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RHAYANY JUVÊNCIO COSTA

# MARGINAL REEFS IN THE EQUATORIAL SOUTHWESTERN ATLANTIC: BENTHIC COMMUNITY HETEROGENEITY, MACROALGAL BLOOMS, AND ZOOPLANKTON BIOMASS

FORTALEZA - CE
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**Thesis submitted to the Coordination of the Post-Graduation Course in Tropical Marine Sciences - PPGCMT, of the Federal University of Ceará (UFC), as a requirement for the Completion of the PhD in Tropical Marine Sciences in the area of Concentration in Science, Technology and Coastal and Ocean Management.**

**Advisor: Prof. Dr. Marcelo de Oliveira Soares**

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## SUMMARY

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# RESUMO

Os recifes marginais são aqueles que ocorrem em ambientes sob condições restritas, i.e., onde corais ocorrem próximos a limites ambientais de sobrevivência ou em condições consideradas sub-ótimas, extremas ou flutuantes. Sendo assim, os recifes marginais estão geralmente associados a turbidez moderada, a condições mesotróficas ou eutróficas, a amplas variações de temperatura e/ou ressuspensão de sedimentos, sendo ocupados por organismos bioconstrutores adaptados a tais condições. Nesses recifes geralmente há uma menor diversidade de corais escleractíneos que se adaptaram ao longo da história evolutiva. A resistência a distúrbios ambientais das espécies de corais nos recifes marginais reforça o possível potencial desses ecossistemas marinhos como refúgio de parte da biodiversidade recifal em face das mudanças climáticas em curso. No entanto, apesar da existência do interesse global crescente em como os recifes tropicais serão afetados, pouco se sabe sobre a estrutura e dinâmica de recifes marginais quando comparados aos recifes de corais “clássicos”, incluindo aspectos da heterogeneidade das comunidades bentônicas e planctônicas, cuja importância para a ecologia recifal é reconhecida. Nesse contexto, os recifes brasileiros são os únicos ambientes recifais tropicais do Atlântico Sudoeste que se encontram em uma área considerada marginal, podendo ser utilizados como importante modelo para avanço das pesquisas. O objetivo desta pesquisa foi aprofundar o conhecimento sobre a ecologia de recifes marginais no Atlântico Sul Equatorial a partir do estudo em três capítulos em formato de artigos: (1) a variação espacial da estrutura das comunidades bentônicas recifais, (2) as florações das algas *Rhizoclonium*-like, e (3) a variação da biomassa do zooplâncton relacionada aos ambientes recifais. Em relação a estrutura da comunidade bentônica (capítulo 1), nossos resultados apontam para uma forte heterogeneidade espacial com recifes dominados por macroalgas (1 - 60%), algas filamentosas (0 - 47%) e cobertura variável de corais escleractíneos (0 - 18%). Nestes recifes ocorreram apenas quatro corais massivos tolerantes ao estresse, sendo *Siderastrea stellata* e *Montastraea cavernosa* as mais abundantes. A profundidade e o efeito de ondas do tipo *swell* que induzem assoreamento dos recifes marginais mais rasos (16,6 - 16,7) representam importantes fatores de distribuição da comunidade bentônica como esponjas, algas e corais. Outro resultado observado se refere a ocorrência de blooms sazonais de *Rhizoclonium*-like nesses ambientes marginais detalhado no capítulo 2 da tese. O bloom de macroalgas foi registrado, somente entre os meses de Maio e Agosto (2010 – 2018), formando densos tapetes próximos ao substrato recifal, nas quais cobriram outros organismos tais como corais escleractíneos, octocorais, esponjas e outras algas. A análise multivariada indica que as florações nestes recifes moderadamente turvos estão ligadas ao aumento da pressão atmosférica, à direção predominante norte do vento e ao aumento da amplitude térmica. Por fim, no capítulo 3, foi observado que em recifes marginais de zonas turvas e de baixa latitude a biomassa zooplanctônica apresenta uma distribuição heterogênea entre diferentes redes (65, 200 e 300 µm), com a característica oligotrófica das águas e a presença das formações recifais parecendo ter importante papel na distribuição da biomassa orgânica. Nesse contexto, compreender a estrutura e ocorrência dessas comunidades bentônicas e planctônicas e como essas ocorrem nos recifes marginais representa uma estratégia de suma importância para prever possíveis cenários futuros, contribuindo para o gerenciamento desses ecossistemas recifais tropicais em todo o planeta.

**PALAVRAS-CHAVE**: Recifes marginas; Estrutura da comunidade bentônica; Bloom de algas; Biomassa do zooplâncton.

# ABSTRACT

Marginal reefs are those that occur in environments under restricted conditions, i.e., where corals occur close to environmental limits of survival or under conditions considered sub-optimal, extreme or fluctuating. Thus, marginal reefs are generally associated with moderate turbidity, mesotrophic or eutrophic conditions, wide temperature variations, and/or resuspension of sediments, and are occupied by bioconstructing organisms adapted to such conditions. On these reefs there is generally a lower diversity of scleractinian corals that have adapted over evolutionary history. The resilience to environmental disturbance of coral species on marginal reefs reinforces the possible potential of these marine ecosystems as a refuge for part of the reef biodiversity in the face of ongoing climate change. However, despite growing global interest in how tropical reefs will be affected, little is known about the structure and dynamics of marginal reefs as compared to "classic" coral reefs, including aspects of the heterogeneity of benthic and planktonic communities, whose importance to reef ecology is recognized. In this context, Brazilian reefs are the only tropical reef environments in the Southwest Atlantic that are in an area considered marginal, and can be used as an important model to advance research. The objective of this research was to deepen the knowledge of the ecology of marginal reefs in the South Equatorial Atlantic from the study in three chapters in article format: (1) the spatial variation of the structure of benthic reef communities, (2) *Rhizoclonium*-like algal blooms, and (3) the variation in zooplankton biomass related to reef environments. Regarding benthic community structure (chapter 1), our results point to a strong spatial heterogeneity with reefs dominated by macroalgae (1 - 60%), filamentous algae (0 - 47%) and variable coverage of scleractinian corals (0 - 18%). On these reefs only four stress-tolerant massive corals occurred, with *Siderastrea stellata* and *Montastraea cavernosa* being the most abundant. The depth and the effect of swell-type waves that induce siltation of the shallower marginal reefs (16.6 - 16.7) represent important factors in the distribution of the benthic community such as sponges, algae, and corals. Another observed result refers to the occurrence of seasonal *Rhizoclonium*-like blooms in these marginal environments detailed in chapter 2 of the thesis. The macroalgae bloom was recorded, only between the months of May and August (2010 - 2018), forming dense mats near the reef substrate, in which they covered other organisms such as scleractinian corals, octocorals, sponges and other algae. Multivariate analysis indicates that blooms on these moderately turbid reefs are linked to increased atmospheric pressure, predominant north wind direction, and increased temperature range. Finally, in chapter 3, it was observed that in marginal reefs of turbid and low latitude zones the zooplankton biomass shows a heterogeneous distribution between different nets (65, 200 and 300 µm), with the oligotrophic characteristic of the waters and the presence of the reef formations seeming to play an important role in the distribution of the organic biomass. In this context, understanding the structure and occurrence of these benthic and planktonic communities and how they occur on marginal reefs represents a strategy of paramount importance to predict possible future scenarios, contributing to the management of these tropical reef ecosystems across the planet.

**KEYWORDS:** Marginal reefs; Benthic community structure; Algal blooms; Zooplankton biomass.

# 1. GENERAL INTRODUCTION

## 1.1. “Traditional” clear and shalllow-water and marginal reefs

Coral reefs have relevant marine biodiversity, in addition to keystone ecosystem goods and services for humanity (BARBIER, 2017). However, with intensifying human impacts and environmental degradation of tropical reefs, it is estimated that 30% of these ecosystems are already damaged, and that by 2030 about 60% may not persist (HUGHES et al. 2003, 2018). Such alarming ongoing predictions have led to numerous studies that try to identify how tropical shallo-water reefs respond to various conditions aiming to understand their dynamics in the face of local and global environmental changes (HUGHES et al. 2007; SPALDING & BROWN, 2015; PANDOLFI, 2015).

The occurrence of shallow-water reefs (<30m depth) in tropical regions with oligotrophic, transparent, warm waters (with a well-defined and narrow temperature range between 22 and 30°C), and at low latitude is well known in the literature (NEWELL, 1971; POTTS & JACOB, 2000). These coral reefs are characterized by high coral cover on the reef substrate and high species richness (e.g, Coral Triangle), as they occur under environmental parameters conducive to optimal carbonate bioconstruction and high benthic productivity (ZILBERBERG et al., 2016; HUTCHINGS et al, 2019). However, if environmental conditions move away from those considered "optimal" for growth of reef-building corals (such as scleractinians), carbonate productivity and three-dimensional reef complexity can be drastically modified (PERRY & ALVAREZ-FILIP, 2019). These shallow reefs with these aforementioned characteristics are considered "traditional", as they correspond to the shallow-water tropical reefs first described and most historically studied as in the Caribbean Sea region and on the Great Barrier Reef in Australia (MORAIS et al., 2018).

Distinctively, tropical reefs also occur in environmentally constrained marginal environments, where reef-building coral communities occur near environmental limits of survival or in areas with suboptimal, extreme, or fluctuating conditions that experience wide environmental variation (PERRY & LARCOMBE, 2003) (Figure 1). These are known as marginal or extreme reefs, generally associated with a lower richness of scleractinian corals (SOARES et al., 2021) but fully adapted throughout evolutionary history to unique local conditions, such as extreme temperatures and salinities (CHUI & ANG JR, 2017), low aragonite saturation status (GUINOTTE, BUDDEMEIER & KLEYPAS, 2003), mesotrophic or eutrophic waters (KLEYPAS et al. 1999), occurrence in the mesophotic zone (SOARES et al., 2018), andmoderate turbidity, which may be (or not) associated with high latitudes (CACCIAPAGLIA & VAN WOESIK, 2016) (Figure 2).

Figure 1 - Marginal reefs (five types) in the world. Source: Soares et al. (2021).

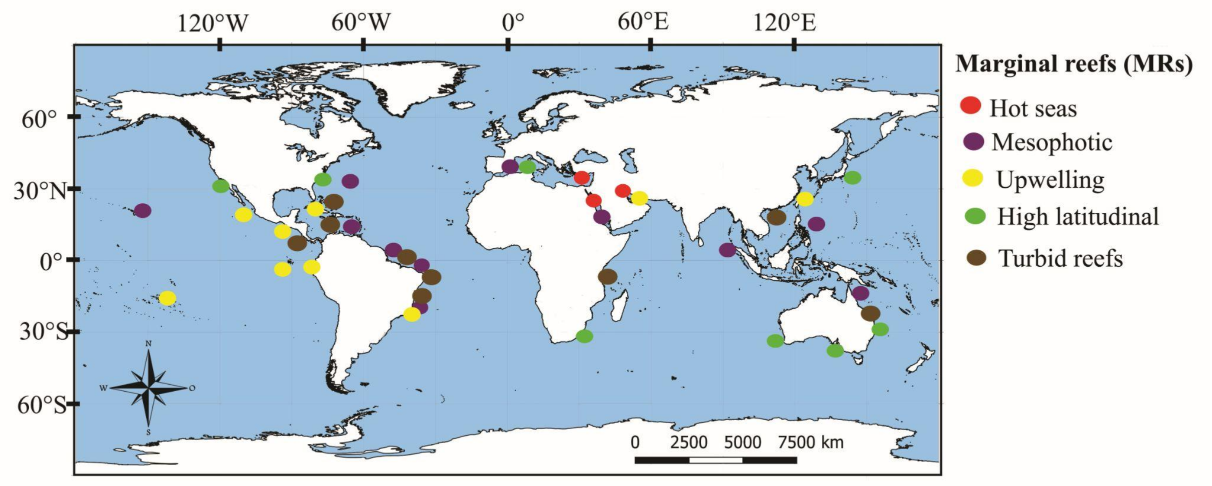
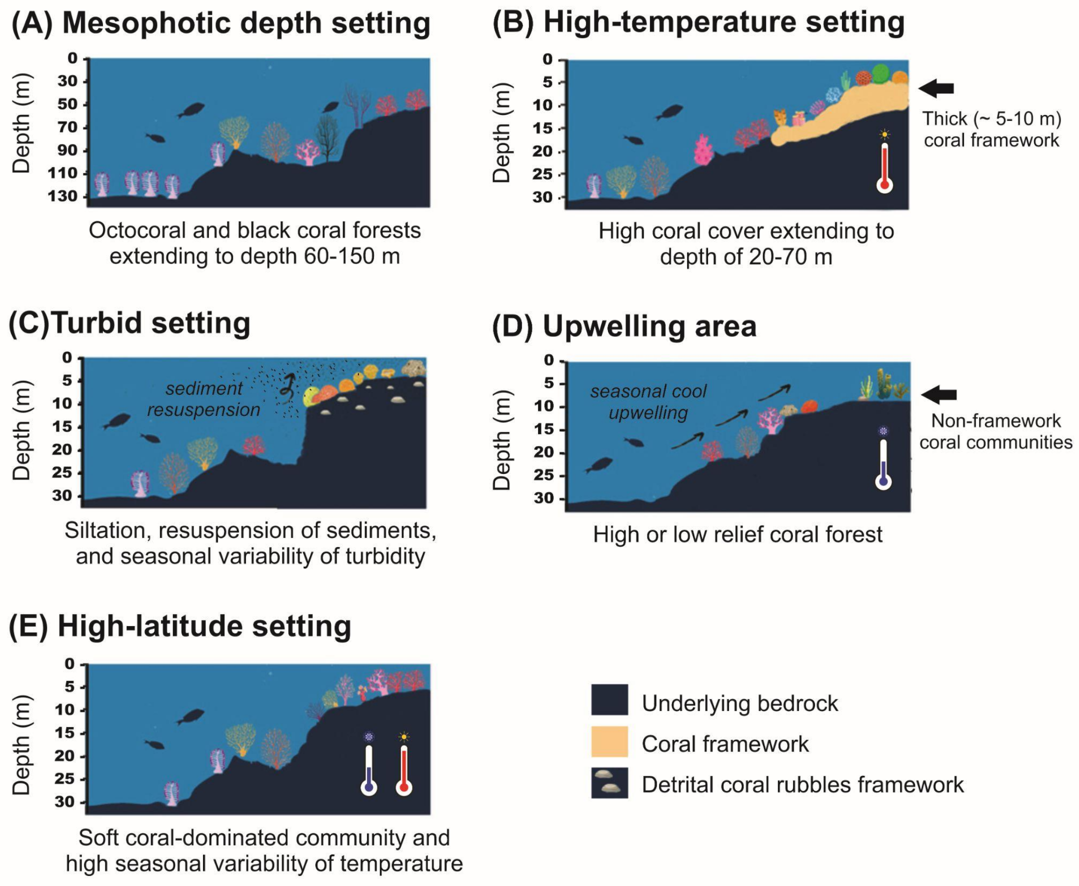


Figure 2 - Suboptimal environmental conditions for coral growth on distinct five marginal reefs. Source: Soares et al. (2021).

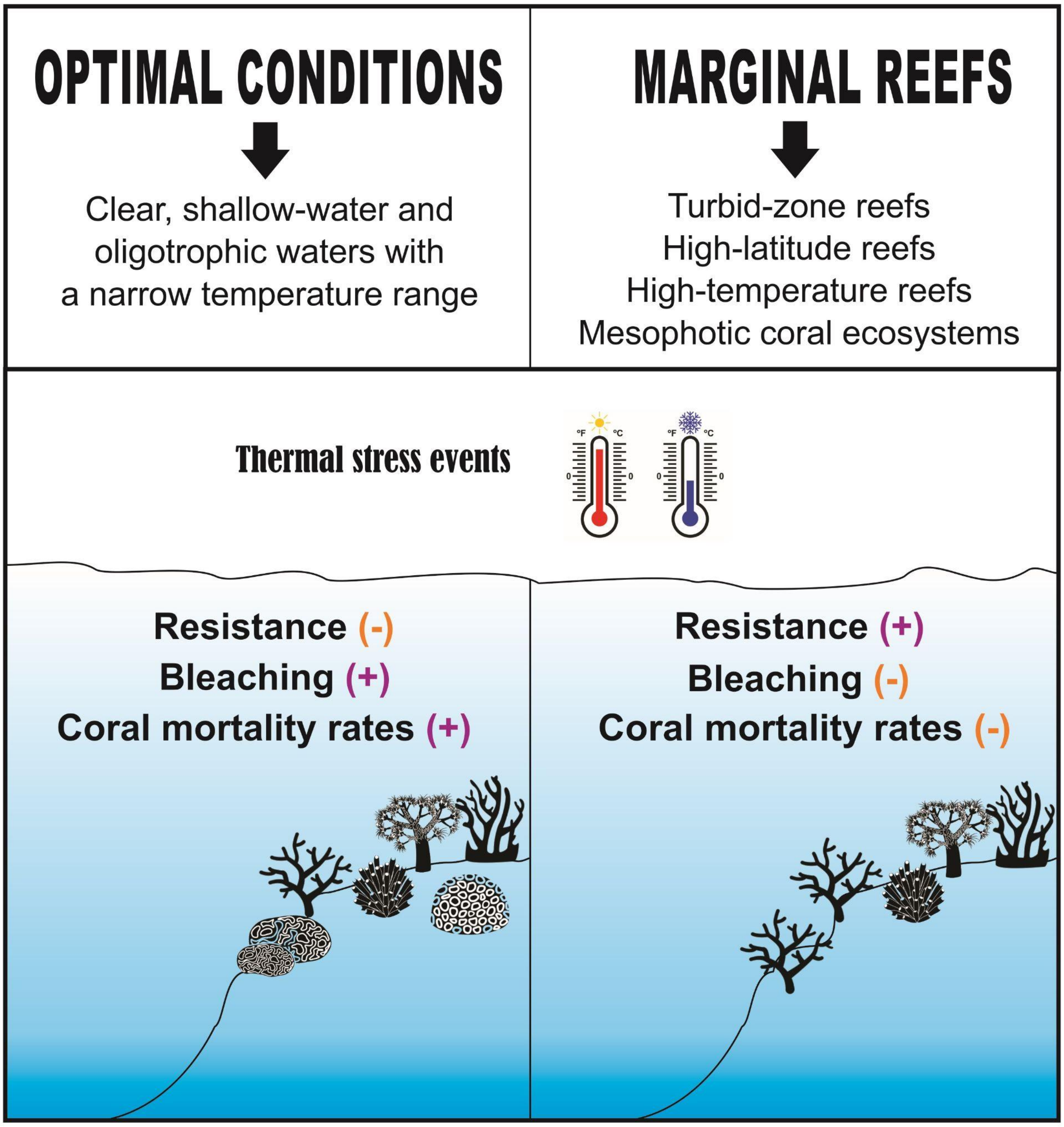


The resilience of stress-tolerant reef-building corals on marginal reefs in the face of stressors such as marine heatwaves (CACCIAPAGLIA & VAN WOESIK, 2016; TEIXEIRA et al., 2019) suggests that these unique environments may act as limited refugia for some species (SOARES, 2020a). Limited refugia because despite being resilient systems to short-term and acute environmental disturbances, they are not completely immune to the long-term synergestic and cumulative impacts of them, such as the local impacts (e.g., marine pollution and silting) and growing climate change impacts (SOARES, 2020a; DIXON et al., 2022). Under this perspective, resistance (the ability of a system to withstand an external disturbance), resilience (speed of a system to return to the original structure after a disturbance) and persistence (the ability of a system, even in the face of disturbances, to remain within defined limits) are important processes linked to the stability of these extreme reef ecosystems in the face of external disturbances (SOARES et al., 2021), for example thermal stresses resulting from global warming and marine heatwaves (WU & LOUCKS, 1995; SOARES, 2020a).

The benthic community structure in marginal reefs is still poorly studied when compared to tropical "traditional" shallow-water reefs. Despite the low richness of scleractinian corals in marginal reefs, the species that dominate these environments stand out for their tolerance to some disturbances (BURT et al., 2020; SOARES et al., 2021). This resilience can even confer high coral cover rates (SOARES et al., 2021), along with algae and sponges (SOARES et al., 2017). Furthermore, these extreme reefs may exhibit strong heterogeneity in composition and benthic cover, associated with high levels of endemism, a topic that still needs to be further investigated worldwide (CAMP et al., 2018; BURT et al., 2020).

Stress-tolerant corals can be resistant to different stressors, such as temperature, turbidity or reduced luminosity. For example, some stress-tolerant corals on tropical marginal reefs (e.g., hot-water reefs in Persian Arabian Gulf and Red Sea) are hypothesized to have greater resistance to temperature increase when compared to "traditional" reefs under optimal conditions. Also, studies on turbid-zone reefs (CACCIAPAGLIA & VAN WOESIK, 2016), mesophotic ecosystems (30-150m depth) (SOARES et al., 2020b) and high-latitude reefs, that persist in reduced luminosity, partially support this hypothesis of coral resistance in the face of different stressors (FREEMAN, 2015). It is already known that scleractinian coral communities of high-latitude reefs exposed to extreme environmental conditions are dominated by opportunistic species that are more tolerant to short-term thermal stress but not long-term multiple disturbances (BEGER et al., 2013). Furthermore, it is known that in mesophotic ecosystems, due to the depth, these corals could be subjected to less light and temperature stress, especially in upwelling zones (SOARES et al., 2018; SOARES et al., 2020b). Another important fact is that turbid waters can protect, by shading, corals from the detrimental interaction between high light-heat stress , attenuating the bleaching process during acute events (CACCIAPAGLIA & VAN WOESIK, 2016) (Figure 3). In this regard, the specific corals traits in marginal reefs combined with the unique environmental conditions to which they are exposed, can make them more resistant to some disturbances.

Figure 3 - Bleaching and resistance of traditional and suboptimal reef environments. Source: Soares et al. (2021)



In this sense, stress-tolerant corals on turbid-zone reefs are less susceptible to marine heatwaves due to a combination of unique environmental and biological conditions, including shading produced by turbidity, higher levels of coral heterotrophy, and local adaptations of species (TEIXEIRA et al. 2019; SOARES, 2020a). Therefore, in marginal reefs, three factors seem to be differential for their stability: biological tolerance to short-term stress in the case of high-temperature and turbid-water settings (Figure 2), protection from high-light stress due to depth, and turbid waters. This resistance to disturbances of marginal reefs reinforces the possible potential of these ecosystems as a refuge for part of the reef biodiversity in the face of ongoing climate change. In this context, Brazilian reefs are the only tropical Southwestern Atlantic reefs that are located in an area considered marginal (MIES et al., 2020; SOARES et al., 2021), and may be used as an important model to advance research.

Like the structure of benthic communities, zooplankton biomass is also a little explored topic in moderately turbid and low-latitude marginal reefs when compared to shallow-water ‘traditional” reefs (PERRY & LARCOMBE, 2003; NAKAJIMA et al., 2009). Zooplankton act at the base of the reef food chain by mediating the transfer of energy from phytoplankton to higher trophic levels (PEIJNENBURG & GOETZE, 2013). Given such importance, knowledge of the local factors that influence the distribution of zooplankton biomass in these marginal reef ecosystems is of great relevance to the advancement of marine sciences. In marginal reefs, under sub-optimal environmental conditions as those studied here, the oligotrophic waters and the active nutrient recycling characteristic of the region seem to play a paramount role in the distribution of zooplankton biomass.

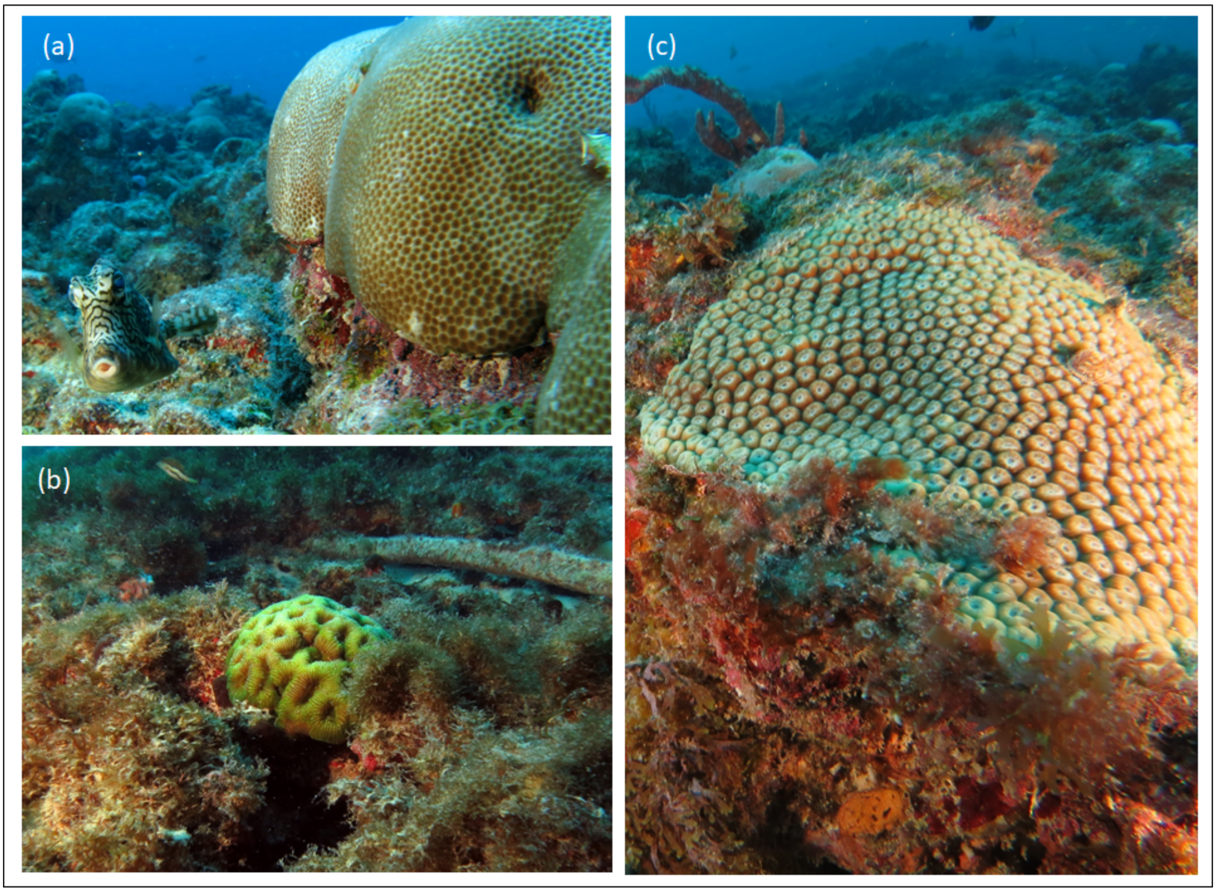
## 1.2. South Atlantic Reefs (Brazil)

Brazilian shallow coral reefs occur under significant conditions of sedimentation, turbidity, and nutrient inputs (LEÃO et al., 2016; BANHA et al. 2019; TEIXEIRA et al. 2019) (Figure 4). Therefore, they are considered marginal reefs due to these suboptimal conditions and their intrinsic characteristics, such as low coral richness, presence of massive and endemic corals, and current resilience to thermal stress events (LEÃO et al., 2016; MIES et al., 2020; SOARES et al., 2021). Previous studies point out that most of the massive coral species that compose the Brazilian reefs, such as *Montastraea cavernosa*, *Siderastrea stellata*, and *Mussismilia* spp., express tolerance to past bleaching events (MAYAL et al. 2009; FERREIRA et al. 2013; LEÃO et al. 2016; MIES et al., 2020; SOARES et al., 2021) (Figure 5).

Figure 4 - Aerial photographs of different marginal reef areas on the Southwest Atlantic coast (Brazil) (a) Reefs of Porto de Galinhas in Pernambuco state; (b) Reefs of Picãozinho in Paraíba state; (c) Reefs of the Abrolhos Archipelago Islands in Bahia state; (d) Reefs of the Coral Coast APA between Pernambuco and Alagoas states. Source: Leão et al. (2016); Prefeitura Municipal de João Pessoa/Secretaria do Turismo; and Ministry of the Environment (2020).

In addition to the low diversity of stress-tolerant massive corals present on marginal reefs, algae and sponges also constitute key components of the reef seascape (SOARES et al. 2017; CAMP et al., 2018; BURT et al., 2020). Such eco-engineers organisms confer strong spatial heterogeneity with respect to abundance, cover, and composition of the benthic communities on marginal reefs (SOARES et al. 2017).

Figure 5 - Coral species found on the studied marginal low-latitude reefs (Equatorial Southwestern Atlantic, Ceará coast) in this PhD. thesis: (a) *Siderastrea stellata*. (b) *Mussismilia hispida*. (c) *Montastraea cavernosa*. Source: SEMA/FCPC/LABOMAR (2019)



Brazilian reefs have unique characteristics that make corals more tolerant in the short term to environmental disturbances. This resistance can be explained by numerous adaptations, among which we can exemplify three. The first characteristic would be related to the composition of photosynthetic endosymbionts in the tissue of host corals in Brazil (MIES et al., 2020). The identity of the symbiont itself in the coral-dinoflagellate symbiosis represents a key factor, because different phylotypes present different physiological *optimum*, making a coral more or less susceptible to environmental disturbances and photobiological performance (BAKER, 2001). Another important feature related to the Symbiodinaceae would be the presence of more flexible symbiotic relationships composed of generalist organisms (corals and symbiont phylotypes). In this regard, coral species are considered generalists when associated with more than one clade of symbionts, on the other hand, species associated with a single clade are considered specialists. Regarding endosymbionts, these are considered generalists when found in more than one coral genus; on the other hand, symbiont phylotypes found in a single host coral genus are taken as specialists. It is possible that this flexibility of generalist organisms found on Southwestern Atlantic reefs may contribute to the corals' greater tolerance to bleaching, as the ability to associate with more symbiont types represents an important strategy for adaptation and acclimation under environmental stress (MIES et al. 2020). A study developed with colonies of *Madracis decactis* on Brazilian reefs (Abrolhos Bank and Saint Peter and Saint Paul Archipelago), for example, pointed out that the community of endosymbionts associated with this coral was composed of several types of clades simultaneously, and this multiple occurrence may be related to a greater tolerance (VARASTEH et al., 2021).

A second important feature would be the heterotrophic feeding strategy as a compensatory measure in the face of reduced autotrophic mechanism in bleaching events (MIES et al. 2018). A study developed with bleached and recovering corals of *Montipora capitata* in Hawaii pointed out that increased heterotrophy played an important role in meeting the coral's daily metabolic energy needs, suggesting that corals with high heterotrophic capacity during bleaching and recovery events may become more resilient and dominant in the long term (GROTTOLI et al., 2006). Such a process occurs in several coral species on Brazilian turbid reefs (MIES et al., 2020).

Finally, in turbid zone reefs, protection of massive corals can occur through turbidity, which protects them from light and thermal stress (CACCIAPAGLIA & VAN WOESIK, 2016). This is a third important adaptation strategy in Brazilian marginal reefs. In addition to the adaptations mentioned above, there is the history of thermal stress in the South Atlantic, which, by being exposed to lower frequencies of marine heat waves so far, gives an additional adaptative advantage to corals in the region (BANHA et al., 2019; MIES et al. 2020) however some species are recently affected by the severe and frequent heatwaves (PEREIRA et al., 2022).

Given the predicted scenarios of global climate change and despite the existence of growing global interest in how tropical reefs will be affected, little is known about the structure and benthic cover of marginal reefs compared to "traditional" coral reefs (PERRY & LARCOMBE, 2003; BEGER et al. 2013; SOARES, 2020a). Understanding the structure and occurrence of these communities and how they survive on marginal reefs represents a strategy of paramount importance to predict possible future scenarios of current reefs, contributing to the management of these ecosystems across the planet. The analysis of the structure and functioning of tropical reefs in the South Atlantic (Brazil) can serve as a model to better understand the characteristics of marginal reefs and contribute to this global knowledge gap to improve theories about the heterogeneity of these communities as well as resistance and resilience to environmental impacts. Another virtually unknown topic in marginal reefs is the occurrence of macroalgal blooms, which will be another chapter/theme of this novel PhD thesis.

### 1.3. Environmental factors and occurrence of macroalgae in reef environments

Temperature is a key environmental variable that influences the distribution, growth, coverage, among other indicators of algal conditions (SOUSA-DIAS & MELO, 2008; TAYLOR et al. 2001), with a relevant role in the occurrence of macroalgae blooms (RYBAK & GĄBKA, 2018). Studies point out that temperature plays an important role in controlling macroalgae growth (ZHANG et al., 2019). Generally, marine macroalgae respond with increased biomass to increasing temperature (TAYLOR et al., 2001; THORNBER et al., 2017). Even climate change, due to rising global average temperature and marine heatwaves, may act as potential drivers for increased blooms occurrence in future scenarios (PAERL & HUISMAN, 2008).

Certain species, such as *Rhizoclonium tortuosum*, show higher growth rates at temperatures between 15 and 20 °C, and lower growth rates at higher temperatures (25 to 30 °C) (TAYLOR et al. 2001). However, *Rhizoclonium riparium*, one of the few species of the genus *Rhizoclonium* found in Brazil (ALVES et al. 2009), has its growth strongly influenced by rising temperatures, with 25 °C being optimal for growth of the species (CHAO et al. 2005). In the Pedra da Risca do Meio Marine Park (Ceará state), blooms of the *Rhizoclonium*-like macroalgae have been recorded (COSTA et al. in prep.; i.e., chapter 2). This low-latitude area, located on the marginal reefs studied here, lies under relatively stable temperatures within a narrow range (between 26° and 30°) (SOARES et al., 2017). In this sense, we can hypothesize that small variations in temperature or climate-oceanographic events are sufficient to stimulate and sustain the occurrence of macroalgae blooms, which will be analysed in this PhD. thesis concerning the marginal reefs.

Temperature is also an important driver for the germination of "seed banks" that will form macroalgae blooms. In this context, Song et al. (2015) observed that the optimal germination temperature varied for different green macroalgae, and this altered the biomass and species composition at different times. Moreover, Hall & Walmsley (1991), when analyzing the effects of high temperature (40 °C) on the germination of the filamentous macroalgae *Rhizoclonium riparium*, observed that optimal germination occurred between 15 and 20 °C and in a fast manner. This rapid germination led the authors to confirm the trend already reported for this algae that it produces early reproductive stages (akinetes and zoospores), rather than the usual reproduction by vegetative fragmentation, when under temperature stress conditions.

Wind is also a likely important variable in the study of macroalgal blooms on marginal reefs. It is hypothesized that the speed and direction will interfere with the hydrodynamics of the waters and the characteristic turbidity of these reefs. Weaker winds tend to make the water masses more stable, reducing turbidity and promoting greater light penetration that favors algae. On the other hand, it is hypothesized that stronger winds cause greater turbulence making the waters more turbid (resuspension of sediments) and decreasing the range of light penetration in the water column, not being favorable to macroalgae blooms in deeper reef systems (WU et al., 2015).

Precipitation, nutrients (e.g. Nitrogen and Phosphorus) and chlorophyll are other variables commonly identified as key drivers of algae blooms (PHLIPS et al. 2011; BINDING et al. 2018). On the marginal reefs studied here, precipitation may plays an important role in increasing nutrient loading to the oligotrophic waters of the Brazilian equatorial coast. The increased concentration of nutrients, such as nitrogen and phosphorus, during rainy periods can favor the amount and development of coastal algal blooms (PHLIPS et al. 2011). Besides nutrients, other factors characteristic of each species, such as absorptive capacity, nutritional status and preferences, interfere with the formation of algal blooms (ANDERSON et al. 2002), as well as ecological aspects, such as interspecific competition for nutrients (PHLIPS et al. 2006), and space, in addition to predation. However, the ephemeral and intense characteristics of blooms are closely linked to the rapid uptake of bioavailable nutrients in the system, which results in increased biomass (LEAL et al. 2020). Although in the marginal reefs studied here the macroalgal blooms occur in a non-rainy period and there is no evidence of nutrient input from the shore or by upwelling (SEMA/FCPC/LABOMAR, 2019),the environmental factors involved in macroalgal blooms need to be unraveled and studied.

Regarding chlorophyll, it acts as an indicator of algae biomass (BOYER et al., 2009). Because it is highly related to nutrients, it represents a potential variable to indicate nutrient inputs (BRODIE et al., 2007). Phlips et al. (2011), for example, observed that chlorophyll concentrations were positively correlated with nitrogen and phosphorus. In the case of the reef region studied here, because it is located in the open ocean, in a marine area without resurgence, in deeper regions (~17 to ~27 m depth), and in turbid areas, (SOARES et al.,

2017) changes in the pattern of weather conditions may be related to seasonal blooms of the *Rhizoclonium*-like macroalgae, which will be investigated in this PhD. thesis.

## 1.4. Main research actions to be explored in this PhD. thesis

In this context of marginal reef analysis, this PhD thesis will have three chapters with new themes to be submitted to international peer-reviewed journals after the thesis defence and expertcomments. The structure of the chapters already in English aims at publishing the results of the doctoral thesis in a faster way after the evaluation by the academic committee. In chapter 1, a novel study of the benthic cover of eight marginal reefs in the Equatorial Southwestern Atlantic (Ceará, Brazil) was conducted in order to improve in-depth knowledge about these unique ecosystems in a low-latitude region with high and stable temperatures. Using the PIT (Point Intersept Transect) method, data on the percent benthic cover over these never studied reefs were collected over a depth gradient (~17 to ~27m depth) to investigate spatial heterogeneity in marginal reefs.

Previous benthic studies in the studied area analyzed only one reef and pointed to a low diversity of tolerant corals such as *Montastraea cavernosa* and *Siderastrea stellata*, besides showing sponges and algae as dominant reef components (SOARES et al., 2017). This composition reflects characteristic patterns of low-latitude marginal reefs that, in general, are dominated by a few massive corals resistant to environmental disturbances (HENNIGE et al., 2010), by fast-growing filamentous algae, and by stress-tolerant suspensivorous benthic organisms, such as sponges (BELL et al., 2015). In this context, Hennige et al. (2010) suggests that in marginal reefs the diversity of massive and disturbance-tolerant corals tends to increase, modifying the reef biodiversity, the provision of ecosystem services, and the decreasing carbonate accumulation rates in reefs, since massive coral pecies are slower and non-building species (e.g., fleshy algae and sponges) could dominate. Regarding sponges, these eco-engineering animals have the ability to tolerate or even thrive in environments with significant sedimentation forming dense 3-D marine animal forests (BELL et al., 2015).

On “traditional” coral reefs, as a result of phase shift, filamentous algae and sponges could increase instead the coverage of scleractinian corals that is reduced (BELL et al., 2013; NORSTRÖM et al., 2009). This process occurs when reef-building building corals are replaced by non-building organisms (DONE, 1999). Brazilian reefs are naturally dominated by algae in the reef substrate (VILLAÇA & PITOMBO, 1997; CRUZ et al. 2009; SEGAL & CASTRO, 2011; SOARES et al. 2017). The phase shifts and barrens observed so far in these marginal reefs along the Brazilian coast refer to the change of coral-dominated state towards macroalgae and zoantharian dominance, associated with local impacts such as excessive nutrients of anthropogenic origin (CRUZ et al. 2018; REIMER et al., 2021).

In chapter 2, we analysed for the first time the drivers of seasonal blooms of *Rhizoclonium*-like macroalgae on marginal reefs in the equatorial SW Atlantic (Figure 6). Algal blooms are characterized by the rapid and massive development of algae in aquatic environments, and is usually seasonal and of short duration (JACKSON & LOCHMANN, 2018). Widely studied in shallow-water coral reefs < 10m depth (LAPOINTE, 1999; HUGHES et al. 1999), estuaries and lagoons (GUBELIT & BEREZINA, 2010; ZHANG et al. 2014; LANARI & COPERTINO, 2017), the study of macroalgal blooms in these ecosystems already has a widespread literature. However, it is little studied in deeper marginal reefs (17-30m), from turbid areas and far from the coast. There are many possible drivers for the macroalgal blooms, so natural and anthropogenic stressors may interact in complex ways for this phenomena. Local impacts from overfishing or aquaculture can cause depletion of herbivores and modify food webs contributing to the emergence of blooms (HUGHES, 1994; HEISLER et al. 2008). Similarly, nutrient enrichment (taking into account composition and quantity) by human action or by upwelling are also factors to be considered in nearshore areas (KAMER et al. 2001; HEISLER et al. 2008; TRAINER & HARDY, 2015).

Figure 6 - Bloom of *Rhizoclonium*-like macroalgae on marginal reefs (Equatorial Southwestern Atlantic, Brazil). Source: Prepared by the authors (2022).

Considering the current knowledge, key variables such as temperature, wind intensity/direction, precipitation, chlorophyll, turbidity, PAR (photosynthetically active radiation), among others have been tested in this PhD chapter to analyze the causes of the occurrence of macroalgae blooms in these marginal reefs. This phenomena are increasingly frequent, worldwide (FRANKLIN & FORSTER, 1997; SOUSA-DIAS & MELO, 2008; PHLIPS et al. 2011; HUANG et al. 2014; BINDING et al. 2018) but its never studied in these low-latitude reefs.

Finally, in chapter 3, the spatial variation of zooplankton biomass on moderately turbid and low-latitude marginal reefs was described. Despite acting as the base of the marine food webs, zooplankton biomass on equatorial SW Atlantic reefs is still poorly studied. Therefore, plankton samples were collected at 14 stations, using subsurface trawls, to analyze whether marginal reefs and oligotrophic water characteristics influence the spatial distribution of biomass.

## 2. THESIS HYPOTHESIS

Building on the theoretical concepts discussed in the general introduction and on the three chapters of this PhD Thesis, we suggest three main novel hypothesis as follows:

(1) Marginal reefs can exhibit strong spatial heterogeneity, having massive sponges, algae and massive disturbance-tolerant corals as key components of the benthic structure;

(2) *Rhizoclonium*-like algal blooms on low-latitude marginal reefs in areas far from the coast may be related to small variations in temperature, turbidity, chlorophyll, PAR (photosynthetically active radiation), wind intensity/direction, precipitation, insolation, and cloudiness;

and

(3) The spatial distribution of zooplankton biomass in this turbid-zone region may be influenced by the nutrient-poor waters and location of marginal reefs.

Testing these three hypotheses contributes to the global discussion about the structure and dynamics in extreme reefs. In addition, it helps to understand reef resilience under marginal conditions which is of relevance for improving knowledge on tropical reefs in the world´s oceans, especially in the scarcely known equatorial region.

# 3. OBJECTIVES

## 3.1. General Objective

To analyze the spatial variation in benthic cover, *Rhizoclonium*-like algal blooms, and zooplankton biomass on marginal reefs in the equatorial Southwestern Atlantic.

## 3.2. Specific Objectives

- To examine the benthic cover on marginal reefs in the equatorial SW Atlantic (Ceará state coast, Brazil) and to identify whether depth and sedimentation influence the spatial distribution of Live coral, Macroalgae, *Rhizoclonium*-like, Filamentous algae, Crustose algae, Sponge, Other organisms, and abiotic characteristics (sediment and Rocky ground cover).

- To analyze seasonal occurrence of *Rhizoclonium*-like algal blooms on marginal reefs in the equatorial SW Atlantic (Ceará, Brazil) and to identify whether temperature, turbidity, chlorophyll, PAR (photosynthetically active radiation), wind intensity/direction, precipitation, insolation, and cloudiness influence seasonal blooms.

- To describe the spatial variation of zooplankton biomass in surface waters of the equatorial SW Atlantic (Ceará, Brazil) and to identify whether reef formations influence the spatial distribution of zooplankton biomass in this low-latitude reef region.

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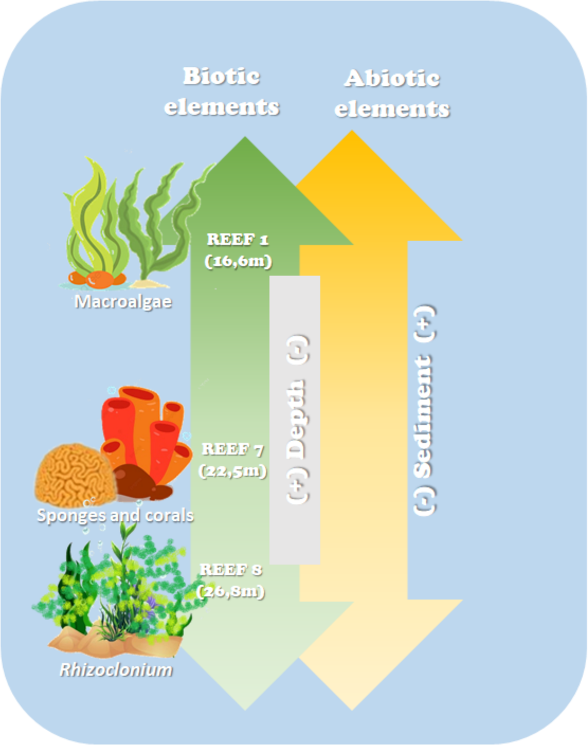
# CHAPTER 1 – LOW-LATITUDE AND TURBID REEFS SHOW HETEROGENEITY IN BENTHIC COVER



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# CHAPTER 1 – LOW-LATITUDE AND TURBID REEFS SHOW HETEROGENEITY IN BENTHIC COVER

## ABSTRACT

We analyzed the spatial patterns of benthic cover on turbid and low-latitude reefs in the equatorial Southwestern Atlantic. Furthermore, we identified how depth and sediment quantity influences the distribution of the main benthic components (macroalgae, corals and sponges). Eight marginal reefs located in a marine protected area with ~17 to ~27m depth were analyzed. Results indicated algae as dominant reef components, in addition to a variable coverage of sponges (3-21%) and four (mainly *Siderastrea stellata* and *Montastraea cavernosa*) massive corals (0-18% of cover). Cluster analysis distinguished two major groups of reefs with significant difference between them (PERMANOVA, $p < 0.05$). The differentiation of the groups was mainly determined by the contribution of algae. All four reefs in group I, are among the shallowest reefs with ~16m to ~18m depth. Macroalgae occurred in higher percentage on the shallower reefs (16.6 and 16.7m) subjected to higher sedimentation rates. *Rhizoclonium*-like algae, and filamentous algae had higher coverage rates on the deeper reefs (22.5 and 26.8m). The highest cover of sponges (21%) and corals (18%) was recorded on the second deepest reef, subject to less siltation. The reefs with the lowest sediment cover (1% - 4%) were the deepest (26.8m and 22.5m). The opposite occurred on the shallower reefs (16.7m and 16.6m), where siltation was higher (29% - 31% cover). Depth was inversely significantly ($p < 0.05$) correlated with macroalgae and sediment quantity. Thus, depth and the effect of swell waves that induce siltation and resuspension of sediments on shallower reefs play an important role on this unique assemblage (formed by stress-tolerant and weedy species) and also on heterogeneity. In this regard, the overall similarity among the marginal reefs was only 40%. The results indicate significant spatial heterogeneity of benthic cover, which indicates that tropical marginal reefs are more heterogeneous than expected by previous published results.

**Keywords:** Marginal reefs; Spatial distribution; Benthic community; Reef-building corals.

## 1. INTRODUCTION

Over the past decades tropical shallow-water reefs have suffered from multiple impacts such as increased sedimentation, pollution, overfishing, and climate change (e.g., sea level rise, ocean acidification, and marine heatwaves) (BENJAMIN et al. 2008; SMITH et al. 2016; EDDY et al., 2021). These pervasive impacts have altered the reef community in some reefs previously dominated by scleractinian corals with the increase of other groups, such as algae, zoantharians, and sponges (BELL et al., 2013; CRUZ et al., 2018). Understanding these spatial patterns in the benthic cover represents an important step toward understanding how human disturbances can modify the reef composition and functioning (ARONSON & PRECHT, 1997; CELLIERS & SCHLEYER, 2008; LIAO et al., 2021). Furthermore, studies of benthic cover can contribute to effective reef management by generating subsidies for conservation and management actions (GABRIÉ et al. 1994; CELLIERS & SCHLEYER, 2008; KNOWLTON, 2021).

In the literature it is possible to find studies addressing the spatial patterns of benthic cover in tropical shallow-water reefs with low nutrient content and low turbidity, which characterizes "traditional" coral reefs dominated by scleractinian corals (VROOM et al., 2005, PRICE et al., 2012; RICHARDSON, et al. 2017). However, there is a lack of knowledge of benthic cover with regard to marginal tropical reefs (PERRY & LARCOMBE, 2003). These reefs are situated under suboptimal conditions such as moderate turbidity, mesotrophic or eutrophic conditions, wide temperature variations, and/or sediment resuspension (CAMP et al., 2018, SOARES, 2020). In this regard, these unique reef systems exhibit low coral diversity and dominance of species tolerant to some disturbances, such as heatwaves, moderate turbidity, and sedimentation (BURT et al., 2020; SOARES et al., 2021b). Despite the extreme (or suboptimal) conditions that characterize marginal reefs and their importance for understanding reef resilience to global environmental change (BURT et al., 2020; SOARES et al., 2021c), these ecosystems still have scarce knowledge about spatial heterogeneity in relation to the benthic cover (ADJEROUD et al. 2016; CAMP et al., 2018).

Turbid reefs have been hypothesized as possible refuges to climate change and a wider debate for and against this hypothesis has occurred recently (CAMP et al., 2018; BURT et al., 2020; MIES et al., 2020; SOARES et al., 2021b). However, one relevant but scarce piece of information concerns the composition and spatial heterogeneity of the benthic cover in these extreme reefs. Abiotic factors such as depth and sedimentation represent important parameters controlling the heterogeneity of marginal reef communities (VROOM et al., 2005). Spatial heterogeneity occurs when the choice of descriptor (e.g., the groups that dominate the benthic cover of a reef) shows different values at different locations in a restricted geographic area (ALLEN et al., 2012). However, this knowledge is scarce especially on marginal turbid-water reefs due to the complicated logistics of navigation, scientific diving, and water visibility. In this paper, we hypothesize that, due to environmental heterogeneity on depth and sedimentation, moderately turbid marginal reefs may exhibit significant spatial heterogeneity in a small geographic area, with sponges, algae and few stress-tolerant corals constituting key components (SOARES et al., 2016). Therefore, we analyse the benthic cover on low-latitude and turbid-zone marginal reefs (Equatorial Southwestern Atlantic) to identify whether depth (~17 to ~27m deep) and siltation events drive the distribution of the major reef components (e.g., algae, sponges, and corals).

## 2. METHODOLOGY

### 2.1. Study area

The Pedra da Risca do Meio Marine State Park (PEMPRIM) is a marine protected area (MPA) located approximately 10 nautical miles (18 km) from the coast of Fortaleza (Ceará, Brazil) (LIMA FILHO, 2006) (Figure 7). This low-latitude MPA covers an area of 33.20 km$^2$ and presents a rectangular shape that is bounded by the geographic coordinates 03°33'80"-03°36'00"S and 038°21'60"- 038°26'00"W (LIMA FILHO, 2006; SOARES et al. 2011) (Figure 1). The park has the peculiarity of being the only fully submerged marine protected area in the Equatorial SW Atlantic. The park has reef formations with a height of one to three meters above the seafloor (SOARES et al. 2011, 2016), with the turbid-zone reefs investigated in this research having depths ranging between ~17 and ~27m (Figure 8).

Figure 7 - Map of the study area location in the South Equatorial Atlantic. Source: (SOARES et al., 2016)

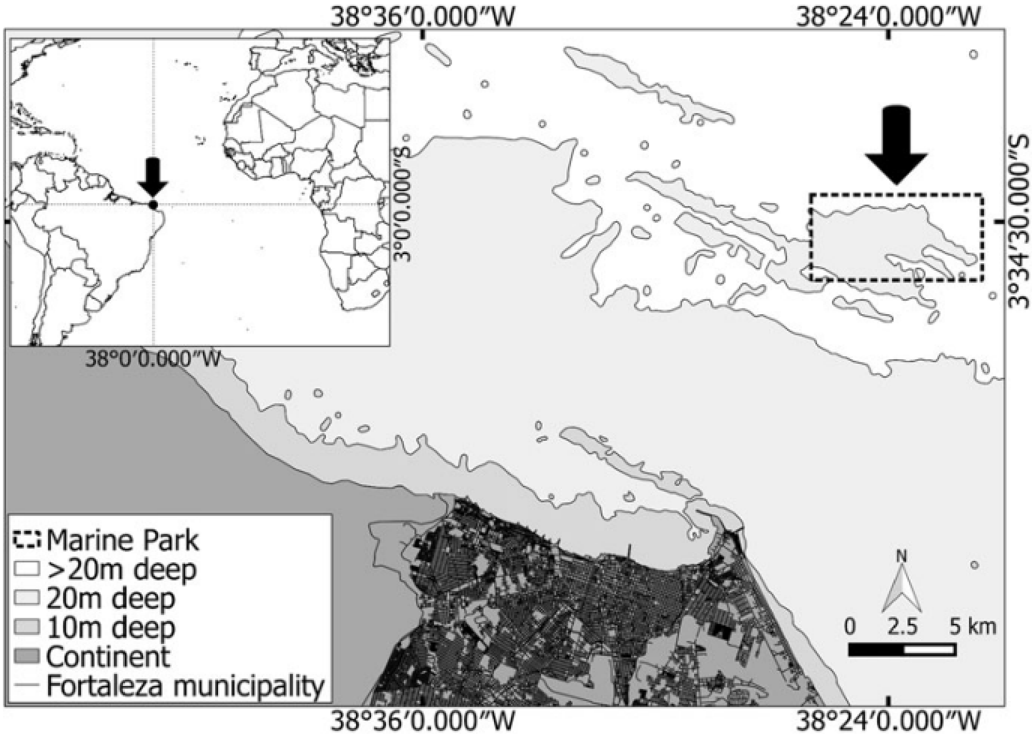
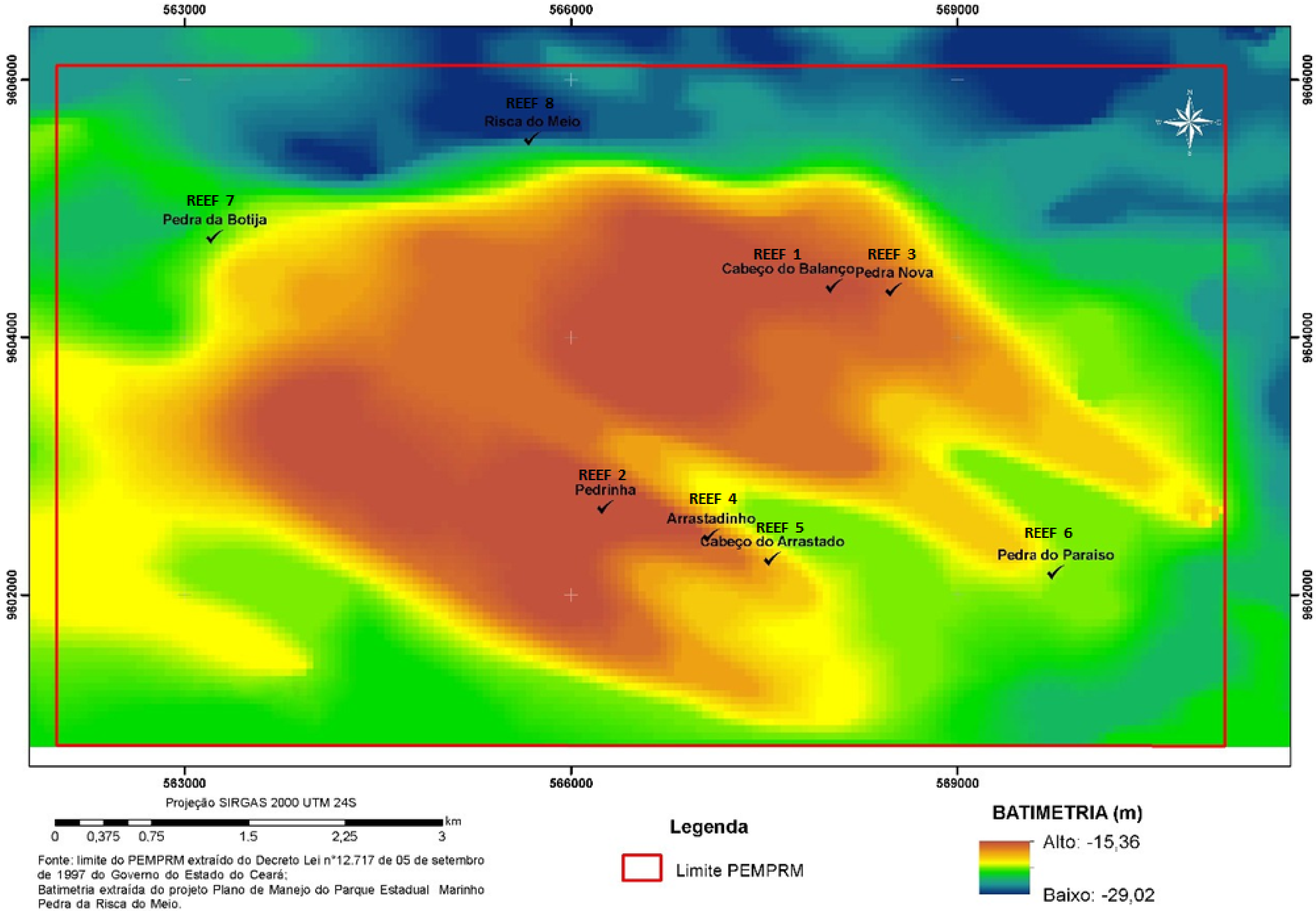


Figure 8 - Bathymetric map of the Parque Estadual Marinho da Risca do Meio (marine protected area delimited by the red line) and respective studied reefs (Equatorial SW Atlantic, Brazil). The different colorations denote the depths of the eight reefs (REEF 1 to 8) ranging from shallower zones (red, orange, yellow tones) to deeper reefs (green and blue). Source: (SEMA/FCPC/LABOMAR, 2019)



Fonte: limite do PEMPRM extraído do Decreto Lei n°12.717 de 05 de setembro de 1997 do Governo do Estado do Ceará;
Batimetria extraída do projeto Plano de Manejo do Parque Estadual Marinho Pedra da Risca do Meio.

The suboptimal conditions of the study area are characterized by intense trade winds, oligotrophic waters, moderate turbidity and low variation of sea surface temperature, ranging between 26° and 30° (SOARES et al. 2016, 2019). The cumulative action of the trade winds, especially in the second half of the year, and the coastal currents are responsible for moderate turbid waters due to the maintenance of suspended particles. Furthermore, high energy swell waves generate disturbances and sediment resuspension on these turbid-zone marginal reefs, selecting organisms resistant to turbidity, intense hydrodynamism, and sediment resuspension (KNOPPERS et al., 1999). In this regard, the silting is relevant in the context of this research and can be indirectly investigated by the percentage of sediment cover on the reefs. Due to the distance from the coast (18km) and low river input due to the semi-arid climate (SOARES et al., 2021a), sediment resuspension by swell waves are the main factor in increasing siltation on these low-latitude and turbid reefs.

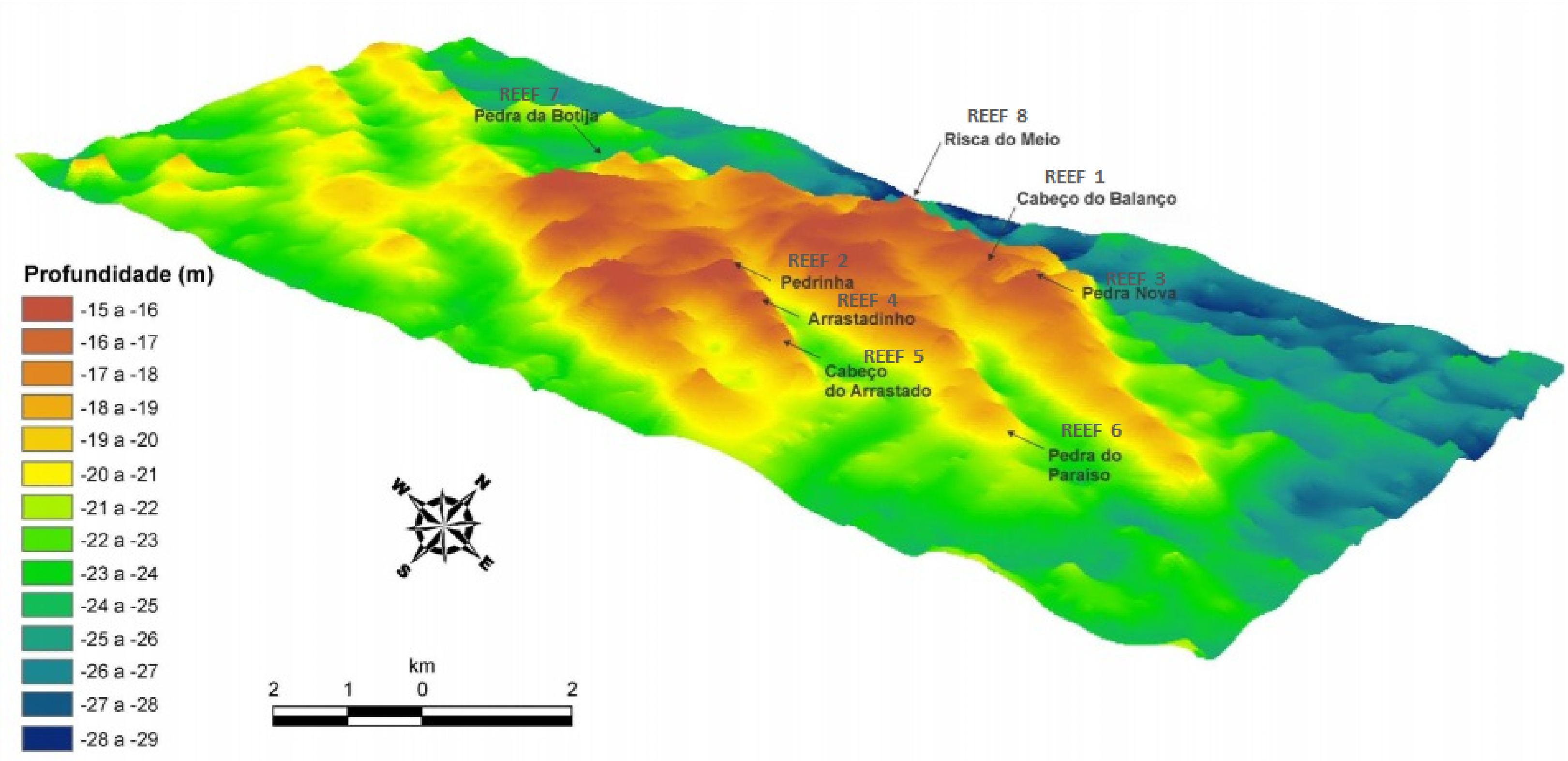
In this study we analyzed the biotic and abiotic elements (e.g., sediment cover) on eight marginal reefs in a restricted geographic area of 33 km² (Figure 8). These low-latitude and turbid-zone reefs had distinct depth ranges (the shallowest at ~17m and the deepest ~27m) as presented in Table 1 and Figure 9. Furthermore, the distance from the shoreline ranged from 14.6 to 17.7 km, and all are outside the area of influence of coastal and estuarine nutrient runoff and sedimentation (SOARES et al., 2021a).

Table 1 - Main characteristics (depth, distance from the coast, geographic coordinates) of the eight marginal reefs studied in the Equatorial SW Atlantic (Ceará, Brazil). Source: (FREITAS & LOTUFO, 2015; SEMA/FCPC/LABOMAR, 2019)

| **Low-Latitude and turbid reefs** | **Depth (m)** | **Distance from coast (km)** | **Geographic coordinates (Lat/Long)** |
|---|---|---|---|
| **REEF 1 (Cabeço do balanço)** | 16,6 | 14,9 | -3.57888/-38.38735 |
| **REEF 2 (Pedrinha)** | 16,7 | 14,3 | -3.59442/-38.40332 |
| **REEF 3 (Pedra nova)** | 17 | 17 | -3.57915/-38.38315 |
| **REEF 4 (Arrastadinho)** | 17,3 | - | -3.59642/-38.39592 |
| **REEF 5 (Cabeço do arrastado)** | 18,7 | 14,6 | -3.59807/-38.39165 |

| | | | |
|---|---|---|---|
| **REEF 6 (Pedra paraíso)** | 21,4 | 17,7 | -3.59898/-38.37183 |
| **REEF 7 (Pedra da botija)** | 22,5 | 14,8 | -3.57543/-38.43063 |
| **REEF 8 (Risca do meio)** | 26,8 | 16,4 | -3.56855/-38.40845 |

Figure 9 - 3D Digital Terrain Model (DTM) highlighting the 8 marginal reefs studied in the Southwestern Equatorial Atlantic (Brazil). Source: (SEMA/FCPC/LABOMAR, 2019)



### 2.2. Field and data sampling

To assess the spatial distribution and heterogeneity of benthic components in the eight turbid-zone and low-latitude reefs, the PIT (Point Intersept Transect) method was adopted according to the methodology established by Leão et al. (2015) for Southwestern Atlantic reefs. We used the following indicators of benthic cover: Live coral; Macroalgae; *Rhizoclonium*-like; Filamentous algae; Crustose algae; Sponge; Other organisms; unconsolidated sediment, and Rocky ground (without biological cover or sand). Cover data were surveyed via four 10-m transects on each reef during July and August in the year 2019 due to favorable sea conditions (e.g., lower wind incidence and temporarily reduced turbidity), availability of oceanographic vessel, and visibility for scientific diving. Benthic cover elements (biotic and abiotic) were identified every 10 cm by scuba diving (SCUBA). Thus, in each transect, 100 points were surveyed. Therefore, there were 400 points per reef. Percent benthic cover was calculated by dividing the number of occurrence of each indicator by the total number of points (400) on each reef.

### 2.3. Statistical Analysis

To assess the spatial similarity of benthic cover among the eight marginal reefs (Q-mode), the non-metric multidimensional scaling (NMDS) ordination method and cluster analysis by the UPGMA method were used, both done based on the Bray-Curtis similarity index (which considers presence/absence of benthic components and abundance - cover). The data were not transformed because the weight of the most abundant elements on each reef was impaired when the data were transformed. That is, when transforming, the weight of the most abundant elements, such as macroalgae, was decreased and this affected the comparison of the most abundant elements between reefs. Therefore, it was chosen not to transform by this reason and also the low distance of relative abundance (between 0 to 66%) between benthic components.

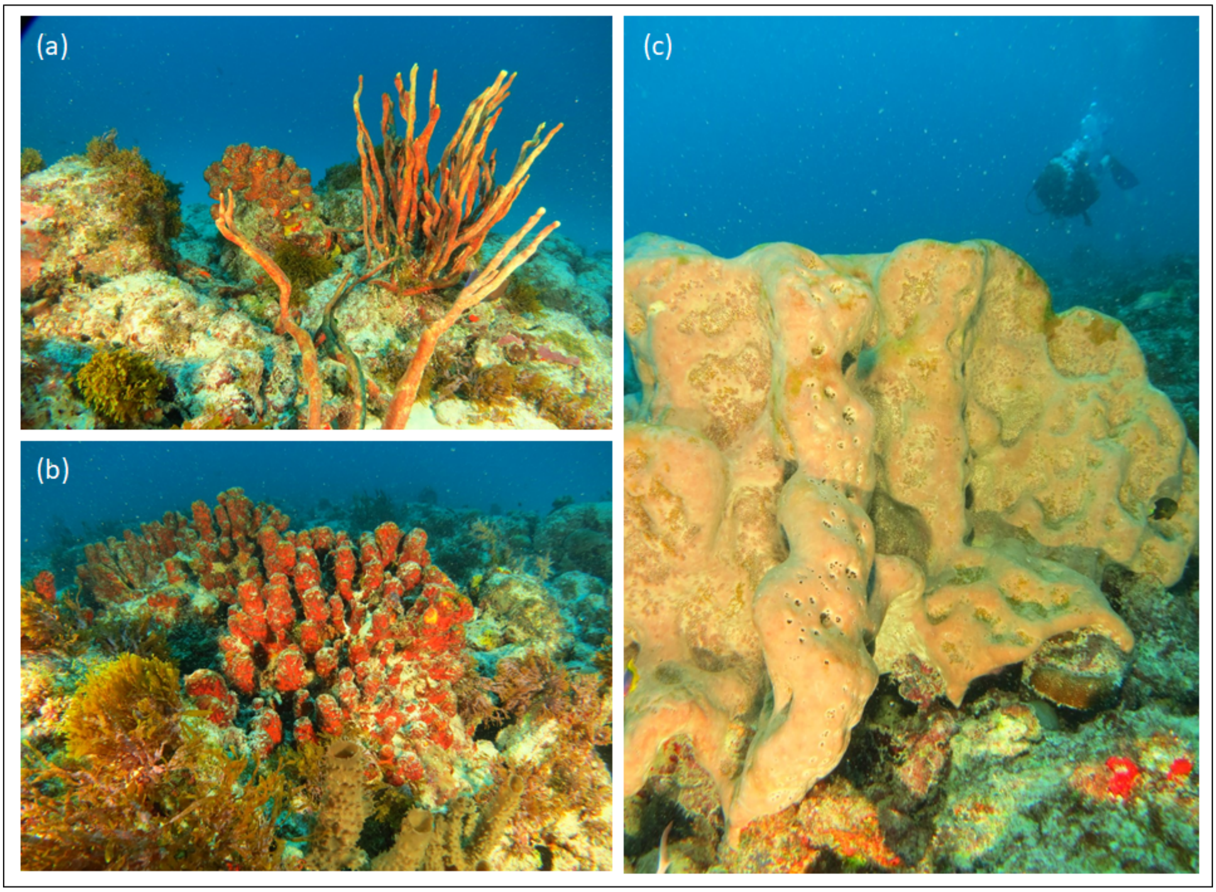
To test the significance of the groups formed by the cluster analysis, the PERMANOVA method was used (Permutations = 9999, Bray-Curtis similarity matrix), with a significance level of $p<0.05$. To identify which benthic components were responsible for the similarity in forming each of the groups, the Percentage of Similarity (SIMPER) test was used. Pearson's correlation analysis was used to evaluate the correlations between all benthic variables with each other, previously transformed by log (x+1). These multivariate statistical analyses were performed in PAST 4.03 (HAMMER et al., 2001) and PRIMER 6.0 (CLARKE & GORLEY 2006) software to analyse the spatial heterogeneity in benthic cover.

## 3. RESULTS

The results indicate that low-latitude and turbid-zone marginal reefs exhibit spatial heterogeneity in the benthic coverage of live coral (0 - 18%), macroalgae (1 - 60%), *Rhizoclonium*-like (0 - 66%), filamentous algae (0 - 47%), crustose algae (2 - 16%), sponges (3 - 21%), other organisms (0 - 1%), unconsolidated sediments (1 - 33%), and rocky bottom (0 - 6%) (Figure 12). The benthic indicators with the greatest range of variation were macroalgae and filamentous algae, even in a restricted geographic area.

The dominance of algae morphotypes (macroalgae, *Rhizoclonium*-like, filamentous algae and crustose algae) (64.6 ± 11.4 %) was observed on the marginal reefs over key benthic animalssuch as sponges (9.2 ± 6.3 %) and scleractinian corals (4.1 ± 6.6 %). Macroalgae and *Rhizoclonium*-like (45.7 ± 22.2 %) were the most abundant, followed by filamentous (11.7 ± 16 %) and encrusting algae (7.2 ± 4.5 %). After algae, sponges presented as the benthic component with the highest coverage on turbid-zone marginal reefs (Figure 10). Moreover, the stress-tolerant and weedy species *Siderastrea stellata* (13.2 ± 20.9 %), *Montastraea cavernosa* (2.8 ± 5.4 %), *Mussismilia hispida* (0.2 ± 0.7 %) and *Meandrina braziliensis* (0.1 ± 0.3 %) demonstrate that the scleractinian community is composed of only four reef-building corals (Figure 11). Regarding abiotic components, a wide variation of siltation by sediment cover was observed over the reefs (19.2 ± 11.9 %). Finally, the coverage without organisms or unconsolidated sediment (rocky ground) was low (2.2 ± 1.9 %).

Figure 10 - Sponges on the studied marginal reefs (Equatorial Soutwestern Atlantic, Brazil): (a) *Aplysina fulva*, (b) *Aplysina* and *Callyspongia* (*Chadochalina*) *aculeata,* and (c) *Agelas dispar*. Source: SEMA/FCPC/LABOMAR (2019)



NMDS and Cluster (Q-mode) cluster analyses classified the low-latitude and turbid-zone reefs into two groups with significant difference (PERMANOVA, $p < 0.05$). The overall similarity among the eight marginal reefs was only 40%, which reveals significant heterogeneity in cover and composition (Figure 12). Group I was composed of REEF 1, REEF 2, REEF 4, and REEF 5. SIMPER analysis (cut-off 70%) indicated that the benthic cover elements that contributed to the 74.85% similarity found in the group were Macroalgae (58.45%) and Sediments (28.90%). All four reefs in this group, are among the shallowest reefs studied, with depths ranging from ~16m to ~18m.

Figure 11 - Scleractinian corals on the studied turbid reefs (Equatorial SW Atlantic): (a) *Siderastrea stellata* and *Montastraea cavernosa*. (b) *Mussismilia hispida*. (c) *Siderastrea stellata* (dominant species of the marginal coral community). Source: SEMA/FCPC/LABOMAR (2019)

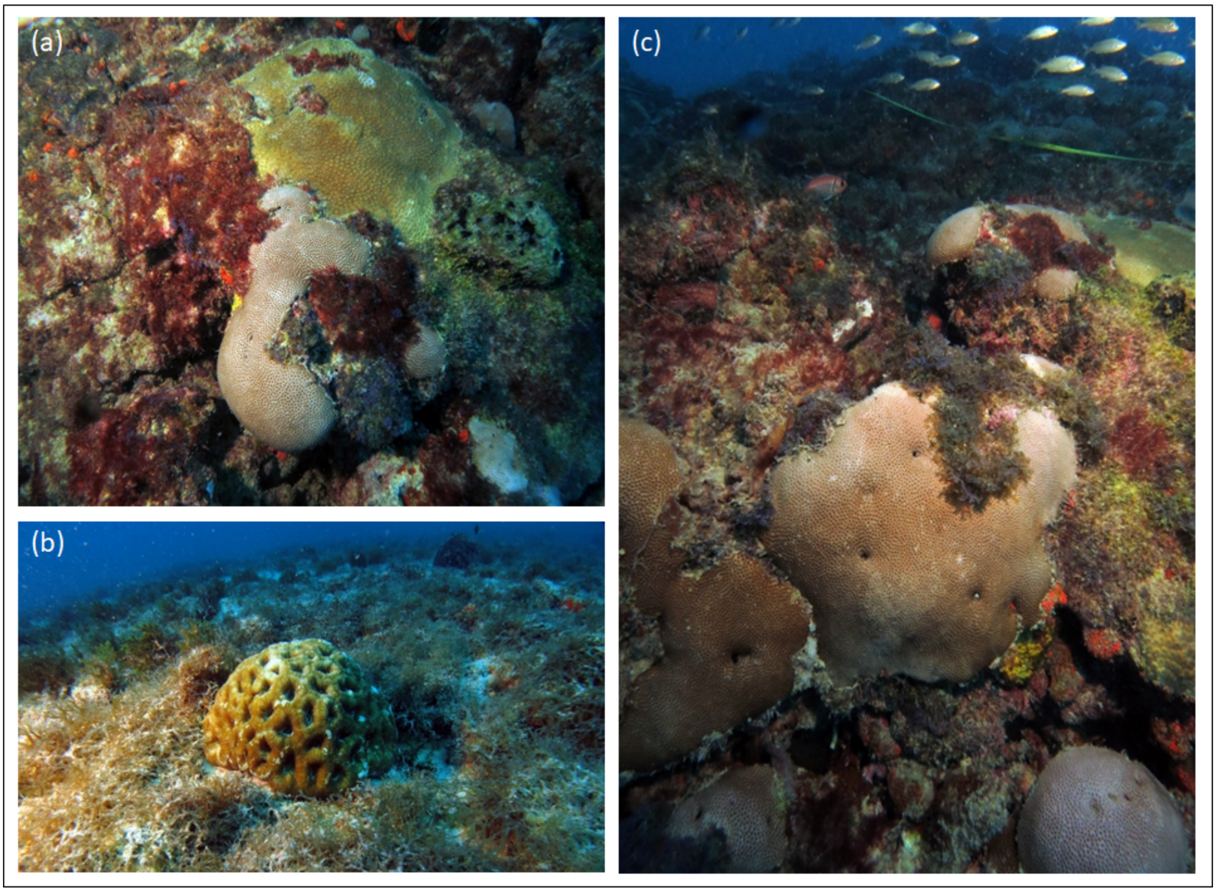
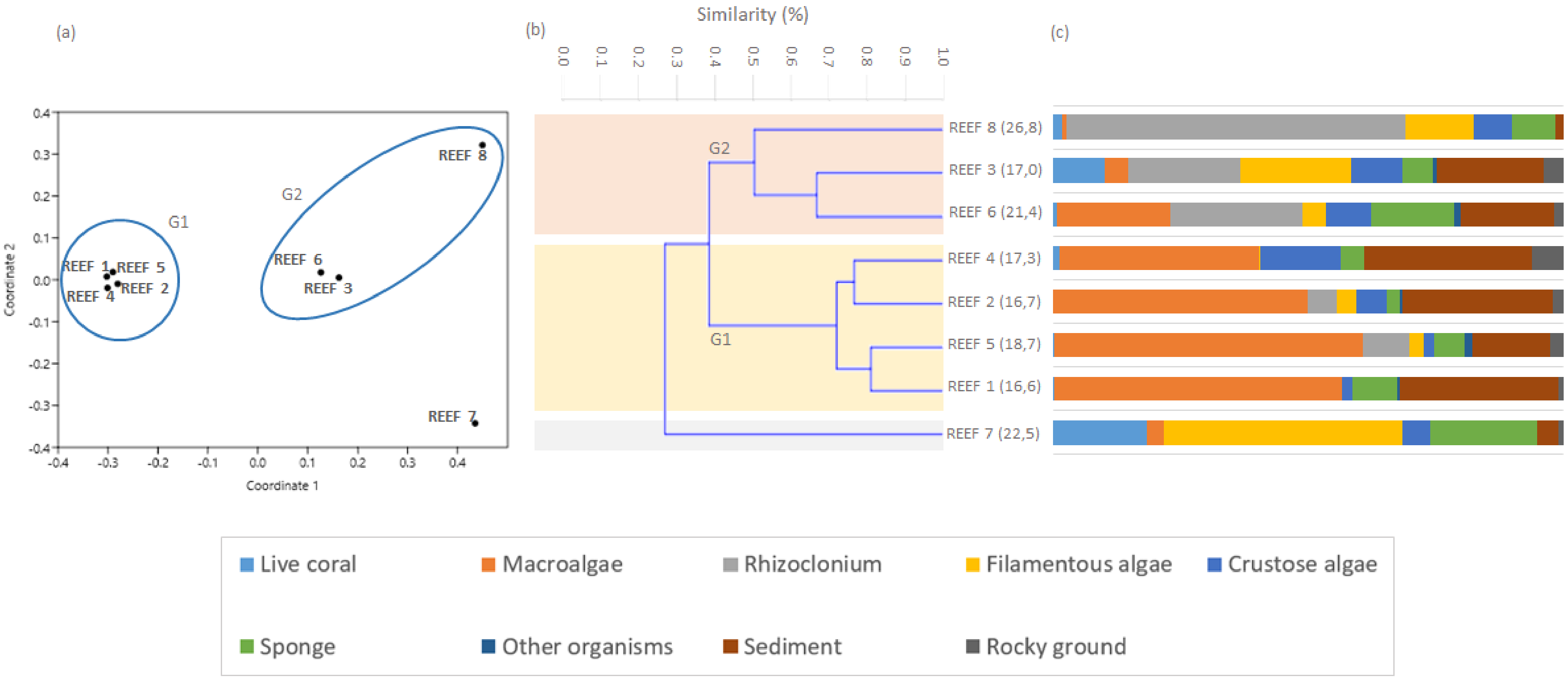

(a)
(b)
(c)

Figure 12 - Spatial heterogeneity of benthic communities on Equatorial SW Atlantic marginal reefs (Ceará, Brazil): (a) Non-metric multidimensional scaling (NMDS) ordination method and (b) Cluster of the eight reefs forming two groups (G1 and G2) based on Bray-Curtis similarity: the G1 reefs have high coverage of macroalgae and sediment; the G2 reefs have high *Rhizoclonium*-like coverage, and the REEF 7 reef has high coverage of filamentous algae and sponges. (c) Histogram showing the variation in the coverage of benthic elements across the eight reefs. The numbers in parentheses after the reef number (REEFs 1 to 8) are the depth of each reef in meters (between 16,7 to 26,8m). Source: Prepared by the authors.



Group II was composed of three reefs (REEF 3, REEF 6, and REEF 8). The benthic components that contributed to the 56.65% similarity found were: *Rhizoclonium*-like (41.21%), Crustose algae (14.22%), Filamentous algae (13.17%), and Sediment (12.48%). The 60.55 % dissimilarity observed between groups I and II was defined by Macroalgae (33.38%), followed by *Rhizoclonium*-like (29.74%) and Sediment (11.17%) (SIMPER (cut-off 70%).

REEF 7, the second deepest studied reef (22.5m depth), in isolation differentiated itself from all other turbid reefs in groups I and II (G1 and G2) (Figure 12). The elements that contributed to 80.40% dissimilarity of REEF 7 in relation to Group I (G1) were Filamentous algae (29.09%), Macroalgae (28.91%), and Sediment (13.74%) (SIMPER). In turn, the elements that contributed to 60.80% dissimilarity of REEF 7 in relation to group II (G2) were: *Rhizoclonium*-like (31.41%), Filamentous algae (27.63%), and Live coral (11.69%).

Another important result refers to the correlation observed between biotic and abiotic elements. Depth were significantly (Pearson, $p<0.05$) and negatively correlated with sediment cover ($r = - 0,87$) and macroalgae ($r = - 0,79$), corroborating that deeper reefs has lower silting and macroalgae (Table 2). Another inverse and significant correlation ($= - 0,70$) was observed between macroalgae and reef-building corals (Pearson, $p<0.05$). Other significant correlations between benthic components was found (Table 2).

Table 2 - Correlation analysis between biotic and abiotic elements in eight marginal reefs in the Equatorial SW Atlantic (Brazil). Bold colors show significant correlations.

| | Live coral | Macroalgae | *Rhizoclonium*-like | Filamentous algae | Crustose algae | Sponges | Other organisms | Sediment | Rocky bottom | Depth |
|---|---|---|---|---|---|---|---|---|---|---|
| **Live coral** | | **-0,70808** | -0,06604 | **0,70784** | 0,44659 | 0,55253 | -0,3404 | -0,42846 | 0,001274 | 0,42513 |
| **Macroalgae** | **-0,70808** | | -0,39942 | **-0,77839** | -0,40253 | -0,38789 | 0,48062 | 0,84661 | 0,6048 | **-0,79232** |
| ***Rhizoclonium*-like** | -0,06604 | -0,39942 | | 0,4495 | 0,16203 | -0,07879 | 0,39364 | -0,34231 | -0,32655 | 0,31219 |
| **Filamentous algae** | **0,70784** | **-0,77839** | 0,4495 | | 0,23122 | 0,36515 | -0,11592 | -0,67556 | -0,30037 | 0,5224 |
| **Crustose algae** | 0,44659 | -0,40253 | 0,16203 | 0,23122 | | -0,00838 | -0,39958 | -0,05669 | 0,24359 | 0,38473 |
| **Sponges** | 0,55253 | -0,38789 | -0,07879 | 0,36515 | -0,00838 | | 0,011243 | -0,43336 | -0,30091 | 0,56626 |
| **Other organisms** | -0,3404 | 0,48062 | 0,39364 | -0,11592 | -0,39958 | 0,011243 | | 0,46914 | 0,32545 | -0,50005 |
| **Sediment** | -0,42846 | 0,84661 | -0,34231 | -0,67556 | -0,05669 | -0,43336 | 0,46914 | | **0,80919** | **-0,87181** |
| **Rocky bottom** | 0,001274 | 0,6048 | -0,32655 | -0,30037 | 0,24359 | -0,30091 | 0,32545 | **0,80919** | | -0,68499 |
| **Depth** | 0,42513 | **-0,79232** | 0,31219 | 0,5224 | 0,38473 | 0,56626 | -0,50005 | **-0,87181** | -0,68499 | |

## 4. DISCUSSION

The macroalgae obtained dominance, with strong spatial heterogeneity, among the studied low-latitude and turbid reefs. Macroalgae occurred in higher cover (50% - 56%) on the shallower reefs (16 to 17m) that are subjected to high sedimentation rates (30% - 31%). On the other hand, the lowest macroalgae cover (1% - 3%) were observed on the deeper reefs (22 to 27m) subjected to low sedimentation rates (1% - 4%). The influence of depth on the spatial distribution of macroalgae is corroborated by the inverse and significant correlation between these variables seen in the results.

The seasonal bloom of the *Rhizoclonium*-like macroalgae, which occurs between the months of July and August, was recorded on five of the eight marginal reefs, with the highest average percentage coverage (66%) observed on the deepest reef (26.8m) and absence on the shallowest reef (16.6m). We hypothesize that the hydrodynamism (waves, tides, and currents) that is more intense on shallower reefs (SOARES et al., 2016) drives the algae dispersion, which is not fixed, to deeper regions. This hypothesis needs further research and dispersion modelling.

After macroalgae (including *Rhizoclonium*-like), filamentous algae had the second highest benthic cover. This can be explained by the opportunistic characteristics of some of these tiny algae in tropical nutrient-poor waters, which morphologically present a high surface area to volume ratio providing high net primary productivity due to high nutrient uptake rates resulting in rapid growth (ROSENBERG & RAMUS, 1984), in addition to the accelerated ability to recover after suffering environmental disturbances (STENECK & DETHIER 1994) such as periodic sedimentation events on these marginal reefs (SOARES et al., 2016). Like the macroalgae, however, with an inverse pattern, filamentous algae shows strong variation in their distribution, being observed high coverage (47%) in the second deepest reef (22.5m).

Sponges, after algae (Figure 4), constitute an important group in these low-latitude and turbid-zone reefs. These sessile suspensivorous organisms are able to tolerate or even thrive in moderately turbid environments with high sedimentation (BELL & BARNES, 2000), which explains their occurrence in the marginal reefs analyzed. It is possible that on these moderately turbid reefs the sponges are more adapted to the resuspension of sediment, allowing a greater ability to survive (BELL et al. 2015) in these extreme turbid reefs (CAMP et al., 2018; BURT et al., 2020). These adaptations may occur through passive responses that prevent sediment deposition on the sponge surface, such as morphological and structural modifications, or active responses that remove sediment from the sponge surface, such as altering or interrupting pumping rates as a way to avoid clogging the feeding and filtration systems (BELL et al. 2015).

Disturbances such as carbonaceous and siliciclastic sediment cover (1 to 33%) described here and higher water temperature (SOARES et al. 2016) may contribute to sponge cover, selecting species to these stressful conditions. Another important observation is that the highest mean percentage coverage of sponges (21%) was recorded on one of the deeper reefs (22.5m) and the lowest (3%) on one of the shallower reefs (16.7m) (Figure 12). This can be explained by the hydrodynamic conditions of the shallowest reefs, which subjected to higher turbulence (swell waves) and higher silting disturbance frequency suggest lower sponge cover (SOARES et al, 2016).

Similar to sponge bathymetric distribution, the highest coral cover (18%) was recorded on deep reef (22.5m) (Figure 12). On the other hand, the lowest percentages (0.2% and absence) of cover occurred on shallower reefs (16 to 18m). The increased coral cover in deeper regions, may be a reflection of more efficient heterotrophic capabilities of these mixotrophic organisms (WILLIAMS et al., 2013) and lower frequency of disturbances such as sediment resuspension and silting by swell waves that mainly occur < 20m depth. Despite the low richness of corals recorded here, the most abundant species, *Siderastrea stellata* and *Montastraea cavernosa*, are known for their tolerance to environmental disturbances and commonly associated with marginal reefs in the Caribbean and South Atlantic due their stress-tolerant and weedy characteristics (MIES et al., 2020; SOARES et al., 2021c).

Morphological and physiological adaptations characteristic of these reef-building corals are keys for persistence on turbid reefs such as survival of the most abundant coral (*S. stellata*) to short-term burial events (LONGO et al., 2020). Moreover, the massive-growth forms, with thicker tissue, confers greater resistance to high-light stress. The endosymbiont community composed of types more flexible to thermal anomalies also seems to be another factor, in addition to the adopted feeding strategy (heterotrophy/autotrophy) under turbid conditions (MIES et al., 2020). Corals with higher heterotrophic feeding capacity (e.g., *S. stellata* in Tunala et al., 2019) and less reliance on autotrophic feeding on marginal reefs are more resilient to stress situations such as bleaching and intense sedimentation (SOARES et al., 2021c). Those aspects might help to understand the resistance of those corals, but need further investigation.

Macroalgae were significantly and inversely correlated with coral cover; this is an important result because it suggests that one component may replace the other. In turbid-zone reefs in the Eastern Brazil, the phase shifts observed so far refer to changes from predominantly coral to macroalgae-dominated states as a result of local and global human impacts (CRUZ et al., 2018).

Regarding substrate, the turbid reefs with the lowest sediment cover (1% - 4%) were the deepest (26.8m and 22.5m). The opposite occurred in the shallower reefs (16 to 17m), where the sediment cover were higher (29% - 31%) which indicates a more intense action of sediment resuspension and silting in the shallower reefs due to the occurrence of swell waves, tides, and coastal currents.

Depth and the effect of swell waves that induce siltation of shallower marginal reefs may play an important role in spatial heterogeneity of cover and composition detected here. This occurs because sedimentation is thought to be a very good predictor of coral cover and changes in community structure (WILLIAMS et al., 2011). It is possible that the cover of organisms such as corals, sponges, and algae is regulated by reduced wave energy and consequent lower turbulence and associated sedimentation, which contributes to higher covers of coral and sponges in deeper regions and lower abundance in shallower ones. In contrast, macroalgae increase with increasing wave energy, which reflects in higher covers in shallower areas and reduced abundance in deeper and less light regions. These results highlight a significant spatial heterogeneity of benthic cover over a small area, which indicates that tropical turbid-zone marginal reefs are heterogeneous as previously suggested in the literature (ROGERS, 1990; FREITAS et al., 2019; SOARES et al., 2021b).

In previously studied marginal reefs significant heterogeneity was observed with benthic communities dominated by algae and low coral cover (AUED et al., 2018). Depth and sedimentation representing keystone factors for reef fish communities (FREITAS et al., 2019). However, in “traditional” shallow- and clear-water coral reefs, such as those in the Caribbean and Indo-Pacific, relative homogeneity of the benthic community was detected (PAWLIK & LOH, 2017), with reefs characterized by high coral cover and high diversity of scleractinian corals (SCHUTTE et al., 2010; JACKSON et al., 2014). In a similar way, sedimentation and depth also influence the distribution of benthic components of “traditional” tropical reefs, with corals showing a lower cover rate in zones that are shallower and more exposed to sedimentation stress (OTAÑO-CRUZ et al., 2019).

In the results presented it is worth noting the influence of the occurrence of the *Rhizoclonium*-like macroalgae bloom during the collection period, which, due to the formation of the characteristic mats of this macroalgae, did not allow the identification of other possible benthic organisms located just below the structure. Further studies needs to understand these seasonal occurrence of these macroalgae blooms (not yet identified in the literature), the environmental drivers, and also their effects on the marginal reef assemblages.

In conclusion, our novel results indicate strong spatial heterogeneity, with turbid and low-latitude reefs dominated by macroalgae, filamentous algae, sponges, and low cover of scleractinian stress-tolerant and weedy corals. These novel results represent a step to understand the composition and abundance on turbid zone marginal reefs. Further studies involving environmental, biological, and ecological factors are still needed for the understanding of these marginal reef ecosystems, which under extreme conditions, are able to harbor species that are more tolerant and resistant to environmental disturbances.

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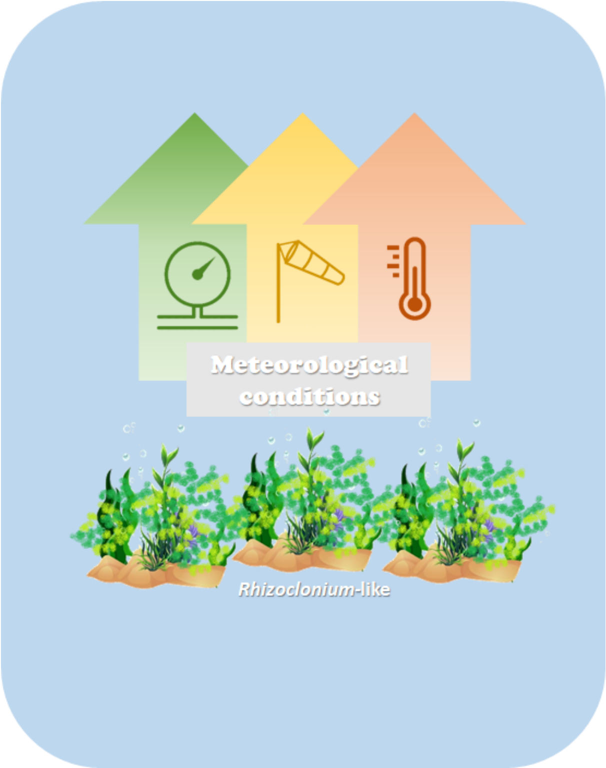
# CHAPTER 2 - TEMPERATURE AND METEREOLOGICAL CONDITIONS DRIVE BLOOMS OF *RHIZOCLONIUM*-LIKE ALGAE ON TROPICAL REEFS



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# CHAPTER 2 – TEMPERATURE AND METEREOLOGICAL CONDITIONS DRIVE BLOOMS OF *RHIZOCLONIUM*-LIKE ALGAE ON TROPICAL REEFS

## ABSTRACT

Blooms of *Rhizoclonium*-like macroalgae are reported for several coastal regions worldwide, mainly in estuarine zones. However, the seasonal occurrence and drivers of *Rhizoclonium*-like blooms on tropical reefs was never described. In this regard, data sampling was conducted between 2005 and 2018 to determine the occurrence of this unique phenomenon and key environmental factors that drive this bloom in low-latitude reefs. The bloom of *Rhizoclonium* was a seasonal phenomenon occurring in 2006 and is more frequent in recent times (occurring every year between 2010 and 2018). Moreover, this bloom only occurs in a restricted time window (between May and August). The algae were recorded forming dense carpets close to the reef substrate and interacting with other organisms such as scleractinian corals, octocorals, sponges, and other algae. The multivariate analysis indicates that the blooms in these turbid-zone reefs are linked to the increase in atmospheric pressure, the predominant north wind direction, and the increase in temperature range. Because it is located in the open sea, in a marine area without upwelling, in deeper areas (20-30m deep), and without the influence of nearshore nutrients, the main factors to explain the seasonal flowering may be slight changes in these metereological and oceanographic factors. This is the first record of large blooms of *Rhizoclonium*-like in South Atlantic tropical reefs and also worldwide. The novel results described here indicate that the frequent occurrence and impact of algae blooms in marginal tropical reefs developed in suboptimal conditions are belittled and need to be better studied especially considering the climate change scenarios.

**Keywords:** Macroalgae; Temperature; Tropical reef; Turbidity; Bloom.

## 1. INTRODUCTION

Algal blooms consist of the rapid and massive growth of micro- or macroalgae in marine or freshwater environments, being usually fast and seasonal events (VALIELA et al. 1997; JACKSON & LOCHMANN, 2018). These episodes may have serious environmental consequences, such as changes in water colour and turbidity, reduction of light penetration and oxygen (BREITBURG et al., 2018; SELLNER et al., 2003), and increased competition among species (MCCOOK et al. 2001). However, the causes of these phenomena are multiple and are not yet fully understood, being usually attributed to both natural (e.g. input of nutrients by upwelling zones and/or estuarine river flow) and/or anthropogenic (e.g. overfishing decreasing the rate of herbivory and/or nutrient input by organic pollution) factors (HUGHES et al., 1999; HUGHES & CONNELL, 1999; SELLNER et al., 2003; LAPOINTE et al., 2005; QI et al., 2017; BREITBURG et al., 2018; VAN BEUSEKOM, 2018).

Although it is recognized that the occurrence of macroalgae blooms is increasing worldwide, most studies so far focused on shallow tropical regions (e.g. VAN TUSSENBROEK et al. 2017; ARELLANO-VERDEJO, 2019). In nearshore and shallow-water coral reefs (< 10m), algae blooms are especially important because the reduction of the euphotic zone and the increased competition may significantly impact the structure and functioning of the reef communities (MCCOOK et al. 2001; JOMPA & MCCOOK, 2003). On the other hand, reefs may also experience seasonal blooms of ephemeral algae that interact with and grow on reef-building corals without driving significant impacts (MCCOOK et al. 2001). Despite the increasing studies on clear- and shallow-water regions, the occurrence and impacts of macroalgae blooms on turbid-zone reefs have not yet been properly documented. These marginal reefs developed under sub-optimal conditions such as moderate or higher sedimentation and turbidity and they are an important component of marine environments, providing essential ecosystem services and hosting a unique biodiversity (PERRY & LARCOMBE, 2003; SOARES et al. 2019; SOARES et al., 2021).

Blooms of the filamentous green macroalgae genus *Rhizoclonium* Kützing (Cladophoraceae, Chlorophyta) have been reported in several coastal regions worldwide, mainly within estuaries (ALVES et al. 2009; GIANASI et al. 2011; NEVEUX et al. 2018). *Rhizoclonium* usually grows entangled with other algae forming dense mats. There are more than 65 described taxa, however, this macroalgae presents taxonomic uncertainties mainly due to the lack of definition of diagnostic morphological characters (GUIRY & GUIRY, 2021; (BOEDEKER et al., 2016). The paucity of morphological simplicity (the morphology of this group of green algae includes uniseriate unbranched filamentous thalli, and branched species, such as *Rhizoclonium ramosum*) together with the phenotypic plasticity and convergent evolution, which is common in this group of algae make taxonomy very complicated, making the current use of the nomenclature *Rhizoclonium*-like widely accepted (AROCA et al., 2020; ICHIHARA et al., 2013). The seasonal occurrence of *Rhizoclonium*-like blooms on tropical reefs are still unknown in marine science. Thus, this article aims to report, for the first time, blooms of *Rhizoclonium*-like in turbid-zone reefs located on the Tropical Southwestern Atlantic (Brazil).

## 2. MATERIAL AND METHODS

### 2.1. Study area

The only coral reefs of the South Atlantic belong to the Brazilian coast and occur under marginal conditions such as moderate turbidity and sediment resuspension (CASTRO & PIRES, 1999; BANHA et al. 2019; MIES et al., 2020). The marginal reefs studied in this research are located in the Equatorial Southwestern Atlantic (northeastern Brazil, Ceará state coast) in a region characterized by stable inter- and intrannual sea surface temperatures (26-30 ºC), oligotrophic waters influenced by the North Brazilian Current and strong trade winds (mainly in the second semester) (SOARES et al. 2017) due to the action of ITCZ (Intertropical Convergence Zone). This low-latitude region also presents a marked seasonality, with a rainy period from January to June and a dry period from July to December, but with significant interannual variations in the rainfall pattern due to occurrence of intense droughts (DIAS et al. 2013).

Long-term data collection was done at the Pedra da Risca do Meio Marine State Park via SCUBA diving between the years 2005 and 2018 (Table 3). The diving activities were usually conducted between January to December and were focused in determining the qualitative presence (or not) of the *Rhizoclonium*-like blooms. This park is a marine protected area located about 18 km (i.e. 10 nautical miles) from the coast, and it houses submerged marginal reefs with depths varying between 17 and 27m (FREITAS & LOTUFO, 2015; SOARES et al. 2019). This location far from the coast is important because the marine park is not directly influenced by nutrients from the continent (either from estuaries or urban areas) or upwelling (SEMA/ FCPC/LABOMAR, 2020), which is especially important to analyse the algae blooms. In this context, the classical hypothesis of the influence of coastal nutrients (and/or urban runoff) on the formation of blooms is prompt rejected due to study area characteristics.

### 2.2. Data collection and analysis

Remote sensing was used to assess environmental factors over the years (2005-2018) in the study area. The data for sea surface temperature (SST), chlorophyll, coefficient of attenuation of diffuse light at 490 nm (Kd490), which is an indicator of water transparency, and available photosynthetic radiation (PAR) were extracted from the Giovanni NASA platform (https://giovanni.gsfc.nasa.gov/giovanni/). For these environmental parameters, monthly values were used from the MODIS-Aqua sensor with a spatial resolution of 4km that also covered the entire period from 2005 to 2018 when the diving activities were conducted.

The meteorological data were downloaded from the National Institute of Meteorology - INMET (https://portal.inmet.gov.br/). Monthly values covering the period from 2005 to 2018 were used, using averages for all parameters, except for insolation and precipitation, where the monthly accumulated was employed. In the case of precipitation, the number of days during the month with precipitation was also applied at the time of the analyses.

## 2.3. Statistical analysis

A logistic model was used to evaluate which environmental parameters influenced the flowering of the species. Initially, 19 environmental parameters were considered, estimated both for the area of Pedra da Risca do Meio by satellite measurements and from a meteorological station in Fortaleza (Ceará state, Brazil).

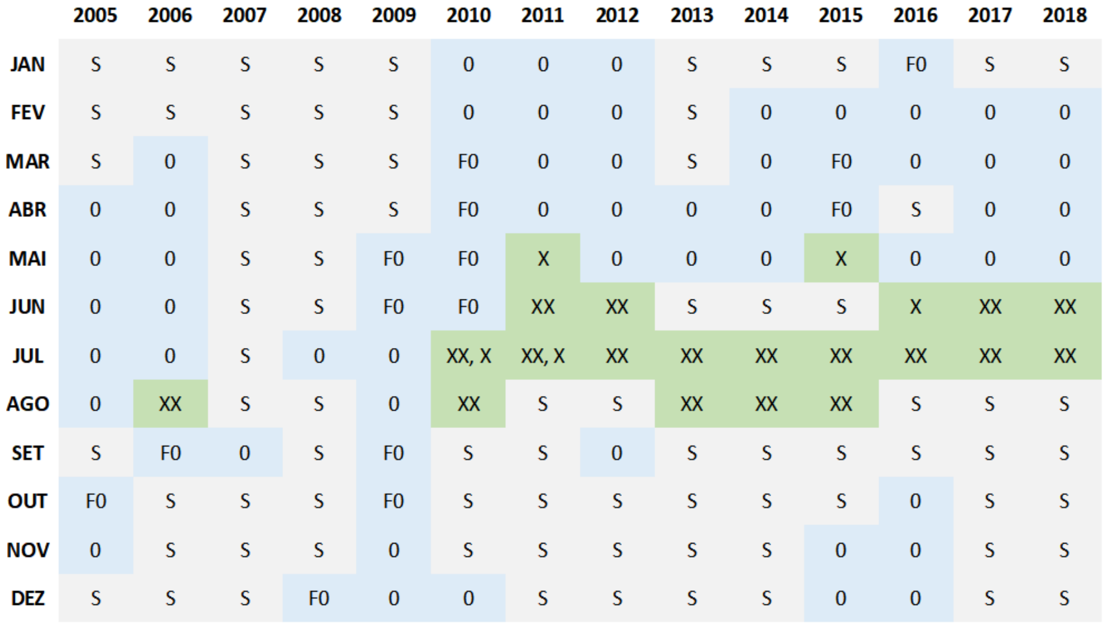
As many of these environmental parameters are strongly correlated, pairs of variables with Pearson correlation index greater than 0.8 were selected and, from each pair, the variable with the highest average absolute correlation was excluded from further analysis. This procedure retained only 11 variables, which were used in a LASSO-regularized logistic regression. For this, the remaining flowering occurrence and environmental parameter data were randomly subdivided into training set (70% of observations) and test set (30% of observations) of the model. The training set was then used to estimate the model parameters, and the test set to evaluate its performance. LASSO regression computes the coefficients of variables and applies a penalty to them that can ultimately reduce them to zero, which excludes that variable from the model. In this way, LASSO acts as yet another variable selection step. The value of the coefficients and the size of the penalty applied by LASSO was estimated through leave-one-out cross-validation, and the penalty that resulted in the smallest classification error was chosen for the logistic model.

The performance of the model was evaluated on the test set. The environmental variables contained in this new data set were used in the model generated through LASSO, and the resulting *Rhizoclonium*-like bloom predictions were compared with the actual observed bloom events. The model results in flowering probability by month. To make the comparison between predicted and observed, these probabilities were first converted to occurrence. Since the number of months with flowering is much smaller than the number of months without flowering (an approximate ratio of 1:3), this conversion was done based on a threshold chosen to equalize the true positive and true negative rates. In the present study, this value was P = 0.35. In other words, whenever the model estimated a probability greater than 0.35 of flowering occurring, we considered it a positive prediction. Probabilities equal to or less than 0.35 were considered negative predictions for flowering. From the comparison of predicted and observed data, the model's accuracy, sensitivity, specificity, and precision were calculated.

## 3. RESULTS AND DISCUSSION

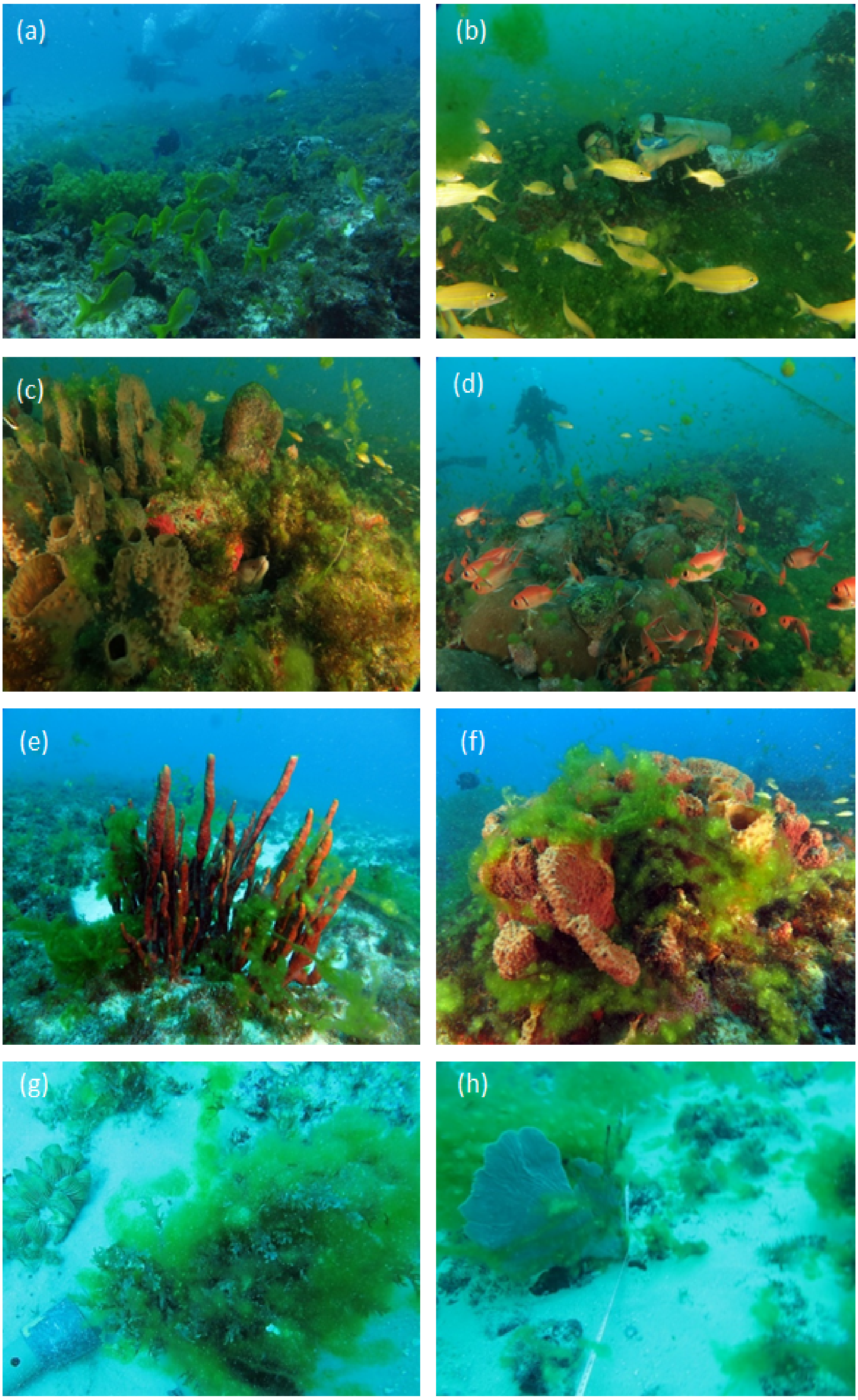
*Rhizoclonium*-like blooms occurred in the year 2006 and in all years from 2010 onwards (2010-2018) (Table 3). Seasonal bloom was recorded in a narrow temporal windom, between the months of May and August, occurring in all July months starting in 2010. The algae were recorded interacting with other reef organisms (Figure 13) such as massive reef-building corals *Siderastrea stellata, Meandrina braziliensis* and *Montastraea cavernosa*, octocorals of the species *Phyllogorgia dilatata*, ascidians *Eudistoma* sp. and *Stomozoa gigantea* and large sponges such as *Callyspongia vaginalis*, *Ircinia felix* and *Aplysina fistularis* that are major components in these turbid-zone and low-latitude reefs.

Table 3 - Date of diving activities made between the years 2005 and 2018 on the Equatorial Southwestern Atlantic reefs (Pedra da Risca do Meio Marine State Park, Ceará coast, Brazil) and reports of visual record of the algae. Source: Prepared by the authors (2022). (0) Dive with no record of the algae in the park; (XX) Dive with record of the algae in the park; (X) Dive with record of the algae outside the park; (S) No dive in the park; (F0) Dive outside the park without record of the algae.



| | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **JAN** | S | S | S | S | S | 0 | 0 | 0 | S | S | S | F0 | S | S |
| **FEV** | S | S | S | S | S | 0 | 0 | 0 | S | 0 | 0 | 0 | 0 | 0 |
| **MAR** | S | 0 | S | S | S | F0 | 0 | 0 | S | 0 | F0 | 0 | 0 | 0 |
| **ABR** | 0 | 0 | S | S | S | F0 | 0 | 0 | 0 | 0 | F0 | S | 0 | 0 |
| **MAI** | 0 | 0 | S | S | F0 | F0 | X | 0 | 0 | 0 | X | 0 | 0 | 0 |
| **JUN** | 0 | 0 | S | S | F0 | F0 | XX | XX | S | S | S | X | XX | XX |
| **JUL** | 0 | 0 | S | 0 | 0 | XX, X | XX, X | XX | XX | XX | XX | XX | XX | XX |
| **AGO** | 0 | XX | S | S | 0 | XX | S | S | XX | XX | XX | S | S | S |
| **SET** | S | F0 | 0 | S | F0 | S | S | 0 | S | S | S | S | S | S |
| **OUT** | F0 | S | S | S | F0 | S | S | S | S | S | S | 0 | S | S |
| **NOV** | 0 | S | S | S | 0 | S | S | S | S | S | 0 | 0 | S | S |
| **DEZ** | S | S | S | F0 | 0 | 0 | S | S | S | S | 0 | 0 | S | S |

Figura 13 - Algae bloom of the genus *Rhizoclonium*-like in the Southwestern Atlantic reefs (Ceará coast, Brazil). A and B - Algae forming carpet (2012/2016). C and D - Algae associated with sponges *Callyspongia vaginalis* and scleractinian corals *Siderastrea stellata* (2016). E and F - Algae associate with macroalgae *Dictyota/Dictyopteris*, coral *Meandrina braziliensis* (G) and octocoral *Phyllogorgia dilatata* (H) (2019). Source: Prepared by the authors (2021).



In the tropical and subtropical Western Atlantic, five species of the genus *Rhizoclonium* have been recorded (WYNNE, 2005). In Brazil, the occurrence of at least two species, *R. africanum* and *R. riparium,* have been reported along the coast, usually growing on mangroves and intertidal rocky reefs under the influence of freshwater and river runoff

(COTO, 2007; ALVES et al., 2009). This is the first record of blooms of *Rhizoclonium*-like in South Atlantic reefs. Both species may occur in the seasonal blooms described in this study, however new taxonomic studies (e.g., molecular identification) are needed to analyse this hypothesis. In this way, we used in this research the widely used and accepted term *Rhizoclonium*-like proposed by Ichihara et al. (2013).

These macroalgae generally grew wrapped on other algae or forming dense carpets near the tropical reef substrate (Figure 13). As in shallow tropical reefs, the impact of these extensive algae turfs on turbid-zone reefs may include at least a seasonal increase in competition for space and resources, particularly light, with other photosynthetic (algae) or mixotrophic organisms (corals, octocorals, and sponges) (MCCOOK et al. 2001) (Figure 14). In a study carried out in the same study area, Costa et al. (in prep.) show that *Rhizoclonium*-like blooms can reach up to 66% of the benthic cover in tropical reefs. In this research, this macroalgae became the dominant morpho-functional group on most of these low-latitude reefs for at least 3 months.

Figura 14 - Main causes, characteristics and consequences of Rhizoclonium-like bloom in the marginal reefs (Equatorial Southwestern Atlantic). Source: Prepared by the authors.

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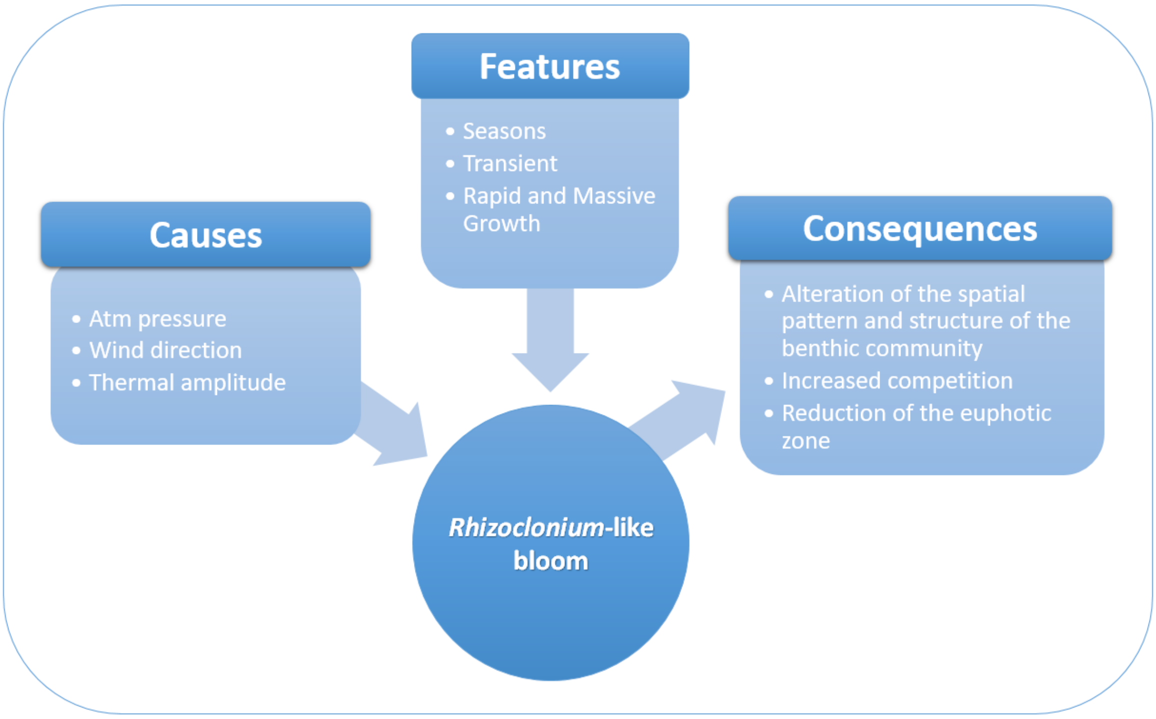


Regarding their causes, an explosive *Rhizoclonium*-like nearshore growth is usually associated with nutrient inputs from the estuaries and continental runoff (GIANASI et al. 2011). However, the occurrence of blooms due to the continental runoff is not the explanation considering that they occur mainly in the dry season and far away from the coast (~18 km). This temporal and spatial pattern prevents the arrival of terrestrial nearshore nutrients and organic/urban pollution into the turbid-zone reef area (SEMA/FCPC/LABOMAR, 2019), suggesting that continental contributions do not influence *Rhizoclonium*-like outbreaks. Moreover, the lack of upwelling in this tropical reef area (SOARES et al., 2017, 2019) further indicates that nutrient inputs are not the main factor generating these accumulations. Therefore, other meteo-oceanographic conditions in this unique low-latitude and oligotrophic area should be the main driver  for these blooms as suggested by statistical analyses.

The final statistical LASSO model retained only three explanatory variables, all of which had a positive influence on the occurrence of macroalgae blooms (Table 4). Comparing the predictions of this model with flowering observations, this model had an accuracy of 92% and a precision of 83.3% (Table 5). In this regard, the results showed that temperature range, wind direction and atmospheric pressure showed a positive relationship with the probability of *Rhizoclonium*-like algae occurrence in these tropical reefs.

Table 4 - Environmental parameters and variable selection methods used in the creation of logistic model to predict the occurrence of *Rhizoclonium*-like blooms in the area of the Pedra da Risca do Meio Marine State Park (Equatorial Southwestern Atlantic, Brazil). Source: Prepared by the authors (2022)

| **Starter Set** | **Low correlation** | **LASSO** |
|---|---|---|
| Chlorophyll | Chlorophyll | |
| Sea surface temperature | Sea surface temperature | |
| Turbidity | Turbidity | |
| Photosynthetically active radiation | | |
| Humidity | | |
| Atmospheric pressure | Atmospheric pressure | Atmospheric pressure |
| Wind speed | | |
| Gust wind speed | Gust wind speed | |
| Mean wind direction | Mean wind direction | |
| Prevailing wind direction | Prevailing wind direction | Prevailing wind direction |
| Cloudiness | | |
| Insolation | | |
| Total insolation | | |

| | | |
|---|---|---|
| Maximum air temperature | Maximum air temperature | |
| Minimum air temperature | Minimum air temperature | |
| Temperature range | Temperature range | Temperature range |
| Average daily rainfall | | |
| Total monthly rainfall | Total monthly rainfall | |
| Number of days with rain in the month | | |

Table 5 - Variables with positive relationship on the occurrence of *Rhizoclonium*-like macroalgae blooms in the Equatorial Southwestern Atlantic (Ceará, Brazil). Source: Prepared by the authors.

| **Variable** | **Coefficient** |
|---|---|
| Intercept | -1,38 |
| Atmospheric pressure | 0,53 |
| Prevailing wind direction | 0,04 |
| Thermal amplitude | 0,50 |

The formation of blooms is affected by meteorological variables (OLIVER et al., 2020), and several studies have already tried to investigate the blooms response with respect to interannual variations in atmospheric pressure (MANGIALAJO et al., 2008), wind action (WU et al. 2015) and thermal amplitude (HOHAM, 1975). However, these studies were developed in urban coastal areas, lakes and reservoirs. In this study we make the first relationship of these variables with Rhizoclonium-like blooms on reefs.

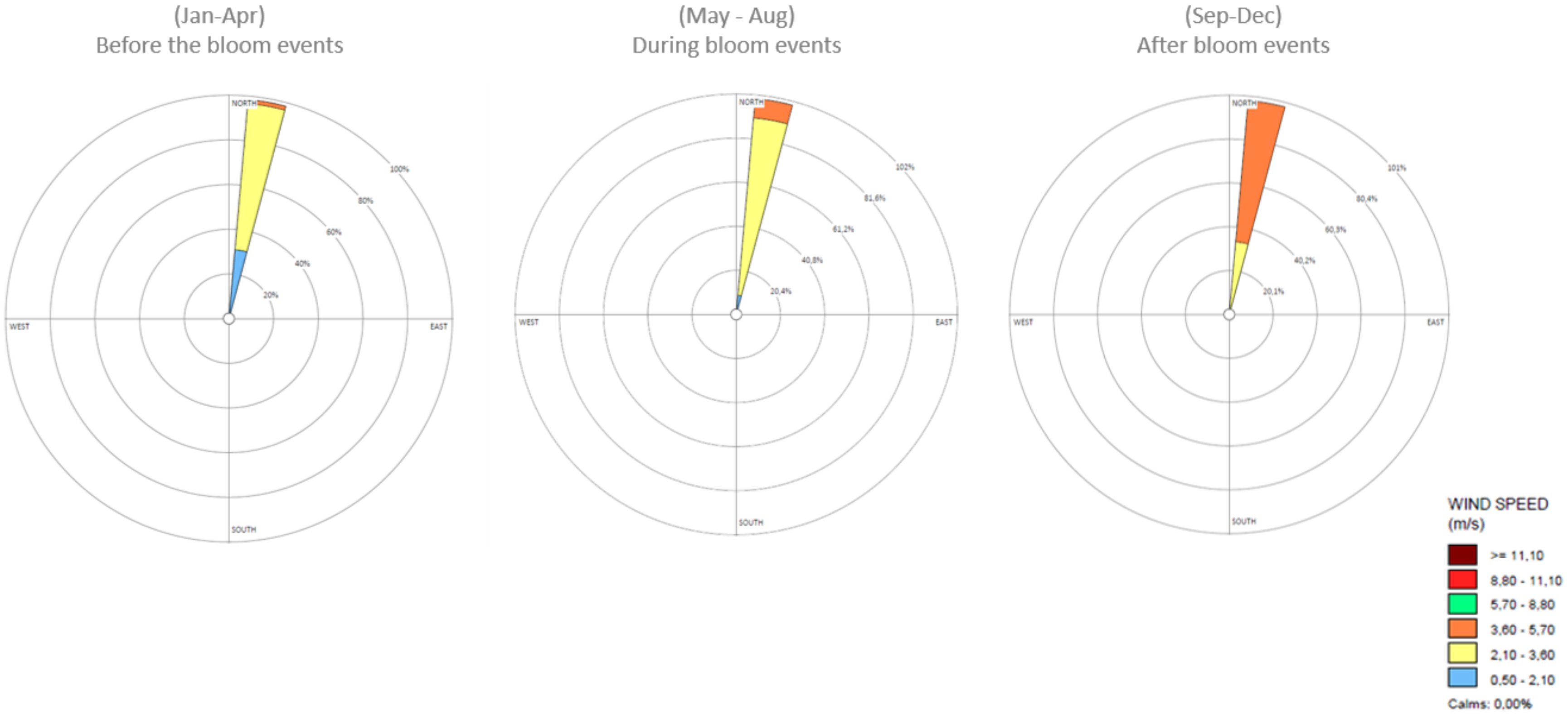
Atmospheric pressure is the variable that defines wind intensity and direction (GILLILAND & KEIM, 2018). Thus, changes in atmospheric pressure are important for assessing the meteorological conditions that affect the formation of algal blooms. Increased atmospheric pressure associated with calm sea conditions are thought to be important factors favoring algal blooms (MANGIALAJO et al., 2008; FEKI-SAHNOUN et al., 2020). In this regard, weaker winds associated with more stable waters are noted as prerequisites for algae accumulation, unlike stronger winds that impair algae accumulation and bloom formation (FANG et a., 2018). The increased atmospheric pressure associated with winds in transition phase from weaker to stronger (2.2 - 3.5 m/s), observed during bloom events in the study area, suggest that such atmospheric conditions are important for the occurrence of *Rhizoclonium*-like macroalgae blooms, and may have an influence on biomass accumulation in marginal reefs (Figure 15A and 15B).

Wind direction and intensity play an important role in the spatial distribution of algae during blooms (WU et al. 2015; ZHANG et al. 2021). A study in Brazil pointed out that wind direction and intensity are important in defining the location of algae prevalence (intertidal/subtidal zone) during bloom events in estuarine waters (LANARI & COPERTINO, 2016). It has been observed that more intense winds from the north - east direction favor the accumulation of algae in the intertidal regions and weaker winds from the same direction contribute to the predominance of algae in the lagoonregions (LANARI & COPERTINO, 2016). In our novel results, the north wind direction showed a positive relationship with the probability of occurrence of the *Rhizoclonium*-like algae on tropical marginal reefs. The transition phase where wind speed change from weaker to stronger (2.2 - 3.5 m/s), observed exactly during the months when blooms occured, and the predominant north direction may be contributing to the prevalence of the *Rhizoclonium*-like algae in the deeper reef regions (Figure 15B e Figure 16). This is aligned with a study developed in the same reef area (COSTA et al., in preparation), in July and August 2019 (months of seasonal bloom occurrence) where was observed that the highest percentage of *Rhizoclonium*-like macroalgae cover occurred on the deepest reefs.

Temperature fluctuations exert a strong influence on the growth rate of macroalgae (WANG et al., 2007), sometimes even acting as triggers for bloom formation and persistence (KONOPKA & BROCK, 1978; HOHAM, 1975), and are commonly employed in the study of algal blooms worldwide (WELLS et al. 2015). Our results indicate that the higher the thermal amplitude (monthly atmospheric temperature), the higher the probability of occurrence of *Rhizoclonium*-like algae in tropical reefs. Considering that the monthly temperature amplitude presents a narrow range of annual mean variation (6.8 - 8.3 ºC), which confers relative thermal stability to this equatorial region, we hypothesize, according to the results, that the highest thermal variation observed mainly between July and August (Figure 15C) is a key driver for blooms. This variation seems to be small because it is an low-latitude habitat with relatively stable temperature, however it's the highest in the region (Figure 15C) and sufficient to improve optimal conditions for the occurrence of *Rhizoclonium*-like blooms.

Figura 15 - Atmospheric pressure (hPa), wind speed (m/s), and thermal amplitude (C°). Data recorded between 2005 and 2018 in the studied region (Equatorial Southwestern Atlantic, Brazil). Green markings correspond to the months in which bloom occurs on tropical marginal reefs. Source: INMET and Giovanni NASA Platform (2021).

Figura 16 - Average wind Speed (m/s) and Direction (°) on the study area (Equatorial Southwestern Atlantic, Brazil). Data recorded between 2005 and 2018 in the studied region. The Rhizoclonium-like macroalgae blooms happens exacly during the transition phase between weaker (January to April) and stronger (September- December) wind speed. Source: Authors based on INMET (2021).



(Jan-Apr)
Before the bloom events

(May - Aug)
During bloom events

(Sep-Dec)
After bloom events

Our results indicate that atmospheric pressure, wind direction and temperature range show a positive relationship with the occurrence of blooms. Furthermore, our results also indicate for the first time that the seasonal occurrence and impacts of macroalgae such as *Rhizoclonium*-like on turbid-zone reefs have been scarcely studied and should be further investigated especially with regard to their impacts on reef structure and dynamics. Lastly, further studies are needed to clarify many aspects of the *Rhizoclonium*-like blooms on marginal turbid-zone reefs, such as their long-term impacts on benthic cover, carbon inputs to the coral reef trophic webs, influences on biogeochemical cycles, and improvement of taxonomic identification by molecular analysis.

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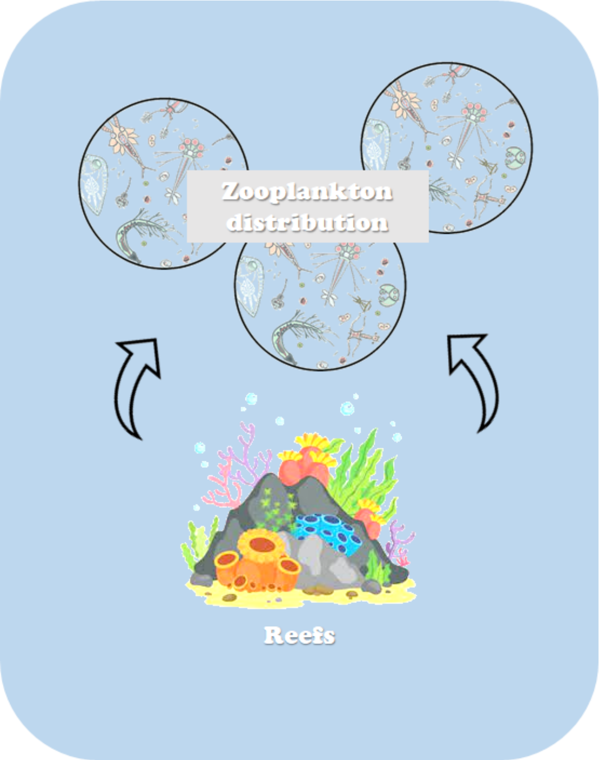
# CHAPTER 3 - ZOOPLANKTON BIOMASS IS DOMINATED BY SMALL-SIZE INDIVIDUALS IN TURBID REEFS UNDER NUTRIENT-POOR WATERS



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# CHAPTER 3 - ZOOPLANKTON BIOMASS IS DOMINATED BY SMALL-SIZE INDIVIDUALS IN TURBID REEFS UNDER NUTRIENT-POOR WATERS

## ABSTRACT

Zooplankton biomass is poorly studied on turbid-zone reefs despite being the basis of marine food webs. We describe the spatial variation of zooplankton biomass in nutrient-poor surface waters influenced by marginal reefs (equatorial Southwestern Atlantic). The studied area is located within this Marine Protected Area (MPA) and its immediate surroundings (buffer zone), which occurs under marginal conditions of oligotrophic waters, high and stable sea surface temperature (range 26-30 ºC), moderate turbidity, and sediment resuspension. Zooplankton samples were collected at 14 stations by subsurface trawls with nets of different mesh sizes (65, 200 and 300 µm). We described what was the dominant zooplanktonic biomass fraction and whether turbid-reef formations in these nutrient-poor waters influence their spatial distribution. To determine the dry weight, the samples were dried in an oven at 60 ºC for 24 hours and subsequently weighed on an analytical balance (0.0001g precision). A heterogeneous distribution of organic zooplankton biomass was observed among the different nets used (65, 200 and 300 µm). Zooplankton biomass from 200 and 300 µm nets were significantly lower in MPA than in buffer zone ($p < 0.05$), suggesting that MPA may be a more favorable area for the settlement of animal larvae present in the larger zooplankton fractions. It is also possible that predation on planktonic reef fish contributes to the reduction of zooplankton in the MPA. In turn, considering all the area, the 300 µm net, biomass was reduced (0.05 - 0.61 mg/m$^3$) at almost all stations when compared to the 65 (0.44 - 2.22 mg/m$^3$) and 200 µm (0.16 - 1.33 mg/m$^3$) nets. In fact, the biomass was significantly higher in the smallest net (65 µm) when compared to the 200 and 300 µm nets ($p < 0.05$), showing that most of the zooplankton biomass is composed of small organisms. Since the studied reef area is subject to low fluvial input, with no evidence of upwelling, and with restricted nutrient loading, it is possible that microbial loop play an important role in the reef region, driving dissolver organic matter to higher trophic levels and in the consequent distribution of consumers in the food chain, including the zooplankton studied here. Our results showed that turbid reefs in these nutrient-poor waters play an important role in the spatial distribution of larger zooplankton biomass, and the community is dominated by small organisms.

**key words:** Zooplankton biomass; Marginal reefs; Oligotrophic waters.

## 1. INTRODUCTION

The zooplankton constitutes the animal fraction of the plankton and it is responsible for energy transfer from the phytoplankton to the higher trophic levels (PEIJNENBURG & GOETZE, 2013). Formed by a complex set of organisms from different phylogenetic origins, zooplankton can be classified as holoplankton (those that perform the complete life cycle in the plankton) and meroplankton (those that present only the first life stages, egg or larvae, in the plankton) (BONECKER et al., 2009). Zooplankton can also be formed by epibenthic species (those residing near or on the reef surface) (SALE et al., 1976) and by demersal migratory species (PORTER & PORTER, 1977).

In reef ecosystems, zooplankton organisms act as an important source of energy for several nectonic and benthic organisms, such as fishes, reef-building corals, ascidians, sponges, among others (HEIDELBERG et al., 2010). Because they play this important trophic role and are significantly abundant (BATHMANN et al, 2001) and underspin important interconnected ecosystems such as coral reefs (SANTOS et al., 2019) and seagrass and rhodolith beds (COSTA et al., 2020), zooplankton biomass is an important variable in tropical reefs functioning but it is commonly understudied due to the focus of reef studies being on benthic suspension feeders (RICCIARDI, 1999; DE LÉO & PIRES-VANIN, 2006) and necton, such as reef fishes and elasmobranchs (HAIMOVICI, 1998; MARTINS & HAIMOVICI, 2017).

The knowledge of size-fractions of zooplankton biomass is still underestimated in studies developed worldwide. In these studies (SUÁREZ-MORALES & GASCA, 2000; CHANG & FANG, 2004; CHOU et al., 2012; DORADO-RONCANCIO et al., 2021), where plankton nets with larger mesh sizes are widely used, smaller and important plankton fractions are neglected (TSENG et al., 2011). Distinctly, in research conducted in the South Atlantic, the use of nets of different mesh sizes has already been employed (FIGUEIRÊDO et al., 2018; GARCIA et al., 2021). The use of this technique is especially important due to its efficiency in representing the smaller plankton fractions, such as juvenile stages and copepods, dominant organisms in the trophic chain in tropical oligotrophic systems (GARCIA et al., 2021).

The marginal turbid-zone reefs of the equatorial Southwestern Atlantic are characterized by oligotrophic waters and active nutrient recycling (CAMPELO et al, 2019; MOTA et al. 2017), being little studied in relation to zooplankton biomass. In some marginal reefs of the South Atlantic, a significant influence of fluvial discharge and consequent high primary production rate due to high nutrient content is observed (MIES et al., 2020). Distinctly, due to low coastal nutrient input and absence of upwelling (BARROSO et al., under review), the primary productivity rate on low-latitude and turbid South Atlantic reefs is generally based on nutrient regeneration and we could hypothesize that reef formations can be a determining factor in the distribution of size-fractioned zooplankton biomass of these marginal reefs whose functioning is unknown. In this way, we investigated what was the dominant zooplanktonic biomass fraction in reef surface waters in the South Atlantic and whether turbid reef formations in these nutrient-poor waters influence their spatial distribution.

## 2. MATERIAL AND METHODS

### 2.1. Study area

The Pedra da Risca do Meio Marine State Park is a Marine Protected Area (MPA) located approximately 10 nautical miles (18 km) from Fortaleza coast, Ceará (Brazil) (SOARES et al. 2011). The rectangular-shaped MPA has depths ranging from 16 to 30 meters (LIMA FILHO, 2006; SOARES et al., 2011), presenting reef formations from one to three meters high, completely submerged, which harbor a rich marine biota of plankton, benthos and necton (MOTA et al. 2017; SOARES et al. 2017; FREITAS et al. 2019; SEMA/FCPC/LABOMAR, 2019).

The studied reef area is located within this MPA and its immediate surroundings called Buffer zone (Figure 1), which occurs under marginal conditions of oligotrophic waters, high but stable sea surface temperature (range 26-30 ºC), moderate turbidity, and strong trade winds in the second semester that together with coastal currents cause sediment transport and resuspension (DIAS et al., 2013; SOARES et al. 2017). The oligotrophic waters of the MPA is related to its location far from the coast and without estuarine and upwelling influences leading to low nutrient concentrations (BARROSO et al., under review).

### 2.2. Sampling data

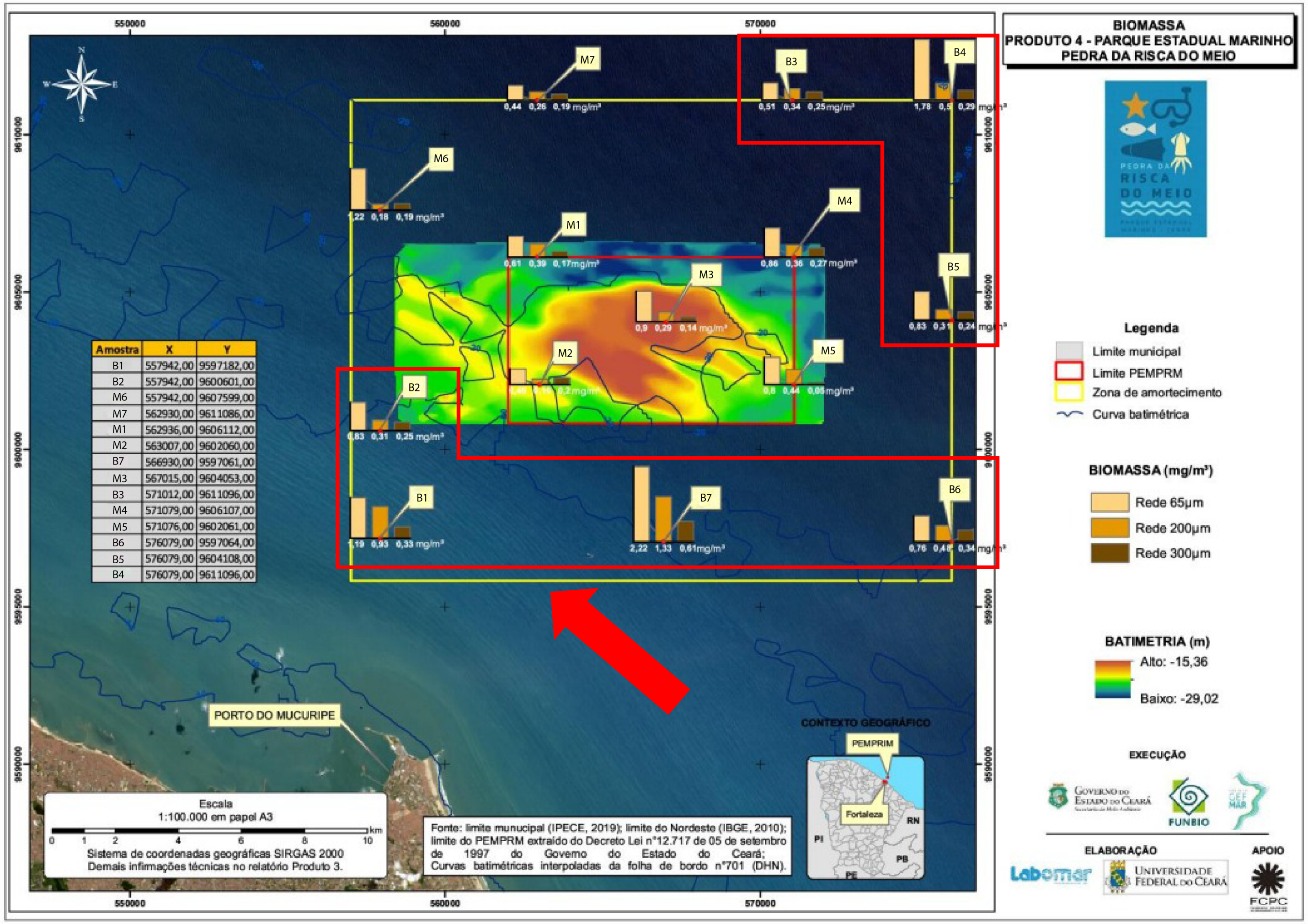
Oceanographic campaigns in the MPA and Buffer zone were carried out in July 2019 for sampling zooplanktonic communities. Zooplankton samples were collected at 14 stations (Figure 17), through subsurface trawls with 65, 200 and 300 µm mesh nets, (50 cm mouth diameter) and coupled with a flowmeter "General Oceanic" to obtain the filtered volume. Seven stations were located in the buffer zone and seven inside t or under influence of the MPA (Figure 17). The stations were classified according to the influence of the reef environment, following the direction of the coastal currents (SEMA/FCPC/LABOMAR, 2019). After collection, the samples were immediately fixed with 4% formalin bufferedwith 4 g/L sodium tetraborate. The use of three nets in this study allows the evaluation of several size strata of zooplankton biomass in a complementary way.

To determine the dry weight, the samples were dried in an oven at 60 ºC for 24 hours and subsequently weighed on an analytical balance (0.0001g precision). To determine the ash-free dry weight (organic biomass), the samples were incinerated in a muffle furnace at 500 ºC. Finally, the samples were placed in a desiccator and, after cooling, were weighed again. The organic biomass data were grouped according to the size of the nets (65, 200 and 300 µm) for each of the 14 stations studied (Figure 17).

### 2.3. Data analysis

Analysis of variance (ANOVA) was used to test differences among the organic biomass from zoopplankton nets (65, 200 and 300 µm) considering all the area (n= 14), and between MPA and Buffer area for each net. For post-hoc analyses, Tukey's Honest Significant Difference (HSD) test was used for multiple comparisons (65 x 200 x 300 µm), and Student's t-tests were used to compare two factors (MPA x Buffer area). All data were previously transformed by fourth root and the analysis were performed in PAST 4.03 software

Figura 17 - Location map of the stations studied. From M1 to M7 are the stations located inside the marine park (MPA). From B1 to B7 are stations located around the park (BUFFER ZONE). Source: SEMA/FCPC/LABOMAR (2019)



| Amostra | X | Y |
|---|---|---|
| B1 | 557942,00 | 9597182,00 |
| B2 | 557942,00 | 9600601,00 |
| M6 | 557942,00 | 9607599,00 |
| M7 | 562930,00 | 9611086,00 |
| M1 | 562936,00 | 9606112,00 |
| M2 | 563007,00 | 9602060,00 |
| B7 | 566930,00 | 9597061,00 |
| M3 | 567015,00 | 9604053,00 |
| B3 | 571012,00 | 9611096,00 |
| M4 | 571079,00 | 9606107,00 |
| M5 | 571076,00 | 9602061,00 |
| B6 | 576079,00 | 9597064,00 |
| B5 | 576079,00 | 9604108,00 |
| B4 | 576079,00 | 9611096,00 |

## 3. RESULTS AND DISCUSSIONS

The organic biomass of zooplankton showed heterogeneous distribution among the different nets used (65, 200 and 300 µm), both in the MPA and in the Buffer zone (Figure 18). At the 300 µm net, biomass was reduced (0.05 - 0.61 mg/m$^3$) at almost all stations when compared to the 65 (0.44 - 2.22 mg/m$^3$) and 200 µm (0.16 - 1.33 mg/m$^3$) nets. The biomass was always significantly higher in the smallest net (65 µm) when compared to the 200 and 300 µm nets ($p < 0.05$) (Figure 19). Such results indicate that most of the zooplankton biomass on the marginal reefs is composed of small organisms at the expense of large organisms. When MPA and Buffer zone were compared considering each net, significant differences were found to 200 and 300 µm nets ($p < 0.05$), but not to 65 µm, showing the small zooplankton that dominated all the studied area (Figure 20, 21 and 22). In addition, significant lower zooplankton biomass from 200 and 300 µm nets in MPA than in buffer zone ($p < 0.05$), suggests that MPA may be a more favorable area for the settlement of animal larvae present in the larger zooplankton fractions, as well as, that larger zooplankton could be being more consumed by planktivorous fishes in MPA zone.

In freshwater environments, zooplankton predation by planktonic fishes has a relevant importance in the structure of plankton communities (LAZZARO, 1987; BONECKER et al., 2011). In reef environments, despite the scarcity of studies, it is believed that planktonic fishes influence the distribution of zooplankton in a localized way, contributing to its reduction through predation (GAINES & ROUGHGARDEN, 1987; KINGSFORD & MACDIARMID, 1988). Thus it is possible that predation on planktonic fishes contributed to the reduced zooplankton biomass observed in the 200 and 300 nets (inside MPA) when compared to the buffer zone. However, other variables such as abundance/density of fish on the reefs, competition and predation need to be better studied to understand the relationship between reef fishes and zooplankton.

Figura 18 - Biomass of zooplankton on marginal reefs of the Tropical South Atlantic (Ceará, Brazil). The area shaded in blue represents stations located within the Marine State Park Pedra da Risca do Meio (MPA - M1 to M7). Shaded area in red represents stations located in Buffer zone (B1 to B7).

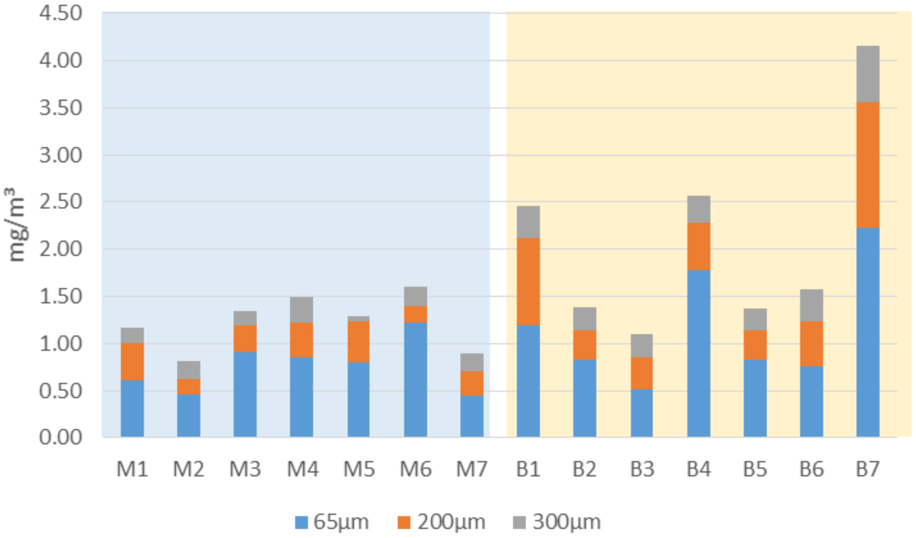


Figure 19 - Mean organic biomass of zooplankton in 65, 200 and 300 µm nets. All nets were significantly different from each other (ANOVA, $p < 0.05$ ).

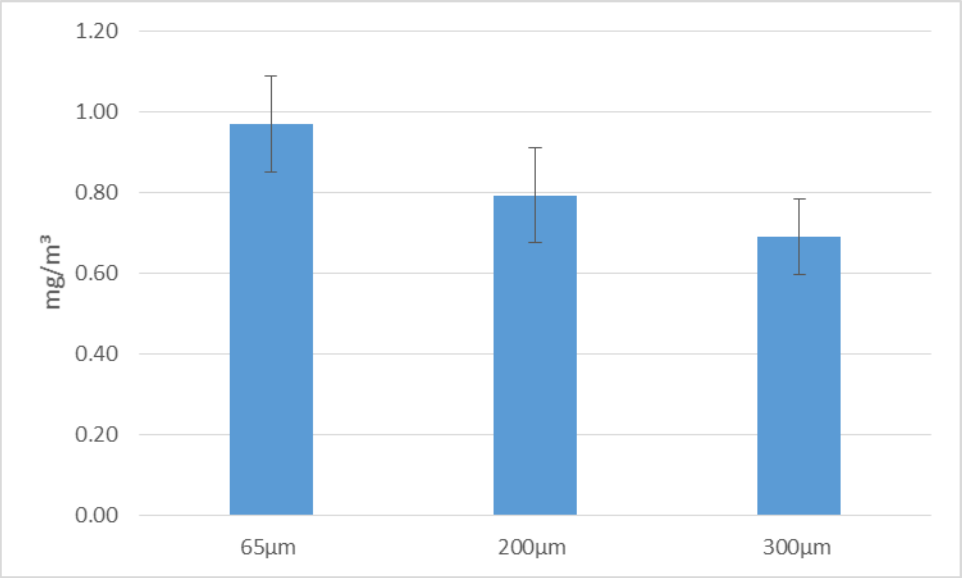


Figure 20 - Averages of zooplankton organic biomass in the 65 µm net between MPA and Buffer zone. Averages were not significantly different (t student, $p > 0.05$ ).

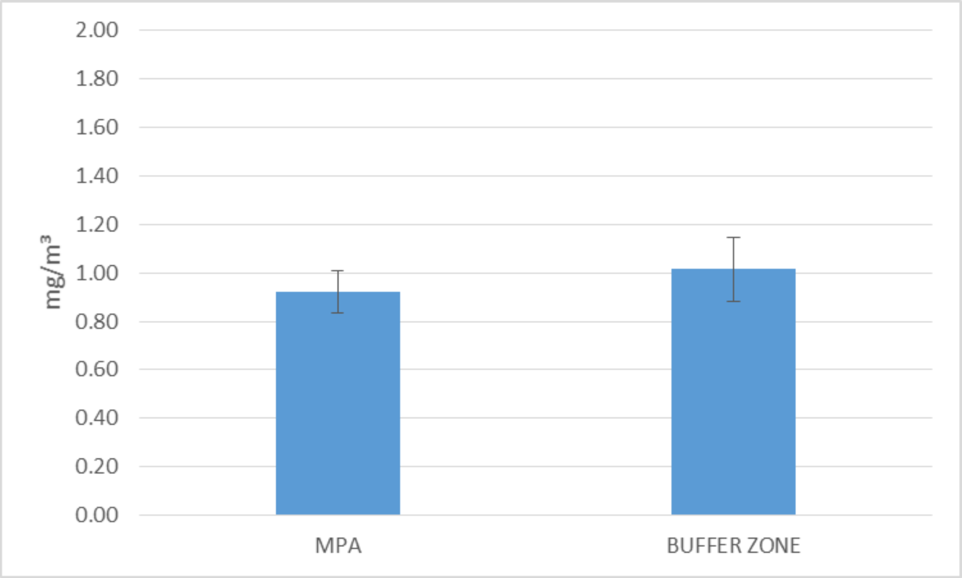


Figure 21 - Averages of zooplankton organic biomass in the 200 µm net between MPA and Buffer zone. Averages were significantly different (t student, $p < 0.05$ ).

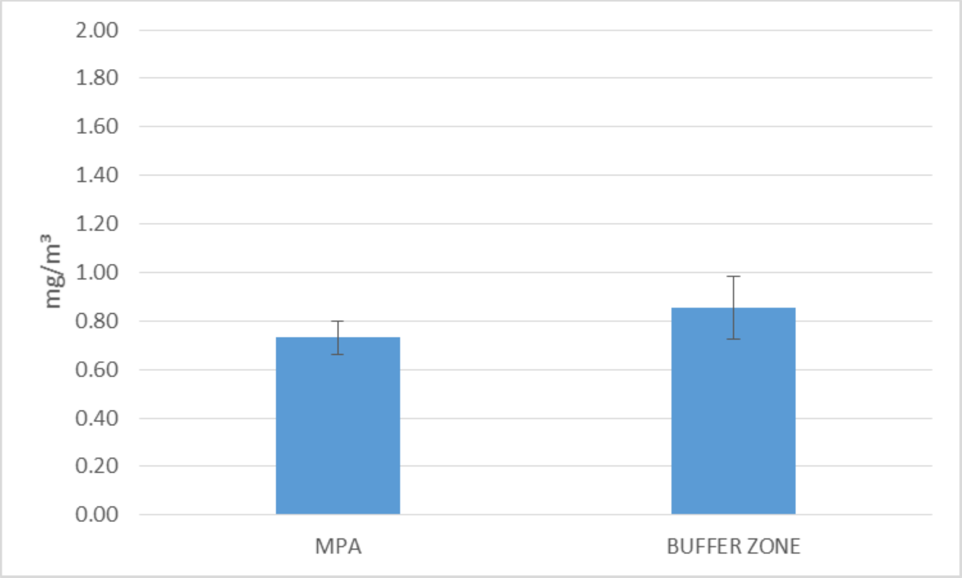
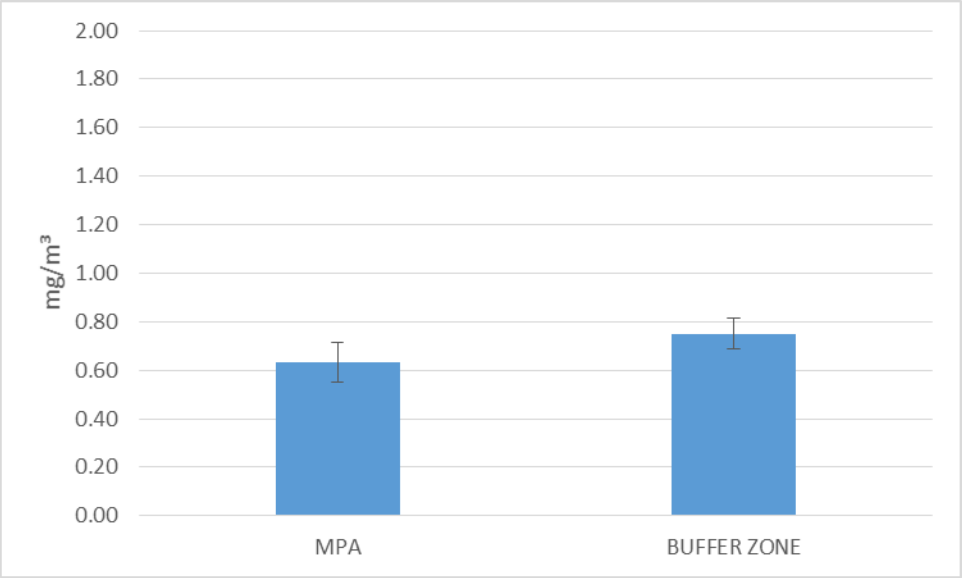


Figure 22 - Averages of zooplankton organic biomass in the 300 µm net between MPA and Buffer zone. Averages were significantly different (t student, $p < 0.05$).



In this study, three nets were used which allowed to evaluate size-fractioning zooplankton biomass. The use of only one net size does not assess the contribution of the remaining relevant zooplankton community, and this hinders the understanding of the reef dynamics as a whole (SANTOS et al., 2017; FIGUEIRÊDO et al., 2018). In "classic" shallow-water reefs it is common to use only one net to assess zooplankton biomass (SCHMUKER & SCHIEBEL, 2002; HEIDELBERG et al., 2004). On the other hand, in turbid-zone marginal reefs, such as those in South Atlantic, the use of more than one net reinforces the importance of this technique, capable of identifying and comparing the abundance of species of different size fractions, avoiding the underrepresentation of organisms (e.g., small-size) with an important role for the community composition (FIGUEIRÊDO et al., 2018). The small-size zooplankton biomass reported at sampling stations is characteristic of oligotrophic ecosystems (BRITO-LOLAIA et al., 2020).

Studies have pointed out that in oligotrophic systems the planktonic microbial community plays an important role in the energy transfer in the food chain, even more than the classical phytoplankton-metazooplankton food chains (MODENUTTI et al., 2003). This happens because, as in these systems the nutrient input is low, the primary production rate is strongly influenced by nutrient recycling (BURNS & SCHALLENBERG, 1998). What happens is that the heterotrophic bacteria absorb a large part of the dissolved organic matter (DOM) that is released by the phytoplankton, and with this they avoid the loss of carbon, introducing it back into the food web (STEELE, 1998). Thus, heterotrophic bacterioplankton are consumed by heterotrophic flagellates, which in turn will be preyed upon by microzooplankton and so on (JÜRGENS et al. 1994).

Since the studied area is subject to low fluvial input, with no evidence of upwelling zones, and with restricted coastal nutrient loading (BARROSO et al., under review), it is possible that bacterioplankton play an important role in the region, channeling DOM to higher trophic levels and in the consequent distribution of consumers in the food chain, including the zooplankton studied here.

Studies that address horizontal patterns of zooplankton distribution on coral reefs and their surroundings are still scarce (MORALES & MURILLO, 1996) when compared to studies on vertical distribution, which relate zooplankton distribution to several elements, such as the type of substrate cover, predation, lunar periodicity (ALLDREDGE & KING, 2009), among others. This implies the need for further studies that address the spatial distribution of zooplankton on marginal reefs in turbid zones and in oligotrophic waters. The sampling areas outside the marine park may have unmapped reefs which may have influenced the similarities between the MPA and the buffer zone. This topic needs further studies. In summary, our results showed that the zooplankton community is dominated by the small organisms, and that turbid reef formations in these nutrient-poor waters play an important role in the spatial distribution of larger zooplankton biomass.

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# CONCLUSIONS AND FINAL CONSIDERATIONS

Marginal turbid reefs are considered as important refugia for reef biodiversity in future climate change scenarios due to the resilience of some species to environmental disturbances. Despite the importance of these ecosystems that occur under suboptimal environmental conditions, knowledge about the dynamics and structure of the betony and planktonic community is still scarce when compared to "traditional" reefs. In this context, this thesis advances the knowledge in particular on equatorial reef systems with moderate turbidity.

Unlike "traditional" shallow and transparent water reefs that show relative homogeneity of the benthic community, with high diversity and coverage of scleractinian corals, the reefs of turbid and low latitude zones of the tropical southwest Atlantic show a strong spatial heterogeneity of the benthic cover in a small area, being dominated by marcroalgae, filamentous algae and showing a low coverage of stress-tolerant scleractinian corals (especially Siderastrea stellata and Montastraea cavernosa). On these turbid reefs, depth and sedimentation play an important role in structuring the benthic components. Depth together with the swell effect wave action, which resuspends sediments to the shallower regions of the reef, seems to contribute to the higher cover of macroalgae observed on the shallower reefs where there is more sedimentation and to higher cover of corals and sponges on the deeper reefs where there is less sedimentation rate.

*Rhizoclonium*-like algal blooms on turbid reefs are still poorly explored, and this is the first record of seasonal blooms of this alga in the tropical Southwest Atlantic. *Rhizoclonium*-like algae have been recorded forming dense mats and interacting with other organisms in the benthic community. Seasonal bloom of *Rhizoclonium*-like algae showed a positive relationship with atmospheric pressure, predominant north wind direction, and temperature range. Atmospheric pressure and wind direction so taken as important predictors of algae accumulation/dispersal. Increased atmospheric pressure associated with winds in transition from weaker to stronger and predominantly northerly direction observed during bloom events may be contributing to the accumulation of algae and their predominance in deeper regions. Temperature, in turn, may be interfering with bloom persistence. This theme is unprecedented in tropical reefs, and is a relevant theme.

Finally, in this thesis, the organic biomass of zooplankton in turbid reefs at low latitude was shown to be dominated by small organisms; a typical characteristic of oligotrophic systems that differs from other Brazilian reefs on the east coast that are under the influence of larger amounts of nutrients. The biomass of larger organisms differed in the park area and its surroundings, being lower in the park area. It is possible that the MPA is a more favorable area for the settlement of larvae present in the larger organisms and/or that the reef planktonic fishes of the region are consuming the larger zooplankton and contributing to its depletion in the regions under the influence of the reef formations. However both hypotheses need further studies, in view of the influence of other variables on the larval settlement process and on the predation of planktonic reef fishes. On these reefs as nutrient loading is restricted we hypothesize that the microbial loop plays an important role by reintroducing into the trophic chain and transporting to higher levels dissolved carbon that would be lost.

As final considerations, we argue that further studies addressing the structure and function of benthic and planktonic communities of marginal reefs are still needed, including long-term monitoring. The relationship of the distribution of benthic cover and zooplankton biomass with other variables (oceanographic, biological, and ecological) is important for understanding and managing these ecosystems that are important biodiversity hotspots around the globe.