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# The first biological survey of the Royal Charlotte Bank (SW Atlantic) reveals a large and diverse ecosystem complex

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The Southwestern Atlantic harbors unique reef environments with high proportions of endemic species. The most prominent reefs are located in the Abrolhos Bank, a 46,000 km<sup>2</sup> extension of the South American continental shelf. However, just 100 km north of Abrolhos is the Royal Charlotte Bank (RCB), an area still poorly investigated. From a biological perspective, the only scientific information available is the historical record of lobster fisheries in the region. Hence, we performed an expedition to investigate what macrohabitats are found in the RCB and perform a preliminary biodiversity assessment. A dropcam was deployed in 67 sites and recorded images of macrohabitats and associated biodiversity. Four different macrohabitats were detected: rhodolith beds, macroalgal forests associated with rhodolith beds, calcareous sand deposits and coral reefs. The former two were the most frequent, and both rhodolith and macroalgae densities were higher on the outer shelf. A total of 83 species of fish, invertebrates and algae were identified, which comprises a comparatively high diversity for visual reef biodiversity assessments in the Southwestern Atlantic. Our findings show that the RCB is a large and diverse ecosystem complex mostly composed of rhodoliths, and also that it may be already undergoing anthropogenic impacts associated with climate change and fisheries. Therefore, further investigations are necessary to understand the extent of biodiversity and its main threats and evaluate the possible need of conservation and management measures.

#### 1. Introduction

The Southwestern Atlantic continental shelf harbors several distinctive reef environments, including true coral reefs, sandstone reefs, rocky reefs, algal reefs, and rhodolith beds distributed from the Equator to subtropical latitudes (Castro and Pires, 2001; Leão et al., 2003; Amado-Filho et al., 2012). These reefs are found in a unique

geological setting because the South American shelf displays several large rivers that discharge a considerable amount of nutrients and sediments (Costa et al., 2000; Omachi et al., 2019). Some reefs are directly influenced by river plumes (Leão et al., 2003, 2016; Moura et al., 2016), while others are influenced by the geographical barrier that the rivers impose by limiting gene flow between reef communities (Picciani et al., 2016; Souza et al., 2017). This is especially the case of the

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Amazon-Orinoco plume, which divides the Brazilian and Caribbean Provinces (Leão et al., 2003; Floeter et al., 2008; Cordeiro et al., 2015). This partial isolation of the South Atlantic tropical biodiversity, along with particular environmental features such as high turbidity, led to high levels of endemism for relevant taxa such as fish and shallow-water corals (Castro and Pires, 2001; Leão et al., 2003; Castro and Zilberberg, 2016; Pinheiro et al., 2018).

The largest shelf extension in the Southwestern Atlantic is the Abrolhos Bank, a major biodiversity hotspot of 46,000 km<sup>2</sup> where the main coral reefs of the South Atlantic are located (Castro and Pires, 2001; Leão and Kikuchi, 2001). This region is considered a center of biodiversity and endemism in the South Atlantic, harboring a high diversity of reef fish and coral species (Castro and Pires, 2001; Leão and Kikuchi, 2001; Dutra et al., 2006; Cruz-Motta et al., 2020). Some of the largest rhodolith beds ever described are also found within this area (Amado-Filho et al., 2012; Moura et al., 2013, 2021; Brasileiro et al., 2016). Besides its ecological importance, the Abrolhos Bank is also relevant from an economic perspective, as fisheries and tourism sustain a significant portion of the regional economy (Leão et al., 1996; Giglio et al., 2016; Previero and Gasalla, 2020). Therefore, the Abrolhos Bank is considered one of the highest priorities for conservation in the South Atlantic because of its biological and socio-economic importance.

Approximately 100 km north of Abrolhos lies the Royal Charlotte Bank (RCB). The RCB is the second largest bank within the tropical Southwestern Atlantic, occupying about 7,000 km<sup>2</sup>. Despite such proximity to Abrolhos, the habitats, fauna, and flora of the RCB are still largely unknown to science. Therefore, because of the lack of biological data, the RCB has not yet been considered a priority area for conservation (see Magris et al., 2020; Vilar et al., 2020). However, there are historical records of lobster fisheries (Fonteles-Filho, 2007) and several reports from local fishermen showing significant catches of reef fishes such as groupers. Additional information available for the RCB is mostly limited to its geological origins (Fainstein and Summerhayes, 1982) and ocean circulation patterns (Summerhayes et al., 1976; Ghisolfi et al., 2015). Therefore, apart from reports of the presence of fisheries activity, biological information is still essentially unavailable.

This study provides the first macrohabitat and biological assessment of the RCB based on data obtained using dropcams. It is important to build an appropriate biodiversity baseline for the RCB because of its proximity to the Abrolhos Bank since it may require conservation and management measures due to its potentially high biodiversity. Thus, a biological survey of the Royal Charlotte Bank was considered a priority in the Brazilian Action Plan for the Conservation of Endangered Species in Coral Habitats. Furthermore, Southwestern Atlantic reefs may serve as climate change refugia, highlighting the need to identify areas that are priorities for protection against local disturbances within the region (Mies et al., 2020).

## 2. Materials and methods

In July 2020, we performed a 10-day expedition to the RCB to identify the shallow (20-30 m) and upper mesophotic (30-75 m) benthic macrohabitats and associated fish, macroinvertebrate and macroalgae assemblages. The cruise worked from the outer shelf towards the shore, performing six navigation transects parallel to the coast. Within these transects, 67 stations were assessed at depths between 20 and 75 m. At each station, during daylight, a GoPro Hero 7 dropcam inside an underwater case (Croma®, custom-made) and attached to a rectangular steel frame (1.5 m-long structure, 8 kg) was lowered until reaching the bottom. The dropcam recorded images during descent and ascent and was laid resting on the bottom for 2 min before retrieval. A single deployment was performed for each station. An EchoMap Plus 42cv GPS connected to a GT20-TM transducer recorded geographical coordinates and depth. After the footage was retrieved from the camera, macrohabitats were described and a census of observed organisms during each 2-min-long video was performed.

Presence-absence data for fishes, invertebrates and macroalgae were used to create biotope (*sensu* Olenin and Ducrotoy, 2006) classifications using multivariate analyses in Primer 6 + Permanova software (Clarke et al., 2014). Biotopes were grouped under a 25% Sørensen-Dice similarity after a UPGMA hierarchical agglomerative cluster analysis. Similarity Percentages (SIMPER) analysis was used to rank the most relevant species present in each biotope. Rhodolith bed (see Results section) coverage was visually estimated from the video footage and classified into four broad categories (adapted from Matsuda and Iryu, 2011; Rocha et al., 2020): sparse (1–25% bottom cover), moderately dense (25–50%), dense (50–75%) and very dense (75–100%).

# 3. Results

Four macrohabitats were identified in the shallow areas of the RCB (Videos S1-S8): rhodolith beds, macroalgal forests, calcareous sand deposits and coral reefs (Fig. 1). Most of the surveyed sites (84%) were composed of flat rhodolith beds (unidentified species), ranging from very sparse to very dense (Fig. 2). Fourteen of the rhodolith-dominated sites presented turf assemblages composed of cyanobacterial and/or other algal mats in the surroundings, visually similar to those previously recorded for the Abrolhos Bank (Coni et al., 2017) and elsewhere (Ford et al., 2018). Forty of the sites dominated by rhodolith beds were interspersed with macroalgal forests, largely composed of Sargassum spp. and Dictyota spp. The outer RCB shelf is characterized by macroalgal forests associated with dense rhodolith beds, but the density of both rhodolith and macroalgae decline coastwards (Fig. 2). Fine white sand deposits, likely of calcareous origin, were observed in 10 sites, and a single coral reef site was detected in the internal shelf near the northern border of the bank (station 59). Largely built by Montastraea cavernosa colonies, this small reef was found at 37 m surrounded by a dense Sargassum spp. forest. Some of the colonies were severely bleached (Fig. 1D). Additional tridimensional features suggestive of coral reefs were detected in the background of some of the other surveyed sites, but their presence could not be confirmed.

Supplementary video related to this article can be found at htt ps://doi.org/10.1016/j.ecss.2021.107363

Eighty-three species were identified (Table 1), including 36 fishes, three reef-building corals (Montastraea cavernosa, Mussismilia hispida and Siderastrea stellata), and 26 macroalgae (most species could be only identified at genus level), including Laminaria cf. abyssalis at sporophyte stage. Sponges were abundant in several rhodolith sites, and nine different morphotypes were detected. Agglutinated rhodolith mounds associated with the sand tilefish Malacanthus plumieri were also frequent. The lowest species richness was observed in the calcareous sand sites, in some of which no species were detected (Table S1). The Montastraea cavernosa-dominated coral reef site displayed the highest diversity (N = 34 species) for a single station. Nineteen of the 36 fish species were found at this site, 11 of which were not found in any of the other 66 sites. This included the only two parrotfish species observed, Scarus trispinosus and Sparisoma axillare (including terminal phase individuals). A total of eight Southwestern Atlantic endemic species were detected at the RCB, of which six were fishes (Chromis jubauna, Elacatinus figaro, Haemulon squamipinna, Scarus trispinosus, Sparisoma axillare and T. noronhanum), one coral (Mussismilia hispida) and one alga (Laminaria cf. abyssalis). Three of the fish species detected (Epinephelus morio, Scarus trispinosus and Sparisoma axillare) are currently classified as either endangered or vulnerable in the Brazilian red list (ICMBio, 2018) and the global International Union for Conservation of Nature red list (IUCN, 2020).

Five biotopes were identified through cluster analysis (Fig. 3). Macroalgae were responsible for defining four of these biotopes (SIMPER analysis). Dense and diverse phaeophycean assemblages attached to rhodolith beds defined Groups 1 and 2; these algae dominated most of the RCB, defining 53 stations. Phaeophytes (*Sargassum* spp., *Padina* sp. and *Laminaria* cf. *abyssalis*) dominate Group 1, with the occurrence of the triggerfish *Balistes vetula* and large sponges.



**Fig. 1.** The four macrohabitats identified during a survey in the Royal Charlotte Bank, a 7000-km<sup>2</sup> area located 100 km to the north of the Abrolhos Bank in the South American continental shelf in the South Atlantic: dense rhodolith beds (A), macroalgal forests associated with rhodoliths (**B**), calcareous sand deposits (**C**), and coral reefs (**D**). The latter are composed of the reef-building coral *Montastraea cavernosa* and some colonies display white coloration associated with severe bleaching.

Unidentified Ectocarpaceae and *Dictyota* sp. characterized Group 2 together with the occurrence of the wrasse *Halichoeres dimidiatus* and the tilefish *Malacanthus plumieri* in five stations clumped in an area near the slope of the northeastern RCB. Two stations near the northern slope of the RCB devoid of fleshy macroalgae formed Group 3 and had the notable presence of large sponges, corals and the ubiquitous *B. vetula*. The presence of various and unidentified phaeophyceans, *Stypopodium* sp., *Padina* sp. and turf characterized Group 4, which occurred in five stations nearest the coast. Four stations in the southern RCB, near sandy areas, were dominated by turf algae, characterizing Group 5. Station 59, where the coral reef was identified, formed a unique biotope and did not group with any of the remaining groups described above. Two stations located in calcareous sand areas registered less than two species (station 41) or did not register any organism (station 45).

#### 4. Discussion

Despite previous modeling investigations suggesting that this area was likely diverse (Carvalho et al., 2020), the only biological information available for the RCB and its surroundings until now were reports of fisheries activity (Costa et al., 2003; Fonteles-Filho, 2007; Freitas et al., 2011; Previero and Gasalla, 2020) and two records of coral species collected during an oceanographic cruise (*Ellisella elongata* and *Siderastrea stellata* – Castro et al., 2006). This study produced the first images and diversity assessment for macroorganisms and macrohabitats associated with the RCB. Our findings show that the RCB is a large and diverse tropical rhodolith bed and the third-largest in the South Atlantic, only behind the Abrolhos Bank and the Great Amazon Reef System (Amado-Filho et al., 2012; Francini-Filho et al., 2018).

Rhodolith beds are extensive areas covered with non-geniculate coralline rhodophytes that form free-living "boulder-like" structures (Bossellini and Ginsburg, 1971; Bosence, 1983; Foster, 2001). They usually require intense hydrodynamic conditions to develop to prevent burial by fine particles (Foster et al., 1997; Marrack, 1999). The Brazil Current flows over the RCB and provides intense motion and removes

suspended sediments, thus creating ideal conditions for rhodolith development (Soutelino et al., 2013). The massive presence of rhodoliths at the RCB solves a missing piece of the puzzle on the Southwestern Atlantic continental shelf. Together with large rhodolith beds at the Amazon-Orinoco Plume, Abrolhos, the northeastern and southeastern coasts, the RCB is part of a nearly continuous rhodolith bed extending for more than 4,000 km in latitude in the South American outer shelf (Kempf, 1970; Riul et al., 2009; Amado-Filho et al., 2012; Horta et al., 2016: Moura et al., 2016). This reinforces that rhodolith beds stand out as a major feature of South Atlantic continental shelf environments and are large carbonate biofactories (Amado-Filho et al., 2012; Carvalho et al., 2020). Since they constitute a large and consolidated substrate environment, rhodolith beds may also serve as key areas for sustaining gene flow and demographic connectivity among different benthic environments within continental shelves (Moura et al., 2013, 2021; Amado-Filho et al., 2016), possibly connecting shallow and mesophotic reefs.

RCB rhodolith beds were largely associated with macroalgal forests. This kind of environment engages in intensive primary production (Bruno et al., 2005) and typically harbors a diverse and specific phytal community composed of small crustaceans and other invertebrates associated with the algal fronds (Gee and Warwick, 1994; Cunha et al., 2013; Thiriet et al., 2016). Also, macroalgal forests are important nursery habitats for the reproduction, feeding and shelter of several larger fish and invertebrate species (Wells and Rooker, 2004; Eggertsen et al., 2017). The presence of Laminaria cf. abyssalis should also receive major attention, considering that this organism is among the most severely threatened marine plants in the Atlantic Ocean (Wernberg et al., 2019). This species had not been detected north of Espírito Santo State before; therefore, our findings expand its known distribution in approximately 500 km. It has been reported that the abundance and biomass of macroalgal forests may vary seasonally in Southwestern Atlantic rhodolith beds and coral reefs (Costa et al., 2002; Pascelli et al., 2013). Therefore, the RCB macroalgal forests may likely undergo significant structural changes throughout the year, and it is unclear



Fig. 2. Macrohabitat map for the Royal Charlotte Bank, located in the South American continental shelf. Four different macrohabitats were described: rhodolith beds (ranging from very sparse to very dense), macroalgal forests (associated with the rhodolith beds), calcareous sand deposits and a coral reef.

#### Table 1

Species richness (refer to Table S1 for full list) for the four macrohabitat types (rhodolith beds, macroalgal forests, calcareous sand deposits and coral reefs) found during the survey of 67 stations at the Royal Charlotte Bank in the Southwestern Atlantic Ocean.

Macrohabitat	Number of stations and relative percentage	Richness			
		Fish	Macroalgae	Other organisms	Total
Rhodolith beds	16 (0.24)	16	15	11	42
Rhodolith beds with macroalgal forests	40 (0.60)	13	23	15	51
Calcareous sand deposits	10 (0.15)	8	12	0	20
Coral reefs	1 (0.01)	19	10	4	34
All macrohabitats	67 (1.00)	36	26	21	83

whether we documented them at a stage of high or low biomass.

A single coral reef site was found at the RCB, although several colonies of reef-building species were detected in rhodolith-dominated sites. At 37 m, this reef site was built primarily by Montastraea cavernosa, a species that often predominates in shallow turbid reefs and deeper mesophotic reefs in the Southwestern Atlantic (Francini-Filho et al., 2013). Although it is a single site, the biodiversity was much higher than the surroundings. The tridimensional structural complexity of coral reefs provides shelter, food sources, and nesting sites, increasing niche partitioning and specialization (Roberts and Ormond, 1987; Graham and Nash, 2013). There are likely more coral reefs in the RCB that went undetected during our survey. Therefore, further expeditions devoted to assessing coral reef presence in the RCB are required. The CaCO<sub>3</sub>-rich bottom associated with the rhodoliths may serve as a cue for the larval settlement and recruitment of reef-building corals (Negri et al., 2001; Ritson-Williams et al., 2010), thus facilitating coral reef formation. Rhodolith beds are also an important successional stage for the early formation of coral reefs, largely due to the mounds produced by Malacanthus plumieri, which were widely detected in the RCB, along



Biotope	Average similarity	Taxonomic unit	Frequency of occurrence	Contribution %	Cumulative contribution %
	I	1			
Group 1	Avg. sim.: 41.23	Turf	0.90	32.0	32.0
		Sargassum sp.	0.75	23.5	55.6
	N = 48 stations	Padina sp.	0.50	10.8	66.4
		Balistes vetula	0.48	7.5	73.9
		Laminaria cf. abyssalis	0.33	5.4	79.3
		Porifera	0.38	5.2	84.5
		Dictyota sp.	0.38	5.1	89.6
		Stypopodium sp.	0.31	3.7	93.2
Group 2	Avg. sim.: 39.31	Ectocarpaceae NI	1	87.9	87.9
	U U	Dictyota sp.	0.4	4.2	92.2
	N = 5 stations	Halichoeres dimidiatus	0.4	3.9	96.1
		Malacanthus plumieri	0.4	3.9	100.0
Group 3	Avg. sim.: 46.15	Balistes vetula	1	33.3	33.3
1	U	Scleractinia	1	33.3	66.7
$\bigcirc$	N = 2 stations	Sponge	1	33.3	100.0
Group 4	Avg sim · 54 43	Phaeophyceae spp (PNI)	1	61.6	61.6
Group /	110g. 5111. 5 1. 15	Stypopodium sp	0.6	21.5	83.1
	N = 5 stations	Turf	0.6	13.6	96.7
	it 5 stations	Padina sp.	0.4	3.4	100.0
Group 5	Avg. sim.: 40.60 N = 4 stations	Turf	1.00	100.0	100.0
Ungrouped stations*:	Station 59 Station 41 Station 45	Coral Reef Calcareous sand w/ <i>Padina</i> sp Bare calcareous sand	L.		

Fig. 3. Map of the Royal Charlotte Bank in the Southwestern Atlantic showing the biotope classification after cluster analysis (UPGMA). Legend shows the species that most contributed for each biotope classification after SIMPER (Similarities Percentages) analysis; groups share at least 25 Bray-Curtis similarity. (\*): ungrouped stations with unique biotic (station 59) or richness lower than 2 species stations 41 and 45).

with the binding action of sponges and other invertebrates (see Pereir-a-Filho et al., 2015a,b).

A total number of 83 species was recorded for the RCB. In general, the biodiversity observed in the RCB is very similar to that of the

Abrolhos Bank and other Southwestern Atlantic reef hotspots (Dutra et al., 2006). However, the true RCB biodiversity is certainly much higher than our assessment because of our relatively low sampling effort and because visual surveys greatly underestimate diversity (Willis,

2001). For instance, this technique will not detect the cryptofauna, an important component that comprises most of the animal diversity in rhodolith beds, macroalgal forests and coral reefs (De Grave and Whi-taker, 1999; Leray and Knowlton, 2015). Future efforts including the collection of biological samples are essential to confirm species identification and to assess components of biodiversity of the RCB overlooked in this study.

The fauna detected in the RCB also displays high trophic diversity, which is an important trait for sustaining environmental stability and resilience (Petchey and Gaston, 2006). Among fish, we detected carnivores, cleaners, herbivores, and corallivores (e.g., *Balistes vetula, Elacatinus figaro, Sparisoma axillare* and *Chaetodon striatus*, respectively), among others. The presence of several terminal-phase *S. axillare* individuals, rarer at Abrolhos suggests that the RCB is a potential spawning ground for fish species (see Francini-Filho et al., 2008). Also, there is evidence that rhodolith beds are important for macroalgal reproduction and may serve as seed banks (Fredericq et al., 2019).

The RCB may be already undergoing the impacts of multiple stressors. The coral reef site displayed intense bleaching symptoms, usually triggered by global warming (Glynn, 1993; Hughes et al., 2018). Bleaching is, in most cases, associated with shallow areas (<20 m -Donner et al., 2017). Therefore deeper reefs are usually considered safer from this kind of impact (Glynn, 1996). However, the low turbidity found at the RCB means that light and heat may reach deeper areas and produce impacts similar to those in shallow reefs (Cacciapaglia and van Woesik, 2016). Furthermore, we detected cyanobacterial mats, which are also present at similar isobaths at Abrolhos (R. B. Francini-Filho, unpubl. data). These are often associated with warmer waters and may overgrow and reduce benthic fauna cover (Coni et al., 2017; Ford et al., 2018). Although our expedition was performed during austral winter, we observed three phenomena that are usually associated with warmer conditions: coral bleaching, cyanobacterial mats, and the sporophytic stage of Laminaria cf. abyssalis (usually only found during summer - see Yoneshigue-Valentin, 1990). Although the temperature and oceanographic conditions surrounding these mesophotic rhodolith beds at the RCB are poorly understood, the area is likely undergoing the influence of heat waves (Teixeira et al., 2019). Besides global warming, the RCB is also under intense fishing pressure, with comprehensive stock assessments and fisheries impacts still lacking. Lobster fisheries in the region date back to the 1970's (Fonteles-Filho, 2007) and local fishermen currently reported 252 sites within the RCB associated with lobster fishing (data not shown). In addition to harming the rhodoliths due to weighted nets, this activity often produces bycatch (Steller et al., 2003; Brock and Ward, 2004; Rendina et al., 2020). This is supported by the historical lobster fisheries activity in the area (Fonteles-Filho, 2007). Therefore, evaluations of the status of fish stocks in the RCB are urgently needed. It has also been recently suggested that fisheries activity at the RCB has affected whale shark populations (Barbosa-Filho et al., 2016). Thus, the combined impacts of climate change and fisheries on the RCB may require conservation measures, especially considering the presence of both endemic and endangered species.

#### 5. Conclusions

Our findings show that the RCB is a complex and diverse ecosystem formed by rhodolith beds, macroalgae forests and coral reefs. This first assessment already detected signs of anthropogenic impacts, but there are still no marine protected areas in the RCB. Until now, the lack of biological data meant that the RCB did not rank among priority areas for conservation in the Southwestern Atlantic (Magris et al., 2020; Vilar et al., 2020). Our findings may help to fill this gap in future spatial conservation planning efforts for the Southwestern Atlantic Ocean.

#### Author contributions

FN, CHFL, AB, ENC, CBC, RJSD, FMG, AZG, MM, DOP, PYGS planned

and/or organized the expedition; FN, CHFL, THM collected field data; RTSC, RJSD, TMCL, MMM, PYGS contributed with infrastructure/material/technical support; FN, RBFF, AZG, BH, PAH, MM, KPS processed and analyzed the data; and all authors contributed to the manuscript.

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# Declaration of competing interest

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

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#### Appendix A. Supplementary data

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#### References

- Amado-Filho, G.M., Moura, R.L., Bastos, A.C., Francini-Filho, R.B., Pereira-Filho, G.H., Bahia, R.G., Moraes, F.C., Motta, F.S., 2016. Mesophotic ecosystems of the unique South Atlantic atoll are composed by rhodolith beds and scattered consolidated reefs. Mar. Biodivers. 46, 933–936.
- Amado-Filho, G.M., Moura, R.L., Bastos, A.C., Salgado, L.T., Sumida, P.Y.G., Güth, A.Z., Francini-Filho, R.B., Pereira-Filho, G.H., Abrantes, D.P., Brasileiro, P.S., Bahia, R.G., Leal, R.N., Kaufman, L., Kleypas, J.A., Farina, M., Thompson, F.L., 2012. Rhodolith beds are major CaCO3 bio-factories in the tropical South West Atlantic. PloS One 7, e35171.
- Barbosa-Filho, M.L., Tavares, D.C., Siciliano, S., de Moura, J.F., Costa-Neto, E.M., dos Santos Motta, F., Koike, C.D.V., 2016. Interactions between whale sharks, *Rhincodon typus* Smith, 1928 (Orectolobiformes, Rhincodontidae), and Brazilian fisheries: the need for effective conservation measures. Mar. Pol. 73, 210–215.
- Bosence, D.W.J., 1983. The Occurrence and Ecology of Recent Rhodoliths a Review. In: Peryt, T.M. (Ed.), Coated Grains. Springer, Berlin, pp. 225–242.
- Bossellini, A., Ginsburg, R.N., 1971. Form and internal structure of recent algal nodules (rhodolites) from Bermuda. J. Geol. 79, 669–682.
- Brasileiro, P.S., Pereira-Filho, G.H., Bahia, R.G., Abrantes, D.P., Guimarães, S.M., Moura, R.L., Francini-Filho, R.B., Bastos, A.C., Amado-Filho, G.M., 2016. Macroalgal composition and community structure of the largest rhodolith beds in the world. Mar. Biodivers. 46, 407–420.
- Brock, D.J., Ward, T.M., 2004. Maori octopus (*Octopus maorum*) bycatch and southern rock lobster (*Jasus edwardsii*) mortality in the South Australian lobster fishery. Fish. Bull. 102, 430–440.
- Bruno, J.F., Boyer, K.E., Duffy, J.E., Lee, S.C., Kertesz, J.S., 2005. Effects of macroalgal species identity and richness on primary production in benthic marine communities. Ecol. Lett. 8, 1165–1174.
- Cacciapaglia, C., van Woesik, R., 2016. Climate-change refugia: shading reef corals by turbidity. Global Change Biol. 22, 1145–1154.
- Carvalho, V.F., Assis, J., Serrão, E.A., Nunes, J.M., Anderson, A.B., Batista, M.B., Barufi, J.B., Silva, J., Pereira, S.M., Horta, P.A., 2020. Environmental drivers of rhodolith beds and epiphytes community along the South Western Atlantic coast. Mar. Environ. Res. 154, 104827.
- Castro, C.B., Pires, D.O., 2001. Brazilian coral reefs: what we already know and what is still missing. Bull. Mar. Sci. 69, 357–371.
- Castro, C.B., Pires, D.O., Medeiros, M.S., Loiola, L., Arantes, R.C.M., Thiago, C.M., Berman, E., 2006. Capítulo 4 - Filo Cnidaria. In: Lavrado, H.P., Ignacio, B.L. (Eds.), Biodiversidade bentônica da região central da Zona Econômica Exclusiva brasileira, vol. 18. Museu Nacional, Série Livros n., Rio de Janeiro, pp. 147–192.
- Castro, C.B., Zilberberg, 2016. Recifes brasileiros: sua importância e conservação. In: Zilberberg, C., Abrantes, D.P., Marques, J.A., Machado, L.F., Marangoni, L.F.B. (Eds.), Conhecendo os Recifes Brasileiros: Rede de Pesquisas Coral Vivo. Museu Nacional, UFRJ, Rio de Janeiro, pp. 17–26.
- Coni, E.O., Ferreira, C.M., Meirelles, P.M., Menezes, R., Santana, E.F., Moreira, A.P., Amado-Filho, G.M., Ferreira, B.P., Pereira-Filho, G.H., Thompson, F.L., Moura, R.L.,

#### F. Negrão et al.

Francini-Filho, R.B., 2017. Modeling abundance, growth, and health of the solitary coral Scolymia wellsi (Mussidae) in turbid SW Atlantic coral reefs. Mar. Biol. 164, 66.

Cordeiro, R.T.S., Neves, B.M., Rosa-Filho, J.S., Pérez, C.D., 2015. Mesophotic coral ecosystems occur offshore and north of the Amazon River. Bull. Mar. Sci. 91, 491–510.

- Costa Jr., O.S., Attrill, M.J., Pedrini, A.G., de Paula, J.C., 2002. Spatial and seasonal distribution of seaweeds on coral reefs from Southern Bahia, Brazil. Bot. Mar. 45, 346–355.
- Costa Jr., O.S., Leão, Z.M.A.N., Nimmo, M., Attrill, M.J., 2000. Nutrification impacts on coral reefs from northern Bahia, Brazil. Hydrobiologia 440, 307–315.
- Costa, P.A., Braga, A.C., Rocha, L.O.F., 2003. Reef fisheries in Porto Seguro, eastern Brazilian coast. Fish. Res. 60, 577–583.

Cruz Motta, J.J., Miloslavich, P., Guerra-Castro, E., Hernández-Agreda, A., Herrera, C., Barros, F., Navarrete, S.A., Sepúlveda, R.D., Glasby, T.M., Bigatti, G., Cardenas-Calle, M., Carneiro, P.B.M., Carranza, A., Flores, A.A.V., Gil-Kodaka, P., Gobin, J., Gutiérrez, J.L., Klein, E., Krull, M., Lazarus, J.F., Londoño-Cruz, E., Lotufo, T., Macaya, E.C., Mora, C., Mora, E., Palomo, G., Parragué, M., Pellizzari, F., Retamales, R., Rocha, R.M., Romero, L., 2020. Latitudinal patterns of species diversity on South American rocky shores: local processes lead to contrasting trends in regional and local species diversity. J. Biogeogr. 47, 1966–1979.

- Cunha, T.J., Güth, A.Z., Bromberg, S., Sumida, P.Y.G., 2013. Macrofauna associated with the brown algae *Dictyota* spp. (Phaeophyceae, Dictyotaceae) in the Sebastião Gomes reef and Abrolhos Archipelago, Bahia, Brazil. Continent. Shelf Res. 70, 140–149.
- De Grave, S., Whitaker, A., 1999. Benthic community re-adjustment following dredging of a muddy-maerl matrix. Mar. Pollut. Bull. 38, 102–108.

Donner, S.D., Rickbeil, G.J.M., Heron, S.F., 2017. A new, high-resolution global mass coral bleaching database. PloS One 12, e0175490.

- Dutra, G.F., Allen, G.R., Werner, T., McKenna, S.A., 2006. A Rapid Marine Biodiversity Assessment of the Abrolhos Bank, Bahia, Brazil. RAP Bulletin of Biological Assessment, vol. 38. Conservation International, Washington, DC, USA.
- Eggertsen, L., Ferreira, C.E.L., Fontoura, L., Kautsky, N., Gullström, M., Berkström, C., 2017. Seaweed beds support more juvenile reef fish than seagrass beds in a southwestern Atlantic tropical seascape. Estuar. Coast Shelf Sci. 196, 97–108.

Fainstein, R., Summerhayes, C.P., 1982. Structure and origin of marginal banks off Eastern Brazil. Mar. Geol. 46, 199–215.

- Floeter, S.R., Rocha, L.A., Robertson, D.R., Joyeux, J.-C., Smith-Vaniz, W.F., Wirtz, P., Edwards, A.J., Barreiros, J.P., Ferreira, C.E.L., Gasparini, J.L., Brito, A., Falcón, J.M., Bowen, B.W., Bernardi, G., 2008. Atlantic reef fish biogeography and evolution. J. Biogeogr. 35, 22–47.
- Fonteles-Filho, A.A., 2007. Síntese sobre a lagosta-vermelha (*Panulirus argus*) e a lagosta-verde (*Panulirus laevicauda*). In: Haimovic, M. (Ed.), A prospecção pesqueira e abundância de estoques marinhos no Brasil nas décadas de 1960 a 1990: levantamento de dados e avaliação crítica. Ministério do Meio Ambiente, Brasília, pp. 257–265.
- Ford, A.K., Bejarano, S., Nugues, M.M., Visser, P.M., Albert, S., Ferse, S.C., 2018. Reefs under siege—the rise, putative drivers, and consequences of benthic cyanobacterial mats. Frontiers in Marine Science 5, 18.
- Foster, M.S., 2001. Rhodoliths: between rocks and soft places. J. Phycol. 37, 659–667.
- Foster, M.S., Riosmena-Rodriguez, R., Steller, D.L., Woelkerling, W.J., 1997. Living rhodolith beds in the Gulf of California and their implications. In: Johnson, M.E., Ledesma-Vázquez, J. (Eds.), Pliocene Carbonates and Related Facies Flanking the Gulf of California, Baja California, Mexico. Geological Society of America, pp. 127–139.
- Francini-Filho, R.B., Asp, N.E., Siegle, E., Hocevar, J., Lowyck, K., D'Avila, N., Vasconcelos, A.A., Baitelo, R., Rezende, C.E., Omachi, C.Y., Thompson, C.C., Thompson, F.L., 2018. Perspectives on the Great Amazon reef: extension, biodiversity, and threats. Frontiers in Marine Science 5, 142.
- Francini-Filho, R.B., Coni, E.O.C., Meirelles, P.M., Amado-Filho, G.M., Thompson, F.L., Pereira-Filho, G.H., Bastos, A.C., Abrantes, D.P., Ferreira, C.M., Gibran, F.Z., Güth, A. Z., Sumida, P.Y.G., Oliveira, N.L., Kaufman, L., Minte-Vera, C.V., Moura, R.L., 2013. Dynamics of coral reef benthic assemblages of the Abrolhos Bank, Eastern Brazil: inferences on natural and anthropogenic drivers. PloS One 8, e54260.

Francini-Filho, R.B., Moura, R.L., Ferreira, C.M., Coni, E.O., 2008. Live coral predation by parrotfishes (Perciformes: Scaridae) in the Abrolhos Bank, eastern Brazil, with comments on the classification of species into functional groups. Neotrop. Ichthyol. 6, 191–200.

Fredericq, S., Krayesky-Self, S., Sauvage, T., Richards, J., Kittle, R., Arakaki, N., Hickerson, E., Schmidt, W.E., 2019. The critical importance of rhodoliths in the life cycle completion of both macro-and microalgae, and as holobionts for the establishment and maintenance of marine biodiversity. Frontiers in Marine Science 5, 502.

Freitas, M.O., Moura, R.L., Francini-Filho, R.B., Minte-Vera, C.V., 2011. Spawning patterns of commercially important reef fish (Lutjanidae and Serranidae) in the tropical western South Atlantic. Sci. Mar. 75, 135–146.

Gee, J.M., Warwick, R.M., 1994. Metazoan community structure in relation to the fractal dimensions of marine macroalgae. Mar. Ecol. Prog. Ser. 103, 141–150.

Ghisolfi, R.D., Silva, M.P., Santos, F.T., Servino, R.N., Cirano, M., Thompson, F.L., 2015. Physical forcing mechanisms controlling the variability of chlorophyll-a over the Royal-Charlotte and Abrolhos banks — eastern Brazilian shelf. PloS One 10 e0117082.

Giglio, V.J., Luiz, O.J., Schiavetti, A., 2016. Recreational diver behavior and contacts with benthic organisms in the Abrolhos National Marine Park, Brazil. Environ. Manag. 57, 637–648. Glynn, P.W., 1996. Coral reef bleaching: facts, hypotheses and implications. Global Change Biol. 2, 495–509.

Graham, N.A., Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. Coral Reefs 32, 315–326.

- Horta, P.A., Riul, P., Amado-Filho, G.M., Gurgel, C.F., Berchez, F., Nunes, J.M.C., Scherner, F., Pereira, S., Lotufo, T., Peres, L., Sissini, M., Bastos, E.O., Rosa, J., Munoz, P., Martins, C., Gouvêa, L., Carvalho, V., Bergstrom, E., Schubert, N., Bahia, R.G., Rodrigues, A.C., Rörig, L., Barufi, J.B., Figueiredo, M., 2016. Rhodoliths in Brazil: Current knowledge and potential impacts of climate change. Braz. J. Oceanogr. 64, 117–136.
- 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 359, 80–83.

ICMBio, 2018. Livro vermelho da fauna brasileira ameaçada de extinção. Brasília, Brazil. IUCN, 2020. The IUCN Red List of Threatened Species. Version 2020-2. https://www. iucnredlist.org. (Accessed 9 July 2020).

- Kempf, M., 1970. Notes on the benchic bionomy of the N-NE Brazilian shelf. Mar. Biol. 5, 213–224.
- Leão, Z.M.A.N., Kikuchi, R.K.P., 2001. The Abrolhos reefs of Brazil. In: Seeliger, U., Kjerfve, B. (Eds.), Coastal Marine Ecosystems of Latin America. Springer-Verlag, Berlin, pp. 83–96.

Leão, Z.M.A.N., Kikuchi, R.K.P., Ferreira, B.P., Neves, E.G., Sovierzoski, H.H., Oliveira, M.D., Maida, M., Correia, M.D., Johnsson, R., 2016. Brazilian coral reefs in a period of global change: a synthesis. Braz. J. Oceanogr. 64, 97–116.

Leão, Z.M.A.N., Kikuchi, R.K.P., Testa, V., 2003. Corals and coral reefs of Brazil. In: Cortes, J. (Ed.), Latin American Coral Reefs. Elsevier, Amsterdam, pp. 9–52.

Leão, Z.M., Telles, M.D., Sforza, R., Bulhões, H.A., Kikuchi, R.K.P., 1996. Impact of tourism development on the coral reefs of the Abrolhos area. Brazil. Biological Conservation 2, 215–216.

Leray, M., Knowlton, N., 2015. DNA barcoding and metabarcoding of standardized samples reveal patterns of marine benthic diversity. Proceedings of the National Academy of Sciences USA 112, 2076–2081.

Magris, R.A., Costa, M.D., Ferreira, C.E., Vilar, C.C., Joyeux, J.C., Creed, J.C., Copertino, M.S., Horta, P.A., Sumida, P.Y., Francini-Filho, R.B., Floeter, S.R., 2020. A blueprint for securing Brazil's marine biodiversity and supporting the achievement of global conservation goals. Divers. Distrib. 27, 198–215.

Marrack, E.C., 1999. The relationship between water motion and living rhodolith beds in the southwestern Gulf of California, Mexico. Palaios 14, 159–171.

Matsuda, S., Iryu, Y., 2011. Rhodoliths from deep fore-reef to shelf areas around Okinawa-jima, Ryukyu Islands, Japan. Mar. Geol. 282, 215–230.

Mies, M., Francini-Filho, R.B., Zilberberg, C., Garrido, A.G., Longo, G.O., Laurentino, E., Güth, A.Z., Sumida, P.Y.G., Banha, T.N.S., 2020. South Atlantic coral reefs are major global warming refugia and less susceptible to bleaching. Frontiers in Marine Science 7, 514.

Moura, R.L., Abieri, M.L., Castro, G.M., Carlos-Júnior, L.A., Chiroque-Solano, P.M., Fernandes, N.C., Teixeira, C.D., Ribeiro, F.V., Salomon, P.S., Freitas, M.O., Gonçalves, J.T., Neves, L.M., Hackradt, C.W., Felix-Hackradt, F., Rolim, F.A., Motta, F.S., Gadig, O.B.F., Pereira-Filho, G.H., Bastos, A.C., 2021. Tropical rhodolith beds are a major and belittled reef fish habitat. Sci. Rep. 11, 794.

- Moura, R.L., Amado-Filho, G.M., Moraes, F.C., Brasileiro, P.S., Salomon, P.S., Mahiques, M.M., Bastos, A.C., Almeida, M.G., Silva Jr., J.M., Araujo, B.F., Brito, F.P., Rangel, T.P., Oliveira, B.C.V., Bahia, R.G., Paranhos, R.P., Dias, R.J.S., Siegle, E., Figueiredo Jr., A.G., Pereira, R.C., Leal, C.V., Hajdu, E., Asp, N.E., Gregoracci, G.B., Neumann-Leitão, S., Yager, P.L., Francini-Filho, R.B., Fróes, A., Campeão, M., Silva, B.S., Moreira, A.P.B., Oliveira, L., Soares, A.C., Araujo, L., Oliveira, N.L., Teixeira, J.B., Valle, R.A.B., Thompson, C.C., Rezende, C.E., Thompson, F.L., 2016. An extensive reef system at the Amazon River mouth. Science Advances 2, e1501252
- Moura, R.L., Secchin, N.A., Amado-Filho, G.M., Francini-Filho, R.B., Freitas, M.O., Minte-Vera, C.V., Teixeira, J.B., Thompson, F.L., Dutra, G.F., Sumida, P.Y.G., Guth, A.Z., Lopes, R.M., Bastos, A.C., 2013. Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. Continent. Shelf Res. 70, 109–117.
- Negri, A.P., Webster, N.S., Hill, R.T., Heyward, A.J., 2001. Metamorphosis of broadcast spawning corals in response to bacteria isolated from crustose algae. Mar. Ecol. Prog. Ser. 223, 121–131.
- Olenin, S., Ducrotoy, J.P., 2006. The concept of biotope in marine ecology and coastal management. Mar. Pollut. Bull. 53, 20–29.
- Omachi, C.Y., Asp, N.E., Siegle, E., Couceiro, M.A.A., Francini-Filho, R.B., Thompson, F. L., 2019. Light availability for reef-building organisms in a plume-influenced shelf. Continent. Shelf Res. 181, 25–33.

Pascelli, C., Riul, P., Riosmena-Rodríguez, R., Scherner, F., Nunes, M., Hall-Spencer, J. M., de Oliveira, E.C., Horta, P.A., 2013. Seasonal and depth-driven changes in rhodolith bed structure and associated macroalgae off Arvoredo island (southeastern Brazil). Aquat. Bot. 111, 62–65.

- Pereira-Filho, G.H., Cerqueira Veras, P., Francini-Filho, R.B., Moura, R.L., Pinheiro, H.T., Gibran, F.Z., Matheus, Z., Neves, L.M., Amado-Filho, G.M., 2015a. Effects of the sand tilefish *Malacanthus plumieri* on the structure and dynamics of a rhodolith bed in the Fernando de Noronha Archipelago, tropical West Atlantic. Mar. Ecol. Prog. Ser. 541, 65–73.
- Pereira-Filho, G.H., Francini-Filho, R.B., Pierozzi Jr., I., Pinheiro, H.T., Bastos, A.C., Moura, R.L., Moraes, F.C., Matheus, Z., Bahia, R.D., Amado-Filho, G.M., 2015b. Sponges and fish facilitate succession from rhodolith beds to reefs. Bull. Mar. Sci. 91, 45–46.

Glynn, P.W., 1993. Coral reef bleaching: ecological perspectives. Coral Reefs 12, 1-17.

#### F. Negrão et al.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.

- Picciani, N., Seiblitz, I.G.L., Paiva, P.C., Castro, C.B., Zilberberg, C., 2016. Geographic patterns of *Symbiodinium* diversity associated with the coral *Mussismilia hispida* (Cnidaria, Scleractinia) correlate with major reef regions in the Southwestern Atlantic Ocean. Mar. Biol. 163, 236.
- Pinheiro, H.T., Rocha, L.A., Macieira, R.M., Carvalho-Filho, A., Anderson, A.B., Bender, M.G., Di Dario, F., Ferreira, C.E.L., Figueiredo-Filho, J., Francini-Filho, R.B., Gasparini, J.L., Joyeux, J.-C., Luiz, O.J., Mincarone, M.M., Moura, R.L., Nunes, J.A. C.C., Quimbayo, J.P., Rosa, R.S., Sampaio, C.L.S., Sazima, I., Simon, T., Vila-Nova, D. A., Floeter, S.R., 2018. South-western Atlantic reef fishes: zoogeographical patterns and ecological drivers reveal a secondary biodiversity centre in the Atlantic Ocean. Divers. Distrib. 24, 951–965.
- Previero, M., Gasalla, M.A., 2020. Risk assessment of small-scale reef fisheries off the Abrolhos Bank: Snappers and groupers under a multidimensional evaluation. Fish. Manag. Ecol. 27, 231–247.
- Rendina, F., Ferrigno, F., Appolloni, L., Donnarumma, L., Sandulli, R., Fulvio Russo, G., 2020. Anthropic pressure due to lost fishing gears and marine litter on different rhodolith beds off the Campania Coast (Tyrrhenian Sea, Italy). Ecol. Quest. 31, 1–7.
- Ritson-Williams, R., Paul, V.J., Arnold, S.N., Steneck, R.S., 2010. Larval settlement preferences and post-settlement survival of the threatened Caribbean corals Acropora palmata and A. cervicornis. Coral Reefs 29, 71–81.
- Riul, P., Lacouth, P., Pagliosa, P.R., Christoffersen, M.L., Horta, P.A., 2009. Rhodolith beds at the easternmost extreme of South America: community structure of an endangered environment. Aquat. Bot. 90, 315–320.
- Roberts, C.M., Ormond, R.F., 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar. Ecol. Prog. Ser. 25, 1–8.
- Rocha, G.A., Bastos, A.C., Amado-Filho, G.M., Boni, G.C., Moura, R.L., Oliveira, N., 2020. Heterogeneity of rhodolith beds expressed in backscatter data. Mar. Geol. 423, 106–136.
- Soutelino, R.G., Gangopadhyay, A., Silveira, I.C., 2013. The roles of vertical shear and topography on the eddy formation near the site of origin of the Brazil Current. Continent. Shelf Res. 70, 46–60.

- Souza, J.N., Nunes, F.L., Zilberberg, C., Sanchez, J.A., Migotto, A.E., Hoeksema, B.W., Serrano, X.M., Baker, A.C., Lindner, A., 2017. Contrasting patterns of connectivity among endemic and widespread fire coral species (*Millepora* spp.) in the tropical Southwestern Atlantic. Coral Reefs 36, 701–716.
- Steller, D.L., Riosmena-Rodríguez, R., Foster, M.S., Roberts, C.A., 2003. Rhodolith bed diversity in the Gulf of California: the importance of rhodolith structure and consequences of disturbance. Aquat. Conserv. Mar. Freshw. Ecosyst. 13, S5–S20.
- Summerhayes, C.P., Melo, U., Barretto, H.T., 1976. The influence of upwelling on suspended matter and shelf sediments off southeastern Brazil. J. Sediment. Res. 46, 819–828.
- Teixeira, C.D., Leitão, R.L., Ribeiro, F.V., Moraes, F.C., Neves, L.M., Bastos, A.C., Pereira-Filho, G.H., Kampel, M., Salomon, P.S., Sá, J.A., Falsarella, L.N., Amario, M., Abieri, M.L., Pereira, R.C., Amado-Filho, G.M., Moura, R.L., 2019. Sustained mass coral bleaching (2016–2017) in Brazilian turbid-zone reefs: taxonomic, cross-shelf and habitat-related trends. Coral Reefs 38, 801–813.
- Thiriet, P.D., Di Franco, A., Cheminee, A., Guidetti, P., Bianchimani, O., Basthard-Bogain, S., Cottalorda, J.M., Arceo, H., Moranta, J., Lejeune, P., Francour, P., Mangialajo, L., 2016. Abundance and diversity of crypto-and necto-benthic coastal fish are higher in marine forests than in structurally less complex macroalgal assemblages. PloS One 11, e0164121.
- Vilar, C.C., Magris, R.A., Loyola, R., Joyeux, J.C., 2020. Strengthening the synergies among global biodiversity targets to reconcile conservation and socio-economic demands. Aquat. Conserv. Mar. Freshw. Ecosyst. 30, 497–513.
- Wells, R.J., Rooker, J.R., 2004. Spatial and temporal patterns of habitat use by fishes associated with *Sargassum* mats in the northwestern Gulf of Mexico. Bull. Mar. Sci. 74, 81–99.
- Wernberg, T., Krumhansl, K., Filbee-Dexter, K., Pedersen, M.F., 2019. Status and trends for the world's kelp forests. In: World Seas: an Environmental Evaluation. Academic Press, pp. 57–78.
- Willis, T.J., 2001. Visual census methods underestimate density and diversity of cryptic reef fishes. J. Fish. Biol. 59, 1408–1411.
- Yoneshigue-Valentin, Y., 1990. The life cycle of Laminaria abyssalis (Laminariales, Phaeophyta) in culture. In: Proceedings of the 13th International Seaweed Symposium, pp. 461–466.