



## ECOSYSTEMS

# Effect of fine-scale habitat differences on algal colonisation in a coral-dominated subtropical reef

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**Abstract:** Maintaining the coexistence of algae and corals depends on the interactions between them. We investigated these interactions to assess: (1) recruitment patterns of algal turfs over time in dead areas on live corals; (2) the influence of fine-scale differences in coral-dominated environments on algal colonisation; (3) the influence of coral as a substrate for algal recruitment; (4) the invasion potential of algal turf on live coral tissue. This study compared algal colonisation directly on dead or damaged coral areas with algal colonisation on recruitment plates in coral-dominated or -free areas at 23, 154, and 230 days. We also monitored coral colonies over 1.5 years. Filamentous and articulated coralline algae were primarily evident in the early colonisation, reaching stability after 154 days. On a fine scale, the coral-dominated environment showed an increase in number of algal species and coverage. However, coral substrate was selective, with fewer species recruited to this substrate compared to the artificial plates. Furthermore, the competitive dynamics between corals and algal turfs did not result in a winner over time. Thus, algal turf colonisation was influenced not only by coral substrate but also by the reef environment on a fine scale.

**Key words:** Algal turfs, corals, marginal reef, rocky reef, Scleractinian, *Siderastrea*.

## INTRODUCTION

Algal turfs are considered competitors against corals for space (Wild et al. 2004). However, definitions of algal turfs or epilithic algal matrix (EAM) are highly varied (Connell et al. 2014). In an important review about algal turf sediments on coral reefs, Tebbett & Bellwood (2019) defined algal turfs to be shorter than 2 cm and generally composed of filamentous macroscopic algae associated with sediment. In contrast, Copertino et al. (2005) considered turfs to be multi-specific short filaments with less than 1cm. Furthermore, Connell et al. (2014) noted that several studies have defined algal turfs as multispecies assemblages ranging from 1 to 10 cm in height and associated with different

groups of algae, such as coralline and foliose algae. Thus, Connell et al. (2014) concluded that the term turfs represents several types of micro- and macro-algae which share an extensive low-lying morphology and are densely aggregated. These different definitions of algal turfs clearly share some common features; however, it is also clear that based on these definitions of algal turfs the community composition, morphology, and size of turfs can vary on local and global scales (Connell et al. 2014). Herein, we considered turfs to be consortia of green, red, and brown algae, which are less than 10 cm in height (Odum & Odum 1955, Morrissey 1980, Connell et al. 2014). These turfs form dense mats often associated with sediments (Stewart 1983, Kendrick 1991, Airoldi 1998, Littler & Littler

2011, Tebbett & Bellwood 2019). Although we recognized that other groups, such as diatoms and cyanobacteria, are part of the algal turf community (Diaz-Pulido & McCook 2002, Connell et al. 2014, Tebbett & Bellwood 2019), our work focuses on assessing the interaction between algae in turfs and corals.

Algal turfs constantly colonise the surface of scleractinian corals in damaged or dead areas, which are normally caused by acute disturbances such as storms and hurricanes (Diaz-Pulido & McCook 2002, 2004a, b, Titlyanov et al. 2005) or chronic disturbances such as ocean warming and subsequent coral bleaching (i.e. Douglas 2003, Bellwood et al. 2006). In addition, scleractinian corals, such as *Siderastrea stellata*, can be damaged from direct excavations of the living tissue by barnacles, gall-crabs, and bivalves (Oigman-Pszczol & Creed 2006). However, regardless of the exact mechanism, O'Brien & Scheibling (2018) suggested that algal turfs can occupy new areas of coral in two ways: (1) if the disturbance is strong enough to damage or kill coral tissue, algal turfs can occupy the dead areas without changes in the competitive potential of either the coral or algal turfs involved in interactions, or (2) the competitive potential of turfs can be increased by chronic stressors to corals. In recent works, such stressors have been reported to drive changes in both temperate and tropical benthic environments towards the dominance of macroalgae and algal turfs (Johnson et al. 2017, Filbee-Dexter & Wernberg 2018, Rilov et al. 2018).

A meta-analysis study by Cruz et al. (2018) showed that marginal reefs in Brazil have changed dominance by macroalgae and Zoanthids, while algal turfs and sponges have declined, along with corals, as reef degradation intensifies. The meta-analysis suggests that the responses of corals and algal turfs to disturbance

are similar in marginal reefs of Brazil. As these patterns appear to differ from other coral reef areas, the relationship and interaction dynamics between corals and algal turfs in marginal reefs of Brazil is warranted. Furthermore, although there is a substantial body of literature that has examined the nature of interactions between corals and macroalgae (i.e. McCook et al. 2001, Jompa & McCook 2002, Burkepille & Hay 2006, 2009, Smith et al. 2006, Diaz-Pulido et al. 2010, Andras et al. 2012, Barott et al. 2012, Thinesh et al. 2019), these examinations are more limited (e.g. Nugues & Bak 2006, Swierts & Vermeij 2016, Brown et al. 2017, Speare et al. 2019).

The composition of turfs and their colonisation trajectories may be important factors to understand the nature of competitive interactions between algal turfs and corals (Fricke et al. 2011). Accordingly, Wild et al. (2004) reported that turfs dominated by filamentous algae are potentially damaging to corals, Jompa & McCook (2003a) emphasized that depending on their composition, turfs may not cause deleterious effects. Furthermore, on marginal reefs, such as Brazilian rocky reefs where algal turfs and coral coexist, the abundance of turfs and corals may vary spatially within the same reef (Oigman-Pszczol et al. 2004). This suggests that different environmental factors can act on the interaction between coral and algal turfs.

*Armação dos Búzios* (Rio de Janeiro State coast) is considered a marginal reef environment in the southwest coast of Brazil and is a marine protected area (Parque Natural Municipal Marinho de Armação dos Búzios, 2009). In these marginal reefs, turfs and coral interactions are poorly understood, and concerns about the health of corals have already been raised (Rogers et al. 2014). To address this knowledge gap on coral-algal turf interactions in these marginal reefs, we conducted a series of studies to provide an initial understanding of the

interaction dynamics between these two groups. Specifically, this study consisted of four key questions: (1) what is the pattern of algal turf recruitment in areas of partial mortality on live coral colonies over time? (2) how is colonisation of algal turfs influenced by environments dominated by corals on fine scales? (3) is algal recruitment influenced by coral as a settlement substrate? (4) what is the invasion potential of turfs on live coral tissue?

## MATERIALS AND METHODS

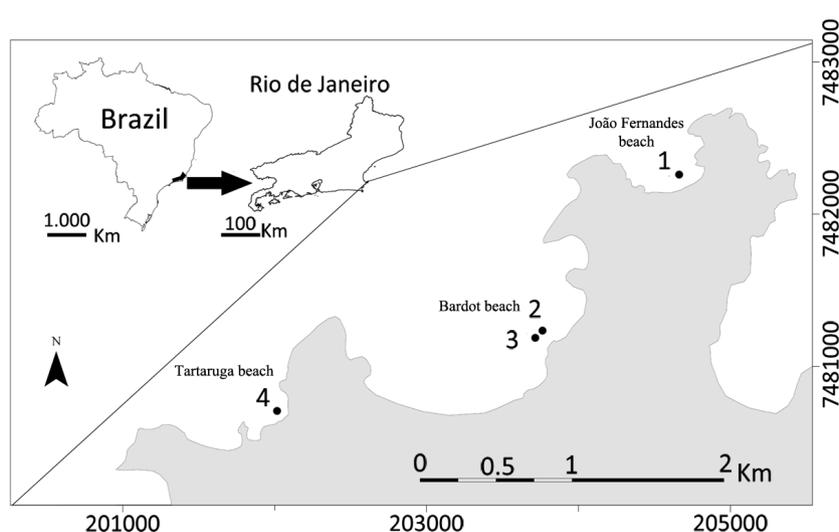
### Study area

This study was carried out in *Armação dos Búzios*, state of Rio de Janeiro, Brazil (Fig. 1). The study area was a shallow water rocky substratum, with a gentle slope extending approximately 100 meters seaward (Carvalho et al. 2018). At some locations, the substratum is dominated by the coral *Siderastrea stellata* Verrill, 1868 (Oigman-Pszczol et al. 2004). This species often has small areas of algal turfs around the living tissue surface, forming patches ranging in size from 20 to 40 cm<sup>2</sup> (personal observation). These turfs usually consist of a mixture of articulated coralline, filamentous, and corticated algae

(Oigman-Pszczol et al. 2004). The water depth in the subtidal area varies between 2 to 4 m, following the local tide cycle (Carvalho et al. 2018). In addition to the coral *S. stellata*, the benthos are covered by zoanthids, leafy macroalgae, algal turfs, sponges, and other coral species to a lesser extent (Oigman-Pszczol & Creed 2004, Oigman-Pszczol et al. 2004).

### Experimental design

A set of experiments were developed to assess the nature of algal turf colonisation and interaction with *S. stellata* coral species by providing substrate for algal colonisation under different conditions and monitoring the potential for algal turfs to overgrow the coral. Specifically, this study assessed: (1) algal turf recruitment patterns in dead or damaged areas of live coral colonies (n=15) at three different times, which were defined here as early, middle, and late (23, 154, and 230 days, respectively); (2) fine-scale differences in algal colonisation on artificial recruitment plates deployed at coral-dominated and -absent sites (n=30), which were monitored at the same times as in (1); (3) differences in algal recruitment between coral substrata (1) and recruitment plates (2); (4) the invasion potential of turfs on live coral tissue



**Figure 1.** Study area. *Armação dos Búzios* rocky shore, Rio de Janeiro. Monitoring areas of coral colonies (1, 3 and 4). Recruiting experiment in an area without coral (2) and coral dominated (3).

by monitoring changes in areas occupied by algae and corals in interaction regions of three rocky reefs (n=15) over 1.5 years. Furthermore, as sea urchins are among the most abundant benthic organisms in the study region, we also investigated the relationship between their presence and algal turf colonisation in areas dominated by or absent of corals (n=8). This investigation was carried out in the late colonisation period.

### **Algal colonisation on dead surfaces of coral**

We investigated algal colonisation on coral substratum in dead regions of coral colonies where algal turfs had already colonised. These areas were scraped and considered to be clear recruitment substrate after the turfs were removed (n=15). The live coral tissue surrounding the area occupied by turfs was not damaged during scraping. The algal turfs were scraped with a spatula and steel brush to ensure removal of epilithic algae. However, as 100% algae removal cannot be ensured, we considered it as a secondary succession. To ensure that the exact location of the scraped region could be found on subsequent trips, two stainless steel pins were fixed into the colonies in adjacent regions, outlining two vertices of an imaginary rectangle of 9 x 11cm [modified from McCook et al. (2001)]. Areas were then randomly selected (n=5) at 23, 154, and 230 days after first scraping and scraped again for later sampling of algae. The area occupied by the colonizing algae within the imaginary rectangle ranged from 20 to 40 cm<sup>2</sup> and was estimated from photographs taken with the aid of a PVC structure [modified from Preskitt et al. (2004)], which were previously calibrated based on the known distance between the steel pins. Algae collected after scraping were packed in hermetically sealed bags and taken to the laboratory. The samples were preserved until identification and quantified by

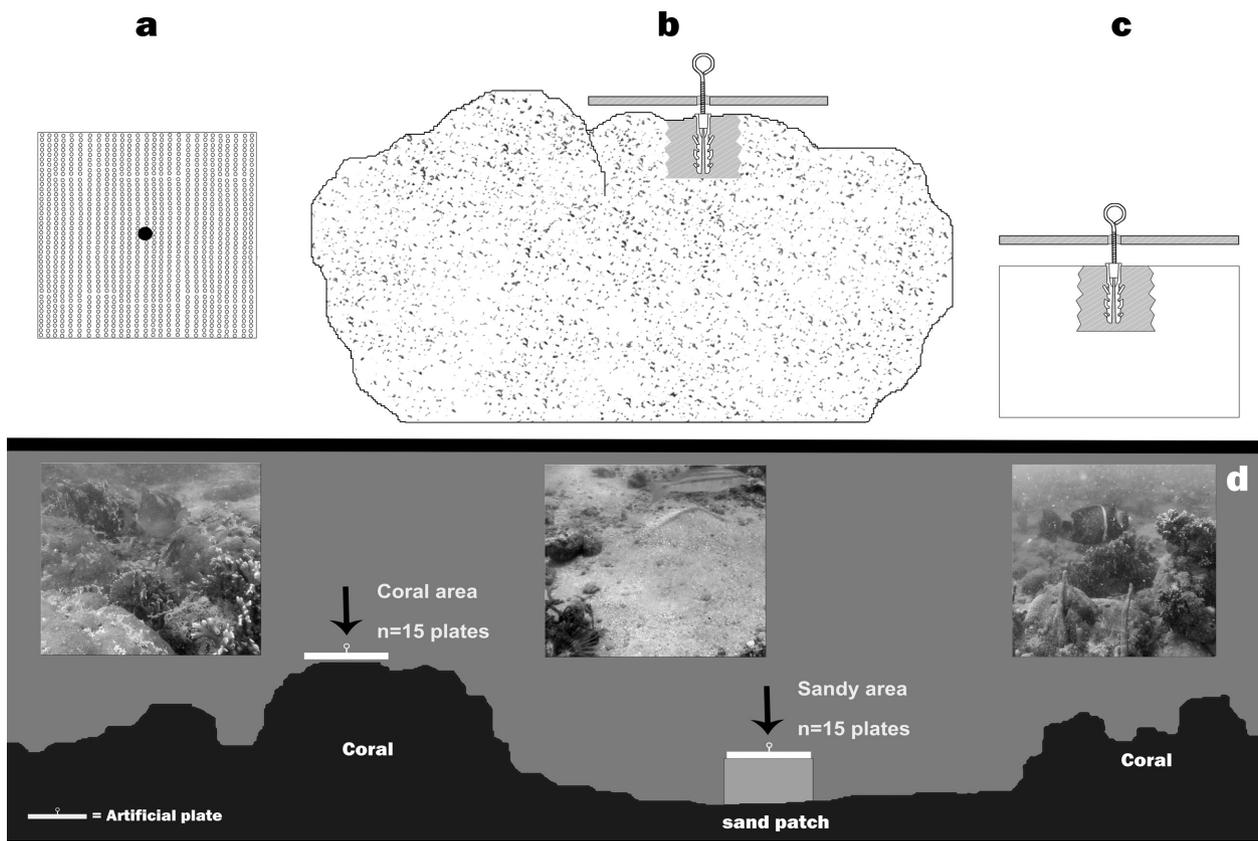
immersion in a 4% formaldehyde solution. Algae collection was authorized by the environmental agencies responsible (N 35309-1).

The abundance of each algal species was estimated inside a 1-cm<sup>2</sup> visual field grid. We estimated the percentage coverage of each species within the visual range into six categories: >0-5%, >5-15%, >15-25%, >25-50%, >50-75%, >75-100%. Relative coverage was estimated as the ratio of the sum of coverage quantified in all visual fields for each species by the total area occupied by algal turfs on the coral (calculated through photographic records). Algae were identified to the lowest taxonomic group possible. However, small, and difficult-to-visualize species which lacked reproductive structures or other important morphological structures were grouped at the genus or family levels. When all structures were present, individuals were identified at the species level by inspecting samples under a compound microscope (Hund H500 - Wetzlar). Other non-algal constituents of turfs, such as diatoms and cyanobacteria, were not quantified except for barnacles.

### **Coral environment influence**

To investigate whether algal turf colonisation is influenced by the reef environment on a fine-scale, we compared algal recruitment in a coral-dominated environment with that in an area without coral colonies over time. Coral-free areas occurred in "patches" on the studied rocky reef. These regions have low structural complexity and are almost always composed of sand and small rocks (Fig. 2). The distance between both regions (with and without corals) was about 15 m, and they were positioned on the same line parallel to the coast and at the same depth.

Artificial substrates in the form of recruitment plates were used in both experimental areas to compare algal colonisation (n=30). We installed



**Figure 2.** Schematic representation of recruitment plates (a), fixed on the coral (b), and on ceramic blocks (c). Representation of the sand patches within the reef and the positioning of the recruitment plates (d).

fifteen plates in each area to monitor colonisation over time. At each period (23, 154, and 230 days after the experiment started), five plates were randomly collected from each treatment. The collected plates were packed into hermetically sealed bags and taken to the laboratory. The samples were preserved until identification and quantification could be conducted by immersion in a 4% formaldehyde solution.

Artificial recruitment plates were manufactured using a nontoxic underwater epoxy (Tubolit® MEP). This is widely used in benthic organism recruitment experiments (Spotorno-Oliveira et al. 2015). The plates measured 9.5 x 9.5 x 1.0 cm and were used to simulate *S. stellata* in the artificial substrate, we moulded depressions 1 mm in depth and 5 mm in diameter, spaced 2 mm evenly apart (Fig. 2a).

Recruitment plates were fixed directly to *S. stellata* colonies by using 5-mm-diameter eye-shaped stainless-steel screws, screwed in the central part of the plate. We used these screws to facilitate and speed up plate removal, reducing effort and time during field collection. Holes were drilled into the corals using a hand drill. We inserted a polyethylene wall plug into each hole to ensure screws were firm (Fig. 2b). In coral-free regions, plates were fixed to ceramic blocks (9.5 x 9.5 x 6.0 cm) using screws through the central holes in the plates, as well as the coral-dominated areas (Fig. 2c, d).

Algal colonisation was assessed by estimating the percentage of coverage per species on each recruitment plate, under a regular grid in the same format as plates (9/9 divisions, 1 cm<sup>2</sup> per visual field), using a binocular microscope (Stemi

DV4 - Zeiss, 8 - 32x). The plates were rinsed with distilled water to remove coarse sediment, and fine sediment was removed gently with a fine-tip brush. Estimates were made with plates immersed in water to reduce error due to loss of visualization of collapsed filamentous algae on air-exposed surfaces. To avoid edge effects, we excluded 32 cm<sup>2</sup> from the outermost perimeter of the plates. We also excluded the 9-cm<sup>2</sup> area in the centre of each plate to eliminate possible screw influence on recruitment of algae species. Afterwards, we analysed a 40-cm<sup>2</sup> area of each plate (average area of algal turfs on dead areas of *S. stellata* colonies in experiment 1). Each 1-cm<sup>2</sup> visual field was estimated for percentage coverage following the same classification used previously for algae colonizing the corals directly. Due to species overlapping one another under a three-dimensional environment, sums of coverage percentages sometimes exceeded 100%. As in coral surface analysis, individuals were identified to the lowest taxonomic level possible.

### Coral-algal turf monitoring

Coral-algal turf interaction dynamics were assessed at three sites along *Armação dos Búzios*: Tartaruga, Bardot, and João Fernandes beach. All locations had similar algal turf compositions (Oigman-Pszczol et al. 2004). The dynamics were evaluated by analysing the increase or decrease of algal turfs on live coral tissue in successive photographs at fixed points over 1.5 years. At each time-point, five 9 x 11 cm photographs were taken from the area, including the border between algal turfs and live coral tissue (n=15) [modified from McCook et al. (2001)]. To ensure that photographs taken next covered the same exact location, two stainless steel pins were attached to the colonies, outlining two corners of an imaginary rectangle. After taking the photographs, we quantified the areas occupied

by coral and turf, using the software Photoquad®. An index (I) was built to examine variations in coral tissue coverage. This index consists of the proportion of the area occupied by coral tissue at each specific sampling time (A<sub>t</sub>) and that in the first sampling (A<sub>1</sub>), as the following equation:

$$I = \left( \frac{A_t}{A_1} \right) - 1 \quad (1)$$

With the index, we could assess if there were gains in coral tissue area to first sampling, at the expense of turfs (values > 0), or if there was a loss of coral tissue area due to increases in turf coverage (values < 0). Values close to zero indicate that the occupied areas were like that of the first sampling.

### Density of sea urchins

The population of sea urchins was quantified as an indirect estimate of herbivory pressure. The species found in the studied depth range was *Lytechinus variegatus* Lamarck (1816), which is considered an omnivore with a broad diet, including macroalgae (Watts et al. 2007). It is usually found in shallow regions and may live on algae-covered rocks, seagrass banks, or sandy bottoms (Hill & Lawrence 2003, Watts et al. 2007, Gondim et al. 2008). The density of sea urchins was estimated by counting the average number of individuals per square meter. Urchins were accounted in coral-covered and coral-free areas along 10 x 1-m transects (n=8). All specimens found within transect limits were recorded. The structural complexity of the environment was estimated using a ballast rope to contour the physical habitat structure and determine the ratio between cable length and linear distance between its ends (Aronson & Precht 1995). Ratios close to 1 indicate a flat surface, while values >1 suggest increasing roughness; therefore, the higher the ratio, the more complex the environment.

## Statistical analysis

Analysis of variance (ANOVA) was used to test a single factor between treatments, using data previously processed by square root to meet homogeneity assumptions using Levene's test (Sokal & Rohlf 2012). Different time samples were compared using repeated-measures ANOVA. A permutational multifactorial analysis of variance (PERMANOVA) (Anderson 2001) was used for comparison of algal species composition at different succession stages between coral-dominated and free areas, as well as different settlement substrates (coral substratum or artificial plates). Area covered by algae was a dependent variable on the analysis. Treatments and periods were independent variables in the ANOVA, and both are fixed variables. Therefore, the analysis had two factors: treatments (3 levels, i.e. colonisation on scraped areas of coral, artificial plates on corals, and artificial plates on coral-free areas) and time (3 levels, i.e. 23, 154, and 230 days). In addition, we also assessed the interaction between factors. We used 9999 permutations. Significantly distinct groups were identified using post-hoc pairwise tests when needed.

Patterns of algal colonisation were visualised using a non-metric multidimensional scaling (nMDS) ordination, with vectors calculated using Pearson's correlation coefficients. Only the most influential algal genera identified by a SIMPER analysis (Clarke & Gorley 2006) were plotted. Similarity percentages analysis (SIMPER) was used to examine how each algal morphological group contributed to similarities between algae composition in coral-covered and -free areas (Warwick & Clarke 1990). While a similarity analysis (ANOSIM) tested for differences in algal composition (Clarke 1993). Both sets of analyses, PERMANOVA with nMDS and ANOSIM with Simper, were conducted on Bray-Curtis similarity matrices (Clarke 1993).

The correlation between urchin density and habitat complexity was assessed using the Pearson's method at a 0.05 significance level. Data were normalised using a log (X +1) transformation.

## RESULTS

### Colonisation of algae on dead or damaged coral surfaces

Scraped areas of *S. stellata* were colonised by nine algal genera at all sampling times (*Amphiroa*, *Cladophora*, *Colpomenia*, *Enteromorpha*, *Hypnea*, *Jania*, *Polysiphonia*, *Sargassum*, and *Spyridia*), but one algal specimen belonged to the family Ceramiaceae (Table I). However, not all species were present during the early period (day 23), appearing only after day 154 (henceforth referred to as middle period). Likewise, some species present at the beginning of colonisation were not present in late periods, leading to different compositions throughout the succession periods. However, the significance test (PERMANOVA,  $p < 0.05$ ) and *post-hoc* analysis showed that only the early period had a different composition (Table II); therefore, after day 154, composition tended to be the same as that after day 230 (hereinafter referred to as the late period). Thus, community structure in the early period had a different pattern from those in the following times (ANOSIM,  $p < 0.05$ , global R 0.498), as represented by the two groupings in then MDS ordination (Fig. 3). More detailed analyses (SIMPER) of community structure showed that the morphological algal group contributing most to differentiate species composition in the early period from subsequent periods was articulated coralline algae. This morphological group is represented by the species *Amphiroa* sp. and *Jania* sp. The early colonisation was marked by an increase in some filamentous algae (*Polysiphonia* sp.,

**Table I. Percentage ( $\pm$  SD) of colonised algal coverage on scraped coral (C) and recruitment plates in the region with corals (P [c]) and without corals (P[wc]).**

Algal colonisation (%)	Early colonisation			Intermediate colonisation			Late colonisation		
	C	P[c]	P[wc]	C	P[c]	P[wc]	C	P[c]	P[wc]
<b>Rhodophyceae</b>									
Ceramiaceae	2.8 $\pm$ 3.7	0.8 $\pm$ 1.5			0.9 $\pm$ 1.9	1.6 $\pm$ 3.0		< 0.1 $\pm$ 0.1	0.2 $\pm$ 0.2
<i>Ceramium</i> sp.	0.5 $\pm$ 0.8			0.4 $\pm$ 0.6			0.1 $\pm$ 3.4	0.5 $\pm$ 0.8	
<i>Hypnea</i> sp.	1.3 $\pm$ 2.2	0.9 $\pm$ 0.8	< 0.1 $\pm$ 0.1	6.3 $\pm$ 9.0	2.2 $\pm$ 2.6		7.3 $\pm$ 4.5	4.7 $\pm$ 6.3	
<i>Spyridia</i> sp.		< 0.1 $\pm$ 0.1		1.8 $\pm$ 3.2			0.9 $\pm$ 1.8	0.5 $\pm$ 0.8	
<i>Polysiphonia</i> sp.	6.6 $\pm$ 6.3	0.4 $\pm$ 0.3			3.1 $\pm$ 7.7		5.1 $\pm$ 4.4	0.7 $\pm$ 0.6	
<i>Laurencia</i> sp.		0.4 $\pm$ 0.8			3.1 $\pm$ 5.5			25.0 $\pm$ 35.6	0.1 $\pm$ 0.1
<i>Jania adhaerens</i>	0.7 $\pm$ 1.2	3.8 $\pm$ 1.7		19.0 $\pm$ 5.1	13.4 $\pm$ 8.4		21.8 $\pm$ 10.7	13.9 $\pm$ 10.5	
<i>Amphiroa beauvoisii</i>	2.6 $\pm$ 4.0	0.1 $\pm$ 0.1		35.5 $\pm$ 43.9	3.8 $\pm$ 5.5		33.2 $\pm$ 20.3	20.8 $\pm$ 16.8	
<i>Pneophyllum</i> sp.		13.3 $\pm$ 8.2	4.1 $\pm$ 1.9		18.8 $\pm$ 8.1	13.4 $\pm$ 4.8		27.4 $\pm$ 6.0	11.6 $\pm$ 4.8
<b>Phaeophyceae</b>									
<i>Colpomenia sinuosa</i>	0.2 $\pm$ 0.3	2.9 $\pm$ 3.3			0.1 $\pm$ 0.2				
<i>Hincksia</i> sp.		6.7 $\pm$ 2.9						0.2 $\pm$ 0.4	
<i>Sphacelaria</i> sp.		1.3 $\pm$ 1.0			1.7 $\pm$ 1.1			6.8 $\pm$ 5.1	
<i>Sargassum</i> sp.	2.4 $\pm$ 4.2			11.7 $\pm$ 20.3	0.1 $\pm$ 0.1		3.7 $\pm$ 6.1	1.2 $\pm$ 1.9	
<b>Chlorophyceae</b>									
<i>Enteromorpha</i> sp.	2.4 $\pm$ 4.1	0.7 $\pm$ 0.4							
<i>Cladophora</i> sp.		3.5 $\pm$ 1.7		3.9 $\pm$ 6.8	2.5 $\pm$ 2.1		4.1 $\pm$ 3.7	4.7 $\pm$ 4.2	

Ceramiaceae, and *Enteromorpha* sp.), but they reduced in the subsequent periods.

The total area colonised by algae in coral scrapings (%) was significantly lower in the early period than in subsequent periods (Table III, PERMANOVA,  $p < 0.05$ ). We observed an interaction between factors since algal coverage on corals was lower than that in artificial plates in the early period, but it was inverse in the intermediated period. Likewise, no significant differences were observed for total algal coverage between the middle and late periods (Fig. 4). When compared with direct colonisation (scraping), recruitment plate on coral colonies had four more genera (*Hincksia*, *Laurencia*, *Pneophyllum*, and *Sphacelaria*). By contrast,

only crustose coralline (*Pneophyllum* sp.) and rare filamentous algae were found on plates fixed away from corals (Table I). Besides algae, barnacles were observed in both treatments.

### Influence of coral-dominated environment and substrate

Species composition of recruited algae was significantly different between treatments in all colonisation times (Table II - PERMANOVA,  $p < 0.05$ ). The nMDS analysis (Fig. 3) showed that community structure in the coral-free area (mainly crustose coralline algae and barnacles) was different from those in plates fixed on corals or the scraped coral surfaces (ANOSIM,  $p < 0.05$ , Global R 0.706). In terms of coral-free area,

**Table II.** Permutational multivariate analysis of variance (PERMANOVA). Comparison of the algal species compositions recruited among the factors: treatment (scraped coral (C)), recruitment plates in the region with corals (P[c]) and without corals (P [wc]), and time (early, intermediated, and late). Degrees of freedom (df), sum of squares (SS), and mean squares (MS). \*Significant results in bold.

	df	SS	MS	F	p
Treatment (Tr)	2	5361228.9	2680614.4	144.4	<b>0.0001</b>
Time (t)	2	519663.4	259831.7	1.6	0.2740
Tr x t	4	635104.4	158776.1	8.5	<b>0.0001</b>
Residual	36	667922.4	18553.4		
Total	44	7183919.2			
<b>Tukey's pairwise test</b>					
Level	Factor: Tr		Level	Factor: t	
<b>Early</b>	p - value		<b>Coral</b>	p - value	
C x P[c]	0.0069		Early x Interm.	0.0073	
C x P[wc]	0.0077		Early x Late	0.0093	
P[c] x P[wc]	0.0083		Interm. x Late	0.5774	
<b>Intermediated</b>			<b>P[c]</b>		
C x P[c]	0.0092		Early x Interm.	0.0065	
C x P[wc]	0.0076		Early x Late	0.0082	
P[c] x P[wc]	0.0083		Interm. x Late	0.0875	
<b>Late</b>			<b>P[wc]</b>		
C x P[c]	0.0096		Early x Interm.	0.0072	
C x P[wc]	0.0070		Early x Late	0.0082	
P[c] x P[wc]	0.0107		Interm. x Late	0.2275	

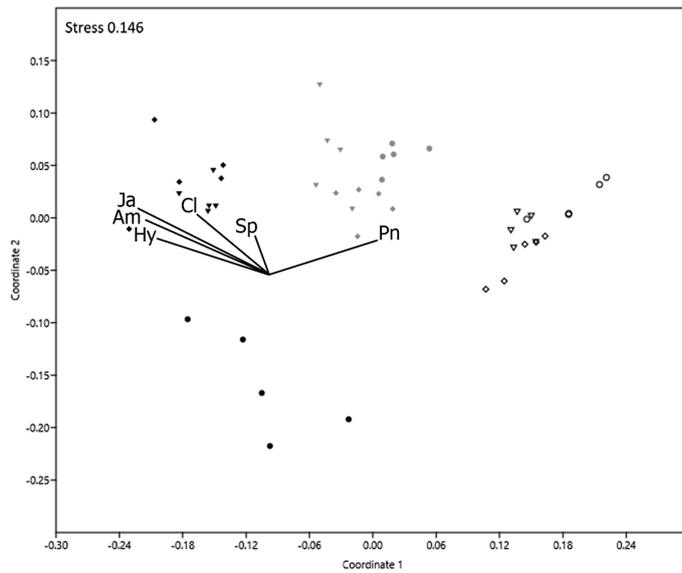
although crustose algae dominated recruitment plates in the late colonisation period, such coverage was lower in the early period. The percentage of algal cover in the coral-free area was lower (ANOVA,  $p < 0.05$ ) when compared to that on scraped coral surfaces in all periods (Fig. 4).

Algal turf composition on plates near corals was distinct from that living directly on scraped coral (Table II, PERMANOVA,  $p < 0.05$ ). It can also be seen in Fig. 3 (ANOSIM,  $p < 0.05$ ). Such difference can be explained by the absence of

crustose coralline algae in scraped corals and higher coverage of articulated coralline algae on plates near coral (SIMPER, 42.76% contribution). Yet, significant differences between treatments were only registered in the early period (PERMANOVA,  $p < 0.05$ ). Changes from the middle period onwards were not significant (Table II).

#### Assessment of herbivores (sea urchins)

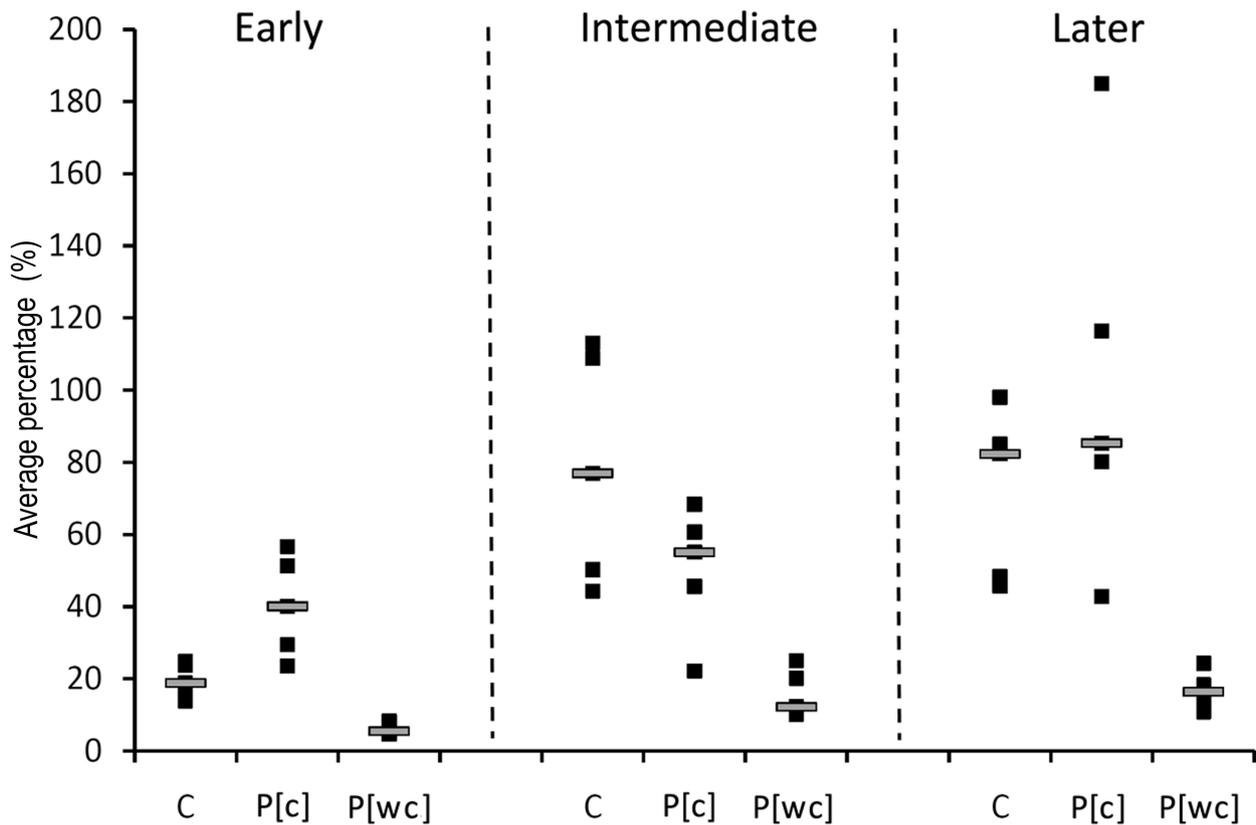
Sea urchin density was higher in coral-free areas ( $p < 0.05$ ). *Lytechinus variegatus* was the species commonly found along transects



**Figure 3.** nMDS plot of algal assemblages. Circles, diamonds, and inverted triangles represent the early, intermediate, and late colonisation, respectively. Vectors are based on Pearson correlation coefficients and display the key genera based on a SIMPER analysis that typify certain groupings: (black) algal colonisation directly on dead or damaged coral areas [*Amphiroa* (Am), *Jania* (Ja), *Hypnea* (Hy)]; (grey) algal colonisation on recruitment plates in coral-covered areas [*Pneophyllum* (Pn), (Ja); *Cladophora* (Cl), *Sphacelaria* (Sp)]; and (clear) algal colonisation on recruitment plates in coral-free areas [(Pn)].

**Table III.** Permutational multivariate analysis of variance (PERMANOVA). Comparison of the average percentage of colonised algal coverage among the factors: treatment (scraped coral (C)), recruitment plates in the region with coral (P[c]) and without coral (P [wc]), and time (early, intermediated, and late). Degrees of freedom (df), sum of squares (SS), and mean squares (MS). \*Significant results in bold.

	df	SS	MS	F	p
Treatment (Tr)	2	23059.8	11529.9	20.67	<b>1.06E-06</b>
Time (t)	2	13413.5	6706.74	12.02	<b>0.0001003</b>
Tr x t	4	8488.71	2122.18	3.804	<b>0.01114</b>
Residual	36	20085.8	557.938		
Total	44	65047.7			
<b>Tukey's pairwise test</b>					
Level	Factor: Tr		Level	Factor: t	
<b>Early</b>	p - value		<b>Coral</b>	p - value	
C x P[c]	<b>0.0064</b>		Early x Intermed.	<b>0.0003</b>	
C x P[wc]	<b>0.0003</b>		Early x Late	<b>0.0004</b>	
P[c] x P[wc]	<b>0.0002</b>		Intermed. x Late	0.9537	
<b>Intermediated</b>			<b>P[c]</b>		
C x P[c]	0.2617		Early x Intermed.	0.7509	
C x P[wc]	<b>0.0003</b>		Early x Late	<b>0.0269</b>	
P[c] x P[wc]	<b>0.0029</b>		Intermed. x Late	0.09618	
<b>Late</b>			<b>P[wc]</b>		
C x P[c]	0.5331		Early x Intermed.	<b>0.001</b>	
C x P[wc]	<b>0.0005</b>		Early x Late	<b>0.001</b>	
P[c] x P[wc]	<b>0.0002</b>		Intermed. x Late	0.9131	



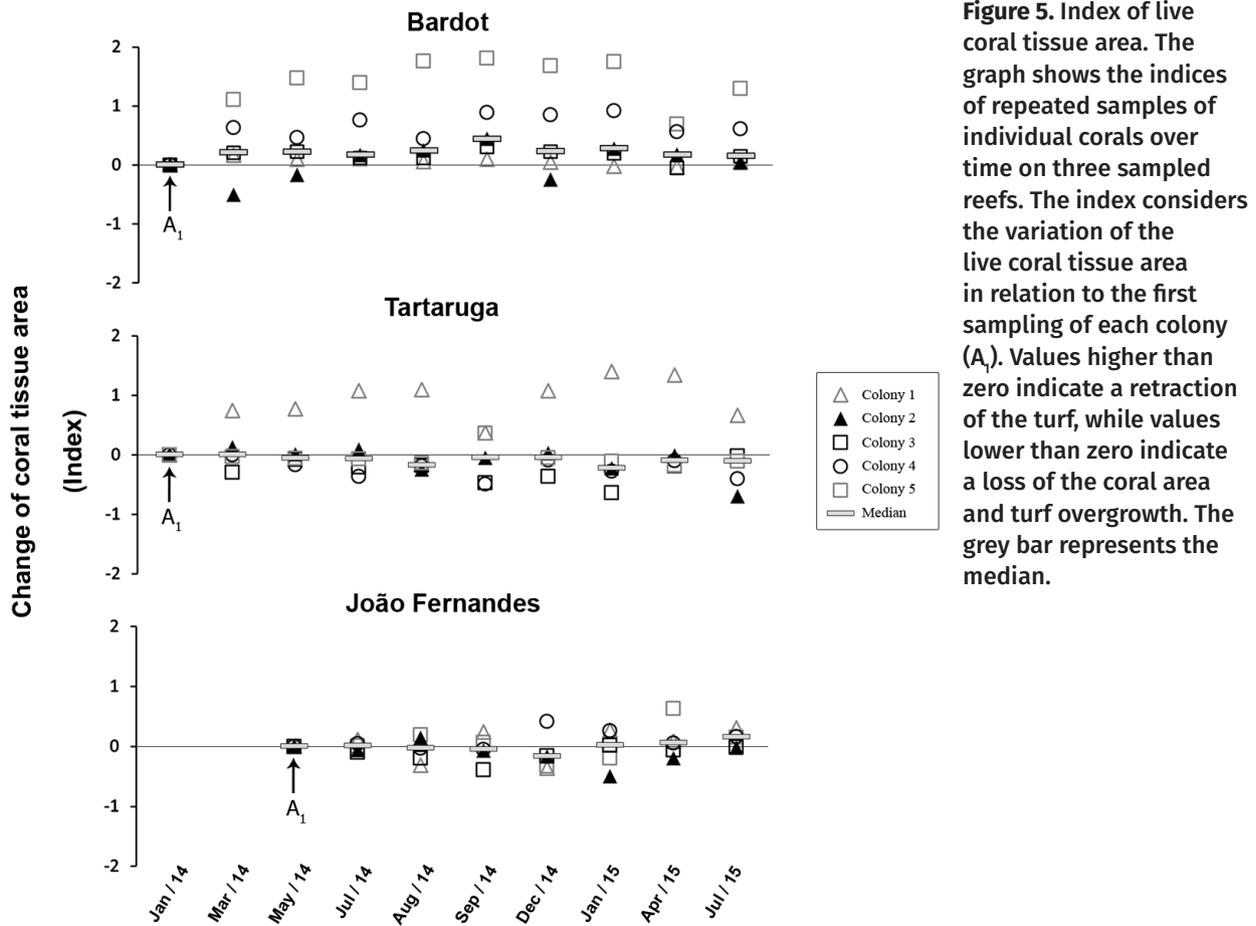
**Figure 4.** Graph comparing the average percentage of colonised algal coverages on scraped coral (C) and recruitment plates in the region with corals (P[c]) and without corals (P [wc]). Comparisons made during the early, intermediate, and late colonisation. The grey bar represents the median.

and on recruitment plates in coral-free areas. Urchin presence was negatively correlated with the structural complexity of the environment (Pearson correlation  $R^2$  0.721 /  $p$  = 0.007), as only one individual was recorded along all transects from a coral-covered area (0.025 individuals/ $m^2$  - roughness 1.35). However, density in coral-free areas was, on average, 2.325 individuals/ $m^2$  - roughness 1.05). Other individuals of the same urchin species were observed in coral-covered areas but outside the limits of transects and at quite low density. Moreover, no urchins were observed on *S. stellata* colonies in coral-dominated areas but the sand, algae-covered rocks, and hydrocoral (*Millepora braziliensis* Verrill, 1868), located around corals.

### Coral-algal monitoring

During the 1.5 years of monitoring, there were no new algal turfs in areas previously occupied by live coral tissue, on reefs located on the beaches of Tartaruga, Bardot, and João Fernandes. Sediments occasionally mixed with coral mucus accumulated at points adhered to living tissue surfaces. However, these sediment accumulation areas were temporary and disappeared in the subsequent months.

Interaction dynamics between live coral tissue and algal turfs varied over the 1.5 years. Fig. 5 shows size variations between coral- and algae-occupied areas over time concerning the first record. Sometimes algal turfs grew on coral tissues ( $I < 0$ ), at other times turf-covered areas decreased and coral tissue grew ( $I > 0$ ). Although



**Figure 5.** Index of live coral tissue area. The graph shows the indices of repeated samples of individual corals over time on three sampled reefs. The index considers the variation of the live coral tissue area in relation to the first sampling of each colony ( $A_1$ ). Values higher than zero indicate a retraction of the turf, while values lower than zero indicate a loss of the coral area and turf overgrowth. The grey bar represents the median.

these results showed significant variations in a few months (repeated measures ANOVA,  $p < 0.05$ ), when considering the entire monitoring period, no clear competitive trends were observed by either corals or algae (Fig. 5).

## DISCUSSION

Herein we revealed that (1) the occupation of dead areas of coral initially starts with filamentous algae and stabilizes after five months with the presence of articulated coralline algae. However, we observed that (2) algal turf colonisations were influenced by coral coverage, with higher percentage of algae coverage and number of algal species in coral dominated environments. We also noted that (3) dead or damaged areas of

coral offer a more selective substrate, benefiting filamentous and articulated algae growth, but crustose coralline algae did not develop on this substrate. Thus, the colonisation of algal turfs is not only influenced by the substrate provided by dead areas of coral but also by the presence of live corals. After colonisation, (4) the invasion potential of turfs on live coral tissue appeared to vary over time and did not show any trend of retraction or advancement. Thus, the coral dominated areas somehow benefit algal turf colonisation although an apparent inhibition of turf growth was registered on live coral tissue.

### Algal turf recruitment patterns

Bare substrate (coral-damaged or -dead areas) was rapidly colonised by filamentous algae. This

group of algae is composed of many opportunistic species. In the absence of space competitors, these species rapidly occupy vacant areas before slowing down in subsequent stages, and they may even be replaced with other species in latter successional stages (Dodds & Gudder 1992). Our results confirm such opportunistic pattern as we documented an initial increase in filamentous algae, followed by a subsequent decline. Moreover, it should be noted that the initial algal turf colonisation had previously been associated with a rapid colonisation by cyanobacteria, before or concurrently with filamentous algae recruitment (Diaz-Pulido & McCook 2002). However, in our study, non-macroalgal constituents in turf formation were not assessed. In the late period, algal turf composition was similar to that observed previously in a study conducted in the same area (Oigman-Pszczol & Creed 2004). However, Oigman-Pszczol et al. (2004) recorded a higher abundance of articulated coralline algae of the species *Amphiroa beauvoisii* J. V. Lamouroux 1816, and *Jania adhaerens* J.V. Lamouroux 1816, in addition to other less abundant taxa. Other than the groups that have already been described, we also found the algal genera *Colpomenia* sp. and *Enteromorpha* sp. (in its juvenile state) in the turfs, but in lower abundances.

The rapid growth of articulated coralline algae suggests that the calcareous substrate in areas free of live coral tissue facilitated their colonisation and development. Furthermore, a progressive increase in articulated coralline coverage suggests that *S. stellata* did not pose allelopathic inhibition on these algae. After the day 154 (middle period), total coverage of colonised algae in scraped areas was close to 100%, and it did not differ in the late colonisation. When compared with our long-term monitoring (1.5 years), increase in algal turf colonisation on live coral tissue was not progressive and,

although certain groups of algae were not inhibited in areas of dead coral, such increase in live coral tissue appeared to be limited.

Coral inhibition by algal growth has previously been described elsewhere (Vansteveninck et al. 1988, Diaz-Pulido & McCook 2002, 2004a, Jompa & McCook 2003a, Venera-Ponton et al. 2011) and suggests that coral absence benefits algae growth due to the lack of competitors (Vansteveninck et al. 1988). In our study, algal species composition differed in the presence of corals but was richer in coral-dominated areas compared to coral-free areas. Constant low coverage or absence of filamentous algae in coral-free areas throughout the entire study suggests that other limiting factors might have acted more intensely than in coral-dominated areas, but exactly which factors were important remains unclear. Moreover, the low algal species richness on plates fixed in coral-free areas points to limiting factors for filamentous algae settlement and growth. It also indicates that crustose coralline algae are more resistance to possible stress factors present in these areas (Airoldi 1998) and may be competitively dominant under these environmental conditions. Crustose coralline algae occupation is not always considered to be an exclusion factor for other algal groups. In some habitats, they can coexist without apparently competing with other groups (Airoldi 2000), as we observed in coral-covered areas. Steneck (1997) reported that algal turfs and crustose coralline algae coexistence only occurs under intense herbivory conditions. However, Airoldi (2000) noted such co-occurrence in environments of extremely low herbivory and claimed that tolerance to other algal groups, in some environments, may be an important factor rather than pure competition.

The higher algal cover in areas dominated by *S. stellata* compared to coral-free regions suggests that coral-dominated reefs may

have a direct or indirect effect on algae recruitment dynamics. Since several factors may be associated with the coral-dominated environment, it becomes difficult to explain what was controlling algal recruitment and growth mechanisms. Thus, the differences between the treatments could be associated with factors such as herbivorous attraction, hydrodynamics, and sedimentation, which seems to shape algal recruitment. These factors seem to vary on a local scale since coral-free regions are arranged in patches within the reef.

### **Small-scale environmental influence**

#### ***Structural complexity and urchin herbivory***

Among the factors mentioned above, habitat structural complexity can increase herbivory pressure, for example by sea urchins (Lee 2006), acting as a top-down force over the algae community. Studies on sea urchin density have shown that herbivore species are key controllers of algal coverage on some reefs (McClanahan 1997, Lee 2006, Bronstein & Loya 2014). On the other hand, high numbers of sea urchins can act oppositely and lead to reef degradation (McClanahan & Shafir 1990). Furthermore, on the Great Barrier Reef (a relatively healthy reef system), sea urchins are exceedingly rare when compared to other reef systems globally (Tebbett & Bellwood 2018).

Our study revealed higher algal recruitment and growth in coral regions with *S. stellata* colonies and low density of sea urchins (*L. variegatus*). Furthermore, we did not observe the species *Echinometra lucunter* and *Arbacia lixula*, which are sea urchins commonly found on hard substrata in this region. Indeed, algal coverage on recruitment plates in coral-free areas was five times lower and sea urchin density about ten times higher. These herbivores were often seen grazing recruitment plates. Here, although the coral-dominated region

had greater structural complexity, these corals can form a physical barrier blocking sea urchin movements and limiting access to food resources (van de Koppel et al. 1996). This would favour algal recruitment and growth by reducing herbivory pressure. Such macroalgae herbivory reduction due to corals has already been described by Littler et al. (1987) and Bennett et al. (2010), who revealed that branched coral structures prevent herbivorous fish from accessing algae. Although *S. stellata* has no branches, its semi-spherical massive growth, which is common in the genus *Siderastrea* genus (Lewis 1989), can prevent sea urchins from reaching coral regions far from the bottom. This hypothesis was supported by the fact that we did not find any urchins on the top of the coral.

The increased algae recruitment and growth in coral-dominated areas may have been due to the greater structural complexity of the habitat. Such complexity leads to the formation of microhabitats and shelters against herbivores, which may potentially increase the number of algal species inhabiting the region (MacArthur & MacArthur 1961, Huston 1979). Even though we noticed a strong correlation between urchin absence and algae recruitment and growth in coral-dominated areas, we did not evaluate their significance explicitly. Yet, we highlight that urchin grazing in coral-free areas could be an inhibiting factor to algae recruitment and growth. Reduction in urchin herbivory may also be associated with other factors in synergism, which influence algal recruitment and growth (e.g., negative correlations between sediment load and fish herbivory rate, as discussed below).

#### **Sediment load and herbivorous fishes**

Sedimentation is a factor that is negatively related to algal settlement and growth in early development stages (Schiel et al. 2006). However, sediment accumulation in the epilithic algal matrix can also decrease herbivory rates by fishes, probably due to a reduction in palatability.

Consequently, such accumulation can increase the chances of survival and growth of algal recruits (Goatley & Bellwood 2013). Sediments in algal turfs can also influence fish feeding behaviour by hindering its access to turf filaments (Tebbett & Bellwood 2019, Tebbett et al. 2020). Furthermore, coral reef structural complexity provides a three-dimensional topography with recesses, holes, and elevations, which may reduce water flow over the substrate (Huang et al. 2012a, b) and facilitate sediment accumulation and reduces abrasion to algae. Tebbett et al. (2020) observed that reef complexity is directly related to sediment dynamics and nature of algal turfs. Tebbett et al. (2020) noted that, on a small scale (cm - m), on elevated surfaces where reefs become more exposed to hydrodynamic action and fish feeding, sediment accumulation was lower and algal turf length shorter (Tebbett & Bellwood 2020). In our study, even though we did not assess colonisation at different heights within a coral-dominated area, we clearly noted that elevated coral colonies build a barrier against waves and currents; hence, decreasing the water flow and facilitating sediment deposition and algal turf growth (Gowan et al. 2014). Recruitment plates fixed in structurally complex coral-covered areas visually appeared to have more sediment deposition, while plates attached in coral-free areas had limited sediment accumulation. These results corroborate the hypothesis that sediments reduce herbivory by fish, at least on turfs. Sediments may initially accumulate on the coral surface and favour algal turf growth by reducing herbivore access. Thereby, increasing turf length and further sediment trapping Latrille et al. (2019), leading to a positive feedback (Tebbett & Bellwood 2019). This positive association has a threshold. Tebbett et al. (2018) demonstrated that high sediment loads reduce turf biomass build-up, probably due to the development of

anoxic conditions in layers near the substrate (Clausing et al. 2014).

We observed a greater abundance of corticated algae, represented by *Laurencia* sp. in plates fixed on corals at more advanced succession stages. Since their stems are leafy and flexible, we did not observe deposition of sediment on their apical regions in the last periods of development. This was likely due to constant changes in current directions, which swept deposited sediments off these algae. Even if deposited sediment loss can favour herbivores, *Laurencia* is known to produce secondary metabolites that strongly inhibit herbivory (Pereira et al. 2003). However, as this algal species was absent in coral-free areas, other factors, such as abrasion, may have been more important in the early stages of recruitment and development. These observations suggest that sediment deposits on recruitment plates in coral-free areas might have been removed or resuspended.

Abrasion by sediment movement over recruitment plates may influence the survival of algal recruits more susceptible to mechanical action (Araujo et al. 2012). This hypothesis corroborates our findings on the predominance of coralline algae incrustation only on plates fixed in coral-free areas, as well as the absence of deposited sediments. The maintenance of crustose coralline algae can be explained by their resistance to environments with intense hydrodynamics and wave energy (Adey 1998). Moreover, crustose coralline algae are more affected by sediments, so a decrease in deposition on recruitment plates in coral-free areas was probably a positive factor for their growth and dominance in these areas (Fabricius 2005).

Sediments collected from the top of recruitment plates in coral-dominated sites were associated with a mucilage matrix, forming

a layer of particles adhered to the substrate. These sediment particles trapped in coral mucus may have reduced or prevented abrasion effects, facilitating algae settlement and growth. This hypothesis is supported by the greater algae coverage on recruitment plates with mucilage and sediment in coral-covered areas. This mucilage may have originated from mucilaginous sheaths of filamentous cyanobacteria in algae turfs (Stal 2003) or exudates released by *S. stellata* (Jatkar et al. 2010), given its proximity to recruitment plates. Furthermore, exudates released by corals can contain nutrient concentrations higher than those found in water. Nakajima et al. (2015) observed that mucus released by *Acropora* sp. corals has phosphate concentrations 135 times higher than that found in water samples. Thus, both cyanobacterial and coral exudates could enrich nutrients on a local scale for the algal community, enhancing conditions for turf development.

Scleractinian corals are known to produce mucus to facilitate removal of sediments (Hubbard & Pocock 1972, Richman et al. 1975). Part of the mucus is detached from the coral and released into water, forming clusters of sediments deposited throughout reef areas (Wild et al. 2004). Our study is located in an area influenced by sediments brought from nearby rivers (Godiva et al. 2010), and corals of the *Siderastrea* genus are known to be resistant to intense sedimentation due to their constant removal of sediment particles (Lirman et al. 2002, Lirman & Manzello 2009). Thus, although not quantified here, *S. stellata* could produce mucus constantly to clear sediments. The coral mucus, together with cyanobacteria, could form a sediment mucilage matrix, thereby facilitating algae settlement by reducing abrasion and herbivory, as well as increasing nutrient supplies.

### Substrate selectivity

Although it appeared that an increase in habitat complexity favoured algal recruitment and growth, we observed that the number of species able to settle on the coral substrate was limited. Crustose coralline algae failed to colonise the dead surface of corals but were found on recruitment plate surfaces within the same region. Coral substrate appeared to favour the growth of articulated algae, with high coverages in the middle and late colonisation periods. The lower coverage of articulated algae on the plates in coral-dominated areas compared to those on scraped areas of dead corals may have arisen from the competition with corticated algae, especially *Laurencia*, which grew rapidly. Borowitzka et al. (1978) claimed that some algae such as *Laurencia* would not grow on artificial substrates directly, requiring other species, e.g. crustose corallines, to grow before they colonise. Similarly, we found the same genus on artificial plates in the late recruitment period, when there was a previous presence of crustose corallines.

Substrate topography may also influence the recruitment of algae. Artificial plates were made of epoxy resin; however, its roughness and the depressions moulded in plates (to mimic the coral surface) were not identical to the natural substrate. Harlin & Lindbergh (1977) experimentally observed that algal composition differed among surfaces on different roughness scales, and they observed greater diversity and coverages on rougher surfaces. These data suggest that besides external factors acting on competitive interaction between algae and corals, coral substrate topography could also act as a selective factor on algal recruitment and may even influence fish grazing intensity (Hixon & Brostoff 1985).

### Algal turfs vs. corals

Coexistence of algal turfs and corals was also limited to areas previously damaged or dead, as no consistent growth of algal turfs on live coral tissues was observed for 1.5-year. This result suggests that corals are resistant to algal overgrowth and that previous damages to their tissues were necessary for algal colonisation (Diaz-Pulido & McCook 2004b). Algal turfs have previously been described as poor competitors with the corals (Jompa & McCook 2003a, b), corroborating our findings. We conclude that the balance in competitiveness has not changed, and algae turf growth depends on disturbances affecting coral survival (O'Brien & Scheibling 2018).

The area occupied by live coral tissue was not static and underwent constant changes. This suggests a dynamic interaction between the coral and algal turfs. This could be due to coral growth since *S. stellata* colonies typically have a massive form. An important study carried out in the South China Sea compared interactions among six different growth forms of coral and algae turfs (Swierts & Vermeij 2016). Swierts & Vermeij (2016) revealed that massive forms of coral growth have greater competitive potentials, preventing an over growth of algal turfs. Swierts & Vermeij (2016) also showed that algal turfs were competitively successful only in 38% of the interactions with massive corals, whereas turfs won in 82% of the interactions with branched coral forms.

Other factors may determine competitiveness between corals and algal turfs such as the interaction between water flow and increased sediment loads. This may increase the area of damaged coral tissue and therefore facilitate the expansion of algal turfs (Gowan et al. 2014). We believe that competitive potential between algae and corals in our work was driven by sedimentation, water

stream flow changes, herbivory activities, and substrate characteristics, which depend on reef structure complexity on a small scale. Our results demonstrate a competitive stalemate between corals and algae under the current environmental conditions of the studied reef. But in the event of an acute disturbance, some corals are likely to die and would be colonised by algae. If corals do not recover areas of partial mortality, they will decline in the long-term. The fact that a coral community is dominated by stronger competitors (massive growth form) suggests that such competitiveness will allow corals to persist.

### CONCLUSION

Corals on the marginal reefs studied herein do not appear to be readily overgrown by the turf-forming algae community. Thus, although the presence of coral on a small scale may bring some direct or indirect advantages to algal turf colonisation and development, so their competitiveness remains dynamic but without winners, indicating coral resistance to prevailing environmental conditions. Given the apparent standoff between algal turfs and corals, there is a concern on how corals will recover from any future acute disturbances. Moreover, the patterns documented in this study may also be relevant for other reef areas.

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## REFERENCES

- ADEY WH. 1998. Coral reefs: Algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. *J Phycol* 34: 393-406.
- AIROLDI L. 1998. Roles of Disturbance, Sediment Stress, and Substratum Retention on Spatial Dominance in Algal Turf. *Ecology* 79: 2759-2770.
- AIROLDI L. 2000. Effects of disturbance, life histories, and overgrowth on coexistence of algal crusts and turfs. *Ecology* 81: 798-814.
- ANDERSON MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26: 32-46.
- ANDRAS TD, ALEXANDER TS, GAHLENA A, PARRY RM, FERNANDEZ FM, KUBANEK J, WANG MD & HAY ME. 2012. Seaweed allelopathy against coral: surface distribution of a seaweed secondary metabolite by imaging mass spectrometry. *J Chem Ecol* 38: 1203-1214.
- ARAUJO R, ARENAS F, ÅBERG P, SOUSA-PINTO I & SERRÃO EA. 2012. The role of disturbance in differential regulation of co-occurring brown algae species: Interactive effects of sediment deposition, abrasion and grazing on algae recruits. *J Exp Mar Biol Ecol* 422/423: 1-8.
- ARONSON RB & PRECHT WF. 1995. Landscape patterns of reef coral diversity: a test of the intermediate disturbance hypothesis. *J Exp Mar Biol Ecol* 192: 1-14.
- BAROTT KL, RODRIGUEZ-MUELLER B, YOULE M, MARHAVER KL, VERMEIJ MJA, SMITH JE & ROHWER FL. 2012. Microbial to reef scale interactions between the reef-building coral *Montastraea annularis* and benthic algae. *Proc R Soc B* 279: 1655-1664.
- BELLWOOD DR, HOEY AS, ACKERMAN JL & DEPCZYNSKI M. 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Glob Change Biol* 12: 1587-1594.
- BENNETT S, VERGES A & BELLWOOD DR. 2010. Branching coral as a macroalgal refuge in a marginal coral reef system. *Coral Reefs* 29: 471-480.
- BOROWITZKA MA, LARKUM AW & BOROWITZKA LJ. 1978. A preliminary study of algal turf communities of a shallow coral reef lagoon using an artificial substratum. *Aquat Bot* 5: 365-381.
- BRONSTEIN O & LOYA Y. 2014. Echinoid community structure and rates of herbivory and bioerosion on exposed and sheltered reefs. *J Exp Mar Biol Ecol* 456: 8-17.
- BROWN KT, BENDER-CHAMP D, BRYANT DE, DOVE S & HOEGH-GULDBERG O. 2017. Human activities influence benthic community structure and the composition of the coral-algal interactions in the central Maldives. *J Exp Mar Biol Ecol* 497: 33-40.
- BURKEPILE DE & HAY ME. 2006. Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. *Ecology* 87: 3128-3139.
- BURKEPILE DE & HAY ME. 2009. Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef. *Mar Ecol Prog Ser* 389: 71-84.
- CARVALHO LL, DIAS FF, SOUZA VDSM, SILVA AL, SANTOS PRA, VARGAS R & VILLAÇA RC. 2018. Low-cost solution for correction of tidal changes in the mapping of coastal environments. *Rev Bras Geogr Fís* 11: 904-912.
- CLARKE KR. 1993. Non-parametric multivariate analyses of changes in community structure. *Austral Ecol* 18: 117-143.
- CLAUSING R, ANNUNZIATA C, BAKER G, LEE C, BITTICK S & FONG P. 2014. Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef. *Mar Ecol Prog Ser* 517: 121-129.
- CONNELL SD, FOSTER MS & AIROLDI L. 2014. What are algal turfs? Towards a better description of turfs. *Mar Ecol Prog Ser* 495: 299-307.
- COPERTINO M, CONNELL SD & CHESHIRE A. 2005. The prevalence and production of turf-forming algae on a temperate subtidal coast. *Phycologia* 44: 241-248.
- CRUZ IC, WATERS LG, KIKUCHI RK, LEÃO ZM & TURRA A. 2018. Marginal coral reefs show high susceptibility to phase shift. *Mar Pollut Bull* 135: 551-561.
- DIAZ-PULIDO G, HARI S, MCCOOK LJ & HOEGH-GULDBERG O. 2010. The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs* 29: 203-208.
- DIAZ-PULIDO G & MCCOOK LJ. 2002. The fate of bleached corals: patterns and dynamics of algal recruitment. *Mar Ecol Prog Ser* 232: 115-128.
- DIAZ-PULIDO G & MCCOOK LJ. 2004a. Algal recruitment and interactions. *Coral Reefs* 23: 225-233.
- DIAZ-PULIDO G & MCCOOK LJ. 2004b. Effects of live coral, epilithic algal communities and substrate type on algal recruitment. *Coral Reefs* 23: 225-233.
- DODDS WK & GUDDER DA. 1992. The ecology of *Cladophora*. *J Phycol* 28: 415-427.
- DOUGLAS A. 2003. Coral bleaching—how and why? *Mar Pollut Bull* 46: 385-392.

- FABRICIUS KE. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar Pollut Bull* 50: 125-146.
- FILBEE-DEXTER K & WERNBERG T. 2018. Rise of Turfs: a new battlefield for globally declining kelp forests. *BioScience* 68: 64-76.
- FRICKE A, TEICHBERG M, BEILFUSS S & BISCHOF K. 2011. Succession patterns in algal turf vegetation on a Caribbean coral reef. *Bot Mar* 54: 111-126.
- GOATLEY CHR & BELLWOOD DR. 2013. Ecological Consequences of Sediment on High-Energy Coral Reefs. *PLoS ONE* 8: e77737.
- GODIVA D, EVANGELISTA H, KAMPEL M, LICINIO MV & MUNITA C. 2010. Combined use of aerogammaspectrometry and geochemistry to access sediment sources in a shallow coral site at Armacao dos Buzios, Brazil. *Estuar Coast Shelf Sci* 87: 526-534.
- GONDIM AI, LACOUTH P, ALONSO C & MANSO CLDC. 2008. Echinodermata da Praia do Cabo Branco, João Pessoa, Paraíba, Brasil. *Biota Neotrop* 8.
- GOWAN JC, TOOTELL JS & CARPENTER RC. 2014. The effects of water flow and sedimentation on interactions between massive *Porites* and algal turf. *Coral Reefs* 33: 651-663.
- HARLIN M & LINDBERGH J. 1977. Selection of substrata by seaweeds: optimal surface relief. *Mar Biol* 40: 33-40.
- HILL SK & LAWRENCE JM. 2003. Habitats and Characteristics of the Sea Urchins *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata) on the Florida Gulf-Coast Shelf. *Mar Ecol* 24: 15-30.
- HIXON MA & BROSTOFF WN. 1985. Substrate characteristics, fish grazing, and epibenthic reef assemblages off Hawaii. *Bull Mar Sci* 37: 200-213.
- HUANG ZC, LENAIN L, MELVILLE WK, MIDDLETON JH, REINEMAN B, STATOM N & MCCABE RM. 2012a. Dissipation of wave energy and turbulence in a shallow coral reef lagoon. *J Geophys Res: Oceans* 117.
- HUANG ZC, REINEMAN BD, LENAIN L, MELVILLE WK & MIDDLETON JH. 2012b. Airborne lidar measurements of wave energy dissipation in a coral reef lagoon system. *J Geophys Res: Oceans* 117.
- HUBBARD JEB & POCKOCKY. 1972. Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. *Geol Rundsch* 61: 598-626.
- HUSTON M. 1979. A general hypothesis of species diversity. *The Am Nat* 113: 81-101.
- JATKAR AA, BROWN BE, BYTHELL JC, GUPPY R, MORRIS NJ & PEARSON JP. 2010. Coral Mucus: The Properties of Its Constituent Mucins. *Biomacromolecules* 11: 883-888.
- JOHNSON MD, COMEAU S, LANTZ CA & SMITH JE. 2017. Complex and interactive effects of ocean acidification and temperature on epilithic and endolithic coral-reef turf algal assemblages. *Coral Reefs* 36: 1059-1070.
- JOMPA J & MCCOOK LJ. 2002. Effects of competition and herbivory on interactions between a hard coral and a brown alga. *J Exp Mar Biol Ecol* 271: 25-39.
- JOMPA J & MCCOOK LJ. 2003a. Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*. *Mar Ecol Prog Ser* 258: 79-86.
- JOMPA J & MCCOOK LJ. 2003b. Coral-algal competition: macroalgae with different properties have different effects on corals. *Mar Ecol Prog Ser* 258: 87-95.
- KENDRICK GA. 1991. Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion. *J Exp Mar Biol Ecol* 147: 47-63.
- LATRILLE FX, TEBBETT SB & BELLWOOD DR. 2019. Quantifying sediment dynamics on an inshore coral reef: Putting algal turfs in perspective. *Mar Pollut Bull* 141: 404-415.
- LEE SC. 2006. Habitat complexity and consumer-mediated positive feedbacks on a Caribbean coral reef. *Oikos* 112: 442-447.
- LEWIS JB. 1989. Spherical growth in the caribbean coral *Siderastrea radians* (pallas) and its survival in disturbed habitats. *Coral Reefs* 7: 161-167.
- LIRMAN D & MANZELLO D. 2009. Patterns of resistance and resilience of the stress-tolerant coral *Siderastrea radians* (Pallas) to sub-optimal salinity and sediment burial. *J Exp Mar Biol Ecol* 369: 72-77.
- LIRMAN D, MANZELLO D & MACIA S. 2002. Back from the dead: the resilience of *Siderastrea radians* to severe stress. *Coral Reefs* 21: 291-292.
- LITTLER M & LITTLER D. 2011. Algae, Turf. In: Hopley D (Ed). *Encyclopedia of Modern Coral Reefs*: Springer Netherlands, p. 38-39.
- LITTLER MM, LITTLER DS & TAYLOR PR. 1987. Animal-plant defense associations: Effects on the distribution and abundance of tropical reef macrophytes. *J Exp Mar Biol Ecol* 105: 107-121.
- MACARTHUR RH & MACARTHUR JW. 1961. On bird species diversity. *Ecology* 42: 594-598.

- MCCLANAHAN T & SHAFIR S. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83: 362-370.
- MCCLANAHAN TR. 1997. Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. *J Exp Mar Biol Ecol* 218: 77-102.
- MCCOOK L, JOMPA J & DIAZ-PULIDO G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19: 400-417.
- MORRISSEY J. 1980. Community structure and zonation of microalgae and hermatypic corals on a fringing reef flat of magnetic island (Queensland, Australia). *Aquatic Botany* 8: 91-139.
- NAKAJIMA R, TANAKA Y, YOSHIDA T, FUJISAWA T, NAKAYAMA A, FUCHINOUE Y, OTHMAN BHR & TODA T. 2015. High inorganic phosphate concentration in coral mucus and its utilization by heterotrophic bacteria in a Malaysian coral reef. *Mar Ecol* 36: 835-841.
- NUGUES MM & BAK RP. 2006. Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. *Mar Ecol Prog Ser* 315: 75-86.
- O'BRIEN JM & SCHEIBLING RE. 2018. Turf wars: competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. *Mar Ecol Prog Ser* 590: 1-17.
- ODUM HT & ODUM EP. 1955. Trophic Structure and Productivity of a Windward Coral Reef Community on Eniwetok Atoll. *Ecol Monogr* 25: 291-320.
- OIGMAN-PSZCZOL SS & CREED JC. 2004. Size structure and spatial distribution of the corals *Mussismilia hispida* and *Siderastrea stellata* (Scleractinia) at Armacao dos Buzios, Brazil. *Bull Mar Sci* 74: 433-448.
- OIGMAN-PSZCZOL SS & CREED JC. 2006. Distribution and abundance of fauna on living tissues of two Brazilian hermatypic corals (*Mussismilia hispida* (Verrill 1902) and *Siderastrea stellata* Verrill, 1868). *Hydrobiologia* 563: 143-154.
- OIGMAN-PSZCZOL SS, FIGUEIREDO MAD & CREED JC. 2004. Distribution of benthic communities on the tropical rocky subtidal of Armacao dos Buzios, southeastern Brazil. *Mar Ecol-Pubbl Stn Zool Napoli* 1 25: 173-190.
- PEREIRA RC, DA GAMA BAP, TEIXEIRA VL & YONESHIGUE-VALENTIN Y. 2003. Ecological roles of natural products of the Brazilian red seaweed *Laurencia obtusa*. *Braz J Biol* 63: 665-672.
- PRESKITT LB, VROOM PS & SMITH CM. 2004. A rapid ecological assessment (REA) quantitative survey method for benthic algae using photoquadrats with scuba. *Pac Sci* 58(2): 201-209.
- RICHMAN S, LOYA Y & SLOBOCKIN LB. 1975. The rate of mucus production by corals and its assimilation by the coral reef copepod *Acartia negligens*. *Limnol Oceanogr* 20: 918-923.
- RILOV G, PELEG O, YERUHAM E, GARVAL T, VICHIK A & RAVEH O. 2018. Alien turf: Overfishing, overgrazing and invader domination in south-eastern Levant reef ecosystems. *Aquat Conserv: Mar Freshw Ecosyst* 28: 351-369.
- ROGERS R, DE OLIVEIRA CORREAL G, DE OLIVEIRA TC, DE CARVALHO LL, MAZUREK P, BARBOSA JEF, CHEQUER L, DOMINGOS TFS, DE ANDRADE JANDRE K & LEÃO LSD. 2014. Coral health rapid assessment in marginal reef sites. *Mar Biol Research* 10: 612-624.
- SCHIEL DR, WOOD SA, DUNMORE RA & TAYLOR DI. 2006. Sediment on rocky intertidal reefs: Effects on early post-settlement stages of habitat-forming seaweeds. *J Exp Mar Biol Ecol* 331: 158-172.
- SMITH JE, SHAW M, EDWARDS RA, OBURA D, PANTOS O, SALA E, SANDIN SA, SMRIGA S, HATAY M & ROHWER FL. 2006. Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecol Lett* 9: 835-845.
- SOKAL RR & ROHLF FJ. 2012. *Biometry: the principles and practice of statistics in biological research*. 4<sup>th</sup> ed, New York: W. H. Freeman and Co, 937 p.
- SPEARE KE, DURAN A, MILLER MW & BURKEPILE DE. 2019. Sediment associated with algal turfs inhibits the settlement of two endangered coral species. *Mar Pollut Bull* 144: 189-195.
- SPOTORNO-OLIVEIRA P, FIGUEIREDO MAO & TÂMEGA FTS. 2015. Coralline algae enhance the settlement of the vermetid gastropod *Dendropoma irregulare* (d'Orbigny, 1842) in the southwestern Atlantic. *J Exp Mar Biol Ecol* 471: 137-145.
- STAL LJ. 2003. Microphytobenthos, their extracellular polymeric substances, and the morphogenesis of intertidal sediments. *Geomicrobiol J* 20: 463-478.
- STEWART JG. 1983. Fluctuations in the quantity of sediments trapped among algal thalli on intertidal rock platforms in southern California. *J Exp Mar Biol Ecol* 73: 205-211.
- SWIERTS T & VERMEIJ MJ. 2016. Competitive interactions between corals and turf algae depend on coral colony form. *PeerJ* 4: e1984.

TEBBETT SB & BELLWOOD DR. 2018. Functional links on coral reefs: Urchins and triggerfishes, a cautionary tale. *Mar Environ Res* 141: 255-263.

TEBBETT SB & BELLWOOD DR. 2019. Algal turf sediments on coral reefs: what's known and what's next. *Mar Pollut Bull* 149: 110542.

TEBBETT SB & BELLWOOD DR. 2020. Sediments ratchet-down coral reef algal turf productivity. *Sci Total Environ* 713: 136709.

TEBBETT SB, BELLWOOD DR & PURCELL SW. 2018. Sediment addition drives declines in algal turf yield to herbivorous coral reef fishes: implications for reefs and reef fisheries. *Coral Reefs* 37: 929-937.

TEBBETT SB, STREIT RP & BELLWOOD DR. 2020. A 3D perspective on sediment accumulation in algal turfs: Implications of coral reef flattening. *J Ecol* 108: 70-80.

THINESH T, JOSE PA, RAMASAMY P, MEENATCHI R, SELVAN KM & SELVIN J. 2019. Differential coral response to algae contact: Porites tissue loss, praise for Halimeda interaction at southeast coast of India. *Environ Sci Pollut Res* 26: 17845-17852.

TITLYANOV EA, TITLYANOVA TV, YAKOVLEVA IM, NAKANO Y & BHAGOOOL R. 2005. Regeneration of artificial injuries on scleractinian corals and coral/algal competition for newly formed substrate. *J Exp Mar Biol Ecol* 323: 27-42.

VAN DE KOPPEL J, HUISMAN J, VAN DER WAL R & OLFF H. 1996. Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology* 77: 736-745.

VANSTEVENINCK EDD, VANMULEKOM LL & BREEMAN AM. 1988. Growth-Inhibition of Lobophora-Variegata (Lamouroux) Womersley by Scleractinian Corals. *J Exp Mar Biol Ecol* 115: 169-178.

VENERA-PONTON D, AZ-PULIDO G, MCCOOK L & RANGEL-CAMPO A. 2011. Macroalgae reduce growth of juvenile corals but protect them from parrotfish damage. *Mar Ecol Prog Ser* 421: 109-115.

WARWICK R & CLARKE K. 1990. A statistical analysis of coral community responses to the 1982-83 El Niño in the Thousand Islands, Indonesia. *Coral Reefs* 8: 171-179.

WATTS A, MCCLINTOCK B & LAWRENCE M 2007. Chapter 23 Ecology of Lytechinus. In: John ML (Ed). *Developments in Aquaculture and Fisheries Science*: Elsevier, p. 473-497.

WILD C, HUETTEL M, KLUETER A, KREMB SG, RASHEED MYM & JORGENSEN BB. 2004. Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. *Nature* 428: 66-70.

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Carvalho, L.L and Villaça, R.C. conceived of the presented idea. Carvalho, L.L. conceived, planned, and carried out the experiment. Carvalho, L.L. also performed the analytic calculations and wrote the manuscript with support from Villaça, R.C. All authors discussed the results and contributed to the final manuscript. Villaça, R.C. helped supervise the project, contributed to the interpretation of the results, provided critical feedback, and helped shape the research and analysis. On behalf of all authors, the corresponding author states that there is no conflict of interest.

