Ocean and Coastal Research

BRIEF COMMUNICATION
Special Article Collection
Souza, R. B. and Lopes, R. M. (eds), Environmental variability and hazards on the coastal and continental shelf regions of South America and the Caribbean
http://doi.org/10.1590/2675-2824071.22060mos
ISSN 2675-2824

Marine animal forests in turbid environments are overlooked seascapes in urban areas

Marcelo de Oliveira Soares[1, 2, 5*], Sula Salani[3, 6], Sandra Vieira Paiva[1], Carolina Cerqueira Paiva[1], Pedro Bastos de Macedo Carneiro[4]

[1] Instituto de Ciências do Mar (LABOMAR), Universidade Federal do Ceará (UFC), Abolição Avenue 3207, 60165-081, Fortaleza, Brazil
[2] Reef Systems Group, Leibniz Centre for Tropical Marine Research (ZMT), Fahrenheitstraße 6, 28359, Bremen, Germany
[3] Museu Nacional do Rio de Janeiro, Quinta da Boa Vista, s/n, Rio de Janeiro, Brazil
[4] Universidade Federal do Delta do Parnaíba (UFDPar), São Sebastião Avenue 2819, 64202-020, Parnaíba, Brazil
[5] Center for Marine and Environmental Studies (CMES), University of the Virgin Islands (UVI), Saint Thomas 00802, US Virgin Islands, United States of America
[6] Laboratório de Bentos, Instituto de Ciências Biológicas, Campus Darcy Ribeiro, Universidade de Brasilia (UNB) Asa Norte, 70.910-900, Brazilia, DF

* Corresponding author: marcelosoares@ufc.br

ABSTRACT

Marginal reefs can provide meaningful information about the structure and dynamics of ecosystems under suboptimal environmental conditions. In addition to their different characteristics, these environments can also occur in urbanized areas. In this note, we characterize marine animal forests (MAFs) on turbid-zone reefs on an urban coast in the equatorial southwestern Atlantic. Overall, the sandstone ferruginous reefs (6–10 m depth) exhibited a flat topography and gentle slope (1–2 m above the seabed). Benthic cover is composed mainly of sponge gardens and ascidians. In addition, we found a low-relief coral carpet with only one massive reef-building coral (*Siderastrea stellata*) and Zoantharia. The ascidians and sponges had a higher diversity (at least 15 species) than the cnidarians (two species) in these forests. The main animals forming this seascape are weedy and stress-tolerant species adapted to challenging environmental conditions, such as swell waves, mesotidal regimes, moderate turbidity waters, and periodic burial. In this regard, these conditions and human impacts have shaped a unique MAF. Remarkably, the studied formations seem similar to high-latitude marginal reefs or low-latitude reefs under the influence of upwelling, which sustains soft corals and non-framework building coral communities along with sponges and ascidians. In particular, the shallow MAFs along the semi-arid coast of Brazil seem to lack some of the characteristics of low-latitude reefs under high sedimentation, whose structure was described as coral rubble within sedimentary matrices. This suggests that factors other than periodic burials and low light availability affected these MAFs. These overlooked forests are widespread in this area and have been neglected in studies, despite their richness (> 31 taxa) and valuable ecosystem goods and services. In the context of urbanized areas subject to climate change and pollution impacts, jetties, and dredging activities, it is necessary to consider these lush forests in impact assessments and conservation policies.

Descriptors: Tropical reefs, Sponges, Reef-building corals, Ascidians, Turbidity

Tropical reefs are of great ecological importance because they are biodiversity hubs (Gatwaza and Wang, 2021) hosting a variety of microorganisms, macroalgae, fauna (e.g., corals, sponges, reef fishes), and their interactions (Hughes et al., 2017). These seascapes act as nursery and feeding habitats for biomass maintenance in fisheries (McClanahan, 2020). In addition, they are also economically important because they contribute to tourism, human recreation, shoreline protection, and dissipating wave energy (Elliff and Kikuchi, 2017; Previero and Gasalla, 2018). However, owing to intense local, regional, and global human

Submitted: 30-May-2022
Approved: 06-Jan-2023

Editor: Rubens M. Lopes

actions, these environments are being impacted and degraded, including those on touristic and urbanized coasts (Hughes et al., 2018; Halpern et al., 2019; Fong and Todd, 2021).

The reef ecosystem is an important type of marine animal forest (MAFs) (Rossi, 2013). MAFs are composed of benthic suspension feeders such as cnidarians (e.g., scleractinians and zoantharians), sponges, and ascidians, which act as ecosystem engineers and keystone species in a similar way to trees in terrestrial forests (Rossi et al., 2017). Such eco-engineering (or foundation) benthic organisms create a three-dimensionality of habitat. Investigating their composition is critical for understanding the associated fauna (e.g., fish) and ecosystem functions, such as carbon sequestration and shoreline protection (Rossi et al., 2019, 2022), including on the Brazilian coast (Soares et al., 2017).

The Brazilian reefs are located along the southwestern Atlantic coast (Leão et al., 2003, 2016; Carneiro et al., 2022a) and extend from the northern (Amazon region) (Francini-Filho et al., 2018) to the southeastern (subtropical) regions (Pereira-Filho et al., 2019). In this extensive area, the least known region is the Brazilian semiarid coast (Soares et al., 2017a; Carneiro et al., 2022a). The low-latitude formations in this area are under high and constant temperatures (Teixeira and Machado, 2013) and intense hydrodynamism derived from waves, mesotides, higher wind speed, and coastal currents, which cooperate with intense sediment resuspension and transport (Knoppers et al., 1999; Dias et al., 2013), resulting in moderately turbid waters and periodic burial of shallow seascapes. Therefore, the environmental conditions in this nearshore area are not conducive to the growth of extensive coral-built frameworks. Nevertheless, non-framework-building coral communities and other MAFs are common in this region and play important ecological and economic roles (Carneiro et al., 2022b). Thus, studying such environments can provide important information on the structure and dynamics of MAFs that occur in suboptimal and extreme environmental settings (Camp et al., 2018; Soares 2020; Soares et al., 2021). In addition to these differentiated natural characteristics, these environments can also occur in highly urbanized areas (Burt et al., 2009, 2011; Burt et al., 2020; Fong and Todd, 2021). Therefore, they are subject to human impacts such as pollution, dredging, and coastal constructions such as jetties and breakwaters (Vieira et al., 2002; Portugal et al., 2016).

Research on reef environments on the Brazilian semi-arid coast has focused on the intertidal region (Matthews-Cascon and Lotufo, 2006; Portugal et al., 2016; Baptista, 2021; Barros et al., 2021; Carneiro et al., 2022b) and deeper zones (>20–40m) (Soares et al., 2017b, 2018, 2019). Therefore, a knowledge gap about nearshore formations (up to 20 m deep) situated along the inner continental shelf persists. Despite its proximity to the coast, this region is subject to the most intense fluxes of sediment; the water is usually turbid for most of the year (Tabosa et al., 2007), hindering access to these shallow formations. Despite the widespread presence (Ximenes Neto et al., 2018; Pinheiro et al., 2019; Carneiro et al., 2022a,b) of these low-latitude habitats, the lack of scientific description leads to the neglect of these marine forests in conservation policies and environmental impact assessment (Rossi et al., 2022). Thus, this short communication aims to qualitatively characterize the key benthic groups (i.e., ascidians, cnidarians, and sponges) on turbid-zone MAFs in an urban area on the equatorial semiarid coast of the southwestern Atlantic.

The study area is located in the municipality of Fortaleza, the capital of Ceará State, one of the most densely populated cities in Brazil (Barros et al., 2021) with high-rise development on the sea front (Paula et al., 2013). In particular, the construction of port infrastructure since the mid-19th century has markedly affected the marine geomorphology and sediment dynamics in the region (Paula et al., 2013; Ximenes Neto et al., 2018), with generally negative impacts on the coastal seascape (Paula et al., 2013; Carneiro et al., 2022). Nevertheless, rocky platforms with associated MAFs are still abundant and constitute an important feature of the seabed in the area (Ximenes Neto et al., 2018; Pinheiro et al., 2019). These reefs are likely formed by outcrops of ferruginous sandstones (Morais et al., 2009; Ximenes Neto et al., 2018; Carneiro et al., 2022) and remain fully submerged at shallow depths (6–10m) according to the tide. The present study focused on two of these formations, which are part of a single extensive rocky complex, popularly called the "Recife Grande" and "Recife da Velha" (Ximenes Neto et al., 2018) (Figure 1). Despite their nearshore locations (Figure 1), the biological assemblages associated with these reefs have never been studied. Visibility is quite restricted because of turbidity most of the year (~ 8 of 12 months) and navigational conditions that can make scientific diving difficult, especially during swell wave periods and higher wind speeds (> 7 $m.s^{-1}$) (Soares et al., 2019).

Scientific diving activities were performed with the support of an oceanographic vessel and SCUBA diving equipment. The activities were conducted by four expert divers in June and October 2018. For the qualitative survey of consolidated bottom benthos, scuba dives were conducted using underwater cameras for random analysis. From the videos, images were extracted that allowed the visualization and identification of the organisms as usual in baseline-type visual reef biodiversity assessments never studied before (Negrão et al., 2021). Moreover, taxonomic experts identified the key organisms from comparisons with bibliographic references for ascidians (Lotufo and Silva, 2006; Oliveira-Filho, 2010), corals, zoantharians (Leão et al., 2003; 2016; Rabelo et al., 2013, 2015; Santos et al., 2016) and sponges (Hadju et al., 2011; Moraes, 2011; Muricy et al., 2008).

Overall, the sandstone reefs showed low topographic complexity, appearing as relatively flat platforms, rising 1–2 m above the seabed. The video analysis indicated extensive coverage by turf algae along with sessile benthic suspension feeders, such as sponges, ascidians, zoantharians, and massive scleractinian corals (Figure 2), which provide much of the structural complexity of these ecosystems, thus constituting a MAF.

In these MAFs, 31 taxa were recorded and identified to the lowest taxonomic level (i.e., species, genus, family, or order) (Table 1; Figure 2; Supplementary Material).

Among ecosystem engineers, sponges were the most diverse group, a pattern that was also observed in deeper reefs (~20–50m) in the same region (Soares et al., 2017b; Carneiro et al., 2022a). Common Porifera species in the studied formations included *Aplysina fulva* (Pallas, 1766) (Figure 2A), *Ircinia strobilina* (Lamarck, 1816) (Figure 2B), *Monanchora arbuscula* (Duchassaing and Michelotti, 1864), and *Desmapsamma anchorata* (Carter, 1882). All four species could thrive under the harsh environmental conditions of the studied formations and act as ecosystem engineers, contributing to substrate complexity. *A. fulva* is a stress-tolerant species that

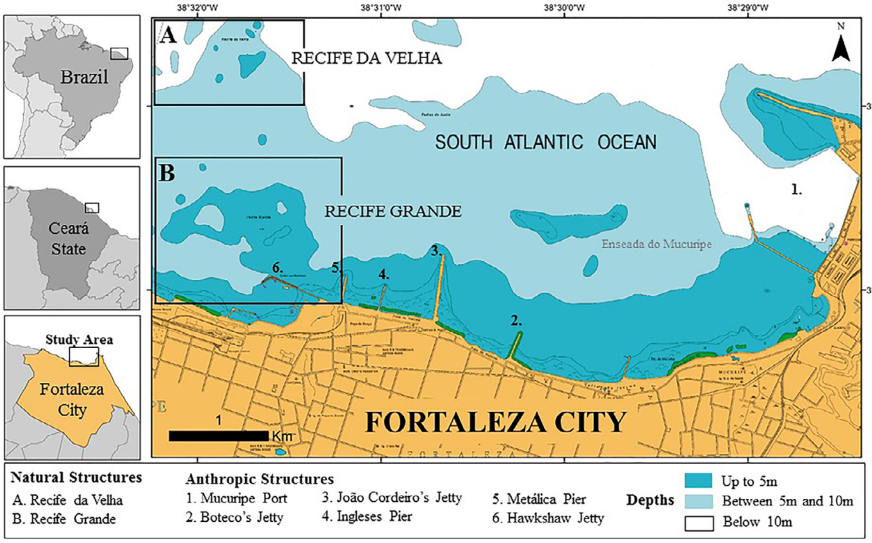

Figure 1. Study area on Fortaleza city coast (Equatorial Southwestern Atlantic, Ceará, Brazil) showing the “Recife da Velha” and “Recife Grande”; previously undescribed shallow-water reefs analyzed here.

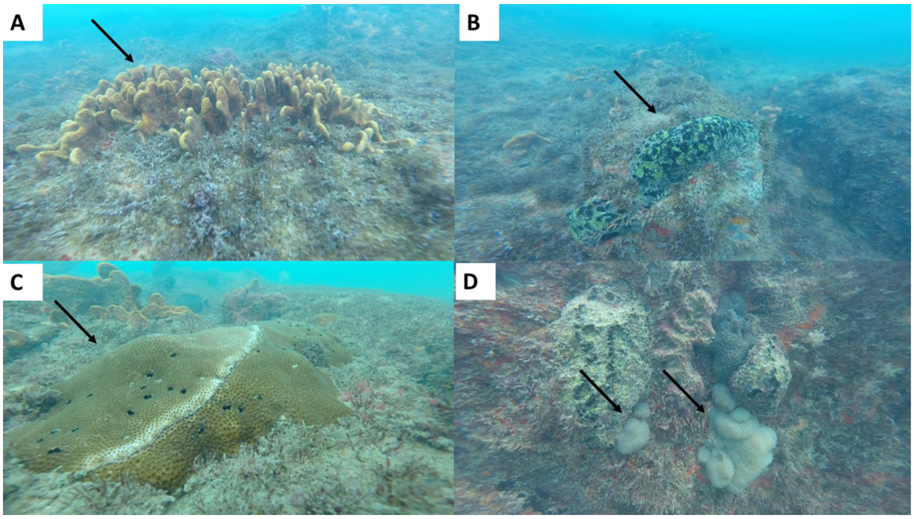

Figure 2. Sponges, massive corals, and ascidians are key components of marine animal forests in turbid-zone reefs (Fortaleza, Equatorial Southwestern Atlantic, Brazil). (A) Sponge *Aplysina fulva*; (B) Sponge *Ircinia strobilina*; (C) Coral *Siderastrea stellata*; (D) Ascidian *Stomozoa gigantea*.

Table 1. List of taxa (identified to the lowest taxonomic level) recorded in MAFs established on subtidal sandstone reefs along the semiarid coast of Brazil (Fortaleza, Equatorial SW Atlantic).

List of taxa
Anthozoa (Scleractinia)
Siderastrea stellata
Anthozoa (Zoantharia)
Palythoa variabilis
Ascidiacea
Cystodytes sp.
Didemnum sp.
Eudistoma saldanhai
Eudistoma vannamei
Stomozoa gigantea
Osteichthyes
Acanthurus chirurgus
Anisotremus virginicus
Halichoeres brasiliensis
Lutjanus sp.
Pomacanthus paru
Sparisoma axillare
Sparisoma frondosum
Phaeophyceae
Dictyota spp.
Dictyopteris spp.
Porifera
Amphimedon sp.
Aplysina fulva (Pallas, 1766)
Axinellidae
Clionaidae
Cliona sp.
Desmapsamma anchorata
Geodia tylastra
Haliclona sp.
Haploscerida
Ircinia strobilina
Lissodendoryx cf. *isodictyalis*
Monanchora arbuscula
Poecilosclerida
Scopalina sp.
Rhodophyta
Gelidium sp.

is known to inhabit a range of environments with significant sedimentation rates, and it thrives in Caribbean coral reefs (Wulff, 2007). *I. strobilina* is a globular sponge that often reaches large sizes and exhibits a massive growth form (Hoppe, 1988). *M. arbuscula* is a sponge that occurs on different substrates, including biogenic and sandstone reefs, such as those in the study area. Due to its generalist characteristics and heterotrophic feeding, it was common in the turbid-zone reefs studied and in the tropical western Atlantic (Leal et al., 2022). *D. anchorata* is a sponge that adheres to the reef substrate and can cover other organisms because of its growth and is one of the main epibiont sponges in the analyzed MAF. It can be observed in extreme environments subject to greater hydrodynamics (McLean and Yoshioka, 2008) such as marine animal forests in the study area.

Other sponges were identified at the order, family, and genus levels (Table 1). Sponges of the orders Poecilosclerida and Haploscerida were found (Figure S1). In the order Poecilosclerida, a massive encrusting species was observed. Sponges of the families Clionaidae and Axinellidae Carter, 1875 were also identified. The family Clionaidae d'Orbigny, 1851, genus *Cliona* Grant, 1825 comprises 81 species worldwide (de Voogd et al., 2022) and nine of them occur in Brazil (Leal et al., 2016). Sponges of the genera *Amphimedon*, *Haliclona*, and *Scopalina* were found at the genus level. The genus *Amphimedon* Duchassaing & Michelotti, 1864 comprises approximately 56 species worldwide (de Voogd et al., 2022), of which six occur in Brazil (Santos et al., 2014). The genus *Haliclona* Grant, 1835 has more than 450 species worldwide (de Voogd et al., 2022), of which 15 occur in Brazil (Muricy et al., 2015). The genus *Scopalina* Schimidt, 1862 comprises 19 species worldwide (de Voogd et al., 2022), of which only one is recorded in Brazil: *Scopalina ruetzleri* (Wiedenmayer, 1977) (Muricy et al., 2011).

Other filter-feeding organisms found on these MAFs were cnidarians (zoantharians and scleractinians), with only two species identified forming low-relief coral carpets. *Palythoa variabilis* (Duerden, 1898) is a Zoantharia that can live buried in the sand because of its long column attached to the rock below the silting layer. It can colonize substrates with a high degree of sedimentation, revealing an adaptation of this species to adverse conditions (Rabelo et al., 2013, 2015) such as that found on marginal reefs. The most common coral species in these turbid-zone reefs was *Siderastrea stellata* (Figure 2C). This reef-building coral is a massive species in Brazilian waters (Barros and Pires, 2006), which generally occurs in intertidal (Portugal et al., 2016), shallow (Costa et al., 2008; Leão et al., 2016), and mesophotic waters (Soares et al., 2018; Carneiro et al., 2022a). It is a weedy species (Darling et al., 2012) resistant to high sedimentation rates, partial burial, and turbidity (Tunala et al., 2019; Longo et al., 2020); which explains its occurrence in these forests. These harsh environmental conditions also explain the absence of stress-sensitive corals (such as branching hydrocorals).

In addition to sponges and cnidarians, ascidians were also observed (Figure S1), which helped to compose these animal forests. Ascidians belonging to the genus *Didemnum* Savignt, 1816 and *Cystodytes* Drasche, 1884 were identified. Moreover, three species (*Stomozoa gigantea*, *Eudistoma vannamei*, *Eudistoma saldanhai*) were common in the studied turbid-zone reefs. In this regard, *Stomozoa gigantea* (Van Name, 1921) has large colonies (Figure 2D) and is present throughout the tropical and subtropical Atlantic. *Eudistoma vannamei* (Millar, 1977) is recognized by its pedunculated colonies, united by a base that sticks to the substrate, and is native to the northeast region of Brazil and numerous in the equatorial Southwest Atlantic. Finally, *Eudistoma saldanhai* (Millar, 1977) is a typical ascidian species found in the subtropical waters of the Tropical SW Atlantic (Lotufo and Silva, 2006).

These unique nearshore reefs are common in this urban area (Figure 1) and have been neglected in many environmental studies. The marine animal forests described here form an extensive habitat for numerous reef fish (Table 1) such as *Anisotremus virginicus* (Linnaeus, 1758) (Figure S2-A), *Pomacanthus paru* (Bloch, 1787) (Figure S2 -B), *Halichoeres brasiliensis* (Bloch, 1791) (Figure S3 -A), *Haemulon plumierii* (Lacepéde, 1801) (Figure S3 -B), *Acanthurus chirurgus* (Bloch,

1787) (Figure S2-C), *Sparisoma frondosum* (Agassiz, 1831) (Figure S3 -C), *Sparisoma axillare* (Steindachner, 1878) (Figure S2-D), and *Lutjanus* sp. (Figure S3 -D). These reef fishes are typical of shallow-water (Freitas et al., 2019) and mesophotic reefs (Soares et al., 2018) in the equatorial SW Atlantic. Moreover, most of these species have ecological and socioeconomic importance (e.g., aquarium trade and/or human consumption), which demonstrates the importance of the MAFs described here for connectivity and conservation policies (Endo et al., 2019). These overlooked forests are widespread in this low-latitude area and are forgotten despite their valuable ecosystem goods and services, such as those for reef fish habitats (Figure S2).

Moderately turbid waters and high sediment resuspension in the study area act as environmental filters that select stress-tolerant marginal reef specialists adapted to the prevailing conditions (Camp et al., 2018; Burt et al., 2020; Soares, 2020). The studied MAFs are located in a shallow area with intense local hydrodynamism owing to the action of waves (i.e., sea and swells) and strong coastal currents (Soares et al., 2017). Such unique oceanographic dynamics in these extreme reefs lead to sediment resuspension and directly drive periodic burial (Portugal et al., 2016). The presence of disturbance-tolerant species adapted to these local extreme factors (Knoppers et al., 1999; Dias et al., 2013; Soares et al., 2019) such as sponges (Bell et al., 2013), *Ircinia strobilina*, *L. isodictyalis*, *S. ruetzleri* and several species of the genera *Haliclona* (Rutzler et al., 2020), cnidarians, *S. stellata* (Leão et al., 2016; Barros et al., 2021), *P. variabilis* (Rabelo et al., 2013, 2015), and ascidians reinforce this idea. Such resilience to turbidity and sedimentation has been observed in the identification of different stress-tolerant and weedy species that compose these MAFs, which have characteristics of resistance to such disturbances (Cruz et al., 2018; Soares et al., 2021; Santana et al., 2023).

Remarkably, the structures of the studied formations seem similar to high-latitude marginal reefs or low-latitude reefs under the influence of upwelling, which sustains soft corals and non-framework building coral communities along with sponges and ascidians (Perry and Larcombe, 2003). In particular, shallow MAFs along the semiarid coast of Brazil seem to lack some of the characteristics of low-latitude reefs under high sedimentation, whose structure was described as coral rubble within sedimentary matrices (Perry and Larcombe, 2003). This suggests that factors other than periodic burials and low light availability affected the studied MAFs. In particular, temperature and nutrient fluctuations may limit the growth of a coral framework while benefiting other suspension feeders in the area.

In the tropical southwestern Atlantic, reef environments are degraded by multiple local and regional human impacts (Leão et al., 2016), including urbanization (Portugal et al., 2016; Barros et al., 2021). In addition, the effects of marine heatwaves and global climate change (Principe et al., 2021; Pereira et al., 2022) have synergistic and cumulative effects (Soares, 2020), especially on marginal reefs, such as those described in this short communication.

Fortaleza is one of Brazil's most developed, densely populated, and heavily modified coastal engineering structures (Paula et al., 2013). In this way, we conclude that the urbanized coast of Fortaleza in the Equatorial Southwestern Atlantic has lush MAFs in turbid-zone reefs with significant diversity (at least 31 taxa) despite the significant high-rise development of the sea front. These animals (and algae) were not collected, and further studies are required for their detailed identification. This hidden biodiversity needs further detailed studies such as quantitative assessment of benthic cover, evaluation of reef fishes including abundance and richness, taxonomic analysis of cryptic diversity and other groups (e.g., hydrozoans, echinoderms, etc.), environmental DNA, and high-resolution mapping of the extent of these underwater forests.

Finally, anthropogenic activities that increase sediment runoff and suspension above the threshold of turbid-zone reefs are local pressures that must be controlled by science-based conservation policies (Soares, 2020). Suspended sediment concentrations through urban and industrial runoff, as well as deforestation, resuspension, and dredging activities, are local drivers of resistance loss and impact in turbid-zone reefs (Fisher et al. 2019; Freitas et al., 2019). Their increase, along with the synergistic interaction between non-climate and climate change pressures threatens marine animal forests and may decrease their overall resistance (Soares et al., 2021). In the context of highly urbanized areas subject to pollution impacts (Vieira et al., 2002), breakwaters (Portugal et al., 2016), jetties, and dredging activities (Paula et al., 2013), it is necessary to consider the existence of these unique marine animal forests (Rossi et al., 2022). They must be included in the impact assessment analysis of large-scale coastal projects and conservation policies because they are underrepresented and outside the current marine protected areas.

ACKNOWLEDGMENTS

The authors thank Cynthia Ogawa, Sarah Maria, Maria Ozilea Menezes, and Carlinhos for the execution of the oceanographic campaigns and undergraduate students at the Institute of Marine Sciences (LABOMAR-UFC) for their help with video analysis. We thank Tatiane Garcia for the maps based on nautical charts. This study was funded by the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico (PELD-CNPq), Project #442337/2020-5, CNPq Research Productivity Fellowship (#313518/2020-3), CAPES PRINT, CAPES/AVH, FUNCAP (Chief-Scientist Program), Fulbright Commission, and the Alexander Von Humboldt Foundation.

AUTHOR CONTRIBUTION

M.O.S.: Conceptualization; Supervision, Project Administration; Funding Acquisition; Formal Analysis; Investigation; Writing – original draft; Writing – review & editing.

S.S.M., S.V.P., C.C.P., P.B.M.C.: Methodology; Formal Analysis; Investigation; Writing – review & editing.

REFERENCES

BAPTISTA, E. M. C. 2021. Caracterização e importância ecológica e econômica dos recifes da zona costeira do estado do Piauí. *Geografia: Publicações Avulsas*, 3(2), 225-250.

BARROS, M. M. L. & PIRES, D. O. 2006. Aspects of the life history of Siderastrea stellata in the tropical Western Atlantic, Brazil. *Invertebrate Reproduction & Development*, 49(4), 237-244, DOI: http://dx.doi.org/10.1080/07924259.2006.9652213

BARROS, Y., LUCAS, C. C. & SOARES, M. O. 2021. An urban intertidal reef is dominated by fleshy macroalgae, sediment, and bleaching of a resilient coral (Siderastrea stellata). *Marine Pollution Bulletin*, 173(Pt A), 112967, DOI: https://doi.org/10.1016/j.marpolbul.2021.112967

BELL, J. J., DAVY, S. K., JONES, T., TAYLOR, M. W. & WEBSTER, N. S. 2013. Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology*, 19(9), 2613-2624, DOI: https://doi.org/10.1111/gcb.12212

BURT, J. A., BARTHOLOMEW, A., BAUMAN, A., SAIF, A. & SALE, P. F. 2009. Coral recruitment and early benthic community development on several materials used in the construction of artificial reefs and breakwaters. *Journal of Experimental Marine Biology and Ecology*, 373(1), 72-78.

BURT, J., BARTHOLOMEW, A. & SALE, P. F. 2011. Benthic development on large-scale engineered reefs: a comparison of communities among breakwaters of different age and natural reefs. *Ecological Engineering*, 37(2), 191-198.

BURT, J. A., CAMP, E. F., ENOCHS, I. C., JOHANSEN, J. L., MORGAN, K. M., RIEGL, B. & HOEY, A. S. 2020. Insights from extreme coral reefs in a changing world. *Coral Reefs*, 39, 495-507, DOI: https://doi.org/10.1007/s00338-020-01966-y

CAMP, E. F., SCHOEPF, V., MUMBY, P. J., HARDTKE, L. A., RODOLFO-METALPA, R., SMITH, D. J. & SUGGETT, D. J. 2018. The future of coral reefs subject to rapid climate change: lessons from natural extreme environments. *Frontiers in Marine Science*, 5(4), 1-15, DOI: https://doi.org/10.3389/fmars.2018.00004

CARNEIRO, P. B. M., XIMENES NETO, A. R., JUCÁ-QUEIROZ, B., TEIXEIRA, C. E. P., FEITOSA, C. V., BARROSO, C. X., MATTHEWS-CASCON, H., MORAIS, J. O., FREITAS, J. E. P., SANTANDER-NETO, J., ARAÚJO, J. T., MONTEIRO, L. H. U., PINHEIRO, L. S., BRAGA, M. D. A., CORDEIRO, R. T. S., ROSSI, S., BEJARANO, S., SALANI, S., GARCIA, T. M., LOTUFO, T. M. C., SMITH, T. B., FARIA, V. V. & SOARES, M. O. 2022. Interconnected marine habitats form a single continental-scale reef system in South America. *Scientific Reports*, 12, 17359, DOI: https://doi.org/10.1038/s41598-022-21341-x

CARNEIRO, P. B. M., XIMENES NETO, A. R., FEITOSA, C. V., BARROSO, C. X., MATTHEWS-CASCON, H., SOARES, M. O. & LOTUFO, T. M. C. 2022. Marine hardbottom environments in the beaches of Ceará State, Equatorial Coast of Brazil. *Arquivos de Ciências do Mar*, 54(2), 120-153, DOI: http://dx.doi.org/10.32360/acmar.v54i2.61440

CRUZ, I. C. S., WATERS, L. G., KIKUCHI, R. K. P., LEÃO, Z. M. A. N. & TURRA, A. 2018. Marginal coral reefs show high susceptibility to phase shift. *Marine Pollution Bulletin*, 135, 551-561, DOI: https://doi.org/10.1016/j.marpolbul.2018.07.043

COSTA, C. F., SASSI, R. & GORLACH-LIRA, K. 2008. Zooxanthellae genotypes in the coral Siderastrea stellata from coastal reefs in northeastern Brazil. *Journal of Experimental Marine Biology and Ecology*, 367(2), 149-152, DOI: http://dx.doi.org/10.1016/j.jembe.2008.09.012

DARLING, E. S., ALVAREZ-FILIP, L., OLIVER, T. A., MCCLANAHAN, T. R. & CÔTÉ, I. M. 2012. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*, 15(12), 1378-1386, DOI: https://doi.org/10.1111/j.1461-0248.2012.01861.x

DE VOOGD, N. J., ALVAREZ, B., BOURY-ESNAULT, N., CARBALLO, J. L., CÁRDENAS, P., DÍAZ, M. C., DOHRMANN, M., DOWNEY, R., HAJDU, E., HOOPER, J. N. A., KELLY, M., KLAUTAU, M., MANCONI, R., MORROW, C. C. PISERA, A. B., RÍOS, P., RÜTZLER, K., SCHÖNBERG, C., VACELET, J. & VAN SOEST, R. W. M. 2022. *Home - The World Porifera Database*. Available at: https://www.marinespecies.org/porifera. [Accessed: 26 May 2022].

DIAS, F. J. S., CASTRO, B. M. & LACERDA, L. D. 2013. Continental shelf water masses off the Jaguaribe River (4S), northeastern Brazil. *Continental Shelf Research*, 66(1), 123-135, DOI: https://doi.org/10.1016/j.csr.2013.06.005

ELLIFF, C. I. & KIKUCHI, R. K. P. 2017. Ecosystem services provided by coral reefs in a Southwestern Atlantic Archipelago. *Ocean & Coastal Management*, 136, 49-55, DOI: https://doi.org/10.1016/j.ocecoaman.2016.11.021

ENDO, C. A. K., GHERARDI, D. F. M., PEZZI, L. P. & LIMA, L. N. 2019. Low connectivity compromises the conservation of reef fishes by marine protected areas in the tropical South Atlantic. *Scientific Reports*, 9, 8634, DOI: https://doi.org/10.1038/s41598-019-45042-0

FISHER, R., BESSELL-BROWNE, P. & JONES, R. 2019. Synergistic and antagonistic impacts of suspended sediments and thermal stress on corals. *Nature Communications*, 10, 2346, DOI: https://doi.org/10.1038/s41467-019-10288-9

FONG, J. & TODD, P. A. 2021. Spatio-temporal dynamics of coral-macroalgal interactions and their impacts on coral growth on urbanised reefs. *Marine Pollution Bulletin*, 172, 112849, DOI: https://doi.org/10.1016/j.marpolbul.2021.112849

FRANCINI-FILHO, R., ASP, N. E., SIEGLE, E., HOCEVAR, J., LOWYCK, K., D'AVILA, N. & THOMPSON, F. L. 2018. Perspectives on the great Amazon reef: extension, biodiversity, and threats. *Frontiers in Marine Science*, 5, 142, DOI: https://doi.org/10.3389/fmars.2018.00142

FREITAS, J. E. P., ARAÚJO, M. E. & LOTUFO, T. M. C. 2019. Composition and structure of the icthyofauna in a marine protected area in the western equatorial Atlantic: a baseline to support conservation management. *Regional Studies in Marine Science*, 25, 100488, DOI: https://doi.org/10.1016/j.rsma.2018.100488

FREITAS, L. M., OLIVEIRA, M. D. M., LEÃO, Z. M. A. N. & KIKUCHI, R. K. P. 2019. Effects of turbidity and depth on the bioconstruction of the Abrolhos reefs. *Coral Reefs*, 38(2), 241-253, DOI: https://doi.org/10.1007/s00338-019-01770-3

GATWAZA, O. C. & WANG, X. 2021. Mapping of biodiversity hubs and key ecosystem services as tool for shaping optimal areas for conservation. *PLoS One,* 16(8), e0253151, DOI: https://doi.org/10.1371/journal.pone.0253151

HALPERN, B. S., FRAZIER, M., AFFLERBACH, J., LOWNDES, J. S., MICHELI, F., O'HARA, C., SCARBOROUGH, C. & SELKOE, K. A. 2019. Recent pace of change in human impact on the world's ocean. *Scientific Reports*, 9, 11609, DOI: https://doi.org/10.1038/s41598-019-47201-9

HADJU, E., PEIXINHO, S. & FERNANDEZ, J. C. C. 2011. *Esponjas marinhas da Bahia. Guia de campo e laboratório*. Rio de Janeiro: Museu Nacional.

HOPPE, W. F. 1988. Growth, regeneration and predation in three species of large coral reef sponges. *Marine Ecology Progress Series*, 50, 117-125.

HUGHES, T. P., ANDERSON, K. D., CONNOLLY, S. R., HERON, S. F., KERRY, J. T., LOUGH, J. M., BAIRD, A. H., BAUM, J. K., BERUMEN, M. L., BRIDGE, T. C., CLAAR, D. C., EAKIN, C. M., GILMOUR, J. P., GRAHAM, N. A. J., HARRISON, H., HOBBS, J. P. A., HOEY, A. S., HOOGENBOOM, M., LOWE, R. J., MCCULLOCH, M. T., PANDOLFI, J. M., PRATCHETT, M., SCHOEPF, V., TORDA, G. & WILSON, S. K. 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, 80(359), 80-83, DOI: https://doi.org/10.1126/science.aan8048

HUGHES, T. P., BARNES, M. L., BELLWOOD, D. R., CINNER, J. E., CUMMING, G. S., JACKSON, J. B. C., KLEYPAS, J., VAN DE LEEMPUT, I. A., LOUGH, J. M., MORRISON, T. H., PALUMBI, S. R., VAN NES, E. H. & SCHEFFER, M. 2017. Coral reefs in the Anthropocene. *Nature*, 546, 82-90, DOI: https://doi.org/10.1038/nature22901

KNOPPERS, B., EKAU, W. & FIGUEIREDO, A. G. 1999. The coast and shelf of east and northeast Brazil and material transport. *Geo-Marine Letters*, 19, 171-178, DOI: https://doi.org/10.1007/s003670050106

LEAL, C. V., AVELINO-ALVES, D., SALAZAR, V., OMACHI, C., THOMPSON, C., BERLINCK, R. G. S., HADJU, E. & THOMPSON, F. 2022. Sponges present a core prokaryotic community stable across Tropical Western Atlantic. *Science of Total Environment,* 835, 155145, DOI: https://doi.org/10.1016/j.scitotenv.2022.155145

LEAL, C. V., PAULA, T. O. S., LÔBO-HAJDU, G., SCHÖNBERG, C. H. L. & ESTEVES, E. L. 2016. Morphological and molecular systematics of the '*Cliona viridis complex*' from south-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom*, 96(2), 313-322, DOI: https://doi.org/10.1017/s0025315415001642

LEÃO, Z. M. A. N., KIKUCHI, R. K. P., FERREIRA, B. P., NEVES, E. G., SOVIERZOSKI, H. H., OLIVEIRA, M. D. M., MAIDA, M., CORREIA, M. D. & JOHNSSON, R. 2016. Brazilian coral reefs in a period of global change: a synthesis. *Brazilian Journal of Oceanography*, 64(spe2), 97-116, DOI: https://doi.org/10.1590/S1679-875920160916064sp2

LEÃO, Z. M. A. N., KIKUCHI, R. K. P. & TESTA, V. 2003. Corals and coral reefs of Brazil. *Latin American Coral Reefs*, 1, 9-52, DOI: https://doi.org/10.1016/B978-044451388-5/50003-5

LOTUFO, T. M. C. & SILVA, A. M. B. 2006. Ascidiacea do litoral cearense. *In:* MATTHEWS-CASCON, H. & LOTUFO, T. M. C. (eds.). *Biota marinha da costa oeste do Ceará*. Brasília (DF): MMA (Ministério do Meio Ambiente), pp. 221-247.

MATTHEWS-CASCON, H. & LOTUFO, T. M. C. 2006. *Biota marinha da costa oeste do Ceará.* Brasília (DF): MMA (Ministério do Meio Ambiente).

McCLANAHAN, T. R. 2020. Wilderness and conservation policies needed to avoid a coral reef fisheries crisis. *Marine Policy*, 119, 104022, DOI: https://doi.org/10.1016/j.marpol.2020.104022

McLEAN, E. L. & YOSHIOKA, P. M. 2008. Substratum effects on the growth and survivorship of the sponge Desmapsamma anchorata. *Caribbean Journal of Science*, 44(1), 83-89, DOI: https://doi.org/10.18475/cjos.v44i1.a9

MORAES, F. C. 2011. *Esponjas das ilhas oceânicas brasileiras. Série Livros 44.* Rio de Janeiro: Museu Nacional. Available from: https://www.marinespecies.org/porifera/aphia.php?p=sourcedetails&id=162782. [Accessed: 01/August/2022].

MORAIS, J. O., IRION, G. F. & PINHEIRO, L. S. 2009. Preliminary results on holocene sea-level changes on Ceará Coast/Brazil. *Journal of Coastal Research*, SI 56, Lisbon, 56, 646-649.

MURICY, G., ESTEVES, E. L., MONTEIRO, L. C., RODRIGUES, B. R. & ALBANO, R. M. 2015. A new species of Haliclona (Demospongiae: Haplosclerida: Chalinidae) from southeastern Brazil and the first record of Haliclona vansoesti from the Brazilian coast. *Zootaxa*, 3925(4), 536-550, DOI: https://doi.org/10.11646/zootaxa.3925.4.3

MURICY, G., ESTEVES, E. L., MORAES, F., SANTOS, J. P., SILVA, S. M., ALMEIDA, E. V. R., KLAUTAU, M. & LANNA, E. 2008. *Biodiversidade Marinha da Bacia Potiguar*: *Porifera*. Rio de Janeiro: Museu Nacional.

MURICY, G., LOPES, D. A., HAJDU, E., CARVALHO, M. S., MORAES, F., KLAUTAU, M., MENEGOLA, C. & PINHEIRO, U. 2011. *Catalogue of Brazilian Porifera. Série Livros 46.* Rio de Janeiro: Museu Nacional.

NEGRÃO, F., LACERDA, C. H. F., MELO, T. H., BIANCHINI, A., CALDERON, E. N., CASTRO, C. B., CORDEIRO, R. T. S., DIAS, R. J. S., FRANCINI-FILHO, R. B., GUEBERT, F. M., GÜTH, A. Z., HETZEL, B., HORTA, P. A., LOTUFO, T. M. C., MAHIQUES, M. M., MIES, M., PIRES, D. O., SALVI, K. P. & SUMIDA, P. Y. G. 2021. The first biological survey of the Royal Charlotte Bank (SW Atlantic) reveals a large and diverse ecosystem complex. *Estuarine, Coastal and Shelf Science*, 255, 107363, DOI: https://doi.org/10.1016/j.ecss.2021.107363

OLIVEIRA-FILHO, R. R. 2010. *Caracterização das ascídias em regiões portuárias do Ceará*. MSc. Fortaleza: UFC (Universidade Federal do Ceará).

PAULA, D. P., DIAS, J. M. A., FERREIRA, O. & MORAIS, J. O. 2013. High-rise development of the sea-front at Fortaleza (Brazil): Perspectives on its valuation and consequences. *Ocean & Coastal Management*, 77, 14-23, DOI: https://doi.org/10.1016/j.ocecoaman.2012.03.004

PEREIRA-FILHO, G., SHINYAYE, G. S., KITAHARA, M. V., MOURA, R. L., AMADO-FILHO, G. M., BAHIA, R., MORAES, F. G., NEVES, L. M., FRANCINI, C. L. B., GIBRAN, F. Z. & MOTTA, F. S. 2019. The southernmost Atlantic coral reef is off the subtropical island of Queimada Grande. *Bulletin of Marine Science*, 95(2), 1-12, DOI: https://doi.org/10.5343/bms.2018.0056

PEREIRA, P. H. C., LIMA, G. V., PONTES, A. V. F., CÔRTES, L. G. F., GOMES, E., SAMPAIO, C. L. S., PINTO, T. K., MIRANDA, R. J., CARDOSO, A. T. C., ARAUJO, J. C. & SEOANE, J. C. S. 2022. Unprecedented coral mortality on Southwestern atlantic coral reefs following major thermal stress. *Frontiers in Marine Science*, 9, 725778, DOI: https://doi.org/10.3389/fmars.2022.725778

PERRY, C. T. & LARCOMBE, P. 2003. Marginal and non-reef-building coral environments. *Coral Reefs*, 22(4), 427-432.

PINHEIRO, L. S., GASTÃO, F. G., JÚNIOR, W. F. & BRANCO, M. P. D. N. C. 2019. Mapeamento de habitats marinhos da plataforma continental interna da praia de Iracema-Fortaleza-Ceará. *Geociências*, 38(3), 813-825.

PRINCIPE, S. C., ACOSTA, A. L., ANDRADE, J. E. & LOTUFO, T. M. C. 2021. Predicted shifts in the Distributions of Atlantic Reef-Building Corals in the Face of Climate Change. *Frontiers in Marine Science*, 8, 673086, DOI: https://doi.org/10.3389/fmars.2021.673086

PORTUGAL, A. B., CARVALHO, F. L., CARNEIRO, P. B. M., ROSSI, S. & SOARES, M. O. 2016. Increased anthropogenic pressure decreases species richness in tropical intertidal reefs. *Marine Environmental Research*, 120, 44-54, DOI: https://doi.org/10.1016/j.marenvres.2016.07.005

PREVIERO, M. & GASALLA, M. A. 2018. Mapping fishing grounds, resource and fleet patterns to enhance management units in data-poor fisheries: The case of snappers and groupers in the Abrolhos Bank coral-reefs (South Atlantic). *Ocean & Coastal Management*, 154, 83-95, DOI: https://doi.org/10.1016/j.ocecoaman.2018.01.007

RABELO, E. F., SOARES, M. O. & MATTHEWS-CASCON, H. 2013. Competitive interactions among zoanthids (Cnidaria: Zoanthidae) in an intertidal zone of northeastern Brazil. *Brazilian Journal of Oceanography*, 61(1), 35-42. Available from: https://www.scielo.br/pdf/bjoce/v61n1/a04v61n1.pdf. [Accessed: 13/August/2022].

RABELO, E. F., SOARES, M. O., BEZERRA, L. E. A. & MATTHEWS-CASCON, H. 2015. Distribution pattern of zoanthids (Cnidaria: Zoantharia) on a tropical reef. *Marine Biology Research,* 11(6), 584-592, DOI: https://doi.org/10.1080/17451000.2014.962542

ROSSI, S. 2013. The destruction of the "animal forests" in the oceans: towards an over-simplification of the benthic ecosystems. *Ocean & Coastal Management,* 84, 77-85.

ROSSI, S., BRAMANTI, L., GORI, A. & OREJAS, C. 2017. Animal forests of the world: an overview. In: ROSSI, S., BRAMANTI, L., GORI, A. & OREJAS, C. (eds.). *Marine animal forests*. Cham: Springer, DOI: https://doi.org/10.1007/978-3-319-21012-4_1

ROSSI, S., BRAMANTI, L., HORTA, P., ALLCOCK, L., CARREIRO-SILVA, M., COPPARI, M., DENIS, V., HADJIOANNOU, L., ISLA, E., JIMENEZ, C., JOHNSON, M., MOHN, C., OREJAS, C., RAMSAK, A., REIMER, J., RINKEVICH, B., RIZZO, L., SALOMIDI, M., SAMAAI, T., SCHUBERT, N., SOARES, M., THURSTAN, R., VASSALLO, P., ZIVERI, P. & ZORRILLA-PUJANA, J. 2022. Protecting global marine animal forests. *Science*, 376(6596), 929.

ROSSI, S., ISLA, E., BOSCH-BELMAR, M., GALLI, G., GORI, A., GRISTINA, M., INGROSSO, G., MILISENDA, G., PIRAINO, S., RIZZO, L., SCHUBERT, N., SOARES, M., SOLIDORO, C., THURSTAN, R. H., VILADRICH, N., WILLIS, T. J. & ZIVERI, P. 2019. Changes of energy fluxes in marine animal forests of the Anthropocene: factors shaping the future seascape. *ICES Journal of Marine Science,* 76(7), 2008-2019, DOI: https://doi.org/10.1093/icesjms/fsz147

RÜTZLER, K., DIAZ, M. C., VAN SOEST, R. W. M., ZEA, S., SMITH, K. P., ALVAREZ, B. & WULFF, J. 2020. Diversity of Sponge Fauna in Mangrove Ponds, Pelican Cays, Belize. *Atoll Research Bulletin*, 476, 231-248.

SANTANA, E. F. C., MIES, M., LONGO, G. O., MENEZES, R., AUED, A. W., LUZA, A. L., BENDER, M. G., SEGAL, B. & FLOETER, S. R. 2023. Turbidity shapes shallow Southwestern Atlantic benthic reef communities. *Marine Environmental Research*, 183, 105807, DOI: https://doi.org/10.1016/j.marenvres.2022.105807

SANTOS, G. G., DOCIO, L. & PINHEIRO, U. 2014. Two new species of the family Niphatidae van Soest, 1980 from Northeastern Brazil (Haplosclerida: Demospongiae: Porifera). *Zootaxa*, 3774(3), 265-274, DOI: https://doi.org/10.11646/zootaxa.3774.3.3

SANTOS, M. E. A., KITAHARA, M. V., LINDNER, A. & REIMER, J. D. 2016. Overview of the order Zoantharia (Cnidaria: Anthozoa) in Brazil. *Marine Biodiversity*, 46, 547-559, DOI: https://doi.org/10.1007/s12526-015-0396-7

SOARES, M. O. 2020. Marginal reef paradox: a possible refuge from environmental changes? *Ocean & Coastal Management*, 185, 105063, DOI: https://doi.org/10.1016/j.ocecoaman.2019.105063

SOARES, M. O., CRUZ, I. C. S., SANTOS, B. A., TAVARES, T. C. L., GARCIA, T. M., MENEZES, N., LOPES, B. D., ARAÚJO, J. T., GURGEL, A. & ROSSI. S. 2021. Marginal reefs in the Anthropocene: they are not Noah's ark. *In:* ROSSI, S. & BRAMANTI, L. (eds.). *Perspectives on the marine animal forests of the world*. Switzerland: Springer Nature, pp. 87-128, DOI: https://doi.org/10.1007/978-3-030-57054-5_4

SOARES, M. O., DAVIS, M., PAIVA, C. C. & CARNEIRO, P. B. M. 2018. Mesophotic ecosystems: Coral and fish assemblages in a tropical marginal reef (Northeastern Brazil). *Marine Biodiversity,* 48, 1631-1636, DOI: https://doi.org/10.1007/s12526-016-0615-x

SOARES, M. O., MARTINS, F. A. S., CARNEIRO, P. B. M. & ROSSI, S. 2017. The forgotten reefs: benthic assemblage coverage on a sandstone reef (Tropical Southwestern Atlantic). *Journal of Marine Biological Association of UK*, 97(8), 1585-1592, DOI: https://doi.org/10.1017/S0025315416000965

SOARES, M. O., MONTEIRO, T., VIEIRA, M., SALANI, S., HADJU, E., MATTHEWS, H., MARGARIDA, Z., NERY, D. A. & KENJI, R. 2017. Brazilian marine animal forests: a new world to discover in Southwestern Atlantic. *In:* ROSSI, S., BRAMANTI, L., GORI A. & OREJAS, C. (eds.). *Marine Animal Forests*. Cham: Springer, pp. 1-38, DOI: https://doi.org/10.1007/978-3-319-17001-5

SOARES, M. O., TEIXEIRA, C. E. P., FERREIRA, S. M. C., GURGEL, A. L. A. R., PAIVA, B. P., MENEZES, M. O. B., DAVIS, M. & TAVARES, T. C. L. 2019. Thermal stress and tropical reefs: mass coral bleaching in a stable temperature environment?. *Marine Biodiversity*, 49(6), 2921-2929, DOI: http://dx.doi.org/10.1007/s12526-019-00994-4

TABOSA, W. F., AMARO, V. E. & VITAL, H. 2007. Análise do ambiente costeiro e marinho, a partir de produtos de sensoriamento remoto na região de São Bento do Norte, NE Brasil*. Revista Brasileira de Geofísica*, 25, 37-48.

TEIXEIRA, C. E. P. & MACHADO, G. T. 2013. On the temporal variability of the Sea Surface Temperature on the Tropical Southwest Atlantic Continental Shelf. *Journal of Coastal Research,* 65(spe2), 2071-2076, DOI: https://doi.org/10.2112/SI65-350.1

TUNALA, L. P., TÂMEGA, F. T. S., DUARTE, H. M. & COUTINHO, R. 2019. Stress factors in the photobiology of the reef coral Siderastrea stellata. *Journal of Experimental Marine Biology and Ecology*, 519, 151188, DOI: http://dx.doi.org/10.1016/j.jembe.2019.151188

XIMENES NETO, A. R. X., MORAIS, J. O. & PINHEIRO, L. S. 2018. Modificações na geomorfologia marinha a partir de estruturas portuárias: o caso do Mucuripe, Fortaleza/CE. *Geociências*, 37(4), 793-805.

WULFF, J. L. 2007. Disease prevalence and population density over time in three common Caribbean coral reef sponge species. *Journal of the Marine Biological Association of the United Kingdow*, 87(6), 1715-1720, DOI: https://doi.org/10.1017/S002531540705881X