

# The forgotten reefs: benthic assemblage coverage on a sandstone reef (Tropical South-western Atlantic)

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*Despite the ecological relevance of tropical reefs, information on species composition and coverage on sandstone reefs is very scarce. Most studies on reef systems have been conducted for true coral reefs, ecosystems that show calcareous formations with extensive coral cover and diversity. The aim of this study was to analyse the coverage of benthic assemblages in a submerged sandstone reef (22–24 m) in a relatively non-explored region (Tropical South-western Atlantic). In this area, filamentous algae (43.6%) and sponges (19.6%) are the main components of the benthic reef assemblages. Other benthic reef fauna (ascidians, corals and zoanths) showed lower coverage, although their importance may vary depending on the area. A negative correlation between filamentous algae and slow-growing reef-building organisms (calcareous algae) was observed. High sand coverage (19.6%) over the reef revealed a high rate of silting. A low coral diversity (only two resilient species) was quantified, and most of the coral colonies were small-sized. The results provide a baseline assessment for a poorly known ecosystem with turbid-water benthic communities and higher sea-surface temperatures near the Earth's equator.*

**Keywords:** benthic assemblages, reef ecology, corals, macroalgae, sponges

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## INTRODUCTION

Tropical reef communities are globally recognized for their high biodiversity and productivity (Mumby *et al.*, 2007; Kiessling *et al.*, 2010; Pimm *et al.*, 2014). These tropical regions show a variety of geological and environmental features that shape different ecosystems; however a huge study effort has been made mostly in calcareous reefs, and other regions of the planet have been almost neglected. In view of the environmental challenges regarding oceans in general and the tropical reefs in particular (Halpern *et al.*, 2008; Rossi, 2013; Palumbi *et al.*, 2014), research on reef assemblages in poorly studied regions is urgently required to provide scientific data for their sustainable use and environmental monitoring.

Sandstone reefs differ from a typical rocky shore and coral reefs mainly because of their gentle slope and sedimentary composition (Rabelo *et al.*, 2015). Previous studies on benthic assemblages mainly focused on Caribbean and Indo-Pacific coral reefs, and few studies have been conducted on the Tropical South-western Atlantic (TSA) reefs. Furthermore, the studies available for TSA were mostly conducted on biogenic reefs (Leão *et al.*, 2010; Francini-Filho *et al.*, 2013; Kelmo *et al.*, 2013; Cruz *et al.*, 2015), and literature on sandstone formations is limited and focused on intertidal or shallow subtidal

environments (Barradas *et al.*, 2010; Rabelo *et al.*, 2015). This is remarkable, since the 4000 kilometres of coastline along TSA contain many areas with sandstone reefs, most of which remain largely unknown. Data on benthic assemblages in underwater sandstone reefs, especially in TSA (*sensu* Spalding *et al.*, 2007), are still very scarce. Most of the information is focused on vagile or semi-vagile organisms (Martínez *et al.*, 2012; Freitas & Lotufo, 2015; Galvão Filho *et al.*, 2015), and information on ecosystem engineering species (*sensu* Jones *et al.*, 1997) is almost non-existent (Rabelo *et al.*, 2015).

In TSA, low-latitude sandstone reefs commonly develop on the continental shelf under environmental stress factors such as high turbidity, intense sedimentation and high temperatures (Morais *et al.*, 2009; Dias *et al.*, 2013). A quantitative analysis of the reef assemblages under these harsh conditions is essential to develop a general understanding of the relationship between environmental changes and marine biodiversity (Sanders & Baron-Szabo, 2005; Silva *et al.*, 2013). In fact, assessments of benthic coverage are necessary to the establishment of useful baselines for predictions related to local or global changes, particularly in poorly known areas (Ruzicka *et al.*, 2013). In many areas, major environmental modifications have already started, and only standardized tools can be used to obtain a good quantification and proper interpretation of these changes (Edmunds & Elahi, 2007).

Sandstone reefs provide shelter and food for commercial species (Martínez *et al.*, 2012; Freitas & Lotufo, 2015), and they are important touristic areas in TSA. Because of this ecological and socioeconomic importance, we urgently need to collect information on the benthos of these formations. The

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aim of this study was to provide a quantitative assessment of benthic assemblages on a tropical sandstone reef of TSA. To achieve this goal, a scuba diving-based study was performed at a depth of 22–24 m in a marine protected area (MPA) off the Brazilian coast in the summer of 2013.

## MATERIALS AND METHODS

### Study site

The study site was the marine protected area ‘Pedra da Risca do Meio’. It is one of the few totally submerged MPAs in TSA (Soares *et al.*, 2011; Santos & Schiavetti, 2014). This MPA is located 18 km from the city of Fortaleza, on the north-east coast of Brazil, and covers an area of 33.2 km<sup>2</sup> (Figure 1). The completely submerged reefs are at depths ranging from 22 to 24 m. The reef evaluated in this study has elevations in a linear arrangement 1–2 m above the sea floor.

The TSA coast (*sensu* Spalding *et al.*, 2007) offers diverse coastal habitats, such as coral reefs, sandstone reefs, sand beaches and dunes. The intertidal and shallow subtidal zones of this coast have sandstone reefs and beach rocks, which are rocky outcrops with flat surfaces tilted slightly seaward (Pereira *et al.*, 2007; Freitas & Lotufo, 2015; Rabelo *et al.*, 2015). The reefs have a tabular format, and consist of sand cemented by calcium carbonate and iron oxide (Morais *et al.*, 2009).

The study site has a tropical wet and dry climate (Aw in Köppen classification), with an annual sea surface temperature (SST) ranging from 27 to 29°C (near the Earth’s equator) and a highly variable precipitation regime, with frequent droughts. The rainy period extends from January to July, but in many years rain is concentrated between February and April (200 to 400 mm per month). The dry period extends from August to December, and during these

months precipitation can be null, even in years of regular rainfall (Dias *et al.*, 2013).

Oceanographic and climate conditions in this semi-arid coast of TSA are different from those in the North Atlantic, eastern Brazilian Coast, and Caribbean Sea. This region exhibits oligotrophic waters, strong trade winds (mainly in the second semester), and high SST (Dias *et al.*, 2013; Teixeira & Machado, 2013; Aguiar, 2014). Despite the oligotrophic waters and SST favourable for coral bioconstruction, the action of trade winds and coastal currents causes strong resuspension and transport of marine sediments (Knoppers *et al.*, 1999). This renders the water turbid and inappropriate for coral reef development, in spite of low fluvial inputs (Dias *et al.*, 2013).

### Sampling methods

Data collection was conducted in the summer of 2013 via linear transects. Biotic data were collected by scuba diving at a depth of 22–24 m. The point-intercept transect (PIT) method was used to analyse the reef benthic assemblages, and the belt transect (BT) method was used to assess the size of the scleractinian coral colonies.

In the PIT method, ten 60-m-long transect lines were used. These transects were distributed in pairs (first pair with transects 1 and 2, second pair with transects 3 and 4, etc.), each composed of parallel lines 2 m apart, haphazardly placed over the reef. Each transect line was analysed by one scuba diver. Quantitative assessment (presence of filamentous algae, coral, ascidians, etc.) was performed every 20 cm of each transect line, totalling 300 points per transect and 3000 points over the reef. At each point, sessile benthic organisms or sand present immediately below the transect line was recorded. Benthic coverage was classified into categories of benthic suspension feeders (corals, sponges, etc.) and morpho-functional groups of algae (filamentous, foliose,

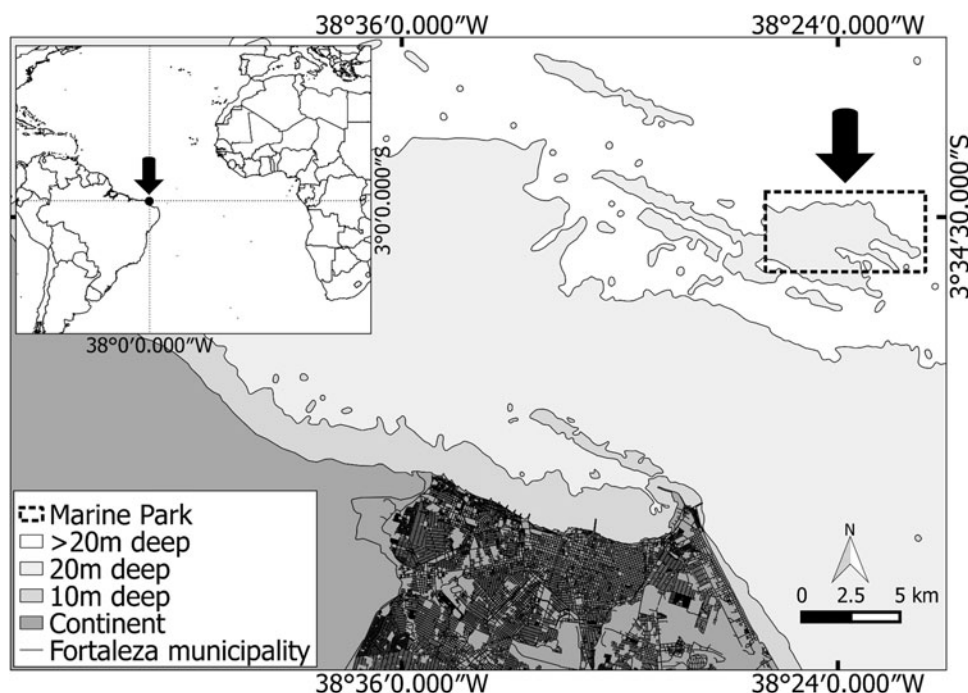


Fig. 1. Location of study site. Tropical South-western Atlantic (left side) and Marine protected area (right side).

etc.), the latter following the approach of Steneck & Dethier (1994). To complement the characterization of reefs, sand covering the hard bottom was quantified to assess the area without sessile organisms. Benthic coverage of each category was measured by dividing the number of points where the taxon (or sand) occurred by the total number of PIT points. Benthic coverage is a common metric for reef monitoring because it can be determined rapidly in the field and has been used for over 50 years for many reefs worldwide (Madin & Madin, 2015).

For the BT method, scuba divers used an underwater camera and a 50 × 50-cm quadrat to record colonies in five 60-m<sup>2</sup> areas (each 30 m × 2 m). These areas were delimited by each pair of transect lines used in the PIT method. We aimed to evaluate the following variables along five belt transects: the number of corals (zoanthid or scleractinian) and scleractinian colony size-frequency distributions. In total, 350 photo-quadrats (N = 70 per transect) were obtained for the BT method and analysed using ImageJ and Coral Point Count with Excel Extensions.

### Statistical analyses

The chi-square test was used to determine variations in benthic assemblages between PITs. Besides the general comparison of transect lines, repeated chi-square tests were used to analyse changes in each benthic category. These latter tests were performed on the basis of the frequency of each category relative to the sum of the remaining groups in each transect. Non-metric multidimensional scaling (NMDS) ordination was used to summarize spatial similarities, measured as Bray–Curtis index, in the structure of the reef benthic assemblages. The morpho-functional groups (algae and benthic

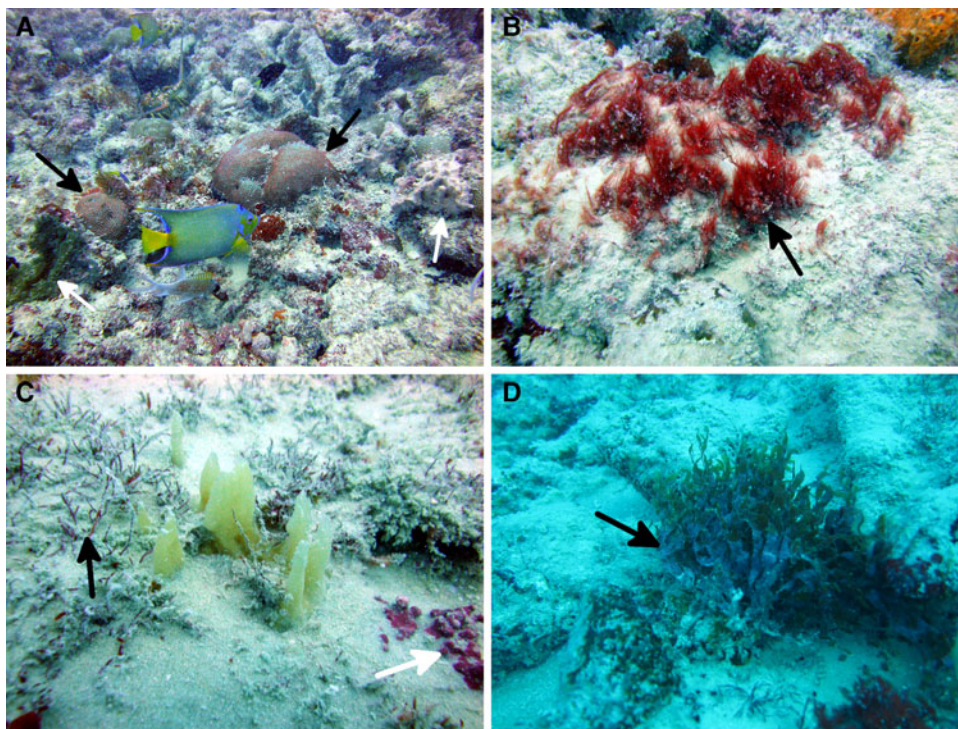
fauna) and sand responsible for multivariate differences were determined using similarity of percentage analysis (SIMPER).

Pearson's correlation analyses were used to evaluate the relative influence of major non-building organisms (i.e. filamentous algae) on the abundance of key reef-building organisms (scleractinians and crustose calcareous algae). Statistical analyses were performed using R software, and differences were considered statistically significant when  $P < 0.05$ , except in the case of the repeated chi-square tests, when the Bonferroni-corrected  $P$ -value ( $P < 0.0083$ ) was applied to prevent type I error.

## RESULTS

### Benthic coverage

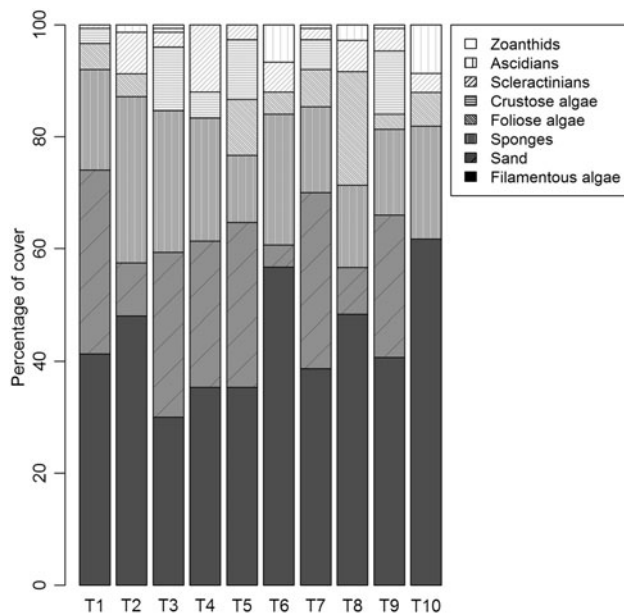
The sandstone reef under study had a diverse benthic community (Figure 2), which could be classified into eight categories: filamentous algae, sponges, sand, foliose algae, crustose algae, scleractinians, ascidians and zoanthids (Table 1). The results indicate the dominance of benthic macroalgae over the sessile benthic fauna (sponges, scleractinian corals, ascidians and zoanthids). Considering only macroalgae, filamentous species were by far the most abundant component (43.6%), followed by foliose (5.8%) and crustose species (4.6%). In general, benthic assemblages were characterized by the high coverage of filamentous algae and sponges (63.2% of coverage in total). Among benthic categories, the scleractinian corals (*Siderastrea stellata* and *Mussismilia* sp.), ascidians and the zoanthid *Protopalyythoa variabilis* showed the lowest coverage values. Additionally, a high coverage of sand (19.6%) was observed on the reef.



**Fig. 2.** Benthic assemblage on a sandstone tropical reef. (A) overview of the reefs highlighting the scleractinian coral *Siderastrea stellata* (Verrill, 1868) (black arrows) and sponges (white arrows); (B) the filamentous red alga *Callithamnion corymbosum* (Smith) Lyngbye (black arrow); (C) a filamentous red alga *Gelidiella* sp. (black arrow) and an unidentified calcareous red alga (white arrow); and (D) the foliose brown alga *Dictyota* sp.

**Table 1.** Benthic categories, main species and coverage percentage in a SW Atlantic sandstone reef.

Group	Example	Coverage (%)
Filamentous algae	<i>Callithamnion corymbosum</i> (Smith) Lyngbye; <i>Gelidiella</i> sp.	43.6
Sponges	<i>Aplysina fistularis</i> (Pallas, 1766); <i>Sigmaxinella cearense</i> Salani, Lotufo & Hadju, 2006	19.6
Sand	–	19.6
Foliose algae	<i>Canistrocarpus cervicornis</i> (Kützting) De Paula & De Clerck; <i>Dictyota mertensii</i> (Martius) Kützting	5.8
Crustose algae	<i>Mesophyllum</i> sp.; <i>Lythothamnion</i> sp.	4.6
Scleractinians	<i>Mussismilia</i> sp.; <i>Siderastrea stellata</i> (Verrill, 1868)	4.6
Ascidians	<i>Didemnum</i> spp., <i>Eudistoma saldanhai</i> Millar, 1977; <i>Stomozoa gigantea</i> (Van Name, 1921)	2.1
Zoanthids	<i>Protopalpythoa variabilis</i> (Duerden, 1898)	0.1

**Fig. 3.** Variation of coverage of benthic categories along 10 transects.

The chi-square test of independence, excluding ascidians and zoanthids because of their low benthic coverage, showed that the differences between the transect lines (PITs) were significant ( $\chi^2 = 342.8$ ,  $P < 0.0001$ ) (Figure 3). The test was repeated to determine the proportion of coverage for each group in each transect line, and the Bonferroni-corrected  $P$ -value (adjusted  $P = 0.0083$ ) showed that all the tested benthic groups varied significantly between transects (Table 2).

The NMDS analysis produced a two-dimensional representation (stress = 0.054) that defined two main groups (solid and dotted lines in Figure 4). The SIMPER analysis showed that these groups of transects differed with respect to the quantity of filamentous algae, calcareous algae, sponges and sand (Table 2). In general, transects 2, 6, 8 and 10 showed the lowest coverage of sand and calcareous algae and the highest coverage of filamentous algae and sponges. The reverse pattern was observed in the other group. The contribution of cnidarians (zoanthids and scleractinian corals) to the differentiation between transects was low.

Pearson's correlation analysis revealed a negative correlation between two morpho-functional groups (filamentous algae and calcareous algae;  $r^2 = 0.58$ ,  $P < 0.05$ ), suggesting competition between these organisms.

### Scleractinian coral and zoanthid colonies

In this study, 202 colonies of Anthozoa, mainly scleractinian corals, were observed: 172 (85.5%) colonies of *Siderastrea stellata*; 19 (9.4%) colonies of *Mussismilia* sp.; and 11 (5.4%) colonies of the zoanthid *Protopalpythoa variabilis*. The belt transects had  $40.4 \pm 15.3$  colonies ( $0.67 \pm 0.25$  colonies per  $m^2$ ). Both scleractinian corals (*S. stellata* and *Mussismilia* sp.) were present in all five transects analysed, whereas *P. variabilis* was found in only two of the transects.

The colony size-frequency of the major coral *S. stellata* varied between 1.6 and 56.9 cm (mean  $\pm$  SD =  $12.9 \pm 9.9$  cm). However, most of the colonies belonged to small-diameter classes, with 83.7% exhibiting a diameter  $< 20$  cm. Because of the skewed distribution of the colony size

**Table 2.** Chi-squared test of independence among 10 transects considering six benthic categories in a SW Atlantic sandstone reef.

Benthic categories	$\chi^2$ test of independence	Contribution to Bray–Curtis dissimilarity	Cumulative contribution (%)
Sand	$\chi^2 (9) = 127.9$ , $P < 0.001$	0.119	0.346
Filamentous algae	$\chi^2 (9) = 73.8$ , $P < 0.001$	0.080	0.579
Calcareous algae	$\chi^2 (9) = 71.2$ , $P < 0.001$	0.039	0.691
Sponges	$\chi^2 (9) = 28.4$ , $P < 0.001$	0.033	0.787
Foliose algae	$\chi^2 (9) = 83.8$ , $P < 0.001$	0.032	0.880
Ascidians	*	0.023	0.946
Scleractinians	$\chi^2 (9) = 32.3$ , $P < 0.001$	0.018	0.998
Zoanthids	*	0.001	1.000

Since these transects could be classified into two groups via multidimensional scaling, the table also shows the relative contribution of each category to the differentiation between these groups (i.e. results of SIMPER analysis).

\*Excluded from the  $\chi^2$  test due to their low benthic coverage.

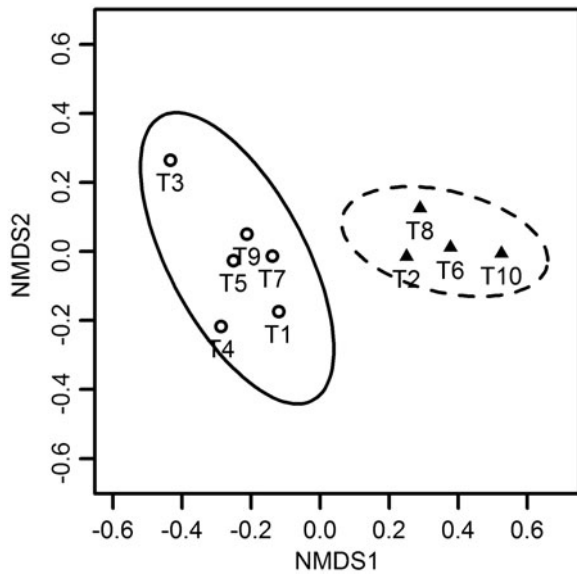


Fig. 4. Non-metric Multidimensional Scaling (NMDS) of 10 transects showing two groups: the transects circled by a solid line had a higher coverage of filamentous algae and sponges, whereas the transects circled by a dotted line had a higher coverage of sand and calcareous algae. Stress = 0.054.

frequency, the central trend is better conveyed by the median (instead of the mean) which was 9.8 cm.

## DISCUSSION

The results of this study establish two singular findings in tropical sandstone reef description and ecosystem functioning: (1) The dominance of benthic algae (mainly filamentous algae) over benthic suspension feeders and (2) low coral diversity, as most of the coral colonies are small-sized.

The tropical subtidal reefs off TSA waters support highly diverse assemblages of macroalgae and sessile invertebrates, yet little is known about the structure of these communities. The present study has described, for the first time, the coverage of these benthic assemblages, which is one of the most important metrics for reef characterization and monitoring (Sarkar & Ghosh, 2013; Cruz *et al.*, 2014; Madin & Madin, 2015).

To discuss these results, it is necessary to understand the environmental conditions of the continental shelf where the tropical sandstone reefs are located. The study site is strongly affected by high-speed winds (Sauermaun *et al.*, 2003; Tsoar *et al.*, 2009) and large swell events that generate resuspension of sediments and turbidity in the pelagic zone (Knoppers *et al.*, 1999). The high percentage of sand (19.6%) found above the reef is the result of these sediment resuspensions. The modern relief of the north-eastern Brazilian Continental Shelf is commonly related to high-energy sedimentary fluxes, oligotrophic waters and hydrodynamic processes (Dias *et al.*, 2013; Teixeira & Machado, 2013; Gomes *et al.*, 2014). According to Aguiar (2014), Secchi depth, which is related to water turbidity, is only 2 m in the first semester in the study site. This low value contrasts with the average value of 6.6 m for the entire continental shelf. Moreover, Dias *et al.* (2013) demonstrated a high concentration of suspended particulate matter on the inner continental shelf,

with an average of 39.7 and 28 mg l<sup>-1</sup> in the first and second semester, respectively. These data demonstrate that the studied reef sustains a very turbid-water benthic assemblage (*sensu* Sanders & Baron-Szabo, 2005).

A high coverage of macroalgae, including filamentous algae, has previously been reported in biogenic reefs in the Tropical South-western Atlantic (Barradas *et al.*, 2010; Segal & Castro, 2011; Francini-Filho *et al.*, 2013), but only for environments in intertidal or shallow subtidal reefs at a maximum depth of 10 m. The present data support the hypothesis that this dominance continues at greater depths (at least 22 m) in TSA, including sandstone reefs. High-current regime and turbidity may be essential factors for understanding the dominance of these sessile organisms. In the Mediterranean, slow-growing calcareous algae are dominant (Ballesteros, 2006), and light limitation and turbidity are essential factors for understanding the absence of certain components such as scleractinian corals (Zabala & Ballesteros, 1989). In the case of TSA, turbidity and harsh living conditions for passive suspension feeders may be the key to understanding this substrate occupation by algae.

Some filamentous algae, the main functional group in the studied reefs, have opportunistic life-history characteristics, including high surface area to volume ratios and the ability to maintain growth rates in oligotrophic waters. Another aspect is that filamentous algae are often able to recover rapidly after being partially removed by physical disturbance (Rosenberg & Ramus, 1984; Littler *et al.*, 2006), for example, re-suspension of sediments and siltation by sand in the sandstone reefs.

The results also indicate that sponges are the second morpho-functional group with the highest coverage and the first among benthic fauna. Despite their ecological importance, sponges are commonly excluded from the characterization of reef assemblages (Bell, 2008). Bell (2008) suggested that the low effort to study sponge coverage is, in part, because sponges are generally less abundant in shallow-water coral reefs than other benthic reef taxa. The results demonstrate that sponges are an important component in sandstone reefs in TSA.

Two hypotheses may explain this high coverage of sponges. The first is related to the depth of the reef surveyed in this study. Pawlik *et al.* (2015) suggested that sponge coverage in shallow waters (2–8 m) is generally low and limited by physical disturbance due to turbulence from storm events. Sponges, in fact, may be deeply affected by rush hydrodynamic conditions, and the first metres of shallow waters may not be suitable for their presence. Ruzicka *et al.* (2013) analysed deeper sites (10–20 m in depth) along the Florida Keys reefs and found a significant increase in sponge coverage. The second hypothesis is the resistance of sponges to environmental stressors such as sedimentation and thermal anomalies (González-Rivero *et al.*, 2011). Bell *et al.* (2015) showed that some sponge taxa are highly resilient to sedimentation, and in some cases, sedimentation has actually been shown to correlate with increased sponge coverage. Salani *et al.* (2006) reported that *Sigmaxinella cearense* Salani, Lotufo & Hadju, 2006, a sponge endemic to the study site, was found even during periods of intense winds and sedimentation. These authors observed that during the time of strong swells (August to January), sand deposited on the top of and around sandstone reefs may be suspended in the water column and increase stress for sponges. Despite this

environmental stress, these authors observed a dominance of sponges during taxonomic surveys in the reef. Kelmo *et al.* (2013) showed that sponges in the Brazilian reefs became more resilient after a very stressful thermal event (El Niño, 1997/98). Both environmental factors (high turbidity and SST) were observed in the study area and may be the reason why the sponges are the best adapted suspension feeders.

Because of the little information on sponge diversity in the sandstone reefs of TSA found in the literature (to date, 37 species; Salani *et al.*, 2006), and the absence of accurate temporal data, it is necessary to monitor over longer temporal scales the benthic coverage of this and other areas. In addition, a better taxonomic resolution and surveys are required in other reef locations to understand the dominance of sponges and to test the effects of depth and sedimentation on these organisms (Kelmo *et al.*, 2013; Ruzicka *et al.*, 2013).

Another remarkable result is the low coverage of reef-building organisms (around 5% coverage of corals and calcareous algae). This is consistent with the findings of previous studies in TSA waters in which the coral cover was 5–11%, depending on the anthropogenic impact (Leão *et al.*, 2010). The benthic coverage of slow-growing reef-building functional groups (for example, calcareous algae and scleractinian corals) and fast-growing non-building organisms (filamentous algae) is an important metric to evaluate reef resilience and recovery (Graham *et al.*, 2015). The presence of a large quantity of sediments above the reefs is an important finding. In general, most South-west Atlantic reefs are characterized by high sedimentation rates (Castro *et al.*, 2012). Although the aim of the present study was not to test the influence of sedimentation on the benthic assemblages, the results of SIMPER suggest that sand is a relevant abiotic factor for the structure of benthic assemblages. The presence of high loads of sand is often negatively related to benthic species on rocky reefs (Díaz-Tapia *et al.*, 2013). Stubler *et al.* (2016) found that the assemblages were primarily composed of filamentous and encrusting algae in Jamaican coral reefs, but the authors observed lower amounts of filamentous algae in locations with the highest sediment supply. Corals also have a negative relationship with the amount of sediment in certain areas (Castro *et al.*, 2012), and resuspension is a major factor that explains turbidity and species presence. Besides the potential for abrasion and burying, availability of suspended organic matter is important to understand the presence of one kind of suspension feeder or another (Rossi & Gili, 2009). In the study site, the presence of carbonates may be as high as 90% in certain areas (Castro *et al.*, 2012), with the available food being very low.

In these tropical reefs, a low coral diversity (two species) was observed, and most of the coral colonies were small-sized. The environmental characteristics of the continental shelf may explain the selection of only two resilient corals (*Siderastrea stellata* and *Monastrea* sp.) in the study site. About 20 scleractinian species have been recorded for the entire TSA coast, and at least six of them are endemic to Brazil (Leão *et al.*, 2010; Francini-Filho *et al.*, 2013). Sedimentation and turbidity affect benthic assemblages (Dutra *et al.*, 2006; Castro *et al.*, 2012) by selecting species most well-adapted to stress and consequently reducing the percentage of coverage and diversity of taxa known to be stress-sensitive, such as scleractinian corals (Fabricius, 2005; Silva *et al.*, 2013). For example, *S. stellata*, a species endemic to the South Atlantic, has been described to have large polyps (Menezes *et al.*, 2014) that are less

susceptible to the effect of sediments (Lirman & Manzello, 2009). Furthermore, this coral species is very resistant to temperature, salinity variations and water turbidity (Costa *et al.*, 2008). In particular, *Symbiodinium* Clade C (present in this species) is well adapted to stressful light and thermal conditions throughout the year, which is a possible explanation for its dominance in a wide area of the Brazilian reefs (Costa *et al.*, 2008). Corals with this Clade C are less sensitive to bleaching events (Glynn *et al.*, 2001). The other coral observed (genus *Montastraea*) is recognized as sediment-resistant with a high capacity for sediment removal, and it is a major component of the 'sediment resistant coral fauna' in the West Atlantic (Francini-Filho *et al.*, 2013). These corals may comprise 'siltation assemblages' (Sanders & Baron-Szabo, 2005) in recent turbid-water reefs.

The present results on benthic coverage reflect a normal characteristic of benthic assemblages of tropical sandstone reefs, with low coverage of reef-building organisms. Holocene turbid-water benthic reef assemblages may be considered as 'alternative states of development rather than as disturbed or restricted versions' of clear-water tropical reefs (Sanders & Baron-Szabo, 2005). In settings of prevalently high turbidity (visibility less than about 5 m), a distinct change occurs in the benthic assemblage. Total diversity and total coral cover are reduced, with an increase in the relative proportion of cover by sediment-resistant corals. Moreover, colony size ranges within wider limits, and smaller-sized specimens become more abundant (Sanders & Baron-Szabo, 2005). Our results demonstrated that most of the coral colonies were small-sized and resilient. Oigman-Pszczol & Creed (2011) observed that the large number of small-diameter colonies (similar to those found in the present study) of *S. stellata* is an adaptive reproductive strategy developed in environments subjected to sedimentation and turbidity stress.

In conclusion, the coverage of benthic species in this area needs to be studied further, and how sedimentation and turbidity act in these reef benthic assemblages needs to be investigated. There is little information on the distribution patterns of benthic assemblages in TSA (*sensu* Spalding *et al.*, 2007), particularly in sandstone reefs. This information is important for expanding the concepts and theories of structure and dynamics of tropical reefs, which are mostly restricted to coral formations. In these sandstone reefs, some of the crucial aspects of tropical photobiology may be tested to establish baselines of warm turbid areas and to better understand how they are facing local and global changes. In particular, temporal changes in the coverage of benthic assemblages can be used as indicators of anthropogenic impacts, which would promote effective management of tropical reefs, particularly when coupled with tests of how the most prominent coral species face the lack of ideal conditions (Hoegh-Guldberg *et al.*, 2007). To establish a baseline against climate changes, a worldwide assessment of sandstone reefs should be included in the list of global 'coral reef' conservation programmes.

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