



The southernmost Atlantic coral reef is off the subtropical island of Queimada Grande (24°S), Brazil

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ABSTRACT.—The Atlantic Ocean encompasses approximately 10% of the global carbonate reef area, but the austral limits of coral reef distribution within this basin are still unclear. The lack of reef area and distribution estimates clearly hampers marine spatial planning and management in several regions, especially in the southwestern Atlantic Ocean. In this area, significant freshwater, nutrient, and terrigenous sediment inputs constrain the detection of subtidal features by remote sensing. Here, we describe the coral reef of Queimada Grande Island (QGI) (24°S). The documented reef covers approximately 75,000 m² between depths of 7 and 12 m, forming a relatively flat-topped plateau that fringes the leeward (W) side of the island. The framework was built mainly by *M. decactis* colonies that were cemented in place by crustose coralline algae (CCA). This peculiar structure lays approximately 1000 km south of the Abrolhos reefs, within a tropical-subtropical transition zone, constituting the southernmost Atlantic carbonate reef built by corals already reported. Our data reveal the enormous scientific and biodiversity conservation value hidden at the coastal islands of the Brazilian Biogeographical Province. Despite the high levels of fisheries activities, we found living coral coverage similar to that of southwestern Atlantic Marine Protected Areas.

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Scleractinian corals (Cnidaria: Scleractinia) and crustose coralline algae (CCA) (Rhodophyta: Corallinales, Hapalidiales and Sporolithales) dominate modern reef-building in shallow tropical and subtropical waters (Stanley 2003). Such

wave-resistant coral accretions cover >280,103 km², yielding complex topographic and hydrodynamic regimes that support highly biodiverse and productive assemblages (Sheppard et al. 2009, Birkeland 2015). In addition to their reef-building role, coralline algae also form beds of free-living nodules (rhodoliths) that cover large, but as yet unknown, portions of the continental shelves and seamount tops in a wide latitudinal and depth range (Foster 2001, Amado-Filho et al. 2017). In the tropical southwestern Atlantic Ocean (SWA), rhodolith beds represent the most extensive biogenic hard bottom habitat, mineralizing more CaCO₃ than the topographically complex coral reefs (Amado-Filho et al. 2012).

Despite their ecological and socioeconomic relevance, shallow-water biogenic reefs are among the most threatened marine ecosystems. More than half of their area has already been severely degraded (Wilkinson and Souter 2008). The rapid global decline of coral ecosystems in the last five decades was driven by the additive and interacting forces of climate and anthropogenic stressors (Bruno and Valdivia 2016, Côté et al. 2016). However, even basic information about reef distribution, range, and large-scale morphological features is still missing for several regions, impeding effective marine spatial planning and management (Moura et al. 2013, 2016).

Nearly 90% of the world's shallow-water coral reefs are in the Indo-Pacific. The remaining 10% are within the much younger and species-poor Atlantic Ocean (Rabinowitz and Labrecque 1979, Stanley 2003), where significant reef building is recorded from Bermuda (approximately 32°30'N) southwards. However, the austral limits of reef-building in this basin are still unclear. The largest SWA reefs and rhodolith beds are located in the Abrolhos Bank, between 16°50'S and 19°40'S (Amado-Filho et al. 2012, 2017, Moura et al. 2013), where all reef-building corals from the Brazilian Province co-occur (Laborel 1960). Coral richness declines sharply moving southwards, with a single reef-building coral species at the southern limit (27°50'S) (Capel et al. 2012). From Abrolhos southward, the coast is dominated by crystalline rocky shores, estuaries, and sandy beaches, with hundreds of coastal islands that were gradually isolated from the mainland during the Pleistocene and Early Holocene.

Here, we describe a coralline reef that fringes Queimada Grande Island (QGI), on the southeastern coast of Brazil (24°S), which also presents a peripheral living rhodolith bed belt (depths of 15–20 m). This peculiar structure lays approximately 1000 km south of the Abrolhos reefs, within a tropical-subtropical transition zone, constituting the southernmost Atlantic carbonate reef built by corals already reported.

MATERIALS AND METHODS

SAMPLING AND HABITAT MAPPING.—Queimada Grande Island is located at 24°29'S and 46°40'W, approximately 32 km off the coastline of São Paulo State, in southeastern Brazil. Surveys of the coralline reef, as well as of the adjacent rhodolith bed, were carried out in March 2015 by scuba diving. Queimada Grande's reef habitats were mapped using measuring tapes, depth gauges, and compasses. Boundary waypoints were recorded using a GPS (Garmin eTrex) and plotted in a digital nautical chart where the area of the polygon was measured using the Blue Chart software. We classified the benthic landscape as three types: (1) rocky reef (intertidal to a depth of 12 m) formed by boulders covered by the coral *Mussismilia hispida* (Verrill, 1901); (2) coralline reef plateau (depths of 7–13 m) formed mainly by dead coalesced branches of the coral *Madracis decactis* (Lyman, 1859) and covered by living corals, sponges,

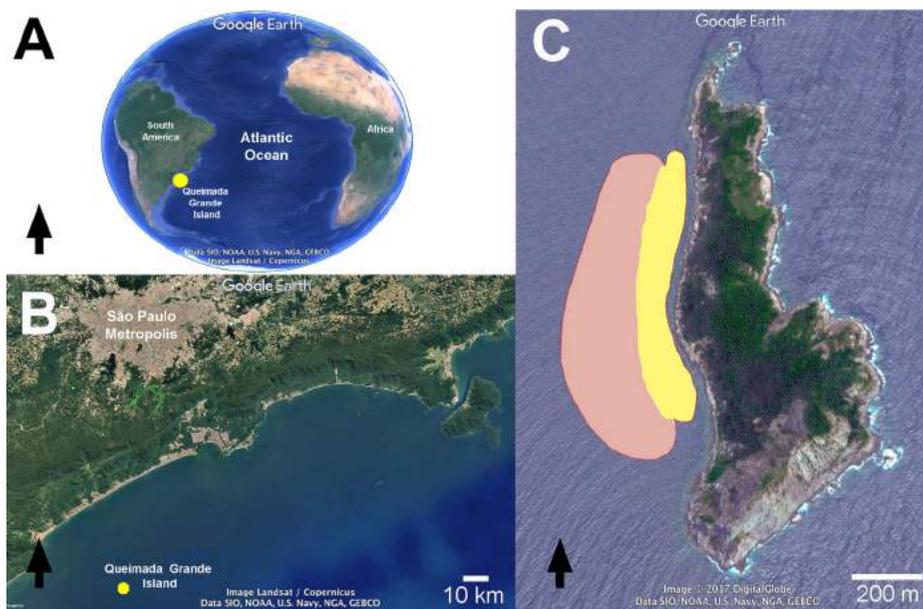


Figure 1. Queimada Grande Island's reefs. (A–B) Queimada Grande geographic position. (C) Coralline reef plateau built mainly by the coral *Madracis decactis* (yellow). Rhodolith beds (pink).

tunicates, and fleshy algae; and (3) rhodolith bed (depths of 12–20 m) formed by nucleated carbonate nodules generated mainly by the overgrowth of CCA on the coral *M. decactis* (Fig. 1).

STRUCTURE OF BENTHIC COMMUNITIES ASSOCIATED WITH THE CARBONATE REEFS.—To quantify the benthic assemblages on the carbonate reef, 90 photoquadrats, measuring 25 × 25 cm, were taken. Thirty photoquadrats were randomly distributed in three strata: (1) coralline reef plateau (depths of 7–12 m), (2) shallow rhodolith bed (depths of 12–15 m), and (3) deep rhodolith bed (depths of 15–20 m); totaling $n = 90$. Images were analyzed using the photoQuad software (Trygonis and Sini 2012). Twenty-five points were randomly generated per photoquadrat and organisms immediately below each point were identified to the highest taxonomic resolution possible, with taxon coverage expressed as percent values. Rhodolith density was also measured between 12 and 25 m using the same sized photoquadrats. To present values as rhodoliths per square meter (rhod m^{-2}), the number of rhodoliths per photoquadrat was multiplied by 16. To describe the rhodolith variables such as volume, diameter, and form, we sampled 50 rhodoliths from both rhodolith strata. Volume was obtained following Amado-Filho et al. (2007) and Riul et al. (2009), while the diameter measurement followed Steller et al. (2003). To classify and quantify the frequency of spheroidal, discoidal, and ellipsoidal shapes, rhodolith measurements were inserted into a tri-plot sheet according to Graham and Midgley (2000). The rhodoliths' diameter, volume, and density were compared between strata using a t -test.

IDENTIFICATION OF RHODOLITH-FORMING ALGAE.—The main morphotypes of rhodolith-forming non-geniculate coralline algae were sampled and identified based on vegetative and reproductive characteristics according to Penrose and Woelkerling

(1991), Irvine and Chamberlain (1994), Harvey and Woelkerling (2007), Villas-Boas et al. (2009), Amado-Filho (2010), and Athanasiadis and Ballantine (2014). Vouchers (including microscope slides) of representative specimens were deposited at the Herbarium of the Rio de Janeiro Botanical Garden (RB), Brazil.

RESULTS

The coralline reef recorded at QGI covers approximately 75,000 m² between depths of 7–12 m, forming a relatively flat-topped plateau that fringes the leeward (W) side of the island (Fig. 1). The framework was built mainly by *M. decactis* colonies that were cemented in place by CCA. Transversally, the reef reaches a height of approximately 0.5 m (Fig. 2A) and its top (i.e., coralline reef plateau) is covered by turf geniculate coralline algae *Jania* and *Amphiroa* [mean = 27.5% (SE 1.8%)], followed by fleshy algae *Dictyota mertensii* (Mart.) Kütz. [14.0% (SE 1.4%)] and *Canistrocarpus cervicornis* (Kütz.) De Paula & De Clerck [12.5% (SE 1.6%)], the zoantharian *Palythoa caribaeorum* (Duchassaing and Michelotti, 1860) [13.0% (SE 2.1%)], turfs composed of small (i.e., <3 cm) filamentous algae [6.8% (SE 2.0%)], and the scleractinian coral *M. hispida* [5.8% (SE 1.0%)]. While *M. decactis* is the most important reef builder, this species covers only 0.5% (SE 0.1%) of the current coralline reef plateau (Figs. 2B–D, 3).

There is a rhodolith bed associated with the coralline reef that covers an area approximately 250,000 m², bordering the deepest sections of the reef and spreading outwards from the island (Fig. 1). Rhodoliths are formed by five species of non-geniculate coralline algae, namely, *Melyvonnea erubescens* (Foslie) Athanasiadis & D.L.Ballantine (RB 772554), *Phymatolithon calcareum* (Pallas) W.H.Adey & D.L.McKibbin (RB 772555, 772556, 772557, 772561), *Lithothamnion muelleri* Lenorm. ex Rosanoff (RB 772558), *Pneophyllum* sp. (RB 772559, RB 772560), and *Lithophyllum* sp. (RB 772562), growing over *M. decactis* fragments that eroded from the reef (Fig. 2E).

Rhodoliths from depths of 12–15 m displayed diameters and volumes 1.6 and 3.1 times lower than those sampled at depths of 15–25 m. In contrast, density was 1.4 times higher in rhodoliths from the shallower strata (Figs. 4A–C). Rhodoliths from both sampled depths are mainly spheroidal and ellipsoidal in shape (Fig. 4D). The most abundant benthic taxa in rhodolith beds from 12 to 15 m are epiphyte-free CCA (i.e., bare rhodoliths), turf, and *P. caribaeorum* [27.3% (SE 0.5%), 17.5% (SE 2.5%), and 15.7% (SE 3.2%); respectively]. Turf [30.7% (SE 2.8%)], CCA [19.6% (SE 0.5%)], and the algae *C. cervicornis* [19.1% (SE 2.1%)] are the main organisms covering the rhodoliths from the 15–20 m depth stratum. Finally, we also detected an initial stage of the invasive coral *Tubastrea* spp. in the subvertical artificial structures of the wreck of the “Tocantins.”

DISCUSSION

Biogenic carbonates cover wide expanses of the tropical SWA shelf (Amado-Filho et al. 2017). These benthic habitats are classified as rhodolith beds and coral reefs and comprise the largest and most highly diverse area of reefs in the SW Atlantic Ocean (Amado-Filho and Pereira-Filho 2012, Moura et al. 2013, Leão et al. 2016, Amado-Filho et al. 2017). Here, we revealed the occurrence of an unnoticed coral

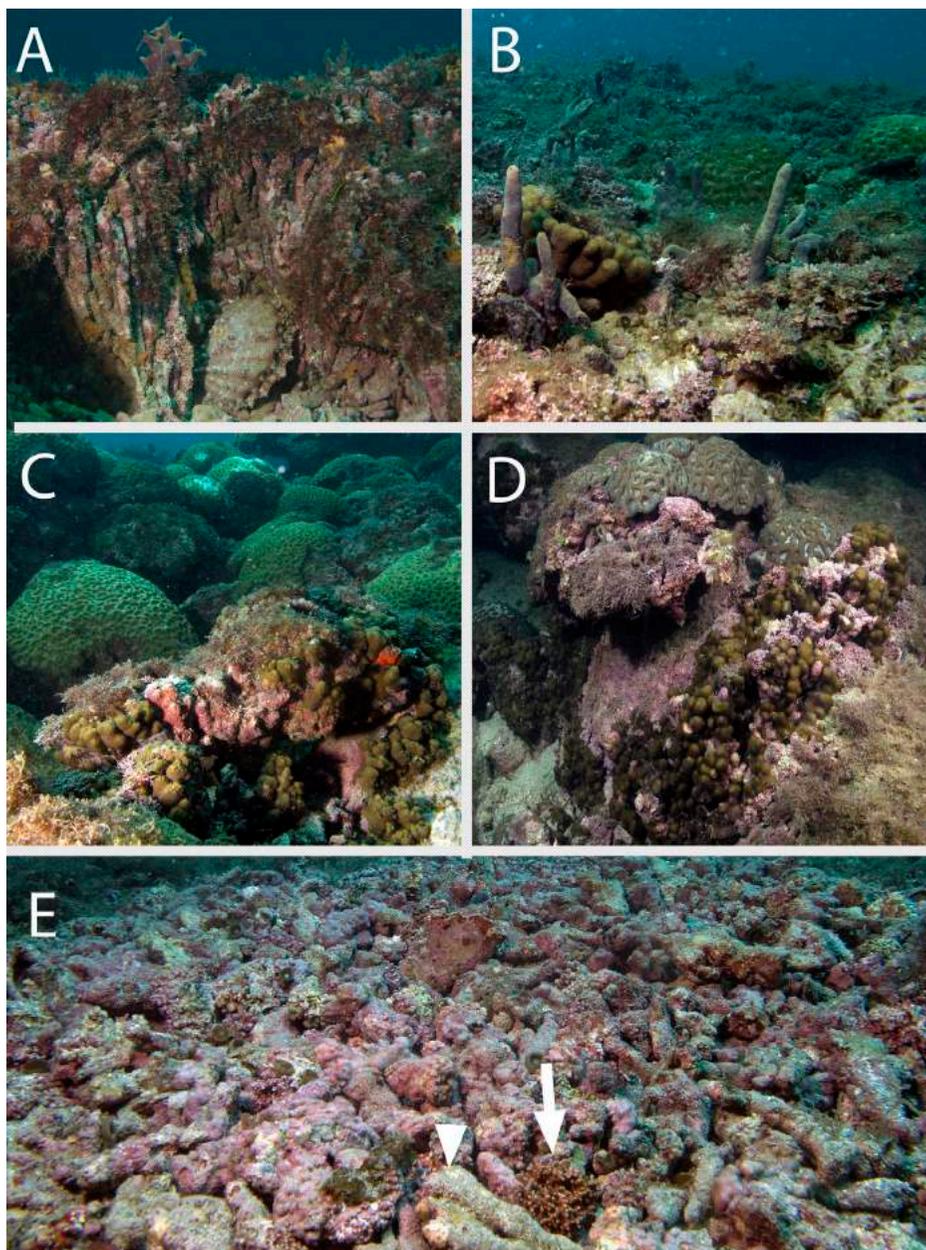


Figure 2. In situ photographs of the coral reef complex from Queimada Grande Island. (A) Deeper border of the coralline reef plateau, showing the *Madracis decactis* framework cross section. (B–D) Coralline plateau. (E) Rhodoliths (arrow) intermixed with conspicuous *M. decactis* rubble (arrowhead) (Photos by CLBF).

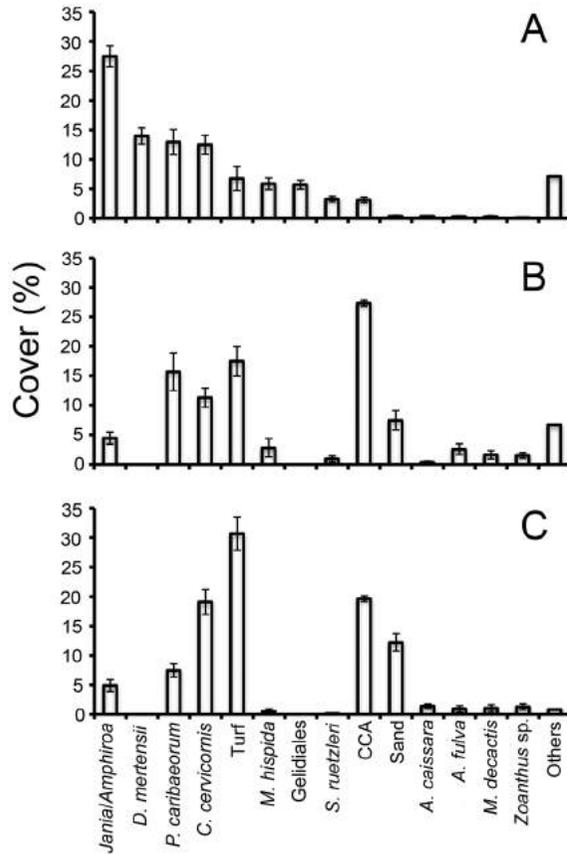


Figure 3. Benthic cover on the Queimada Grande carbonate reefs. (A) Coralline reef plateau. (B) Rhodolith bed between depths of 12–15 m. (C) Rhodolith bed between depths of 15–20 m.

reef associated with a rhodolith bed at 24°29'S, expanding the southern limit for coral reefs in the Atlantic Ocean by >1000 km (4°–5° of latitude).

Akin to some other rhodolith beds (Piller and Rasser 1996), the QGI nodules are formed by CCA growing over fragments of dead coral (*M. decactis*). Rhodolith nucleation by coral fragments colonized by CCA may occur relatively quickly. For instance, a rhodolith bed was formed in no more than three decades in the Galapagos Islands after a widespread coral mortality and fragmentation due to the 1982/1983 and 1997/1998 El Niño–Southern Oscillation (Halfar and Riegl 2013).

Structure-forming coral reefs have a narrower latitudinal range in the SWA, being recorded from the mouth of the Amazon south to Abrolhos, where they reach their maximum range and coral diversity ($n = 20$ species). The QGI reef is located approximately 1000 km south of Abrolhos (Mazzei et al. 2017), representing a considerable range extension of significant carbonate reef-building corals in the SWA, even though coral diversity is very low (two species: *M. hispida* and *M. decactis*). Although displaying a wide depth (0–100 m) and latitudinal range (32°N–25°S), *M. decactis* has not been previously reported as the main framework builder of any other reef. Indeed, *M. decactis* is considered susceptible to high sedimentation and temperature

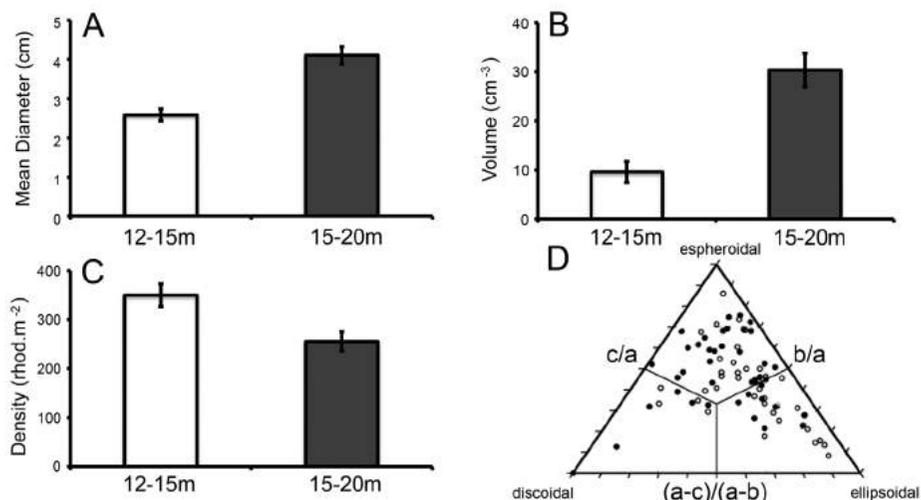


Figure 4. Rhodolith beds from the Queimada Grande Island. (A–C) Mean diameter, volume, and density of rhodoliths from 12–15 m and 15–20 m deep. (D) Sphericity diagram according to Graham and Midgley (2000) applied to rhodoliths from depths of 12–15 m (white points) and 15–20 m (gray square).

extremes (Aronson et al. 2008) and within southeast Brazil, it is primarily found only as small to mid-sized encrusting patches on vertical and horizontal substrates, as well as free-living forms (i.e., Corallith).

The eastern coast of South America is one of the world's wettest regions (rainfall reaches 4000 mm yr⁻¹), being dominated by several subtypes of the Atlantic Forest, including extensive mangrove forests (Schaeffer-Novelli et al. 1990). Such significant freshwater, nutrient, and terrigenous sediment inputs to the ocean constrains reef development (Laborel 1960) and inhibits subtidal feature detection by remote sensing (Spalding et al. 2001). Therefore, reef detection relies largely on in situ surveys (e.g., acoustics, diving, video recording), resulting in significant geographic knowledge gaps. The large mesophotic reef systems in the Abrolhos Bank and off the mouth of the Amazon River (Amado-Filho et al. 2012, Moura et al. 2013, 2016), as well as rhodolith beds and coralline outcrops on seamount tops (Pereira-Filho et al. 2012), comprise emblematic examples of such major knowledge gaps in the SWA. The QGI reef and rhodolith beds reported herein add to this repertoire of novel reef systems that challenge current views of carbonate reef distribution, classification, and evolution (Moura et al. 2016, Amado-Filho et al. 2017).

The so-called South Brazil Bight, an arc-shaped sector of the coast between 22°S and 28°S, represents a broad transition where the warm, south-flowing Brazil Current (BC) interacts with the less-saline coastal waters and with the subjacent and colder South Atlantic Central Water (SACW) (Brandini et al. 2014). This region includes hundreds of rocky coastal islands extending up to 35 km offshore, within a shelf largely dominated by siliciclastic sedimentation (Mahiques et al. 2010). The SACW intrusions intensify in the summer, leading to a strong stratification of the water column that ultimately results in a high diversity of reef-associated organisms, including range overlaps between species with tropical and subtropical affinities (Gibrán and Moura 2012). The coastal islands of the South Brazil Bight are critical to the maintenance of such high regional diversity, as the coastal rocky shores receive

strong riverine, estuarine, and land-based influences that constrain the development of reef-associated organisms (Neves et al. 2016). The results presented herein demonstrate the enormous scientific and biodiversity conservation value hidden at the western South Atlantic coastal islands, most of which still lack effective conservation policies.

Even though QGI is one of the most visited areas for commercial and recreational fisheries (including spearfishing) on the Brazilian coast (e.g., Freire et al. 2016), it still harbors reef fish richness and composition comparable to many southeast Atlantic marine protected areas (MPAs) (Godoy et al. 2004, Luiz Jr et al. 2008, Francini-Filho and Moura 2008, Gibran and Moura 2012). Such diversity may be related to the benthic bottom heterogeneity and higher complexity provided by the three different habitats occurring at the same place, (i.e., rocky shores in alliance with the fringing coral reef and rhodolith bed). Since 2003, there has been a proposal for the creation of a marine national park in the area (Brazilian Ministry of the Environment, process 02027.005038/2003-57), but no effective conservation policy is currently in place (except a multiple-use MPA with low enforcement). In this context, increasing the MPA effectiveness through its zoning is highly dependent on understanding the ecosystem services provided by the southernmost Atlantic coral reef described here.

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