organisms immediately under 300 randomly assigned points using the Coral Point Count with Excel extensions software (CPCe; Kohler and Gill 2006), while images from 25×25 cm quadrats were analyzed by overlaying 50 random points per image using the photoQuad software (Trygonis and Sini 2012). The differences in photos' size and the number of points used for organisms' identification should have a minimal effect on the results obtained, as we considered conspicuous groups using a gross taxonomic resolution. In addition, our sampling size (number of photos and points) is relatively high in comparison to most previous work (Dumas et al., 2009; Molloy et al., 2013; Bryant et al., 2017). Finally, auto similarity curves for relative cover data indicated that sample size was sufficient for all sites. The curves were calculated by iteratively estimating average similarity values (Bray-Curtis) between randomly selected samples (cf. Schneck and Melo 2010) and sufficient sample size (i.e. when resemblance reaches an asymptote) were attained with 4–5 samples for both methods. Species level identification was possible for scleractinians only. To avoid potential bias related to differences in taxonomic resolution among benthic groups, organisms were grouped for further analyses as follows: ascidians, bryozoans, crustose calcareous algae (CCA), cyanobacterial mats, fire-corals, fleshy macroalgae, octocorals, *Palythoa* spp., other zoanthids, scleractinian corals, sponges and turf algae (i.e. < 2 cm multi-specific filamentous algae). The abiotic categories "rock" and "sand" were also considered. The composition and relative abundance of the different coral species were still considered for comparisons among the seven different communities delimited by our regression tree (see below). The full dataset is available at <https://zenodo.org> (under DOI 10.5281/zenodo.7299381).

2.2. Environmental variables

Environmental data were obtained from the *Moderate Resolution*

Imaging Spectroradiometer (MODIS Aqua) (available at <http://oceandata.sci.gsfc.nasa.gov>) with 4 km² resolution. Global means for each site were calculated based on annual means for 2002–2017. Using means from time-series data instead of temporal snapshots is a more comprehensive approach, as benthic communities may be shaped by long-term patterns in environmental conditions (Mumby et al., 2004; Gove et al., 2013). The variables selected are widely known to affect benthic reef communities' structure (Couce et al., 2012; Gove et al., 2013) and include: mean sea surface temperature, chlorophyll concentration (CLO), particulate organic carbon (POC), the diffuse attenuation coefficient (Kd490, a proxy for turbidity; Wang et al., 2009) and photosynthetically active radiation (PAR, at 400 and 700 nm). Additional data (annual means for 2002–2009) for salinity and for nitrate and phosphate concentrations were obtained from Bio-Oracle (Tyberghein et al., 2012) with a 9 km² resolution. Depth was measured *in situ* and distances from the sampling sites to the coast and to the shelf break were estimated using digital nautical charts in QGIS (QGIS Development Team, 2020). Latitude was also added to the list of explanatory variables.

2.3. Statistical analyses

We used a Multivariate Regression Tree (MRT) based on average environmental and benthic cover values for each site to delimit unique benthic communities and to identify thresholds in environmental parameters responsible for their differentiation. The MRT is a constrained clustering algorithm that repeatedly splits samples into groups with the aim of finding the combination leading to the most homogeneous within-group (and the most heterogeneous between-group) variation possible. Homogeneity is measured as the sum of squares about the multivariate mean of each tree node. There are no assumptions on the relationship between variables and the best solution (i.e. the one with the highest predictive accuracy) is obtained through cross-validation (De'ath 2002). To minimize differences in abundance among rare and dominant benthic groups, community data were converted to arcsine square root. We have compared the MRT solution with the result from an unconstrained ordination (Principal Component Analysis, PCA) to estimate the magnitude of unexplained variation due to the possible absence of important explanatory variables not included in the MRT (De'ath 2002).

Univariate regression trees (Boosted Regression Trees, BRT) were used to evaluate the relative influence of different environmental variables on specific benthic groups following the procedures of Elith et al. (2008). Boosted Regression Tree is a method that applies machine learning techniques (boosting) to select the subset of variables with the strongest predictive capacity through recursive binary splits. Iterative training is performed through the combination of three parameters: i) bag-fraction, ii) learning rate and iii) tree complexity. The bag-fraction is the proportion of data selected at random at each step; learning rate indicates the contribution of each additional tree, and tree complexity measures the number of splits (nodes) of each tree. All BRT models were built by checking all possible combinations of values for bag-fraction (0.5 and 0.75), learning rate (0.0001, 0.0005, 0.001, 0.005, 0.01 and 0.05) and tree complexity (1–5) and run with untransformed data based on Gaussian distribution of the dependent variable. Multicollinearity among predictors was verified using the Variance Inflation Factor (VIF), with a value of five set as the cut off (ter Braak and Smilauer, 2002). As a result, the following variables were removed: chlorophyll *a* concentration, distance to the shelf break (100 m isobath), latitude, particulate organic carbon concentration (POC), photosynthetically available radiation (PAR) and phosphate concentration. The correlation matrix for the variables retained for the analyses is given in Fig. S1.

Unpaired student's *t* tests calculated using log₁₀(*x*+1) transformed data were used to compare abundance of each organism/category between the two main groups of communities identified by the MRT: "turbid" and "clear-water" (see below). To avoid bias in interpretation of results from multiple pairwise comparisons (Nakagawa 2004) we

calculated effect sizes with threshold values set at *d* ≤ 0.2 (small), 0.2–0.8 (medium) and >0.8 (large) (Cohen 1992).

All analyses were carried out in R (version 3.5.1) (R Core Team 2021).

3. Results

Brazilian benthic reef communities are largely dominated by turf algae (mean global cover = 44.5%) followed by fleshy macroalgae (17.3%), CCA (8.5%), scleractinians (7.5%), *Palythoa* spp. (5%), sponges (3.1%), and cyanobacterial mats (1.6%). The remaining organisms accounted for <1% of the total cover. The most abundant abiotic component was sand, which represented 7.4% of the total coverage.

The best MRT model delimited seven unique benthic reef communities within the Brazilian Province and explained 42% of the data (cross-validated relative error = 0.7). The first two axes of the PCA explained 88.7% of the data variability, suggesting additional explanation could be obtained in the MRT by adding other (unknown) explanatory variables. The first and most pronounced split of the tree (21.4% of the data variation) discriminated two groups, one with clear waters (<0.066 Kd490.m⁻¹) and dominated by fleshy macroalgae (hereafter called "clear-water" group) and another with turbid waters (≥0.066 Kd490.m⁻¹) and dominated by turf algae (hereafter called "turbid" group). As expected, oceanic islands harbored clear-water communities only, but some clear-water communities were also recorded in the continental reefs of the north (Parcel de Manuel Luís) and northeastern coasts (Paraíba and Rio Grande do Norte states) (Figs. 1 and 2).

The clear-water group was further subdivided into three distinct communities that were delimited according to depth and nitrate concentration. Two deep (≥12.5 m) clear-water communities were identified, one with higher nitrate concentrations (≥0.024 μM) and dominated by sponges, recorded at Fernando de Noronha and SPSPA (community one in Fig. 1), and another with lower nitrate (<0.024 μM) and dominated by sand, recorded at the oceanic islands of Trindade and Martim Vaz and the coastal reefs of the Paraíba state (community two). Both of these deep communities showed relatively high abundances of CCA and a striking dominance of the scleractinian *M. cavernosa* (71–92% of the total coral cover). The remaining clear-water community was relatively shallow (<12.5 m) and was recorded at Fernando de Noronha, Parcel de Manuel Luís, Rio Grande do Norte states, Rocas Atoll, SPSPA and Trindade (community three). It was characterized by an increase in turf algae cover and by the dominance of the scleractinian *Siderastrea* spp., with this species attaining 93.1% of the total coral cover (Figs. 1 and 2).

The turbid group was composed by four distinct communities. The first major split separated the inshore (<8.1 km; dominated by turf algae and sand) and offshore (≥8.1 km; dominated by CCA) turbid communities. Two inshore turbid communities were found, one with mean temperatures <27.8 °C and with the highest turf algae cover among all studied communities (community four) and another with temperatures ≥27.8 °C, dominated by sand and with relatively high macroalgae and cyanobacterial cover (community five). Community four was the most prevalent one in the Brazilian coast, occurring from the northeast to the south, while community five was restricted to the northeast coast (Bahia, Paraíba and Rio Grande do Norte states). Two offshore turbid communities were recorded and discriminated according to nitrate levels, with a threshold at 0.013 μM. The community with lower nitrate was restricted to the Abrolhos Bank (community six). It showed relatively high cover of CCA and the highest covers of *Palythoa* spp and scleractinians, particularly *M. cavernosa* and the Brazilian endemic coral *Mussismilia braziliensis*, among all studied communities. Finally, the turbid assemblage with higher nitrate concentration (community seven) was recorded in the northeast (Paraíba state), central (Espírito Santo state) and southeast coasts (Laje de Santos Island and Alcatraz Archipelago, off São Paulo state). It showed relatively high covers of turf and fleshy macroalgae, as well as high abundances of the reef corals *Mussismilia harti* (particularly at Espírito Santo state), and *Madracis decactis*

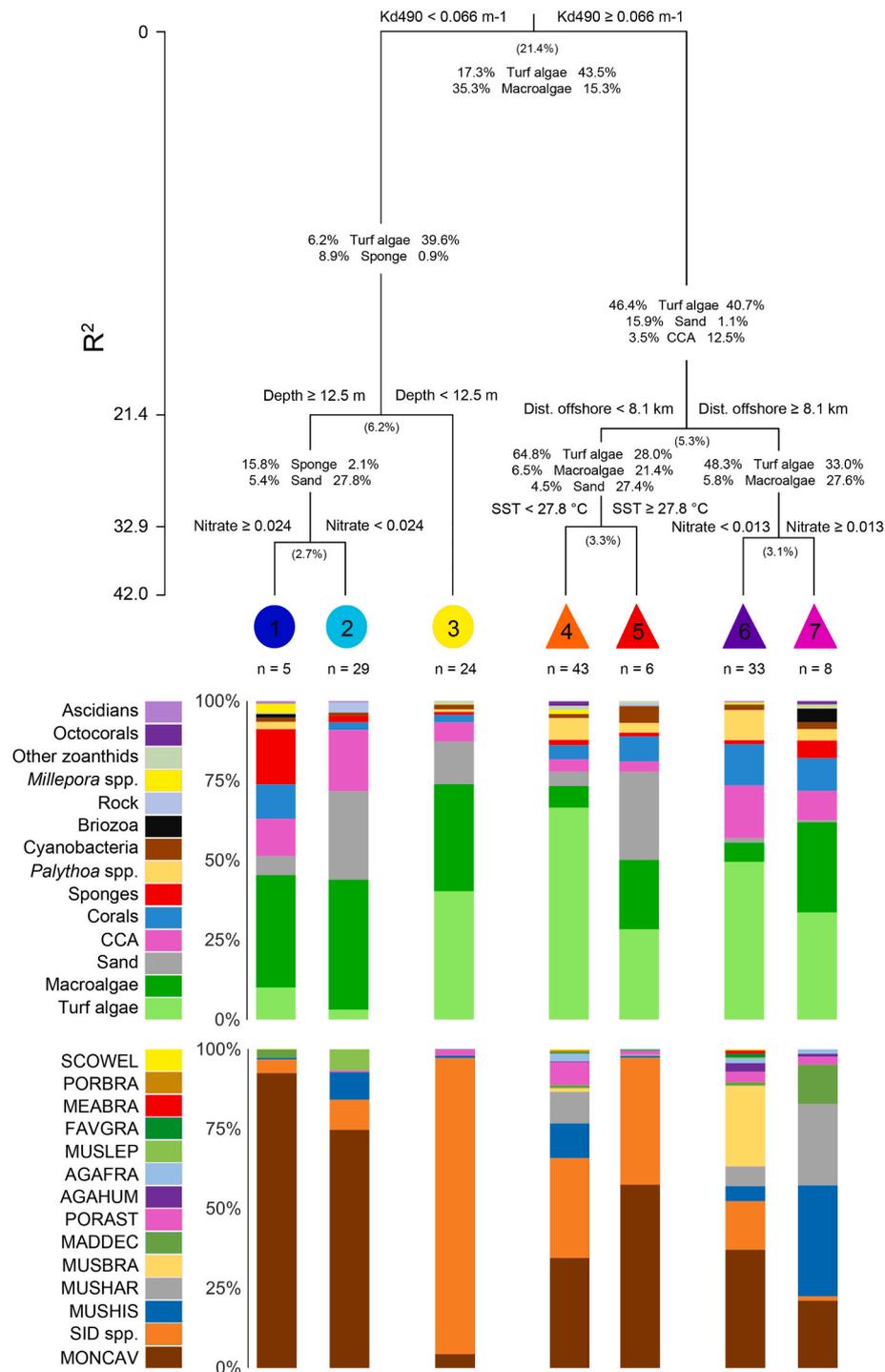


Fig. 1. Multivariate Regression Tree (MRT) for benthic reef communities of the Brazilian Province. Environmental drivers for each split are given in the upper portion, while organisms responsible for the split and the relative contribution of the split to total model variation explained (in parenthesis) are given in the lower portion. Triangles denote the turbid group and circles denote the clear-water ones. Numbers from one to seven denote the individual communities.

and *Mussismilia hispida* (particularly at Espírito Santo and São Paulo states; Figs. 1 and 2).

The univariate BRT models corroborated the major patterns from the MRT. Turbidity was the most important variable affecting the two most abundant benthic organisms within the Brazilian Province: fleshy and turf algae. These benthic groups exhibited opposite patterns, with fleshy macroalgae cover steeply declining and turf algae cover increasing with turbidity values $> 0.05\text{--}0.07 \text{ Kd}_{490} \cdot \text{m}^{-1}$. Turf algae were also particularly abundant at depths $< 15 \text{ m}$. Crustose calcareous algae abundance was higher on deeper reefs (10–25 m) with low nitrate concentrations

($< 0.01 \mu\text{M}$). Scleractinians were more prevalent in depths $> 20 \text{ m}$ and under relatively high salinity (> 37), temperature ($> 26 \text{ }^\circ\text{C}$) and turbidity levels ($> 0.18 \text{ Kd}_{490} \cdot \text{m}^{-1}$). Sponge cover sharply increased with depth and decreased with temperatures $> 24 \text{ }^\circ\text{C}$. Cover of *Palythoa* spp. was highest on reefs shallower than 10 m. Zoanthids other than *Palythoa* spp (mostly *Zoanthus* spp. and *Protospalythoa* sp.) were most abundant on reefs very close to the coast ($< 0.02 \text{ km}$) and with salinity > 37 . Fire-corals (*Millepora* spp.) were more abundant in relatively clear ($< 0.04 \text{ Kd}_{490} \cdot \text{m}^{-1}$) and low salinity (< 36) waters. Finally, octocoral cover was highest in reefs with temperatures ranging 23–24 $^\circ\text{C}$ and with turbidity

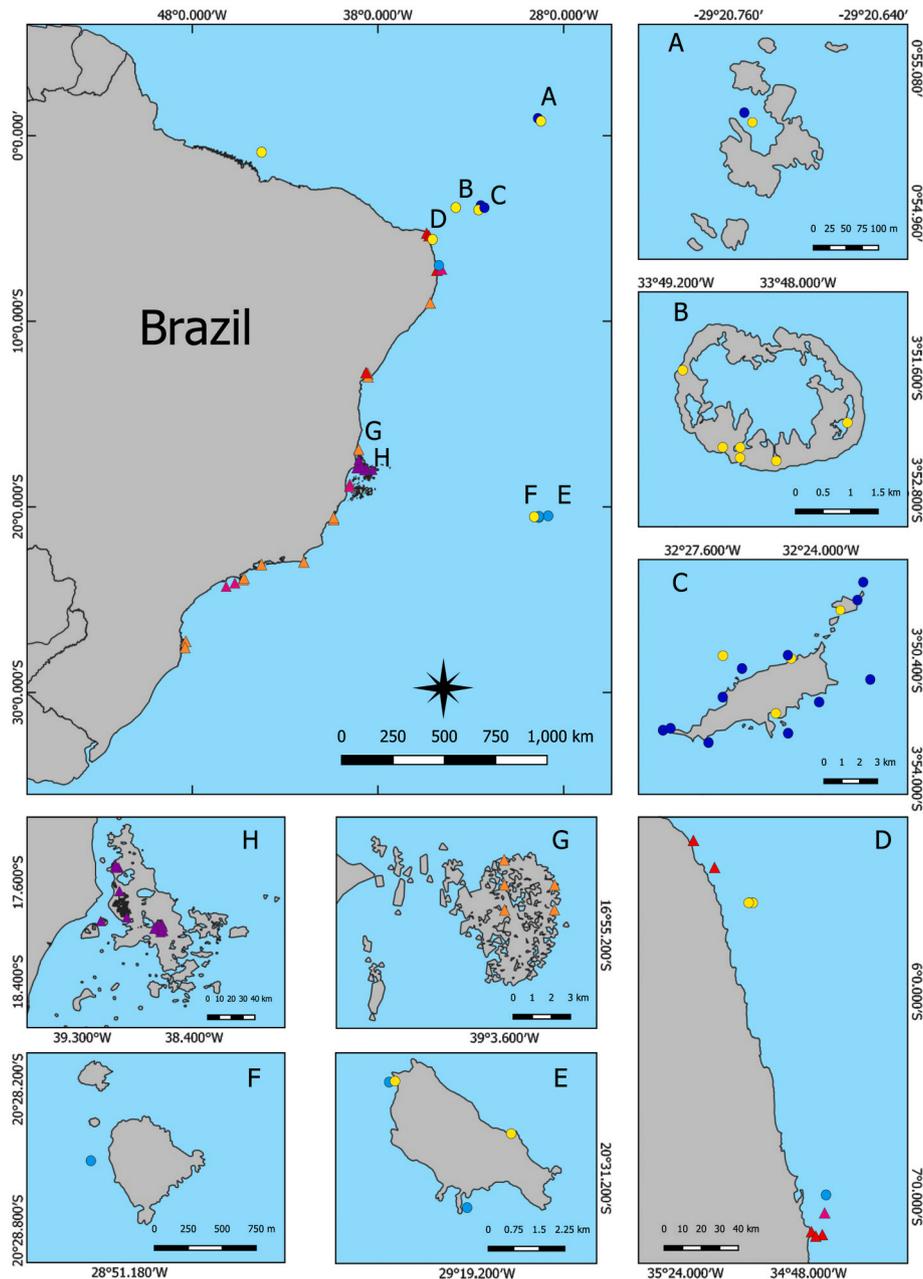


Fig. 2. Spatial distribution of the seven typical communities delimited for the Brazilian Province according to the Multivariate Regression Tree. Triangles denote turbid communities and circles denote clear-water ones. Color codes for sampling stations as in Fig. 1. A – St. Peter and St. Paul’s Archipelago, B – Rocas Atoll, C – Fernando de Noronha, D – NE Brazilian coast (Paraíba and Rio Grande do Norte States), E – Trindade Island, F – Martim Vaz island, G – Itacolomis Reefs and H – Abrolhos Reefs.

$>0.15 \text{ Kd}_{490} \cdot \text{m}^{-1}$ (Fig. 3, Table S2).

Seven out of the 14 scleractinian coral species were more abundant on the turbid group. Octocorals, *Palythoa* spp., scleractinians as a group and turf algae were also more abundant on turbid reefs, while ascidians, fleshy macroalgae and sponges showed higher abundances in the clear-water group (Table 1). All effect sizes for significant differences were in the medium range (0.36–0.8), except for the large effect sizes recorded for turf algae (1.58), flesh macroalgae (1.49) and *M. hispida* (–0.83).

4. Discussion

Sample clustering into the two main groups of benthic reef communities identified within the Brazilian Province (clear-water and turbid) occurred independently from latitudinal gradients in

temperature and productivity, and rather indicated abrupt changes in communities in response to local conditions that affect turbidity (e.g. direct input from rivers along the coast). These relationships illustrate the adaptive response of dominant benthic groups, particularly turf and fleshy macroalgae, to local environmental conditions that end up structuring the entire benthic community.

The high prevalence of turf algae on turbid Brazilian coastal reefs may be explained by a combination of their high tolerance to stress (e.g. low light levels) and the indirect benefits derived from high turbidity (i.e. lower grazing pressure and higher nutrient availability). Turf algae are amongst the most abundant benthic organisms on coral reefs (Goatley and Bellwood 2011) and are fast-growing early-stage colonizers that tolerate stress (Hay 1981, Tebbett and Bellwood, 2019). Their ability to efficiently incorporate sediments from the water column

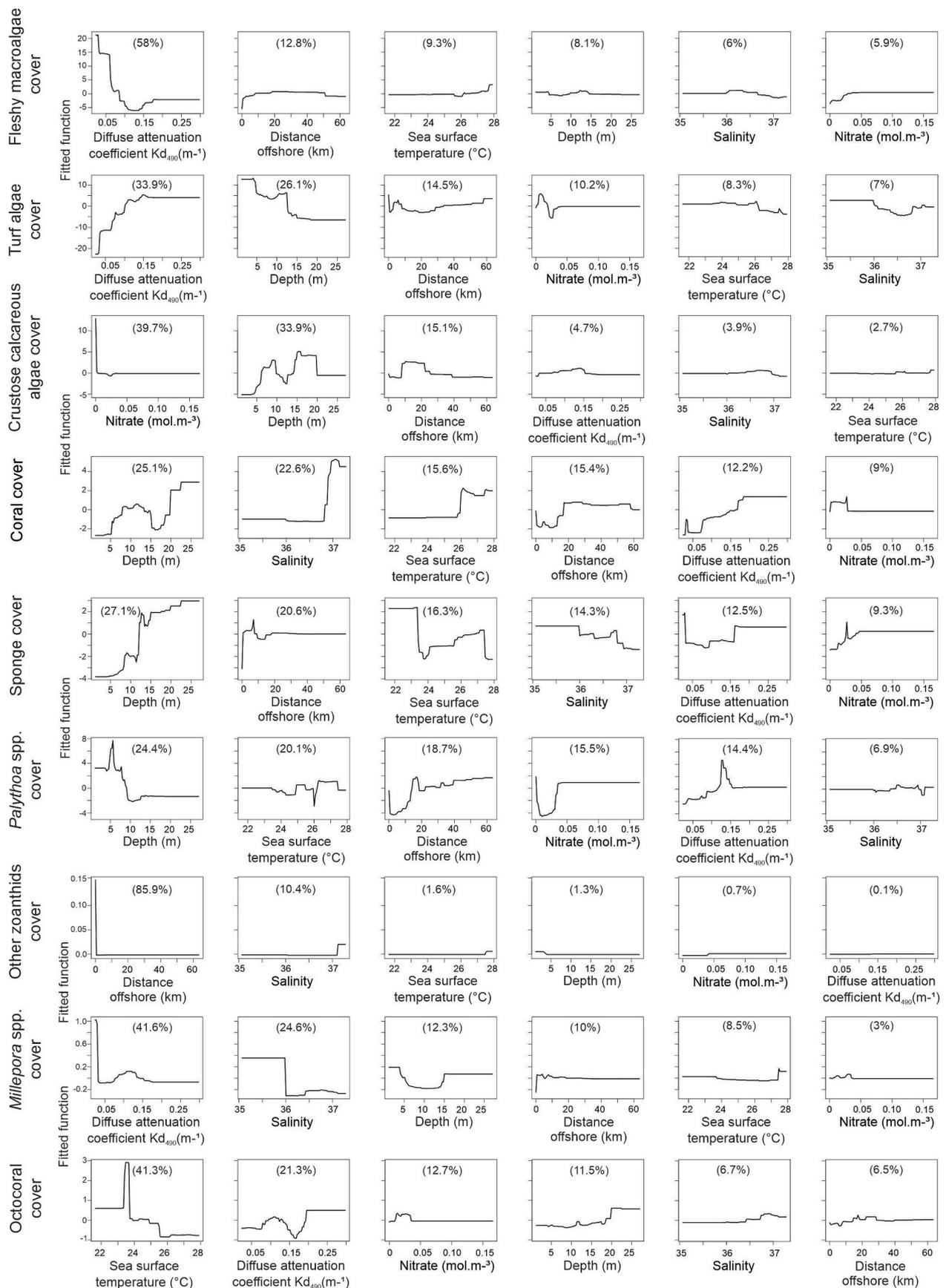


Fig. 3. Partial dependence plots obtained with Boosted Regression Trees (BRT) showing the relative influence of environmental variables on the abundance (% coverage) of different benthic groups. Y axes are centered to have zero mean over the data distribution.

Table 1

Comparison of abundance (cover) of different benthic organisms between the “clear-water” and “turbid” communities, as defined by the Multivariate Regression Tree. Ns = not significant. Significance levels for unpaired t tests and effect sizes (Cohen's d) are given.

Organism	t-value	p	Effect size	comparison
Ascidians	2.58	0.010	0.460	clear-water > turbid
Bryozoans	-1.05	ns	-0.188	clear-water = turbid
Crustose calcareous algae	0.43	ns	0.077	clear-water = turbid
Cyanobacterial mats	0.54	ns	0.09	clear-water = turbid
Fleshy macroalgae	8.38	<0.001	1.49	clear-water > turbid
<i>Millepora</i> spp.	0.51	ns	0.091	clear-water = turbid
Octocorals	-3.41	<0.001	-0.608	clear-water < turbid
Other zoanthids	-1.32	ns	-0.236	clear-water = turbid
<i>Palythoa</i> spp.	-4.48	<0.001	-0.798	clear-water < turbid
Scleractinians (total)	-3.05	0.002	-0.544	clear-water < turbid
<i>Agaricia fragilis</i>	-2.02	0.044	-0.360	clear-water < turbid
<i>Agaricia humilis</i>	-2.86	0.004	-0.510	clear-water < turbid
<i>Favia gravida</i>	-3.47	<0.001	-0.619	clear-water < turbid
<i>Madracis decactis</i>	-0.96	ns	-0.171	clear-water = turbid
<i>Meandrina brasiliensis</i>	-0.82	ns	-0.147	clear-water = turbid
<i>Montastraea cavernosa</i>	0.21	ns	0.038	clear-water = turbid
<i>Mussismilia braziliensis</i>	-3.03	0.002	-0.541	clear-water < turbid
<i>Mussismilia harttii</i>	-3.78	<0.001	-0.674	clear-water < turbid
<i>Mussismilia hispida</i>	-4.66	<0.001	-0.829	clear-water < turbid
<i>Mussismilia leptophylla</i>	-0.03	ns	-0.006	clear-water = turbid
<i>Porites astreoides</i>	-3.15	0.002	-0.560	clear-water < turbid
<i>Porites branneri</i>	-1.46	ns	-0.260	clear-water = turbid
<i>Siderastrea</i> spp.	-1.57	ns	-0.279	clear-water = turbid
<i>Scolymia wellsii</i>	-1.79	ns	-0.319	clear-water = turbid
Sponges	4.35	<0.001	0.774	clear-water > turbid
Turf algae	-8.89	<0.001	1.58	clear-water < turbid

(Goatley et al., 2016; Gordon et al., 2016) leads to a lower grazing pressure (Purcell 2000; Bonaldo and Bellwood 2011) and enhanced growth due to the absorption of sediment-associated nutrients (Entesch et al., 1983; Purcell 2000). An experimental study conducted on coastal Brazilian subtropical reefs detected no influence of fish herbivory on the dynamics of algal assemblages (Cordeiro et al., 2020), but territorial damselfish that are abundant throughout the Brazilian coast can keep algal turfs at early succession stages and enhance algae diversity and biomass (Ferreira et al. 1998). Some fleshy macroalgae, on the other hand, may be negatively impacted by increased sediment loads, mainly through reduced recruitment, growth and survival due to reduced photosynthetically active radiation penetrating the water (Umar et al., 1998; Eriksson and Johansson 2005; Tebbett and Bellwood 2019). Goatley et al. (2016) have suggested that sediment-laden algal turfs may

impede succession and the development of fleshy macroalgae-dominated states. In addition, turbidity is the primary driver of macroalgae loss and turf algae proliferation worldwide (Connell 2005; Tait et al., 2014). Thus, the high natural turbidity along the Brazilian coast may have “trapped” most reefs in a turf-dominated state, while at most clear-water sites, the low turbidity may have favored the development of late successional stages characterized by high fleshy macroalgae cover.

The two shallow and the one mid-depth clear-water communities recorded here showed a sharp increase in abundance and striking dominance of *Siderastrea* spp. corals (up to 97% of the total coral cover). Species within this genus are highly resistant to stress, such as temperature-induced bleaching, fluctuations in salinity, dissection and burial by sediments (Lirman et al., 2002; Lirman and Manzello 2009), with some of these conditions prevailing on the shallow reefs of Brazilian oceanic islands (Longo et al., 2020; Gaspar et al., 2021). The ecological importance of these *Siderastrea* dominated habitats is yet to be determined (see discussion on *Montastraea* reefs below). The two shallow (<4.5 m) clear-water communities dominated Rocas Atoll and were also present at two sites in the Fernando de Noronha Archipelago. They showed remarkably high cover of algal turfs, with similar values to those of some coastal turbid communities (~70%). Variations in turf algae species composition, and differences in the species' ability to colonize and thrive under different environmental conditions (Longo et al., 2015), may explain the dominance of turf algae in both, the shallowest Brazilian clear-water oceanic reefs and turbid coastal reefs (i. e. these communities may be in fact different). For example, Magalhães et al. (2015) showed that the composition of turf algae communities differed along the depth gradient of the SPSPA, with 26 species occurring in the shallow well-lit zone and only a subset (eight species) in the mesophotic zone. In Rocas Atoll, the composition of algal turfs varies between pools that remain connected with the outer reef during low tide, which are predominantly composed of articulated coralline algae, and pools that are isolated in low tide, where algal turfs are mostly filamentous (Longo et al., 2015). Unfortunately, there is no comprehensive data available on turf algae species composition for other Brazilian oceanic and coastal reefs. Future analyses considering a greater taxonomic resolution for algae and other benthic groups may plausibly lead to the identification of a higher number of benthic reef communities within the Brazilian Province.

The deeper clear-water community (14–30 m) showed high abundances of sponges and reef-building organisms (CCA and corals). Increased sponge abundance with depth was expected, as their main food item (picoplankton) also increases with depth (Lesser and Slatery 2013). This pattern led to the proposal of the “sponges increase with depth hypothesis”, which has been supported by several studies in the Caribbean (e.g. Lesser and Slatery 2013; 2018). Further investigations are needed to clarify the role of sponges on energy fluxes on deeper euphotic reefs in Brazil through the “sponge loop” (De Goeij et al., 2013; Silveira et al., 2015). Increased CCA abundance with depth was previously recorded (e.g. Figueiredo and Steneck, 2002; Matheus et al., 2019). Here, this pattern was accompanied by a decrease in abundance of the fast-growing benthic organisms *Palythoa* spp. and turf algae (see Fig. 3), thus corroborating previous studies suggesting spatial competition plays important roles in dominance of CCA across depth gradients (Figueiredo and Steneck, 2002; Francini-Filho et al., 2013).

We recorded a remarkable dominance of *M. cavernosa* on deeper clear-water reefs, where this species comprised up to 93% of the total coral cover. Increased coverage of *M. cavernosa* with depth has been previously recorded for the Caribbean (Lesser et al., 2010) and this species is an important component of mesophotic reefs of the Western Atlantic (Lesser et al., 2010; Francini-Filho et al., 2019). This scleractinian exhibits a multitude of strategies to cope with low light levels at greater depth, such as increased concentrations of photosynthetic pigments, enhanced heterotrophy under enriched cold-water conditions and morphological adaptations to optimize the surface exposed to light

(Lesser et al., 2010). Our data revealed that *M. cavernosa* also dominated turbid coastal reefs, particularly in the central Brazilian coast. In fact, *M. cavernosa* was previously recognized as a major component of the “sediment resistant coral fauna” in the Western Atlantic, including Brazil, and may benefit from the same environmental conditions prevailing in both, shallow turbid and deep clear-water reefs: low light levels and increased nutrient availability (Lasker 1980; Francini-Filho et al., 2013). Morgan et al. (2016) first used the terminology “shallow-water mesophotic reefs” to describe such similarities. Reefs dominated by *Montastraea* spp. (“*Montastraea* reefs”) play critical roles by hosting the highest species richness, ecological processes and ecosystem services among reef habitats in the Caribbean (Mumby et al., 2008). *Montastraea* reefs at the Fernando de Noronha Archipelago are known to harbor a higher fish biomass than surrounding habitats (Krajewski and Floeter 2011) and additional studies evaluating the importance of *Montastraea* reefs in Brazil are warranted.

The inshore (<8.1 km offshore) turf algae-dominated turbid communities were the most prevalent in the Brazilian Province (n = 43 sites), possibly due to the influence of several large rivers along the coast (Leão et al., 2003; Mies et al., 2020). The offshore turbid communities (≥8.1 km offshore) with higher nitrate concentrations (≥0.013 μM) showed the highest macroalgal abundance among all turbid communities, while offshore reefs with lower nitrate levels (<0.013 μM) showed the highest abundance of reef-building organisms (CCA and scleractinians) and the zoanthid *Palythoa* spp. This later community occurred exclusively in the Abrolhos Bank, where the largest and richest reefs in the South Atlantic are located (Leão et al., 2003). Nitrate enrichment may impair skeletogenesis and growth, and decrease the bleaching threshold of reef corals (Marubini and Davies 1996; Ferrier-Pagès et al., 2001; Wooldridge 2009), while favoring the growth of reef algae (Lapointe, 1997; McClanahan et al., 2003). Thus, we hypothesize that the extremely low nitrate concentrations and the turbid waters across the Abrolhos shelf allow photophobic reef-building corals to thrive by increasing their competitive capabilities over algae. The high abundance of *Palythoa* spp. (mostly *P. caribaeorum*) in the Abrolhos reefs was previously recorded (Francini-Filho et al., 2013). This is a fast-growing species that aggressively competes for space (Suchanek and Green 1981; Silva et al., 2015; Lonzett et al., 2022) and may benefit from high turbidity through enhanced heterotrophy and incorporation of sediment particles in its tissue (Haywick and Mueller 1997; Santana et al., 2015). Finally, the offshore turbid reefs with higher nitrate concentrations and with increased macroalgal abundance recorded here were all located near urban centers in the Espírito Santo, Paraíba and São Paulo states, and additional studies may clarify the possible influences of anthropogenic nitrate sources on macroalgal proliferation.

Our results corroborate the photophobic nature of some Brazilian scleractinian corals (Leão et al., 2003; Coni et al., 2017; Mies et al., 2020). Seven species (*Agaricia fragilis*, *Agaricia humilis*, *Favia graxida*, *M. braziliensis*, *Mussismilia harttii*, *Mussismilia hispida* and *Porites astreoides*) were more abundant in the turbid than the clear-water group, while *M. cavernosa* showed similar abundances in both, shallow turbid reefs and deeper clear-water reefs, as explained above. The preferential association with low lit habitats (i.e. turbid/deeper) makes Brazilian corals less susceptible to bleaching and other thermally induced impacts in the face of global warming (Cacciapaglia and van Woesik 2016; Mies et al., 2020). The co-occurrence of corals and turf algae in turbid reefs also suggests that these coral species have efficient mechanisms to cope with the intense spatial competition with turf algae (Jompa and McCook 2003; Vermeij et al., 2010).

Our data show that turbidity is the most important environmental driver of benthic reef communities in the Brazilian Province, thus corroborating previous studies showing its key role on the evolution and dynamics of Brazilian reefs (Leão et al., 2003). The effects of high turbidity were noticed not only for corals, but other organisms as well, particularly algae, which are dominant components of SW Atlantic reefs. Because deep clear-water and shallow turbid reefs, such as the extensive

Montastraea reefs recorded here, may work as climate refugia (Bongaerts and Smith 2019; Mies et al., 2020; Bleuel et al., 2021; Sully et al., 2022), our results have important implications for delimiting potential climate refuges in Brazil. They also highlight the need to avoid local threats (e.g. overfishing, pollution) to these important coral-dominated habitats.

Author statement

Conceptualization: EFCS, RBFF, Data curation: EFCS, RBFF, Formal analysis: EFCS, RBFF, Funding acquisition: RBFF, Investigation: EFCS, RBFF, Methodology: EFCS, RBFF, Project administration: RBFF, Resources: RBFF, Supervision: RBFF, Validation: EFCS, RBFF, Visualization: EFCS, RBFF, RM, Roles/Writing - original draft: EFCS, RBFF, Writing - review & editing: EFCS, MM, GOL, RM, AWA, ALL, MGB, SRF, RBFF

Declaration of competing interest

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

Data availability

All raw data will be made publicly available under acceptance of the manuscript

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2022.105807>.

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