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Extensive Rhodolith Beds Cover the Summits of Southwestern Atlantic Ocean Seamounts

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ABSTRACT

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Calcium carbonate production by marine organisms is an essential process in the global budget of CO_3^{2-}, and coralline reefs are the most important benthic carbonate producers. Crustose coralline algae (CCA) are well recognized as the most important carbonate builders in the tropical Brazilian continental shelf, forming structural reefs and extensive rhodolith beds. However, the distribution of CCA beds, as well as their role in CO_3^{2-} mineralization in mesophotic communities and isolated carbonate banks, is still poorly known. To characterize the bottom features of several seamount summits in the Southwestern Atlantic (SWA), side-scan sonar records, remotely operated vehicle imagery, and benthic samples with mixed-gas scuba diving were acquired during two recent research cruises (March 2009 and February 2011). The tops of several seamounts within this region are relatively shallow ($\sim$60 m), flat, and dominated by rhodolith beds (Vitória, Almirante Saldanha, Davis, and Jaseur seamounts, as well as the Trindade Island shelf). On the basis of abundance, dimensions, vitality, and growth rates of CCA nodules, a mean $CaCO_3$ production was estimated, ranging from 0.4 to 1.8 kg m^{-2} y^{-1}, with a total production reaching 1.5×10^{-3} Gt y^{-1}. Our results indicate that these SWA seamount summits provide extensive areas of shallow reef area and represent 0.3% of the world's carbonate banks. The importance of this habitat has been highly neglected, and immediate management needs must be fulfilled in the short term to ensure long-term persistence of the ecosystem services provided by these offshore carbonate realms.

ADDITIONAL INDEX WORDS: *Calcium carbonate production, mesophotic zone, oceanic banks, crustose coralline algae.*

INTRODUCTION

Rhodoliths are free-living calcareous nodules composed mostly (>50%) of crustose coralline algae (CCA) (Corallinales, Rhodophyta) (Foster, 2001). Rhodolith beds are distributed

worldwide, from the tropics to the poles, from the intertidal zones to depths of up to 200 m (Foster, 2001; Nelson, 2009). They are important "ecosystem engineers" (Foster *et al.*, 2007), providing a structurally complex habitat with high associated diversity encompassing several taxonomic groups, from microbes and fleshy algae to fishes and turtles (*e.g.,* Amado-Filho *et al.*, 2007; Amado-Filho *et al.*, 2010; Peña and Barbara, 2008; Riul *et al.*, 2009). Because rhodolith beds concentrate high biodiversity, provide numerous ecosystem services, and are susceptibile to severe damage from human activities, they are

protected habitats in several countries (*e.g.,* Birkett, Maggs, and Dring, 1999).

Besides growing concerns over habitat destruction due to dredging and trawling in deep reefs (Roberts, 2002), there is a broad record of anthropogenic impacts in shallow coralline habitats (*e.g.,* Birkeland, 1997). Mesophotic reefs that occur in depths between 30 and 40 m and the bottom of the photic layer have been considered as free from major stresses that affect shallow coralline reefs, such as temperature anomalies, overfishing, and water-quality degradation from excessive sedimentation and sewage (Bak, Nieuwland, and Meesters, 2005; Kahng *et al.*, 2010; Lesser, Slattery, and Leichter, 2009). Therefore, reefs from the mesophotic zone may often serve as refugia for several species that also inhabit shallow areas (Bongaerts *et al.*, 2010). However, the 40% increase in levels of atmospheric CO_2 in the past 250 years (Solomon *et al.*, 2007), with a third of this anthropogenic carbon tempered by oceanic uptake (Sabine and Feely, 2007), is already triggering large-scale changes in seawater chemistry that will indistinctly affect both shallow and deep reefs (Doney *et al.*, 2009).

Calcium carbonate production by coralline reefs, which is similar in magnitude to the flux from planktonic carbonate production, is an essential process in the global carbon cycle (Milliman, 1993; Vecsei, 2004), and CCA, especially when forming extensive rhodolith beds, are recognized as foremost carbonate builders. On the basis of growth rate estimates, density, and living branch measurements, Bosence (1980) and Freiwald and Henrich (1994) calculated the $CaCO_3$ production (kg m^{-2} year^{-1}) of rhodolith beds in temperate areas dominated by two CCA species. However, data deficiencies concerning rhodolith beds in the southwestern Atlantic (SWA) have hampered a more detailed appreciation of their relative contribution to the global carbonate production. The Brazilian tropical shelf is one of the world's most important marine $CaCO_3$ deposits, being dominated by extensive rhodolith beds (Foster, 2001; Kempf, 1970; Milliman and Amaral, 1974). Because SWA rhodoliths are generally multispecific (Amado-Filho *et al.*, 2007, 2010; Bahia *et al.*, 2010; Riul *et al.*, 2009), and also have a smoother surface than those studied in temperate seas, direct inferences from production rates estimated elsewhere are not straightforward.

We present novel information from rhodolith beds found on the summits of several SWA seamounts, adding hard data to the ongoing efforts to characterize the extension and role of rhodolith beds in the SWA (*e.g.,* Amado-Filho *et al.*, 2010). We also estimated the unexpectedly high $CaCO_3$ production on the tops of SWA seamounts. Isolated seamounts are of great geological and biological importance, encompassing diverse or unique biotas, as well as high rates of primary productivity due to nutrient upwelling and $CaCO_3$ production (McClain, 2007; Vecsei and Freiburg, 2000). The Vitória–Trindade Chain (VTC), 20–21° S and 29–38° W, within the Brazilian exclusive economic zone, comprises a 1150-km E-W chain of nine seamounts, also bearing two small islands at its eastern outpost (Trindade and Martin Vaz) (Almeida, 2006). We also sampled the more isolated Almirante Saldanha Seamount (22°30′00″ S, 37°30′00″), southward of the VTC. Previous biological sampling on these seamounts was restricted to a few dredging samples, data from commercial fisheries, and scientific diving operations around the Trindade Island shallow reefs (<15-m depth) (O'Hara *et al.*, 2010).

MATERIALS AND METHODS

We obtained data from the insular platforms of Trindade and Martin Vaz islands, as well as from three seamounts within the VTC (Jaseur, Davis, and Vitoria seamounts), and from the Almirante Saldanha Seamount, all of which present predominantly flattened tops lying at average depths around 60 m (10–110 m), within the mesophotic zone. These flattened summits, with horizontal extensions of up to 50 km, apparently result from alternate growth and erosion of carbonate deposits over volcanic pedestals (Skolotnev, Peyve, and Turko, 2010). Benthic habitats were surveyed during two expeditions (March 2009 and February 2011, Figure 1) with a side-scan sonar (SSS) Edgetech 4100 system with a 272TD towfish operated at 100 kHz in 200- and 400-m swaths, as well as with a Seabotix® LBV 150S2 remotely operated vehicle (ROV) equipped with color video camera and a pair of scaling lasers (5 cm apart), used to validate sea-bottom features recorded with SSS. Acoustic data were processed using SonarWis Map4 software; georeferenced mosaics were exported as GeoTiff images with 1 m/pixel resolution into a geographic information system, whereas morphological attributes, such as area and depth, were treated as shapes, using a bathymetric map produced by ETOPO1 data. Footage from the ROV was recorded for at least 40 minutes in each deployment, covering the main benthic features at each site (n = 20). In addition, footage was transformed into one-frame-per-second still images, from which 25 randomly selected frames were used to determine the abundance (individuals m^{-2} by using Coral Point Count (CPCe) software (Kohler and Gill, 2006).

Divers using mixed gas (TRIMIX) collected 30 rhodolith samples at each sample site (Figure 1). Immediately after collections, each specimen was photographed to record the color of the CCA thallus for vitality estimates (*i.e.,* proportion of live tissue). Photographs were analyzed using CPCe, with 50 sampling points randomly positioned over each rhodolith image. The number of points over the living algae thallus (shades of red on the image) was recorded and vitality expressed as a percentage of the total number of sampling points.

Rhodolith volume was estimated from submersion in a graduated beaker filled with water and measured to the nearest millimeter. The largest, intermediate, and smallest diameters were also measured and, thereafter, plotted using the TRIPLOT spreadsheet of Graham and Midgley (2000), who plotted data on the pebble-shaped diagram of Sneed and Folk (1958), and which can be used to separate rhodoliths into spheroidal, discoidal, or ellipsoidal shapes. Analysis of variance (ANOVA) was performed to assess differences between sites for each measured variable (rhodolith volume, diameter, vitality, and densities).

Identification of coralline species that composed the rhodoliths was done on the basis of both vegetative and reproductive characters following Amado-Filho *et al.* (2010), Bahia *et al.* (2011), Harvey *et al.* (2006), Harvey and Woelkerling (2007), and Verheij (1993). Formalin-preserved specimens were decalcified in 10% nitric acid and sequentially immersed in 70%, 90%, and 100% ethanol for a minimum of 30 minutes in each concentration. Specimens were then immersed in Leica Historesin (Leica Microsystems, Wetzlar, Germany) until completely infiltrated. A hardening solution was added and
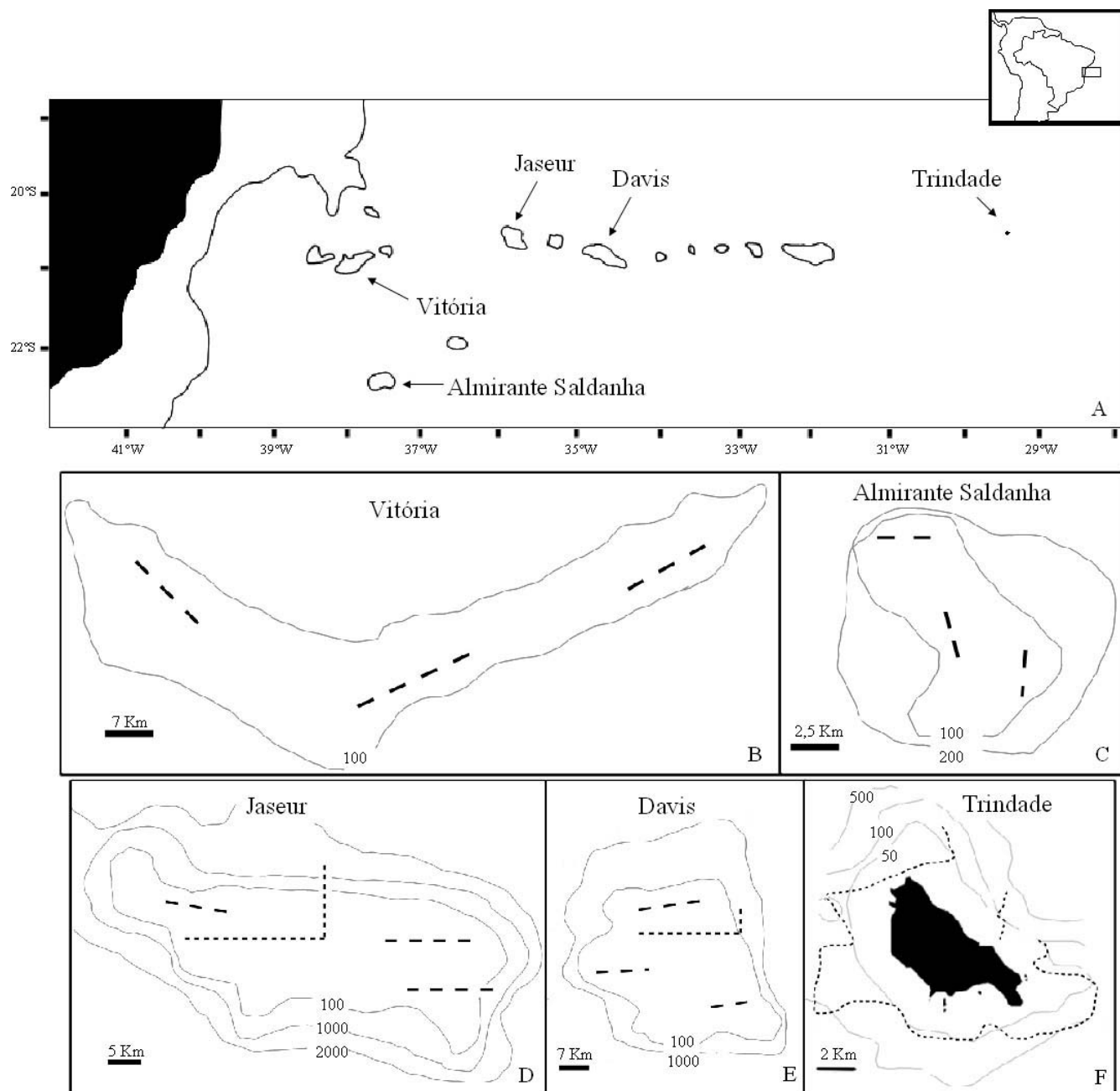
Figure 1. Sampled sites. (A) Map showing the Vitória–Trindade Chain position, (B) Vitória Seamount, (C) Almirante Saldanha Seamount, (D) Jaseur Seamount, (E) Davis Seamount, and (F) Trindade Island. Dotted line shows where the samples by remotely operated vehicle and side-scan sonar were taken. The shorter and larger dotted lines correspond, respectively, to March 2009 and February 2011 expeditions.

the specimens were orientated in this final solution until set. All specimens were sectioned at 5–10μm thickness using a Bright 5030 microtome (Bright Instrument Co. Ltd., Cambs., U.K.). Each section was removed from the microtome blade using a fine sable hair brush and transferred to a slide covered with distilled water. All slides were then placed on a hot plate until dry. Slides were then stained with 1% toluidine blue.

Two main methods have been used to estimate carbonate production in coralline reefs (Vecsei, 2001, 2004). The hydro-chemistry method consists in estimating $CaCO_3$ production from changes in seawater alkalinity (Chisholm and Gattuso, 1991; Kinsey, 1985), but large quantities of biological material are needed to produce measurable changes (Kinsey, 1985). The census-based method uses data on relative cover by reef organisms and their growth/accretion rates (Chave, Smith, and Roy, 1972; Hart and Kenck, 2007). For instance, calcification rates of CCA have been calculated by multiplying algae growth rate (mm) by its bulk skeletal density (g cm^{-3}) (Hart and
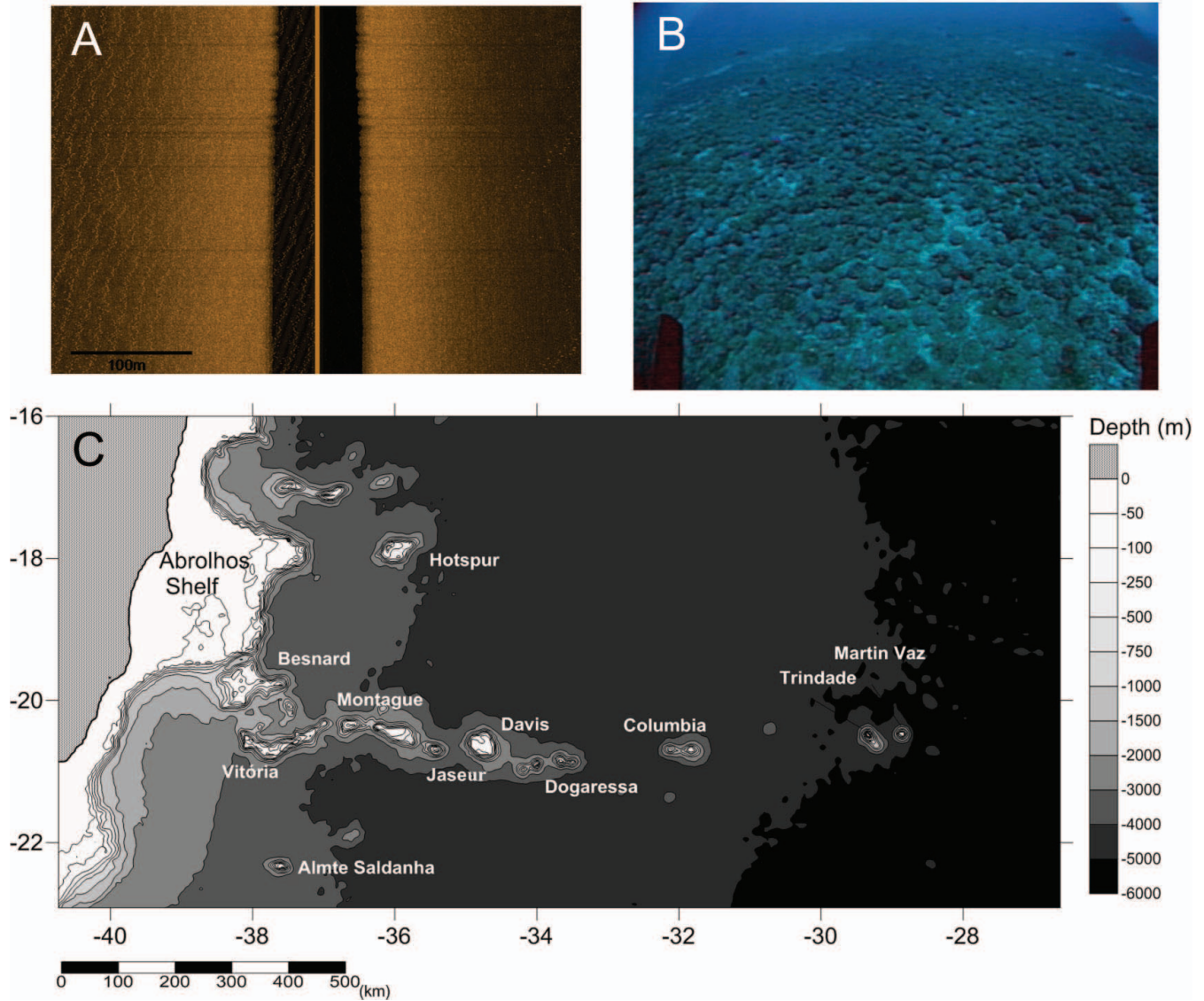
Figure 2. Rhodolith beds from the seamounts Vitória, Almirante Saldanha, Davis, Jaseur, and Trindade Island shelf reaching depths down to 100 m. (A) Side-scan sonar (SSS) image of rhodolith beds at Davis Seamount; (B) image obtained by remotely operated vehicle as ground truth for SSS data, and (C) bathymetric map of Vitoria–Trindade Chain (data source: ETOPO 1).

Kench, 2007). For our estimates, the mass of coralline algae added per square meter after 1 year in a rhodolith bed ($g\,m^{-2}\,y^{-1}$) was calculated on the basis of growth rate, vitality, dimensions, and abundance of rhodolith as follows:

Rhodoliths have an ellipsoid form, with volumes (V) determined by the equation:

$$V = 4/3\pi(R^{a})(R^{b})(R^{c})$$

where R^{a}, R^{b}, and R^{c} are the largest, intermediate, and smallest radii, respectively.

Increases in rhodolith volume after 1 year can be obtained by subtracting initial from final volumes with the following equation:

$$V_{\text{after 1 year}} = \left[4/3\pi(R^{a}+g)(R^{b}+g)(R^{c}+g)\right] - \left[4/3\pi(R^{a})(R^{b})(R^{c})\right]$$

where g is rhodolith growth in centimeters after 1 year. Density (d) is defined as mass/volume, with CCA density estimated at $\sim$1.56 g cm^{-3} (Stearn, Stoffin, and Martindale, 1977).

$CaCO_3$ production rate ($CaCO_3$pr, expressed in g m^{-2} y^{-1}) was obtained with the following equation:

$$CaCO_3pr = 4/3\pi dVitD\left\{\left[(R^{a}+g)(R^{b}+g)(R^{c}+g)\right] - \left[(R^{a})(R^{b})(R^{c})\right]\right\}$$

where *Vit* is rhodolith mean vitality (ranging between 0 and 1) and D is mean rhodolith abundance (individuals^{-1} m^{-2}). The growth thickness value used was 1 mm y^{-1} according to Blake and Maggs (2003).
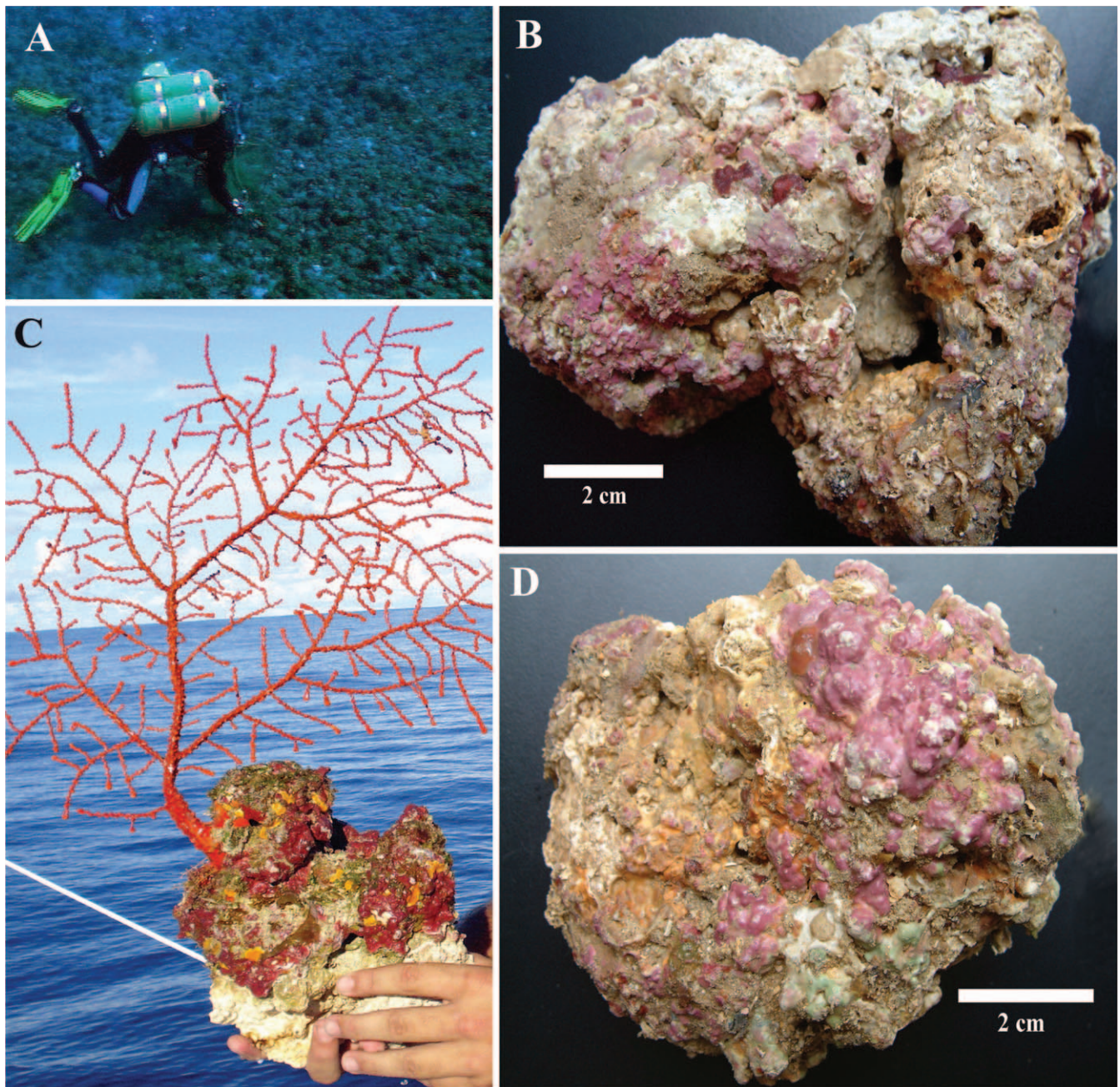
Figure 3. Rhodoliths from sampled sites at Vitória–Trindade Chain. (A) Diver collecting samples on rhodolith bed; (B) and (C) rhodoliths from Jaseur Seamount showing the occurrence of rhodolith fusion and the presence of associated corals, respectively; (D) sample from the Trindade shelf, showing the spheroidal shape and low biomass of associated community.

RESULTS

A representative SSS coverage was acquired from the tops of three seamounts in the VTC (Vitória, Davis, Jaseur), from the Trindade and Martin Vaz islands shelf, and from the Almirante Saldanha Seamount. With the exception of Martin Vaz Island, flat and highly reflective bottoms predominated in depths of up to 100 m, largely corresponding to the low-relief hard bottom typical of rhodolith beds (Figure 2). This benthic feature was explored by ROV across the whole area, confirming its correspondence with rhodolith beds (100% match). On the basis of bathymetry and extension of occurrence, the estimated area covered by rhodolith beds in the studied area is 1511 km² (850, 590, 40, 15, and 16 km², for Davis, Vitória, and Jaseur seamounts and Trindade shelf, respectively) (Figure 3).

Noticeably, rhodolith beds were absent from Martin Vaz Island, where only a few small patches of smaller CCA nodules were sighted by divers in interreefal areas, apparently resulting
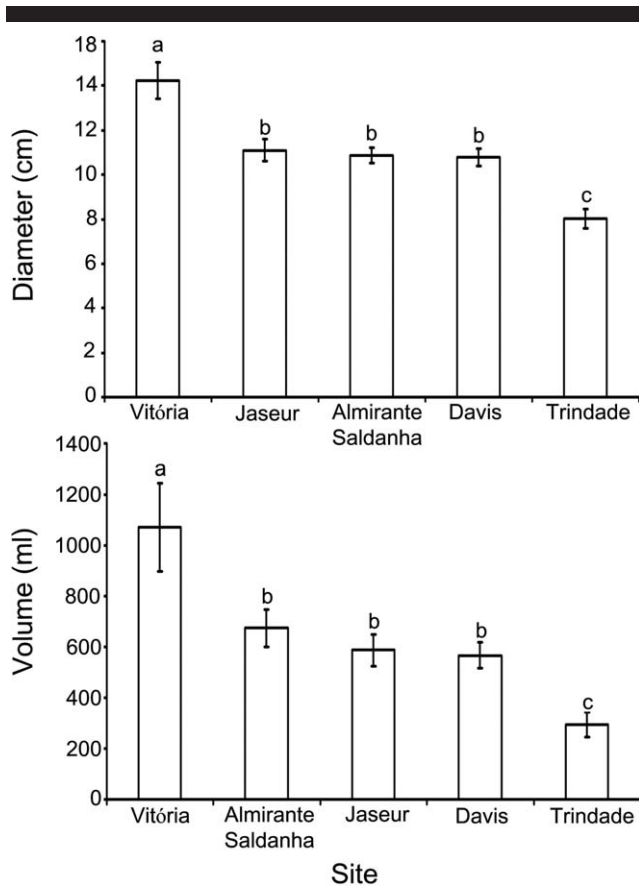
Figure 4. Rhodoliths from sampled seamounts. Mean diameter (cm) and volume (ml) ($\pm$ SE) ($n = 30$).

Figure 5. Rhodolith samples plotted using the TRIPLOT spreadsheet of Graham and Midgley (2000) ($n =30$): rhodolith with a = highest rhodolith diameter, b = intermediate diameter, and c = lowest diameter.

from a detached reef framework. The insular platform of Martin Vaz is largely covered by finer sandy sediments (unpublished data).

Five taxa of coralline algae were identified forming the rhodoliths in the seamounts and islands: *Mesophyllum engelhartii* (Foslie) Adey, *Sporolithon ptychoides* Heydrich, *Sporolithon* sp., *Hydrolithon rupestris* (Foslie) Penrose, and *Lithothamnion* sp. (voucher specimens deposited at Rio de Janeiro Botanical Garden Herbarium: RB 505683, RB 505760, RB 505770, RB 505784, and RB 511250, respectively). The occurrence of *H. rupestris* constitutes a first record of this species for the Atlantic Ocean.

No significant differences among the mean abundance of rhodoliths (individuals m^{-2}) in the different seamounts were observed (ANOVA, $F = 2.3$, $p > 0.05$), with values ranging between 24.2 ± 5 and 48 ± 7 individuals m^{-2} (mean $\pm$ SE) (Vitória and Davis, respectively). The highest diameters and volumes were observed at Vitória Seamount (14.2 ± 0.8 cm and 1071 ± 170 ml), whereas the smallest ones were recorded at the Trindade Island shelf (8.4 ± 0.4 cm and 296 ± 48 ml) (ANOVA, $F = 18.6$, $p < 0.05$ and $F = 12.2$, $p < 0.05$ for diameter and volume, respectively) (Figure 4). Rhodoliths from seamount tops tended to be spheroidal in shape. Differences in the measured proportion between the shortest (or the intermedi-
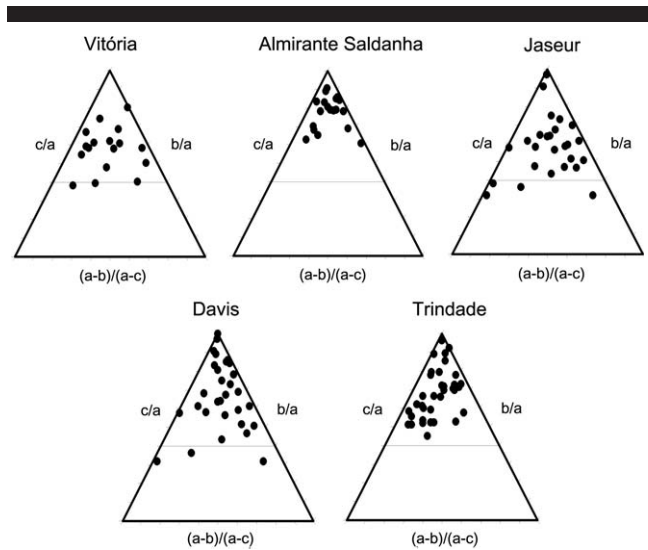
ate) and the largest diameters were observed. Rhodoliths taken at Almirante Saldanha Seamount and Trindade Island shelf tended to be smaller than those collected from the Vitória, Jaseur, and Davis seamounts (Figure 5). Mean vitality ranged between $33 \pm 2.1\%$ and $36 \pm 1.4\%$, with no significant differences among seamounts (ANOVA, $F = 3.2$, $p > 0.05$).

On the basis of rhodolith abundance, dimension, vitality, and a constant growth rate of CCA of 1 mm y^{-1}, the estimated $CaCO_3$ productions were: 1.8 kg m^{-2} y^{-1} for Jaseur Seamount, 1.2 kg m^{-2} y^{-1} for Davis Seamount, 0.85 kg m^{-2} y^{-1} for Vitória Seamount, 0.8 kg m^{-2} y^{-1} for Almirante Saldanha Seamount, and 0.4 kg m^{-2} y^{-1} for the Trindade Island shelf. Taking into account the areas occupied by rhodolith beds, $CaCO_3$ production was estimated at 1.5×10^{-3} Gt y^{-1} in these SWA seamounts (Table 1).

DISCUSSION

Our results show that the flattened mesophotic tops of the seamounts within the VTC, Almirante Saldanha Seamount, and Trindade Island shelf are predominantly covered by rhodolith beds, at least up to 100-m depths. Rhodolith beds along the eastern Brazilian continental shelf are considered to be the most extensive in the world (Foster, 2001; Kempf, 1970; Milliman and Amaral, 1974), and the data presented herein add the VTC seamount tops and the Trindade Island shelf to the large rhodolith realm off the tropical southwestern Atlantic Ocean.

Vecsei and Freiburg (2000) provide data on the distribution, coordinates, size areas, and depth occurrences of the world's isolated carbonate banks in the tropical–subtropical climate zone, but their review lacks data from the SWA. Remarkably, the estimates for carbonate areas presented herein (1511 km²) are higher than those described for the Red Sea (Vecsei and Freiburg, 2000), representing 0.3% of the world's isolated carbonate banks (Table 2).

Table 1. *Measures of the ray maximum, intermediate, and minimum from rodoliths in each seamount; CaCO₃ production; seamount area; and total production for each sampled seamount.*

Seamount	Radius Maximum (cm)	Radius Intermediate (cm)	Radius Minimum (cm)	$CaCO_3(kg.m^{-2}.y^{-1})$	Seamount Area (km²)	$CaCO_3(Gt\ y^{-1})$
Jaseur	7.5	5.9	4,4	1.85	40	7.4×10^{-5}
Trindade	4.8	4.1	3.2	0.41	16	6.5×10^{-6}
Davis	6.3	5.3	6,3	1.19	590	7.0×10^{-4}
Vitória	9.1	7.3	5.1	0.83	850	7.0×10^{-4}
Saldanha	6.2	5.4	4.7	0.82	15	1.2×10^{-5}
Total					1511	1.5×10^{-3}

The high-magnesium calcite produced by CCA is the most soluble form of the common $CaCO_3$ minerals (Martin and Gattuso, 2009; Nelson, 2009), and is thus highly susceptible to ocean acidification (Hoegh-Guldberg *et al.*, 2007; Kleypas, 1997). Recent projections indicate that tropical CCA will stop growing by 2040, and will start to dissolve when the high-magnesium calcite saturation state is less than 1 (Hoegh-Guldberg *et al.*, 2007). By the end of the century, seawater pH may decrease by as much as 0.4 pH units (Doney *et al.*, 2009), indicating that rhodolith beds will rapidly decline across the globe, at faster rates than those expected for coral reefs. The slow growth rate and long life span of CCA (Foster, 2001; Nelson, 2009) indicate a low resilience to such major disturbances. The unprecedented rate of change in seawater chemistry, which is over 1000 times faster than that of the last 420,000 years, makes the adaptation of CCA to such environmental changes unlikely (Anthony *et al.*, 2008). The decline or disappearance of CCA in the near future could have dramatic biological and physicochemical consequences on a

global scale (Veron *et al.*, 2009), and can be even more acute in the eastern tropical shelf of South America, where rhodolith beds are confirmed to occupy vast areas.

Besides the carbonate sink promoted by living rhodoliths on the superficial layer of the studied seamounts, Skolotnev, Peyve, and Turko (2010) remark that these carbonate platforms can be as thick as 300 m, adding to their importance in the oceanic compartment of the carbon cycle. Vecsei (2003) found that the depth window of 0–70 m to the occurrence of carbonate deposits is related to the last postglacial sea-level rise and, therefore, characterizes the tops of most of the world's warm-water carbonate platforms and isolated banks, as also found in our study.

Our estimated $CaCO_3$ production rates (1.8–0.4 kg m^{-2} y^{-1}) are lower than estimates for most reef environments, which range between 0.8 and 30.5 kg m^{-2} y^{-1} (Vecsei 2000). Concerning rhodolith-forming algae, Bosence (1980) found values ranging between 0.029 kg m^{-2} y^{-1} and 0.164 kg m^{-2} y^{-1} with *Lithothamnium corallioides* and between 0.079 kg m^{-2} y^{-1} and 0.249 kg m^{-2} y^{-1} with *Phymatolithon calcareum* from Mannin Bay, Ireland. Freiwald and Hernrich (1994) estimated the $CaCO_3$ production of *Lithothamnium glaciale* from Norway as ranging between 0.895 and 1.432 kg m^{-2} y^{-1}. For the CCA reefs at the Great Barrier Reef, Chisholm (2000) estimated the $CaCO_3$ production ranging from 1.5 kg m^{-2} y^{-1} to 10.3 kg m^{-2} y^{-1} to *Hydrolithon onkodes* and *Neogoniolithon conicum*, respectively. We remark that, although the coralline algal thickness growth for tropical zones varies from 0.1 mm y^{-1} to 5.2 mm y^{-1} (Adey and Vassar, 1975; Eakin, 1992; Rivera, Riosmena-Rodriguez, and Foster, 2004; Stearn, Scoffin, and Martindale, 1977), the mean CCA growth rate of 1 mm y^{-1} used in our study should be considered a conservative value for tropical warm-water regions (see Blake and Maggs, 2003).

The rhodolith beds in the studied seamount tops are located in a highly oligothrophic oceanographic context, and also in deeper waters (60- to 70-m depth) than most studied coralline reefs, with light intensity of 6.9 ± 1.4 µmol s^{-1} m^{-2} (mean ± SE). These conditions are similar to those found in the mesophotic Brazilian continental shelf, where extensive rhodolith beds were found (Amado-Filho *et al.*, 2007), indicating similar oceanographic forcing in both areas. Rhodolith beds in the VTC summits shall constitute a starting point for monitoring the overall state of the huge SWA carbonate banks, constituting an outlying observatory of global significance for the forthcoming impacts from seawater chemistry changes. Also, these seamount tops are in great need of local-scale conservation, because the mesophotic reefs (>30-m depth)

Table 2. *Number and area of the tops of isolated carbonate banks (modified from Vecsei, 2000).*

Ocean, Cluster, or Region	Number of Carbonate Oceanic Banks	Area of the Top (km²)
Caribbean	38	170,557
Northern Caribbean	15	141,398
Nicaragua Rise area	17	22,993
Antilles	6	6165
Western Indian Ocean	23	181,967
Red Sea area	3	972
Seychelles area	11	76,485
Mascarene Ridge area	9	104,510
Eastern Indian Ocean	30	47,270
Laccadives	9	6653
Maldives	17	21,575
Chagos	4	19,042
Southeast Asia	28	53,458
Northern South China Sea	5	9407
Southern South China Sea	18	27,746
Mkassar Strait	5	13,018
Western Pacific	59	53,979
Caroline Island	16	14,639
Bismarck Sea	2	1027
Queensland Plateau	6	14,607
Lord Howe Rise to New Caledonia	18	27,154
Melanesian Boderland	14	5034
Tonga	3	6157
Eastern Pacific	20	15,434
Hawaii Chain	18	14,466
Southwestern Atlantic	4	1511
Total	201	524,875

serve as important shelter for species that inhabit other reef areas, including commercial fishes (Carpenter et al., 2008; Hoegh-Guldberg, 1999; Hoegh-Guldberg *et al.*, 2007; Lesser, Slattery, and Leichter, 2009).

CONCLUSIONS

The summits of several seamounts within the tropical SWA are covered by extensive rhodolith beds formed by CCA. The importance of these large extensions of living hard-bottom beds as $CaCO_3$ sinks has been largely underestimated. Our calculations indicate that they are responsible for 0.3% of the world's carbonate production in isolated oceanic carbonate banks. Although more data are needed to reach a better understanding of the calcium carbonate balance and the relative roles of seamounts, immediate local-level protection and long-term monitoring programs must be included in the priority agenda for environmental conservation in Brazil, the country that owns rights and duties over the unique carbonate realm of the VTC of seamounts.

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