Pontificia Universidad
JAVERIANA
Bogotá

Univ. Sci. 27(1): 34–56, 2022
doi: 10.11144/Javeriana.SC271.ahdp

ORIGINAL ARTICLE

A highly diverse phytobenthic community along a short coastal reef gradient in northeastern Brazil

Sol de Maria César Ferreira*[1], Lucas Assumpção Lolis[1], Pietro Martins Barbosa Noga[1], Helen Michelle de Jesus Affe[2], José Marcos de Castro Nunes[1,3]

Edited by
Juan Carlos Salcedo-Reyes
salcedo.juan@javeriana.edu.co

1. Programa de Pós-Graduação em Ecologia: Teoria, Aplicação e Valores, Universidade Federal da Bahia – UFBA, Instituto de Biologia. Rua Barão de Jeremoabo, s/n. Campus Ondina. Ondina, Salvador – Bahia, Brazil. CEP: 40170-115.

2. Programa de Pós-Graduação em Oceanografia, Universidade do Estado do Rio de Janeiro – UERJ. FAculdade de Oceanografia – FAOC.

3. Laboratório de Algas Marinhas – LAMAR, Universidade Federal da Bahia – UFBA. Instituto de Biologia.

*fcmdsol@gmail.com

Received: 20-02-2021
Accepted: 28-03-2022

Citation: Ferreira SMC, Lolis LA, Noga PM, Affe HMJ, Nunez JM. A highly diverse phytobenthic community along a short coastal reef gradient in northeastern Brazil., *Universitas Scientiarum*, 27(1): 34–56, 2022. doi: 10.11144/Javeriana.SC271.ahdp

Funding: n.a.

Electronic supplementary material: n.a.

Abstract

This study aimed to inventory the species of marine macroalgae and analyze the distribution and biomass patterns of their communities along a short coastal reef gradient in northeastern Brazil. Samples were collected using the technique of random squares, distributed in the three habitats: reef front region (FR), tide pools (TP), and reef plateau (RP). These three make up the reef gradient from the sea to the beach. A total of 56 taxa were identified, with Ochrophyta and Rhodophyta standing out as the phyla with the greater taxonomic richness, and the largest biomass represented by the species *Sargassum vulgare* (30 %, of total biomass) and *Palisada perforata* (16 %). The key emergening patterns along the reef gradient were the occurrence of groups of exclusive taxa in each habitat, and significant variation in biomass, greater in the TP ($166.1\ \mathrm{g\,m^{-2}}$) and lower in the RP ($70.5\ \mathrm{g\,m^{-2}}$). Despite being an environment under marked anthropogenic influence (*i.e.*, tourism and development), we observed a high diversity of species, with a distribution pattern that reflects a high environmental heterogeneity and substantial ecological integrity.

Keywords: Benthic phycoflora, Macroalgae, Midlittoral zone, Tropical reef

1. Introduction

Marine macroalgae are responsible for a large part of primary production in tropical reef environments, which are regarded as systems of high species richness and home to a wide variety of habitats (Lobban and Harrison, 1994; Muñoz and Pereira, 1997). Marine algae themselves function as an important biological substrate in these systems (Moore, 1978; Ramos *et al.*, 2010), providing food and refuge for a large number of species. Macroalgae attenuate the mechanical action of waves, which, in turn, affect the physical structure of the habitat (Fenwick, 1976; Marx and Herrnkind, 1985; Tararam *et al.*, 1986). This enhances habitat complexity and favors the maintenance of high diversity and community abundance due to niche diversification and subsequent colonization (MacArthur *et al.*, 1962; Schoener, 1974; Kohn and Leviten, 1976; Heck and Wetstone, 1977).

The distribution of benthic organisms in an aquatic ecosystem is influenced by abiotic factors, such as substrate type and structure, water physicochemical variables (*e.g.*, temperature, pH, salinity, dissolved oxygen, and turbidity), sunlight intensity, as well as by further ecological factors such as predation, competition, and reproduction. Among these factors, the one that best regulates the presence and distribution of benthic algae communities is wave hydrodynamics (Masunari, 1987;

de Souza *et al.*, 2007). Wave hydrodynamics affects the physical structure of the reef environment, increasing its complexity and, as a consequence, boosting the diversity and abundance of associated organisms (Kohn and Leviten, 1976; Heck and Wetstone, 1977; Moore, 1978; Ramos *et al.*, 2010). This is possible because of increases in available area, in the diversity of structures, and in the number of habitats or niches susceptible to colonization (Schoener, 1974; Heck and Wetstone, 1977).

Coastal environments are among the most threatened marine ecosystems, chiefly impacted by growing urbanization (Halpern *et al.*, 2007; Martins *et al.*, 2012; Vasconcelos *et al.*, 2019). Understanding coastal environment biodiversity is essential to supporting conservation initiatives and highlighting phytobenthic assemblies as important bioindicators of anthropic impacts (Borowitzka, 1972; Ballesteros *et al.*, 2007; Díez *et al.*, 2009). A series of taxonomic studies has demonstrated the richness of macroalgal species (Horta *et al.*, 2001; Marins *et al.*, 2008; Bahia *et al.*, 2010; Nunes, 2010) along the Brazilian northeastern coastline. This research endeavor is now benefiting from a growing effort to deepen the study of the structure of phytobenthic communities in the intertidal regions along the coast the federal state of Bahia. This has meant a substantial shift in research resource allocation and focus from sites in southeastern to northeastern Brazil.

The northern coast of Bahia stands out as a region with a highly diverse marine phycoflora (Nunes and Matos, 2017) (**Figure 1**). Particularly on the reefs facing the locality of Itacimirim, recent studies have shown ecological integrity rates higher than in other urbanized regions of the tropical phytogeographic domain (Caldeira and Reis, 2019). This area is of special interest for the conservation of coastal ecosystems, among those in northeastern Brazil, considering its rampant urbanization process in recent decades (Costa *et al.*, 2012), intensified fishing activity, and the effects of serious environmental disasters, including the 2019 oil spill disaster in Northeastern Brazil (Soares *et al.*, 2020).

Thus, the present study aimed at carrying out an updated taxonomic inventory of the benthic phycoflora of the Itacimirim-BA reef, in addition to analyzing spatial variation in the abundance and diversity of the macroalgal community among the reef habitats in this region. We hypothesized that the structure of phytobenthic assemblies differs among habitats, even in a short spatial gradient, with variations in biomass and taxonomic macroalgae composition.

Our results highlight the importance of understanding community patterns in small scale habitats to better access conservation status of near-shore reef barriers. We suggest that regardless of whether the studied reef is susceptible to high anthropic stressors, the high variability in macroalgae species composition and biomass along different habitats reflect substantial habitat heterogeneity and ecological integrity.

2. Materials and methods

2.1. Study area

The northern coast of the Brazilian state of Bahia has a rainy tropical climate, with no dry season and an average annual rainfall of 1500 mm^3 (SEI, 1998). The average annual air temperature is 25.0 °C, with a maximum of 26.6 °C. The tidal regime has an amplitude of 2.7 m on spring tides and 1.5 m on quadrature tides (Brazil Marine Agency, 1998). In the Itacimirim locality, the reef area experiences average winter and summer temperature values of 28.19 °C to 29.36 °C, respectively, and average salinity of 34.21 ‰ and 33.50 ‰ in the same periods (Moraes, 2001; Moraes and Machado, 2006).

The Itacimirim reef (12°36′5382″ S / 38°2′3187″ W, at Camaçari – Bahia) is a rocky carbonate formation, whose builders are the encrusting corals and coralline algae. These formations have an irregular surface, due to the presence of tide pools of various shapes and sizes, as well as higher and rocky sections covered by soft and calcareous algae. This reef size is 1114 m in length and approximately 471 m in width, reaching depths of 10 m. Reef margins are irregular and are surrounded by sand (Leão *et al.*, 1997) (Figure 1).

The studied reef system entails three habitats defined by their morphologies, wave and sun exposure (Nunes and Paula, 2002): (i) the Reef plateau (RP), characterized by low hydrodynamics, flat topography with permanence of a shallow water layer, completely exposed to the air and direct sunlight in low tide; (ii) Tide pools (TP), featuring medium hydrodynamics, irregular topography, and remaining filled by water even in the lowest tide and may present greater salinity; and (iii) the Frontal region of the reef (FR), this is a highly hydrodynamic habitat with gentle slopes, that remains covered even during the lowest tide and is directly impacted by waves and winds.

2.2. Sampling design

Sample collections were carried out in October 2019 along 20 m transects arranged parallel to the surf line. Three transects were randomly positioned in each of the three reef habitats: reef plateau (RP), tide pools (TP) and reef front (FR). Five plots (20 cm × 20 cm) were systematically positioned along each transect, sampling plots were spaced four meters from each other (resulting in 15 samples per transect and a total of 45 samples per habitat). Inside the sampling plot, we used metal spatulas to remove all macroalgal biomass. The material collected within each plot was separately packed in plastic bags and frozen for preservation according to Costa *et al.* (2012). Qualitative sampling, by active search in each habitat for ten minutes was also carried out to detect low abundant species and to better determine the diversity of each reef habitat.

The taxonomic identification of the samples was performed using specialized keys, up to species level, following (Guiry and Guiry, 2020). After identification, botanic material was archived at the Alexandre Leal Costa Herbarium (Nunes, 2010). To determine biomass, the algae were dried in an oven at 60 °C until a constant weight was obtained. The dry biomass of each species was recorded using a semi-analytical balance (0.001 g).

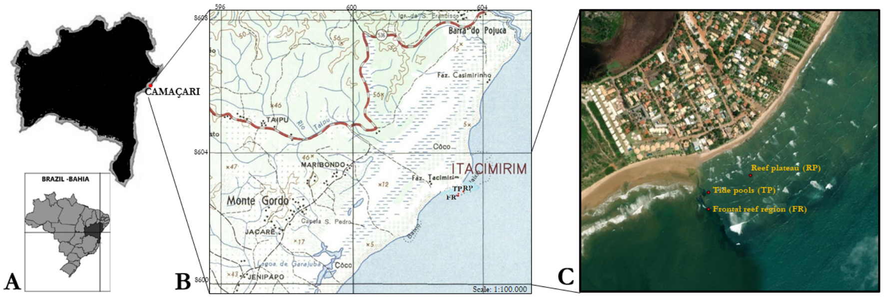

Figure 1. Location of the study area and habitats sampled on the Itacimirim reef–BA. (RP) Reef plateau (RP); Tidal pool (TP); Frontal region of the reef (FR). (A) Brazil, Bahia; (B) Camaçari, Itacimirim; (C) Itacimirim reef.

2.3. Data analysis

In order to characterize the structure of the reef community, the following parameters were calculated: species richness (*i.e.*, number of species), Margalef diversity index (d), Shannon-Wiener diversity (H') (Shannon and Weaver, 1949), and Heip's evenness index was calculated for comparison between habitats (Heip, 1974). The Shannon-Wiener diversity is widely used and enables our data to be comparable, and the Margalef index takes both diversity and abundance into account. After verifying the homogeneity of variances (Levene's test) and normality of the data, the differences between habitats as of Shannon-Wiener index, evenness (Heip's) and Margalef diversity (d) were compared by ANOVA, since assumptions were met. The ANOVA analysis of Shannon-Wiener (H'), this index was expressed as effective number of species (${}^1D = e^{H'}$) for linearity and more intuitive interpretation (Jost, 2006). Owing to data distribution, the analysis of variance of the biomass (g m^{-2}) between habitats was performed using the Kruskal-Wallis non-parametric test. Significant results were submitted to post-hoc analysis (Tukey's test) for peer-to-peer verification between the three habitats. The means of the number of species per square meter (S m^{-2}) were compared using a generalized linear model (Poisson distribution).

The prediction that reef habitats have an effect on the structuring of communities was verified by multivariate analysis of variance (PERMANOVA) (Anderson, 2006). In this analysis a dissimilarity matrix (Clarke and Warwick, 1994) was calculated with the Bray-Curtis coefficient (Bray and Curtis, 1957). The dissimilarity matrix was subjected to the permutational variance homogeneity test (PERMDISP) (Anderson, 2006). This analysis determines which habitat in the reef has the most variable species composition in relation to the others, indicating the beta diversity of the habitats. A principal component analysis and an ordination chart with main coordinates were used to graphically represent the multivariate data. The analyzes were performed using the R Program (The R Project for Statistical Computing), in which the packages *ecodist* (Oksanen *et al.*, 2019) and *labsv* (Roberts, 2013) were used for multivariate analysis and ordination, and *vegan* (Goslee and Urban, 2007) and stats standard R package were employed for the remaining analyses.

2.4. Results and discussion

A total of 56 taxa were identified, distributed among the phyla: Ochrophyta–12 species, 3 families and 2 orders; Rhodophyta–30 species, 17 families and 9 orders; and Chlorophyta–14 species, 8 families and 3 orders. The families Dictyotaceae (Ochrophyta) and Rhodomelaceae (Rhodophyta) were the ones with the highest species richness (**Table 1**). In the Bahia state, a total of 1111 algae species have been described; among these, 60 macroalgal species belong to the Ochrophyta phylum, 132 to the Chlorophyta, and 271 to the Rhodophyta (JBRJ, 2020). In the context of the macroalgal species described in the state of Bahia, the studied area harbors 12 % of all macroalgal flora described in the federal state.

Table 1. Macroalgal species identified in the Itacimirim reef stating habitat and morphotype. Habitats: Reef plateau (RP), Tidal pool (TP), and Frontal reef region (FR). Morphotypes or Macroalgae functional group (FG): Filamentous (FT), Foliate (F), Corticated (C), Coriaceous (CR), and Articulated Calcareous (A). Presence (+) and Absence (−).

Taxa	RP	TP	FR	FG
Ochrophyta				
Phaeophyceae				
Ectocarpales				
Scytosiphonacea				
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier	−	+	+	FT

Taxa	RP	TP	FR	FG
Dictyotales				
Dictyotaceae				
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck	+	+	+	F
Dictyota cervicornis Kützing	+	+	+	F
Dictyota jamaicensis W.R.Taylor	+	+	−	F
Dictyota mertensii (C.Martius) Kützing	−	−	+	F
Dictyopteris delicatula J.V.Lamouroux	+	+	+	F
Lobophora variegata (J.V.Lamouroux) Womersley ex E.C.Oliveira	+	+	+	F
Padina boergesenii Allender & Kraft	+	+	+	F
Padina gymnospora (Kützing) Sonder	−	+	−	F
Spatoglossum schroederi (C. Agardh) Kützing	−	−	−	F
Sargassaceae				
Sargassum cymosum C.Agardh	−	+	+	CR
Sargassum vulgare C.Agardh	−	+	+	CR
Rhodophyta				
Florideophyceae				
Corallinales				
Lithophyllaceae				
Amphiroa anastomosans Weber Bosse	+	−	−	A
Amphiroa fragilissima (Linnaeus) J.V.Lamouroux	−	+	+	A
Amphiroa rigida J.V.Lamouroux	−	−	+	A
Corallinaceae				
Corallina officinalis Linnaeus	−	+	−	A
Corallina panizzoi R.Schnetter & U.Richter	−	+	−	A
Jania pumila J.V.Lamouroux	+	−	−	A
Nemaliales				
Galaxauraceae				
Dichotomaria marginata (J.Ellis & Solander) Lamarck	−	+	+	C
Galaxaura rugosa (J.Ellis & Solander) J.V.Lamouroux	−	−	+	C
Tricleocarpa fragilis (Linnaeus) Huisman & R.A.Townsend	+	+	−	C
Liagoraceae				
Liagora albicans J.V.Lamouroux	−	−	+	F
Ceramiales				
Ceramiaceae				
Centroceras gasparrinii (Meneghini) Kützing	+	−	−	FT
Delesseriaceae				
Dasya baillouviana (S.G.Gmelin) Montagne in Barker Webb & Berthelot	−	−	+	C
Rhodomelaceae				
Acanthophora muscoides (Linnaeus) Bory	−	−	+	C
Acanthophora spicifera (M.Vahl) Børgesen	+	−	−	C
Alsidium triquetrum (S.G.Gmelin) Trevisan	−	+	+	C
Amansia multifida J.V.Lamouroux	−	+	+	C
Digenea simplex (Wulfen) C.Agardh	+	+	+	C
Palisada perforata (Bory) K.W.Nam	+	+	+	C
Osmundaria obtusiloba (C.Agardh) R.E.Norris	−	+	−	C

Taxa	RP	TP	FR	FG
Wrangeliaceae				
Wrangelia argus (Montagne) Montagne	−	−	+	FT
Gelidiales				
Gelidiellaceae				
Gelidiella acerosa (Forsskål) Feldmann & Hamel	+	+	+	C
Gelidiella ligulata E.Y.Dawson	−	+	−	C
Gelidiaceae				
Gelidium coarctatum Kützing	+	−	+	C
Gigartinales				
Gigartinaceae				
Chondracanthus acicularis (Roth) Fredericq in Hommersand & al.	+	−	−	C
Cystocloniaceae				
Hypnea pseudomusciformis Nauer, Cassano & M.C.Oliveira	+	−	+	C
Gracilariales				
Gracilariaceae				
Gracilaria cervicornis (Turner) J.Agardh	−	+	+	C
Halymeniales				
Halymeniaceae				
Cryptonemia seminervis **(**C. Agardh**)** J.Agardh	−	−	+	C
Peyssoneliales				
Peyssoneliaceae				
***Peyssonnelia* sp**. Decaisne	+	−	−	F
Rhodymeniales				
Lomentariaceae				
Ceratodictyon variabile (J.Agardh) R.E.Norris	−	+	−	C
Rhodymeniaceae				
Botryocladia occidentalis (Børgesen) Kylin	−	−	+	C
Chlorophyta				
Ulvophyceae				
Bryopsidales				
Caulerpaceae				
Caulerpa cupressoides (Vahl) C. Agardh	−	+	−	FT
Caulerpa mexicana Sonder ex Kützing	−	+	−	FT
Caulerpa racemosa (Forsskal) J.Agardh	−	−	+	FT
Caulerpa sertularioides (S.G. Gmelin) M. Howe	−	+	+	FT
Codiaceae				
Codium intertextum Collins & Hervey	−	−	+	FT
Codium taylorii P.C. Silva	−	−	+	FT
Halimedaceae				
Halimeda jolyana Ximenes, Bandeira−Pedrosa, Cassano, Oliveira− Carvalho, Verbruggen & S.M.B.Pereira	+	−	+	A
Halimeda opuntia (Linnaeus) J.V.Lamouroux	−	−	+	A
Cladophorales				
Anadyomenaceae				
Anadyomene stellata (Wulfen) C.Agardh	+	+	+	F
Cladophoraceae				

Taxa	RP	TP	FR	FG
Cladophora laetevirens (Dillwyn) Kützing	+	−	−	FT
Siphonocladaceae				
Dictyosphaeria versluysii Weber Bosse	+	−	+	FT
Valoniaceae				
Valonia aegagropila C.Agardh	+	−	−	FT
Ulvales				
Ulvaceae				
Ulva lactuca Linnaeus	+	+	+	F
Ulva rigida C. Agardh	+	+	+	F
TOTAL	**25**	**30**	**37**	

The species that made the greatest contribution to total recorded biomass in the studied reef were: *Sargassum vulgare* (30 %), *Palisada perforata* (16 %), *Dictyopteris delicatulata* (10 %), *Amphiroa fragilissima* (9 %), and *Canistrocarpus cervicornis* (5 %) (**Figure 2**).

The total number of taxa identified in this study agrees with those previously reported in the same region (Altamirano and Nunes, 1997; Nunes and Paula, 2002; Costa *et al.*, 2012). These had different objectives and were carried out in different years and seasons. Altamirano and Nunes (1997) recorded 47 taxa; Nunes and Paula (2002) recorded 37, and Costa *et al.* (2012) identified 44. We recorded 56, of which, 13 were not identified in any of the previous studies, namely: Rhodophyta (*Amphiroa rigida*, *Centroceras gasparrinii*, *Corallina officinalis*, *C. panizzoi*, *Dasya baillouviana*, *Galaxaura rugose*, *Gelidiella ligulata*, *Jania pumila*, *Liagora albicans*, *Peyssonnelia* sp., and *Wrangelia argus*.) Chlorophyta (*Cladophora laetevirens*, and *Halimeda jolyana*). Our sampling effort might be the factor that contributes to the expansion of knowledge about the composition of the phycoflora in this region.

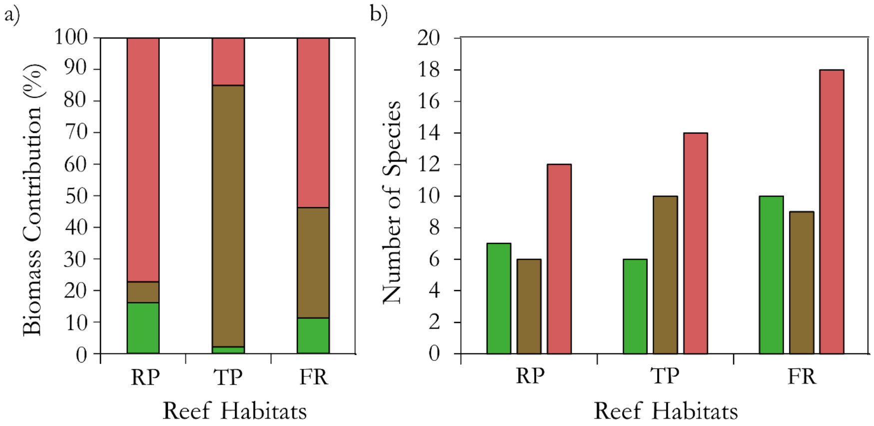

Figure 2. (a) Total reef biomass shares per phylum by habitat (reef zone), and (b) total number of species per phylum in the studied reef zones of Itacimirim–BA. Reef plateau (RP), Tide pools (TP), and Reef front (FR). Phyla: Chlorophyta (Green), Ochrophyta (Brown), and Rhodophyta (Red).

The Rhodophyta predominates in all reports in the area, including ours, and it is followed by Ochrophyta and Chlorophyta. This pattern is observed, in general, in environments with low anthropization, where there are no large nutrient inputs, favoring the substitution of abundance of Ochrophyta and Chlorophyta (Schoener, 1974; Falcão and de Széchy, 2005; Scherner *et al.*, 2013). In the tide pool habitat of the Itacimirim reef, the species *Sargassum vulgare* and *Dictyopteris delicatula* contrbuted largely to biomass. This habitat is characterized by keeping constant water levels and being protected from wave action throughout the low tide period, thus buffering variation in abiotic conditions (Nunes and Paula, 2001). This allows more time for growth without disturbances, favoring species of slow growth and long-life cycle, as is the case of *Sargassum* spp. (Széchy and Paula, 2000; Figueiredo *et al.*, 2004).

The concentration of large macroalgae in places with high hydrodynamics, such as the reef's front, allowed for a greater circulation of dissolved nutrients, being a key aspect of primary production (Villaça *et al.*, 2010). On the other hand, the intense impact of the waves can be a stress factor, limiting the development of some organisms and, therefore, species better adapted to these conditions prevail (Leigh *et al.*, 1987; Nunes and Paula, 2001; Díez *et al.*, 2003).

Both physical factors and organism ecology are central to primary production. The successful distribution of benthic organisms in a marine ecosystem is influenced by abiotic factors, such as substrate type and structure, water physicochemical variables (*e.g.*, temperature, pH, salinity, dissolved oxygen, and turbidity), and sunlight intensity. Among these, wave hydrodynamics best determines the presence and distribution of benthic algae communities (Lyra *et al.*, 2007). Wave hydrodynamics affects the physical structure of the habitat, increasing its complexity and, consequently, the diversity and abundance of associated organisms and their recruitment (Kohn and Leviten, 1976; Heck and Wetstone, 1977; Johns *et al.*, 2018). This is due to an increase in available area, structure diversity, and the number of habitats or niches amenable to colonization (MacArthur *et al.*, 1962).

The reef plateau habitat, in turn, is immersed during low tides and directly exposed to sunlight during this period. Thus, algae growing in this habitat suffer more from desiccation, which may explain their lower biomass (Villaça *et al.*, 2010). The plateu of the Itacimirim reef is a narrow area enduring intense marine sprays, even during low tide. This provides a high degree of humidity, favoring species abundance and diversity, as observed by (Costa *et al.*, 2012).

The Itacimirim reef had an average total biomass of $(127.3 \pm 62.9)\,\mathrm{g\,m^{-2}}$. Considering each habitat individually, we observed average biomass values of $(74.1 \pm 25.8)\,\mathrm{g\,m^{-2}}$ in the reef plateau; $(177.2 \pm 67.7)\,\mathrm{g\,m^{-2}}$ in tidal pools, and $(130.9 \pm 38.8)\,\mathrm{g\,m^{-2}}$ in the reef front. Our Kruskal-Wallis test rvealed that these biomass differences among reef habitats were statistically significant ($H = 21.40$; $p = 0.012$; df = 2), with biomass being lower in the reef plateau than in tidal pool and reef front habitats ($p < 0.01$; z-value 4.50 and 3.16, respectively).

In the reef plateau, 25 species were identified. The species *Palisada perforata* (54 %), *Anadyomene stellata* (8 %), *Amphiroa anastomosans* (7 %), *Gelidiella acerosa* (8 %), and *Padina boergesenii* (5 %) were the ones with major contributions to total biomass. In the tidal pool, 29 species were identified; in this habitat, *Sargassum vulgare* (60 %), *Dictyopteris delicatula* (16 %), *Canistrocarpus cervicornis* (4 %), *Tricleocarpa fragilis* (4 %), and *Dichotomaria marginata* (3 %) had the largest biomass contributions. In the frontal region of the reef, 37 species were identified; *Amphiroa fragilissima* (25 %), *Palisada perforata* (15 %), *Canistrocarpus cervicornis* (9 %), *Dictyopteris deliculata* (8 %), *Halimeda opuntia* (8 %), *Sargassum vulgare* (8 %), and *Lobophora variegata* (7 %) were the species with the greatest contribution to total biomass.

The tidal pool differed from the other two habitats due to its high *Sargassum* biomass. This habitat is a more stable environment in spite of its uneven topography, and it remains covered with water and protected from the direct action of the waves. In contrast, the reef plateau is exposed to air and insolation in the lowest tide due to its low hydrodynamics, and the reef front, facing the ocean and with high hydrodynamics, is directly impacted by waves and wind.

In their studies at Atol das Rocas, an important isolated and protected reef system at western Atlantic, Villaça *et al.* (2010) observed that the proportion of Ochrophyta was probably associated with a more physically stable environment in terms of solar radiation and humidity. The increase in larger macroalgae that pass from internal to external habitats, with small algal coverage, is also a pattern observed in other studies (Morrissey, 1980; Littler *et al.*, 1987; Rodrigues *et al.*, 1997). *Sargasssum* is considered a competitively superior genus, as it hinders the development of other algae under its shade (Vasconcelos *et al.*, 2019). *Corallina panizzoi*, a calcareous articulated species characterized by its slow growth, only occurred in tidal pools. *Corallina* species are abundant in infralittoral or submerged habitats such as tidal pools (Villaça *et al.*, 2010). Figueiredo *et al.* (2004) observed a greater abundance of coriaceous (*Sargassum* spp.) and articulated Corallinaceae (*Amphiroa* spp. and *Jania* spp.) algae. Dominant species with a long life-cycle and slow growth are typical at the end of a succession (Villaça *et al.*, 2008) and are indicative of environments with high productivity and low disturbances degrees, reflecting the action of waves and herbivory (Littler and Littler, 1984; Steneck and Dethier, 1994).

Regarding functional morphotypes, corticated (C) algae (36 %) were largerly represented, followed by foliaceous (F) algae (25 %), filamentous (FT) forms (21 %), articulated calcareous (A) algae (14 %) and coriaceous (CR) algae (2 %). These observations agree with Costa *et al.* (2012). According to Steneck and Dethier (1994), the groups that have enlargement of the cortex, such as the cortical and coriaceous algae *Palisada* and *Sargassum*, are more resistant to physical and biological disturbances, being favored in environments with moderate disturbance and high productivity. The studied beach is a toutist hotspot, ans is known as a surfing beach, thus being in an intermediate state of disturbance. This view is backed up by the large biomass values observed for *Palisada perforata* (C), *Dictyopteris delicatulata* (F), *Canistrocarpus cervicornis* (F), *Amphiroa fragilissima* (A), and *Sargassum vulgare* (CR).

In the study by Costa *et al.* (2012), the species *Acanthophora muscoides*, *Amansia multifida*, *Cryptonemia seminervis*, *Gracilaria* spp., *Padina boergesenii*, *Sargassum cymosum*, and *Ulva* spp. showed higher biomass in the reefs of Stella Maris than in the Itacimirim reef. Stella Maris is the reef most comparable to Itacimirim due to their similar carbonate construction and morphology; both sites have an irregular surface due to the presence of tide pools of varying shapes and sizes, as well as more shallow rocky regions covered by soft and/or calcareous algae (Costa *et al.*, 2012; Nolasco, 1988). The most abundant taxa in Stella Maris were also recorded in Itacimirim's frontal reef, its highest hydrodynamic habitat. This is further evidence of these macroalgal species' adaptation to these environments.

According to Barbosa *et al.* (2008), the great biomass of these taxa reflects their adaptation to strong hydrodynamic conditions. These macroalgae are subject to wave action, allowing greater water oxygenation and partial sediment removal. Of the seven taxa cited by Costa *et al.* (2012), six were recorded in Itacimirim's reef front, where the action of the waves is more intense: *Amansia multifida*, *Cryptonemia seminervis*, *Gracilaria cervicornis*, *Padina boergesenii*, *Sargassum vulgare*, and *Ulva lactuca*. According to Reis and Yoneshigue-Valentin (1998); Barbosa *et al.* (2008); Costa *et al.* (2012), the genus *Ulva* is the most frequent, dominant, opportunistic, and tolerant to wide environmental variation, explaining its presence in all of the studied habitats.

Amphiroa fragilissima, *Dictyopteris delicatula*, and *Sargassum vulgare* are taxa resistant to these conditions and accounted for high biomass in the reef front of Itacimirim. The species *Gelidiella acerosa* and *Palisada perforata* also had an important contribution to biomass values in Itacimirim. When compared to the studies by Costa *et al.* (2012), these two species account for 60 % of the algal biomass in the reef plateau and feature ample desiccation resistance, due to their corticated morphotype. This adaptation is favored in environments like the one studied, where the reef plateau remains fully immersed during low tide and is exposed to sunlight for long periods. This results in intense macroalgal stress and high desiccation risk. In addition, part of the reef plateau extension is covered by sand (Costa Jr *et al.*, 2002; Costa *et al.*, 2012).

The species *Alsidium triquetrum*, *Digenea simplex*, and *Osmundaria obtusiloba* showed significant variation in biomass among the studied reef habitats, and their biomass was highest in the reef front. (Lyra *et al.*, 2007) observe that the gradual increase in wave exposure acts directly on macroalgal biomass; in fact, in the reef front the largest macroalgae were observed. These algae have a preference for regions with strong wave impacts and are less exposed during low tide.

Cladophora spp., *Dictyopteris delicatula*, *Dictyosphaeria versluysii*, *Digenea simplex, Gelidiella acerosa*, and *Halimeda opuntia* were well represented in the plateau and tidal pool in the Itacimirim reef, as they commonly occur in tropical regions (Villaça *et al.*, 2010). According to Taouil and Yoneshigue-Valentin (2002) the genus *Gelidiella*, for instance, occurs in moderately impacted environments. Although the coast of Bahia harbors a diverse marine flora, in the last decades this coastal zone has been going through an intense process of urban development, exerting a significant environmental pressure (Costa *et al.*, 2012). The wide plateau of the Itacimirim reef formation remains totally uncovered during low tide, thus favoring the occurrence of corticated and smaller algae, sandy environments and greater resistance to desiccation. In this context, high biomass values for the species *Palisada perforata* (53 %) and *Amphiroa anastomosans* (8 %) were observed. *Amphiroa* grows in a variety of habitats, but it generally occurs in areas under wave action (Norris and Johansen, 1981).

Itacimirim's reef plateau and reef front were, in that order, the habitats where the greatest richness of macroalgae species was observed. The highest richness:biomass ratio was observed in the reef plateau (**Table 2**). However, the generalized linear regression model revealed that the average number of species recorded did not differ significantly between habitats (Waldstat $= 3.9$; $p = 0.14$; **Figure 3**a). In contrast to the Margalef index, which showed significant variation (ANOVA, $F_{2.42} = 13.51$; $p < 0.001$; Figure 3b), the reef plateau being species richer than the reef front (difference $= 1.82$; $p < 0.01$) and the tide pool (PC) (2.56; $p < 0.01$; Figure 3b). The diversity index ($e^{H'}$) did not differ significantly between habitats (ANOVA, $F_{2.42} = 1.857$; $p = 0.16$; Figure 3c). Differences were found between means of the evenness index (ANOVA, $F_{2.42} = 3.812$; $p = 0.03$; Figure 3d), with the frontal reef region showing higher values than the reef plateau (difference $= 0.17$; $p < 0.05$; Figure 3d).

Our main coordinates analysis revealed that the three reef habitats form distinct groups with regard to community structure (**Figure 4**a). This is confirmed by the multivariate permutation analysis, which revealed a significant habitat effect on species composition (PERMANOVA, $F_{2.42} = 14.61$; p-perm < 0.001; **Table 3**), with habitat explaining 41 % of the variability of the samples ($R^2 = 0.41$). The result of paired comparisons revealed that the three habitats are distinct from each other (Table 3).

According to this result, samples within a habitat are more similar than any pair of samples from different habitats (**Table 4**). Although all pairwise comparisons among habitats revealed significant dissimilarities, the least similar habitats are the tide pools and the reef plateau (Table 4).

Table 2. Diversity univariate parameters of macroalgae communities found in the three habitats of the Itacimirim reef (Bahia, Brazil). Reef plateau (RP), Tide pools (TP), and Reef front (FR).

Habitat	Total species N	Average species number $S\,m^{-2}$	Species Richness (Margalef) D	Equability (Heip) E	Diversity (Shannon) $H'(\log e)$
RP	21	7.6	4.8	0.3	1.2
TP	18	5.7	2.1	0.4	1.0
FR	24	6.8	2.9	0.5	1.3

The dispersion homogeneity analysis between groups (PERMDSISP) revealed that the habitats, or reef zones, differ in their heterogeneity ($F_{2.42} = 10.59$; $p < 0.01$), with the composition within the reef front being more variable than within in the reef plateau ($p < 0.001$) and tide pools ($p < 0.001$; Figure 4b).

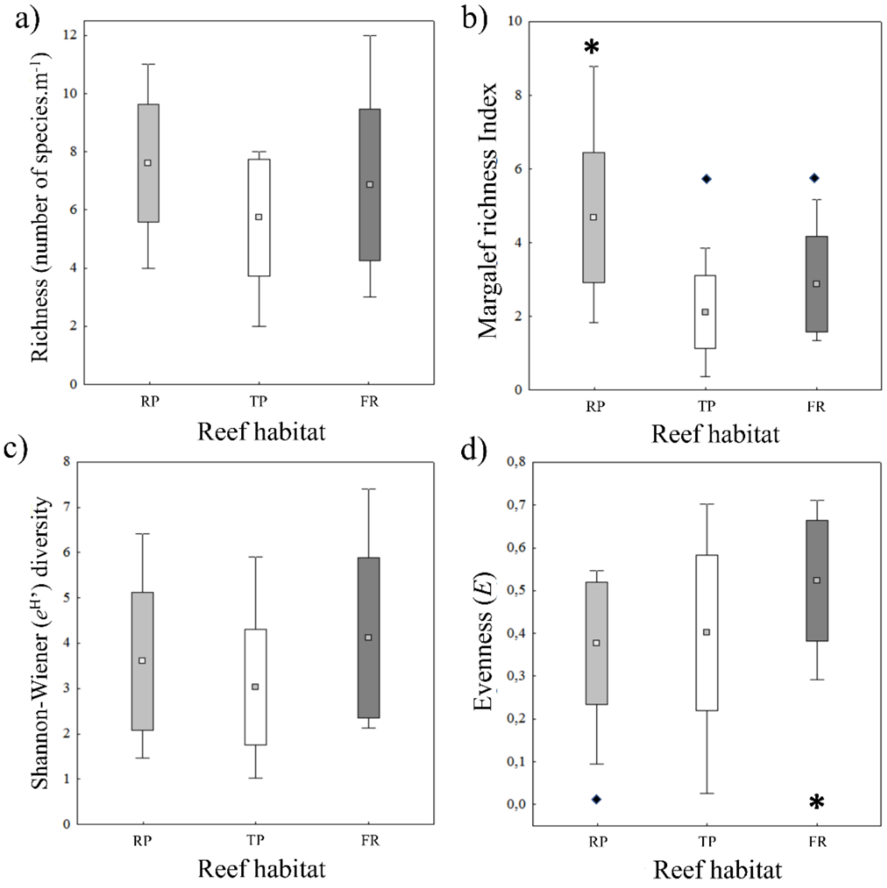

Figure 3. Comparison of average diversity index values of the three habitats (reef zones) of the Itacimirim reef (Bahia, Brazil). (a) Number of species; (b) Margalef Richness Index; (c) Shannon Diversity Index ($e^{H'}$); and (d) 318 Heip's evenness (E) Index. Different symbols indicate significant differences in values between habitats. Reef plateau (RP), Tide pools (TP), Reef front (FR). Squares indicate means, boxes indicate standard deviation, and bars maximum and minimum range.

Table 3. PERMANOVA results of benthic macroalgal communities in the Itacimirim reef (Bahia, Brazil). Results based on bray-curtis dissimilarities. $R^2 = R$-squared values (effect size); Reef habitats: Reef plateau (PR), Tide pools (TP), and Reef front (FR); df = degrees of freedom; MS = mean squares. R-squared values also indicated for each paired comparison between sites.

Source	df	MS	F. model	R^2	p-perm
Reef Habitat	2	2.7048	14.61	0.4102	< 0.001
Residuals	42	0.1851		0.5897	
Total	44			1.000	
RP - TP		4.5719	34.94	0.5551	0.001
RP - FR		1.7845	8.805	0.2392	0.001
TP - FR		1.7580	7.923	0.2205	0.001

The reef front was the habitat with the highest species richness (with 24 recorded species) in the Itacimirim reef. According to Villaça *et al.* (2010) this habitat provides a longer immersion time and less exposure to direct sunlight. These conditions facilitate the occurrence of a wide variety of species, because they are not as restrictive as the conditions of high desiccation by the action

Table 4. Mean similarity values within and between the three habitats (reef zones) communities in the Itacimirim reef (Bahia, Brazil). Reef plateau (PR), Tide pools (TP), and Reef front (FR).

	RP	TP	FR
RP	53.93		
TP	7.92	48.05	
FR	23.13	21.00	26.47

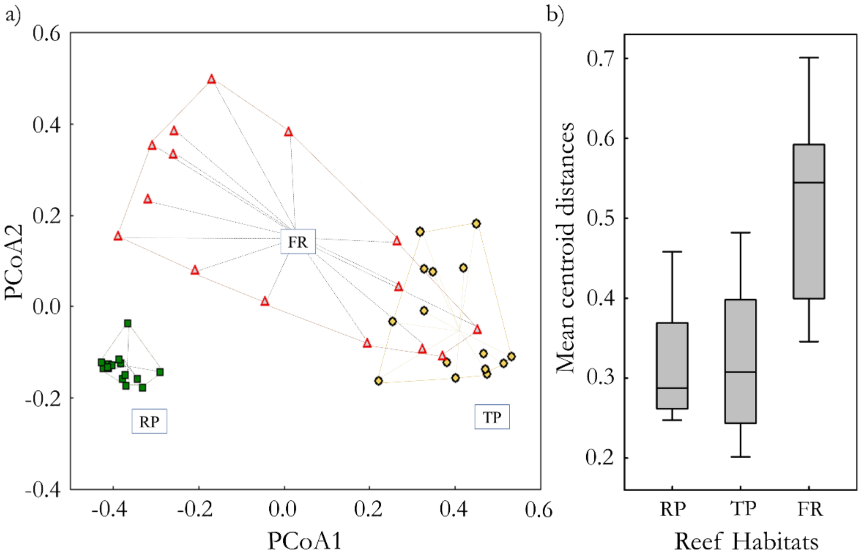

Figure 4. (a) Analysis of main coordinates representing the grouping of samples in the in the three habitats (reef zones) of the Itacimirim reef (Bahia, Brazil) in relation to the ordination axes. (b) Amplitude of variation between samples of each group, indicated by the distance to the centroid. Reef plateau (RP), Tide pools (TP), and Reef front (FR).

of air and an increase in temperature, as observed in other habitats. On the other hand, the intense hydrodynamics in the reef prevents the dominance of species more fragile to the action of the waves (Nunes and Paula, 2001). The reef plateau habitat, in turn, presented greater richness as reveled by a Margalef index of 4.8, compared to 2.1 and 2.9 for the other two habitats. Since this index calculation took into account the ratio between the number of taxa and their total abundance in the area, habitats with a large number of species and low abundance scored high for this metric. Such is the case of the reef plateau with low biomass but featuring a high number of species.

The marked difference in composition between the habitats is probably not the result of variations in the availability of propagules and/or algal spores (Gaylord *et al.*, 2006), which are community structuring factors operating at a scale larger than the actual distances between sampled areas. In this way, we can consider environmental filters and local biotic interactions.

Hypnea pseudomusciformis, *Dictyosphaeria versluysi*, *Chondrachantus acicularis*, *Centroceras gasparini*, and *Acanthophora spicifera* occurred in the reef plateau. Among these species, filamentous and corticate morphological groups predominate. These morphologies are adaptive traits that provide resistance to desiccation during low tide periods (Costa *et al.*, 2012). Also, small species find less competition with leafy or leathery forms in this environment (Vasconcelos *et al.*, 2019). In particular, *Hypnea pseudomusciformis* has biological aspects that favor its occurrence in the reef plateau, such as its reproductive period, that is stimulated by constant nutrients and luminosity (Schenkman, 1989; Caires *et al.*, 2013; Jesus *et al.*, 2019). In addition, the life form in the predominant phase of the reproductive cycle, is composed by an extensive network of basal filaments, which efficiently adhere to the substrate and better cope with desiccation resistance (Reis and Yoneshigue-Valentin, 1998; Bringloe *et al.*, 2020). The reef plateau has a large amount of unconsolidated substrate on its surface, which also allows only for the occurrence of psamophilic algae, which have developed adaptations to survive in sandy locations (Oliveira-Carvalho *et al.*, 2003), for example *Cladophora laetevirens*.

The reef front has a relatively high number of species because of its many depressions and cracks (Villaça *et al.*, 2010). This topography enables the occurrence of a mosaic of microhabitats, explaining the enormous variation in macroalgal composition, evidenced by the performed dispersion test. In this habitat the composition was characterized by a great substitution of species in the samples (beta diversity). Each plot sampled revealed a relatively distinct set of species, with similar biomass values and, therefore, the highest recorded evenness. The reef plateau had less biomass, but greater richness (Table 2). According to Costa *et al.* (2012), despite remaining totally uncovered during low tides, this habitat is sprayed by the waves throughout its length, always providing a supply of water and favoring the occurrence of small, moderately desiccation-resistant algae.

Our principal component analysis and multidimensional ordination approach revealed that space influenced the distribution of macroalgae in the Itacimirim reef, with the number of taxa decreasing in regions with less hydrodynamics (FR = 24, PR = 21, and TP = 18). This finding agrees with data presented in studies carried out on different beaches along the coast of Bahia, revealing that large numbers of taxa occur in the reef front, where the energy of the waves is greater, and that less taxa occur as hydrodynamics decreases, for instance in tide pools (Lucio and Nunes, 2002; Lyra *et al.*, 2007; Nunes and Guimarães, 2010). The high taxonomic richness identified and the differences in species composition between habitats reflected the environmental heterogeneity of the Itacimirim reef. The distribution of abundance among phyla and the observed variation in growth forms are indicative of the ecological integrity of this urban environment. Exposure to waves seems to be the main variable responsible for the spatial distribution of algal species between the studied reef habitats.

3. Conclusions

Our results provide evidence of the importance of understanding community patterns in small scale habitats to better access the conservation status of near-shore reef barriers. We suggest that regardless of reef susceptibility to anthropic stressors, the high variability in macroalgal species and biomass among different habitats is a reflection of the reef's substantial habitat heterogeneity and ecological integrity. The species richness observed the Itacimirim reef agrees with the results from other northern Bahia coast and Northwest Brazilian Coast studies. Exposure to waves is the likely factor modeling species distribution and separating communities into three groups, according to reef zones or habitats. Species adapted to high hydrodynamics were dominant in the reef front, and these were replaced by species resistant to air, light intensity, and desiccation in the reef plateau.

Considering the growing urban occupation of coastal areas, the role of anthropic impacts on macroalgal biodiversity must be investigated, and these results should support decision-making and environmental management. Additionally, our results are a detailed description of community patterns that represent a baseline monitoring for subsequent studies about acute impacts. This is important since this study took place only three months after large oil masses reached the Itacimirim reef and the northeastern Brazil coastline, causing great social and environmental distress. Thus, data shown here could serve as a guide for future understanding and monitoring of benthic community responses after this event. Therefore, enabling good mitigation measures will reduce anthropic impacts, allowing biodiversity maintenance while appropriately sustaining economic activities, such as fishing and tourism.

4. Acknowledgements

J. M. de C. Nunes would like to thank the Brazilian National Council for Scientific and Technological Development (CNPq) for the Research Productivity Fellowship (Proc. 308542/2018-5). Lucas Lolis and Pietro Martins would like to thank the Coordination for the Improvement of Higher Education Personnel (CAPES) for the doctoral scholarship.

5. Conflict of interest

The authors declare that there are no conflicts of interest.

References

Altamirano M, Nunes JMC. Contribuciones al macrofitobentos del municipio de Camacari (Bahía, Brasil), *Acta Botanica Malacitana*, 22: 211–215, 1997.
doi: 10.24310/abm.v22i0.8639

Anderson MJ. Distance-based tests for homogeneity of multivariate dispersions, *Biometrics*, 62(1): 245–253, 2006.
doi: 10.1111/j.1541-0420.2005.00440.x

Anderson MJ. Permutational multivariate analysis of variance, *Wiley StatsRef: Statistics Reference Online*, 1–15, 2017.
doi: 10.1002/9781118445112.stat07841

Bahia RG, Abrantes DP, Brasileiro PS, Pereira Filho GH, Amado Filho GM. Rhodolith bed structure along a depth gradient on the northern coast of Bahia State, Brazil, *Brazilian journal of oceanography*, 58(4): 323–337, 2010.
doi: 10.1590/S1679-87592010000400007

Ballesteros E, Torras X, Pinedo S, García M, Mangialajo L, Torres M. A new methodology based on littoral community cartography dominated by macroalgae for the implementation of the European Water Framework Directive, *Marine Pollution Bulletin*, 55(1-6): 172–180, 2007.
doi: 10.1016/j.marpolbul.2006.08.038

Barbosa SO, Figueiredo MAO, Testa V. Estrutura e dinâmica de comunidades bentônicas dominadas por macrófitas na zona intramareal da Praia de Jacaraípe, Espírito Santo, Brazil, *Hoehnea*, 35(4): 563–575, 2008.
doi: 10.1590/S2236-89062008000400008

Borowitzka MA. Intertidal algal species diversity and the effect of pollution, *Marine and Freshwater Research*, 23(2): 73–84, 1972.
doi: 10.1071/MF9720073

Brazil Marine Agency. Tidal schedule, Hydrography and Navigation Diretory, 1998.
URL: https://www.marinha.mil.br/dhn/

Bray JR, Curtis JT. An ordination of the upland forest communities of southern Wisconsin, *Ecological monographs*, 27(4): 325–349, 1957.
doi: 10.2307/19422688

Bringloe TT, Starko S, Wade RM, Vieira C, Kawai H, De Clerck O, Cock JM, Coelho SM, Destombe C, Valero M, Neiva J, Pearson GA, Faugeron S, Serrão EA, Verbruggen H. Phylogeny and Evolution of the Brown Algae, *Critical Reviews in Plant Sciences*, 39(4): 281–321, 2020.
doi: 10.1080/07352689.2020.1787679

Caires TA, Costa IO, de Matos MRB, Lyra GM, Nunes JMC. Phenological studies in populations of *Hypnea musciformis* (Rhodophyta: Gigartinales) in a tropical region of Brazil, *Brazilian Journal of Botany*, 36(2): 135–140, 2013.
doi: 10.1007/s40415-013-0016-3

Caldeira AQ, Reis RP. Brazilian macroalgae assemblages analyzed using the ecological evaluation index (EEI-c), *Ocean & Coastal Management*, 182: 104927, 2019.
doi: 10.1016/j.ocecoaman.2019.104927

Clarke KR, Warwick RM. An approach to statistical analysis and interpretation, *Change in marine communities*, 2: 117–143, 1994.
doi: 10.5134/144637

Costa IO, Caires TA, Pereira Filho GH, Nunes JMC. Macroalgae associated with banks of *Hypnea musciformis* (Wulfen) J.V. Lamour. (Rhodophyta, Gigartinales) on two beaches on the coast of Bahia, *Acta Botanica Brasilica*, 26(2): 493–507. 507, 2012.
doi: 10.1590/S0102-33062012000200025

Costa Jr OS, Attrill MJ, Pedrini AG, De Paula JC. Spatial and seazonal distribution of seaweeds on coral reefs from Southern Bahia, Brazil, *Botanica Marina*, 45(4): 346–355, 2002.
doi: 10.1515/BOT.2002.035

de Souza AT, Ilarri MI, de Medeiros PR, Sampaio CLS, Horta PA. Small distances, great differences: a case study involving the biomass of reef seaweeds and fishes on the coast of Paraíba, Northeast Brazil, *Biotemas*, 20(2): 9–13, 2007.
doi: 10.5007/%25x

Díez I, Santolaria A, Gorostiaga JM. The relationship of environmental factors to the structure and distribution of subtidal seaweed vegetation of the western Basque coast (N. Spain), *Estuarine, Coastal and Shelf Science,* 56(5-6): 1041–1054, 2003.
doi: 10.1016/S0272-7714(02)00301-3

Díez I, Secilla A, Santolaria A, Gorostiaga JM. Ecological monitoring of intertidal phytobenthic communities of the Basque Coast (N. Spain) following the Prestige oil spill, *Environmental Monitoring and Assessment,* 159(1-4): 555–575, 2009.
doi: 10.1007/s10661-008-0651-5

Falcão C, de Széchy MTM. Changes in shallow phytobenthic assemblages in southeastern Brazil, following the replacement of *Sargassum vulgare* (Phaeophyta) by *Caulerpa scalpelliformis* (Chlorophyta), *Botanica Marina*, 48(3): 208–217, 2005.
doi: 10.1515/BOT.2005.033

Fenwick GD. The effect of wave exposure on the amphipod fauna of the alga *Caulerpa brownie*, *Journal of Experimental Marine Biology and Ecology*, 25(1): 1–18, 1976.
doi: 10.1016/0022-0981(76)90072-1

Figueiredo MA, Barreto MBB, Reis RP. Characterisation of macroalgae in the marine communities of Cairuçú Environmental Protected Area, Parati, RJ: bases for future monitoring, *Brazilian Journal of Botany*, 27(1): 11–17, 2004.
doi: 10.1590/S0100-84042004000100002

Gaylord B, Reed DC, Raimondi PT, Washburn L. Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment, *Ecological Monographs*, 76(4): 481–502, 2006.
doi: 10.1890/0012-9615(2006)076[0481:MSDICE];2

Goslee SC, Urban DL. The ecodist package for dissimilarity-based analysis of ecological data, *Journal of Statistical Software*, 22(7): 1–19, 2007.
doi: 10.18637/jss.v022.i07

Guiry MD & Guiry GM. *AlgaeBase*. World-wide electronic publication, National university of ireland, Galway. 2022.
URL: http://www.algaebase.org

Halpern BS, Selkoe KA, Micheli F, Kappel CV. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats, *Conservation Biology*, 21(5): 1301–1315, 2007.
doi: 10.1111/j.1523-1739.2007.00752.x

Heck Jr KL., Wetstone GS. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows, *Journal of Biogeography*, 4: 135–142, 1977.
doi: 10.2307/3038158

Heip C. A new index measuring evenness, *Journal of the Marine Biological Association of the UK*, 54(3): 555–557, 1974.
doi: 10.1017/S0025315400022736

Horta PA, Amancio E, Coimbra CS, Oliveira EC. Considerações sobre a distribuição e origem da flora de macroalgas marinhas brasileiras, *Hoehnea*, 28(3): 243–265, 2001.
URL: https://www.researchgate.net/publication/283995701_Consideracoes_sobre_a_distribuicao_e_origem_da_flora_de_macroalgas_marinhas_brasileiras

JBRJ (Jardim Botânico do Rio de Janeiro). Flora do Brasil 2020.
URL: http://floradobrasil.jbrj.gov.br/. Accessed on June 2020

Jesus PBD, Pestana EMDS, Affe HMJ., Rocha DSB, Caires TA, Nunes JMC, Schnadelbach AS. Reproductive morphology and phenological aspects of one morphological variant of *Hypnea pseudomusciformis* (Gigartinales, Rhodophyta), *Acta Botanica Brasilica*, 33(1): 67–77, 2019.
doi: 10.1590/0102-33062018abb0247

Johns KA, Emsile MJ, Hoey AS, Osborne K, Jonker MJ, Cheal AJ. Macroalgal feedbacks and substrate properties maintain a coral reef regime shift, *Ecosphere*, 9(7):e02349, 2018.
doi: 0.1002/ecs2.2349

Jost L. Entropy and diversity, *Oikos*, 113(2): 363–375, 2006.
doi: 10.1111/j.2006.0030-1299.14714.x

Kohn AJ, Leviten PJ. Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages, *Oecologia*, 25(3): 199–210, 1976.
doi: 10.1007/BF00345098

Leão ZMAN, Kikuchi RKP, Maia MP, Lago RAL. A catastrophic coral cover decline since 3000 years BP, Northern Bahia, Brazil. In: H.A. Lessios and I.G. Macintyre (eds.) Proceedings of the 8th International Coral Reef Symposium. Smithsonian Tropical Research Institute, Panamá, 1997, 583–588.
URL: http://www.reefbase.org/resource_center/publication/pub_9528.aspx

Leigh EG, Paine RT, Quinn JF, Suchanek TH. Wave energy and intertidal productivity, *Proceedings of the National Academy of Sciences*, 84(5): 1314–1318, 1987.
doi: 10.1073/pnas.84.5.1314

Littler MM, Littler DS. Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system, *Journal of Experimental Marine Biology and Ecology*, 74(1): 13–34, 1984.
doi: 10.1016/0022-0981(84)90035-2

Littler MM, Taylor, PR, Littler DS, Sims RH, Norris JN. Dominant macrophyte standing stocks, productivity and community structure on a Belizean barrier-reef, *Atoll Research Bulletin*, 302: 1–24, 1987.
doi: 10.5479/si.00775630.302.1

Lobban CS, Harrison PJ. Seaweed ecology and physiology, Cambridge University Press, Cambridge-New York-Oakleigh, 1994.

Lucio M, Nunes JMC. Aportación al conocimiento fenológico de las rodofíceas marinas de la playa de Guarajuba (Camaçari, Bahia) Brasil, *Botanica Complutensis*, 26: 17–34, 2002.
URL: https://revistas.ucm.es/index.php/BOCM/article/view/BOCM0202110017A

Lyra GM, dos Santos AC, Nunes JMC. Rodofíceas bentônicas das Praias da Concha e Engenhoca, município de Itacaré Bahia, Brasil, *Acta Botanica Malacitana,* 32: 234–240. 2007.
doi: 10.24310/abm.v32i0.7043

MacArthur RH, MacArthur JW, Preer J. On bird species diversity. II. Prediction of bird census from habitat measurements, *The American Naturalist*, 96(888): 167–174, 1962.
doi: 10.1086/282219

Marins BV, Brasileiro PS, de Barros Barreto MB, Nunes JMC, Yoneshigue-Valentin Y, Amado-Filho GM. Subtidal benthic marine algae of the Todos os Santos bay, Bahia State, Brazil, *Oecologia Brasiliensis*, 12(2): 5, 2008.
doi: 10.4257/oeco.2008.1202.05

Martins CDL, Arantes N, Faveri C, Batista MB, Oliveira EC, Pagliosa PR., Fonseca AL, Nunes JMC, Chow F, Pereira SB, Horta PA. The impact of coastal urbanization on the structure of phytobenthic communities in southern Brazil, *Marine Pollution Bulletin,* 64(4): 772–561, 2012.
doi: 10.1016/j.marpolbul.2012.01.031

Marx J, Herrnkind W. Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*: food and shelter, *Journal of crustacean biology*, 5(4): 650–657, 1985.
doi: 10.2307/1548242

Masunari, S. Ecologia das comunidades fitais. Simpósio sobre ecossistemas da Costa Sul e Sudeste Brasileira, Cananéia-SP, 1987.
URL: http://www.ib.unicamp.br/biblioteca/pubdigitais

Moore JW. Importance of algae in the diet of the oligochaetes *Lumbriculus variegatus* (Müller) and *Rhyacodrilus sodalis* (Eisen), *Oecologia*, 35(3): 357–363, 1978.
doi: 10.1007/BF00345142

Moraes, SS. Interpretações da hidrodinâmica e dos tipos de transporte a partir de análises sedimentológicas e do estudo dos foraminíferos recentes dos recifes costeiros da Praia do Forte e de Itacimirim, litoral norte do Estado da Bahia, *Master's dissertation*, Universidade Federal da Bahia, Salvador, Brazil. 2001.
URL: http://repositorio.ufba.br/ri/handle/ri/23463.

Moraes SS, Machado AJ. Influence of hydrodynamic patterns on foraminifera in reef sediment sat the Praia do Forte beach and Itacimirim, Bahia, Brazil, *Anuario do Instituto de Geociências*, 29: 563–564, 2006.
doi: 10.11137/2006_1_563-564

Morrissey J. Community structure and zonation of microalgae and hermatypic corals on a fringing reef flat of magnetic island (Queensland, Australia), *Aquatic Botany*, 8: 91–139, 1980.
doi: 10.1016/0304-3770(80)90045-5

Muñoz AOM, Pereira SMB. Caracterização quali-quantitativa das comunidades de macroalgas nas formações recifais da Praia do Cupe-Pernambuco (Brasil), *Trabalhos Oceanográficos da Universidade Federal de Pernambuco*, 25: 93–109, 1997.
doi: 10.5914/tropocean.v25i1.2731

Nolasco, MC. Carbonatic constructions of the northeast coast of the state of Bahia, *Master's Dissertation*, Universidade Federal da Bahia, Salvador, Brazil. 1988.
URL: https://repositorio.ufba.br/ri/bitstream/ri/23441/1/Disserta%C3%A7ao-Regina.pdf

Nunes JMC. Taxonomia morfológica: metodologia de trabalho, In: Macroalgas: uma introdução à sua taxonomia. Pedrini AG (Ed.), Technical Books Editora, Rio de Janeiro, Brazil 54–70, 2010.

Nunes JMC, Guimarães SMP. Morfología y taxonomía de *Scinaia halliae* (Scinaiaceae, Rhodophyta) en el litoral de Bahia y Espírito Santo, Brasil, *Revista de biología marina y oceanografía*, 45(1): 159–164, 2010.
doi: 10.4067/S0718-19572010000100017

Nunes JMC, Matos MRB. Litoral norte da Bahia: caracterização ambiental, biodiversidade e conservação, EDUFBA, Salvador, Brazil 2017.

Nunes JMC, Paula EJ. O gênero *Dictyota* Lamouroux (Dictyotaceae-Phaoephyta) no litoral do Estado da Bahia, Brasil, *Acta Botanica Malacitana*, 26: 5–18, 2001.
doi: 10.24310/abm.v26i0.7375

Nunes JMC, Paula, EJ. Composição e distribuição das Phaeophyta nos recifes da região metropolitana de Salvador, Bahia, Brasil, *Iheringia Serie Botânica*, 57(1): 113–130, 2002.

Norris JN, Johansen HW. Articulated coralline algae of the Gulf of California, Mexico, I: *Amphiroa* Lamouroux, *Smithsonian contributions to the marine sciences*, 1981.
doi: 10.5479/si.1943667X.9.1

Oksanen FJ, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O´Hara RB, Simpson GL, Solymos P, … & Wagner HH. Vegan: Community Ecology Package (R package Version 2.5-6, 2019).
URL: https://cran.r-project.org/package=vegan

Oliveira-Carvalho MD, Pereira SMB, Zickel CS. Florística e distribuição espaço-temporal das clorofíceas bentônicas em trechos recifais do litoral norte do estado de Pernambuco-Brasil, *Hoehnea*, 30(3): 201–212, 2003.
URL: https://www.infraestruturameioambiente.sp.gov.br/hoehnea/fasciculos/v30f03/

Ramos RJ, Travassos MP, Leite GR. Characterization of macrofauna associated with articulated calcareous algae (Corallinaceae, Rhodophyta) occurring in a hydrodynamic gradient on the Espírito Santo state coast, Brazil, *Brazilian Journal of Oceanography*, 58(4): 275–285, 2010.
doi: 10.1590/S1679-87592010000400003

Reis RP, Yoneshigue-Valentin Y. Variação espaço-temporal de populações de *Hypnea musciformis* (Rhodophyta, Gigartinales) na Baía de Sepetiba e Armação dos Búzios, RJ, Brasil, *Acta Botanica Brasilica,* 12(3): 465–483, 1998.
doi: 10.1590/S0102-33061998000400015

Roberts, DW. Labdsv: ordination and multivariate analysis for ecology (R package version 2.0-1, 2019).
URL: http://cran.r-project.org/package=labdsv

Rodrigues CL, Caeiro S, Raikar SV. Marine macrophyte communities on the reef flat at Agatti atoll (Lakshadweep, India), *Botanica Marina,* 40(1-6): 557–568, 1997.
doi: 10.1515/botm.1997.40.1-6.557

Schenkman RPF. *Hypnea musciformis* (Rhodophyta): ecological influence on growth, *Journal of Applied Phycology*, 25: 192–196, 1989.
doi: 10.1111/j.0022-3646.1989.00192

Scherner F, Horta PA, de Oliveira EC, Simonassi JC, Hall-Spencer JM, Chow F, Pereira SMB. Coastal urbanization leads to remarkable seaweed species loss and community shifts along the SW Atlantic, *Marine pollution bulletin,* 76(1-2): 106–115, 2013.
doi: 10.1016/j.marpolbul.2013.09.019

Schoener TW. Resource partitioning in ecological communities. *Science*, 185(4145): 27–39, 1974.
doi: 10.1126/science.185.4145.27

SEI (Superintendência de Estudos Econômicos e sociais da Bahia). Análise dos atributos climáticos do estado da Bahia, Série estudos e pesquisas, 38, SEI, Salvador, 1998.

Shannon CE, Weaver W. The Mathematical Theory of Information, University of Illinois Press, Urbana, USA 1949.

Soares MO, Teixeira CEP, Bezerra LEA, Paiva SV, Tavares TCL, Garcia TM, Araújo JT, Ferreira SM, Campos CC, … & Cavalcante RM. Oil spill in South Atlantic (Brazil): environmental and governmental disaster. *Marine Policy*, 115: 103879, 2020.
doi: 10.1016/j.marpol.2020.103879

Sousa WP. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community, *Ecological Monographs*, 49(3): 227–254, 1979.
doi: 10.2307/1942484

Steneck RS, Dethier MN. A functional group approach to the structure of algal-dominated communities, *Oikos*, 69: 476–498, 1994.
doi: 10.2307/3545860

Széchy MTM, Paula EJD. Padrões estruturais quantitativos de bancos de *Sargassum* (Phaeophyta, Fucales) do litoral dos estados do Rio de Janeiro e São Paulo, Brasil, *Brazilian Journal of Botany*, 23(2): 121–132, 2000.
doi: 10.1590/S0100-84042000000200002

Taouil A, Yoneshigue-Valentin Y. Alterações na composição florística das algas da Praia de Boa Viagem (Niterói, RJ), *Brazilian Journal of Botany,* 25(4): 405–412. 2002.
doi: 10.1590/S0100-84042002012000004

Tararam AS, Leite FPP, Wakabara Y. Vertical distribution of amphipods living on algae of a Brazilian intertidal rocky shore, *Crustaceana*, 51(2): 183–187, 1986.
doi: 0.1163/156854086X00665

Vasconcelos ERTPP, Vasconcelos JB, Reis TNV, Cocentino ALM, Mallea AJA, Martins GM, Neto AI, Fujii MT. Macroalgal responses to coastal urbanization: relative abundance of indicator species, *Journal of Applied Phycology,* 31: 893–903, 2019.
doi: 10.1007/s10811-018-1639-3

Villaça R, Fonseca AC, Jensen VK, Knoppers B. Species composition and distribution of macroalgae on Atol das Rocas, Brazil, SW Atlantic, *Botanica Marina,* 53(2): 113–122, 2010.
doi: 10.1515/BOT.2010.013

Villaça R, Yoneshigue-Valentin Y, Boudouresque CF. Estrutura da comunidade de macroalgas do infralitoral do lado exposto da Ilha de Cabo Frio (Arraial do Cabo, RJ), *Oecologia Brasiliensis,* 12(2): 206–221, 2008.
doi: 10.4257/oeco.2008.1202.03

Comunidad macroalgal en el arrecife de Itacimirin

Resumen: En este estudio se inventariaron las especies de macroalgas marinas y se analizó la distribución y patrones de biomasa de sus comunidades a lo largo de un gradiente corto de arrecife costero en el noreste de Brasil. Las muestras se colectaron usando la técnica de bloques al azar, distribuidos en tres hábitats: frente arrecifal (FR), pozas mareales (TP) y plano arrecifal (RP). Estas tres conforman el gradiente arrecifal desde el mar hasta la playa. Se identificó un total de 56 taxa, con Ochrophyta y Phodophyta destacándose como los filos con mayor riqueza taxonómica, y con la mayor biomasa representada por las especies *Sargassum vulgare* (30 % de la biomasa total) y *Palisada perforata* (16 %). Los principales patrones emergentes a lo largo del gradiente arrecifal fueron la ocurrencia de grupos de taxa exclusivos en cada hábitat, y variaciones significativas en biomasa, mayores en las TP ($166.1\,\mathrm{g\,m^{-2}}$) y menores en el RP ($70.5\,\mathrm{g\,m^{-2}}$). A pesar de ser un ambiente marcado por la influencia antropogénica, (p.e. turismo y desarrollo), se observó una alta diversidad de especies, con un patrón de distribución que refleja una alta heterogeneidad ambiental y una sustancial integridad ecológica.

Palabras Clave: ficoflora béntica; macroalgas; zona mesolitoral; arrecife tropical

Comunidade Fitobêntica em um curto gradiente recifal, Nordeste - Brasil

Resumo: Este estudo teve como objetivo inventariar as espécies de macroalgas marinhas e analisar seus padrões de distribuição e biomassa ao longo de um curto gradiente recifal no Nordeste do Brasil. As amostras foram coletadas pela técnica de quadrados aleatórios, distribuídas nas três regiões do recife: Platô Recifal (PR); Poças de Maré (PÇ) e Frente do Recife (FR), contemplando o gradiente da praia até o final da zona intertidal do recife. Foram identificados 56 táxons, com destaque para Ochrophyta e Rhodophyta como os filos com maiores riquezas taxonômicas e biomassas, representados pelas espécies *Sargassum vulgare* (30 % da biomassa total) e *Palisada perforata* (16 %). Os principais padrões observados ao longo do gradiente recifal foram as mudanças de composição, com diferentes táxons ocorrendo de forma exclusiva em cada região do recife (habitat recifal) e variações significativas na biomassa, maior nas PÇ ($166.1\,\mathrm{g\,m^{-2}}$) e menor no PR ($70.5\,\mathrm{g\,m^{-2}}$). Apesar de ser um ambiente sob marcada influência antrópica, devido às atividades turísticas, observamos uma alta diversidade de espécies, com um padrão de distribuição que reflete uma alta heterogeneidade ambiental e integridade ecológica.

Palavras-chave: ficoflora bentônica, macroalgas, médio litoral, recife costeiro.

Sol de Maria César Ferreira Graduated in Biological Sciences at Federal University of Bahia, Master's in Ecology and Biomonitoring and student in Ecology: Theory, Applications and Values. Curator assistant at the Museum of Natural History of Bahia and Research Assistant at the Research Center in Marine and Coastal Ecology. Research fields: Community ecology, taxonomy of Gastropoda and ecology of Mollusca and their interactions with phytobenthos.

Lattes: 2304338128340287

ORCID: 0000-0001-5841-9718

Lucas Assumpção Lolis Biologist, Master in Environmental Sciences at Universidade Estadual de Maringá, PhD student in Ecology at Universidade Federal da Bahia. Research focus on invasion biology, investigating biotic interactions and community structure of invaded communities by non-native species. Developed studies with different groups, such as freshwater fish and plants, and now exotic corals at South Atlantic Ocean.

Lattes: 6593932234021469

ORCID: 0000-0002-9158-3509

Pietro Martins Barbosa Noga Graduated in Natural Sciences at Federal University of Technology – Paraná, Master's Degree in Ecology and Biomonitoring (2018) and PhD student in Ecology: Theory, Applications and Values both at Federal University of Bahia, with a sandwich partnership with University of Quebec at Montréal. Research fields: Community ecology and Science education, acting on palynology, paleoecology, climate changes, community modelling and estuarine dynamics.

Lattes: 0533610941631138

ORCID: 0000-0002-9573-4810

Helen Michelle de Jesus Affe Biologist, Master and Doctor in Ecology, with experience in marine ecology. Member of the marine algae research groups at the Universidade Federal da Bahia, and in Oceanography at the Universidade do Estado do Rio de Janeiro, developing research about the dynamics of phytoplankton, and its role in the marine biological pump, in climate change scenarios.

Lattes: 1086266504352985

ORCID: 0000-0002-0230-3764

José Marcos de Castro Nunes PhD in Sciences from the Universidade de São Paulo, Brazil (2005). Has 38 years of experience in marine algal taxonomy, systematics and ecology. Professor at the Universidade Federal da Bahia, Brazil since 1990. Coordinator of the Laboratório de Algas Marinhas (LAMAR). Associate Researcher at Harvard University Herbaria, where he performs postdoctoral studies on marine macroalgal genomics.

Lattes: 5553350296562020

ORCID: 0000-0001-7142-5995