



Colonization, Growth and Productivity of Crustose Coralline Algae in Sunlit Reefs in the Atlantic Southernmost Coral Reef

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OPEN ACCESS

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Specialty section:

This article was submitted to
Marine Ecosystem Ecology,
a section of the journal
Frontiers in Marine Science

Received: 05 October 2018

Accepted: 12 February 2019

Published: 28 February 2019

Citation:

Tâmega FTS and Figueiredo MAO
(2019) Colonization, Growth
and Productivity of Crustose Coralline
Algae in Sunlit Reefs in the Atlantic
Southernmost Coral Reef.
Front. Mar. Sci. 6:81.
doi: 10.3389/fmars.2019.00081

One of the most important contributions of crustose coralline algae (CCA) to some coral reefs is their structural role in sunlit habitats, but in the Atlantic southernmost coral reef, Abrolhos, these algae are also important components of living communities covering larger areas than corals. Little is known about their competence in occupying reef space and consequently their ecological role. This work compared two CCA species along reef sites and habitats and their responses to different irradiance levels. To study colonization, epoxy disks were placed at four sites and three habitats (reef base, reef flat, and reef edge). Crustose coralline individual pieces were glued onto epoxy disks and their relative growth was estimated. Productivity responses to irradiance levels found on reef habitats was measured on incubated samples. In general, CCA were less abundant than filamentous algae and non-calcareous crusts. Crustose algae showed no seasonal or spatial pattern in cover, contrasting with erect algae that differed in biomass among sites depending on season. Differences among habitats were only found for CCA. The dominant coralline *Porolithon onkodes* was more productive and grew faster than *Lithophyllum stictaeforme* at high irradiance level and both species were inhibited at low light. Dominance of *P. onkodes* in shallow and sunlit reefs was explained by its preference for high-light environments.

Keywords: reef habitats, irradiance levels, Abrolhos, Brazil, crustose coralline algae, growth rates, colonization, productivity

INTRODUCTION

The crustose coralline algae (CCA, Corallinales Rhodophyta) on coral reefs can cover large areas, such as in the Africa (McClanahan et al., 2001b), Australia (Fabricius and De'ath, 2001), Caribbean (Adey and Vassar, 1975; McClanahan et al., 2001a; Williams and Polunin, 2001), Fiji (Littler and Littler, 1997), Hawaii (Vroom et al., 2005), and Brazil (Figueiredo, 1997; Gherardi and Bosence, 2001; Villas-Bôas et al., 2005). Studies have confirmed that together with corals, CCA are important components of the reef framework in shallow environments exposed to strong wave action in the Caribbean (Macintyre, 1997) and Brazilian reefs (Kikuchi and Leão, 1997; Leão and Dominguez, 2000; Gherardi and Bosence, 2001; Leão and Kikuchi, 2001; Lei et al., 2018). The cementation of reefs by CCA maintains reef complexity, reduces erosion (Littler, 1972; Steneck, 1986) and increases resistance to herbivore action due to calcium carbonate deposited in the cell walls (Pitlik and Paul, 1997).

According to models of seaweed (algal) form and function, proposed to describe the distribution and abundance of seaweeds, CCA are classified as a unique functional group that dominates highly productive environments with exposure to high levels of disturbance (Littler and Littler, 1980, 1984; Steneck, 1988; Steneck and Dethier, 1994; Mariath et al., 2013). Morphological characteristics of coralline algae indicate adaptations to many environmental and biological factors, such as wave exposure, light intensity, sediment deposition, competition, and herbivory (Steneck, 1986, 1988; Steneck and Dethier, 1994).

Herbivory is regarded as one of the main processes maintaining the structure and diversity of tropical reefs (Bellwood et al., 2004). In tropical coral ecosystems, herbivorous fishes play key roles in the carbon and energy flux of food webs and are considered some of the primary determinants of the benthic structure (Clements et al., 2009). Herbivorous fish assemblages, dominated by surgeonfishes (Acanthuridae) and parrotfishes (Labridae: Scarini), are widely regarded for their importance in the control of the settlement, growth, and spread of benthic seaweeds (Steneck, 1988; Horn, 1989).

Several descriptive studies have related patterns of distribution and abundance of these algae to environmental parameters that influence coral reefs (Adey and Vassar, 1975; Littler et al., 1995; Steneck, 1997; Fabricius and De'ath, 2001; Figueiredo and Steneck, 2002). The biological limits of CCA were analyzed for a few temperate and subtropical species, showing influence of temperature and light intensity (Adey, 1970; Edyvean and Ford, 1987; Matsuda, 1989; Leukart, 1994), competition and herbivory (Steneck et al., 1991; Keats et al., 1994; Figueiredo et al., 1996). In contrast, experimental studies that test the effect of environmental factors on growth and production of CCA on coral reefs are less common and consist of studies of irradiance (Littler, 1973), sediments (Kendrick, 1991), and herbivory (Steneck and Adey, 1976; Figueiredo, 1997).

Among the most important reef builders on the Atlantic Ocean are the CCA *Porolithon onkodes* (Heydrich) Foslie and *Lithophyllum stictaeforme* (J.E. Areschoug) Hauck, which form algal crests on reefs edges (Adey, 1975; Steneck and Adey, 1976; Tâmega et al., 2014; Spotorno-Oliveira et al., 2015). These two coralline species have distinct growth forms: *P. onkodes* is encrusting and *L. stictaeforme* has branched thalli. Both species are commonly found on shallow reefs of the Abrolhos Archipelago in Brazil (Figueiredo and Steneck, 2002; Tâmega and Figueiredo, 2007; Tâmega et al., 2014). This study aims to describe the early colonization and growth of CCA on the reef flat, edge and base of sheltered and exposed sites in summer and winter, testing the responses of the two most common coralline species to different light levels.

Preliminary observations of seaweeds on the reef community of Abrolhos Archipelago generated three hypotheses that were tested in field and laboratory experiments:

H1: CCA are more abundant than other form-functional seaweeds groups in early stages of colonization in any of the studied reef habitats, sites and seasons.

H2: Encrusting CCA have faster marginal growth than branched CCA in any of the studied reef habitats, sites, and seasons.

H3: Encrusting CCA are more productive than branched CCA in environments under high irradiance.

MATERIALS AND METHODS

Study Sites

The present study was conducted in Abrolhos Archipelago (17° 57'–17° 59'S and 38° 41'–38° 43'W; **Figure 1**) about 70 km off North-eastern Brazil. This archipelago is composed by five volcanic islands bordered by fringing reefs and is included in the Abrolhos Marine National Park. The average seawater temperature ranges from 23 to 27°C (Muehe, 1988) and salinity from 36.5 to 36.7 (Muehe, 1988). In autumn and winter (from March to September), winds are mostly from the south. In spring and summer (September to February), winds are from the east to north. Tides range from ± 2.4 to 0.1 m in the north (Porto de Ilhéus) and ± 1.8 to 0.0 m in the south (Barra do Riacho) (Muehe, 1988).

Study sites at Santa Barbara Island were selected according to reef orientation: Porto Norte (N), Caldeiros (NW), Mato Verde (SW), and Porto Sul (S) (**Figure 1**). Studies were run during two periods: December 2001 to March 2002 (austral summer) and July 2002 to October 2002 (austral winter and spring). Three habitats were studied: reef flat, edge, and slope base in Mato Verde, during austral winter. Reef flats are usually exposed to air on extreme spring low tides. Reef bases are at 4 to 5 m depth. Reefs have a gradual slope on Porto Norte and Porto Sul, while at Caldeiros and Mato Verde they have steep slopes from 50°. Sites were compared only at the reef edge in both seasons, where corallines are more abundant (Figueiredo, 1997; Tâmega and Figueiredo, 2007).

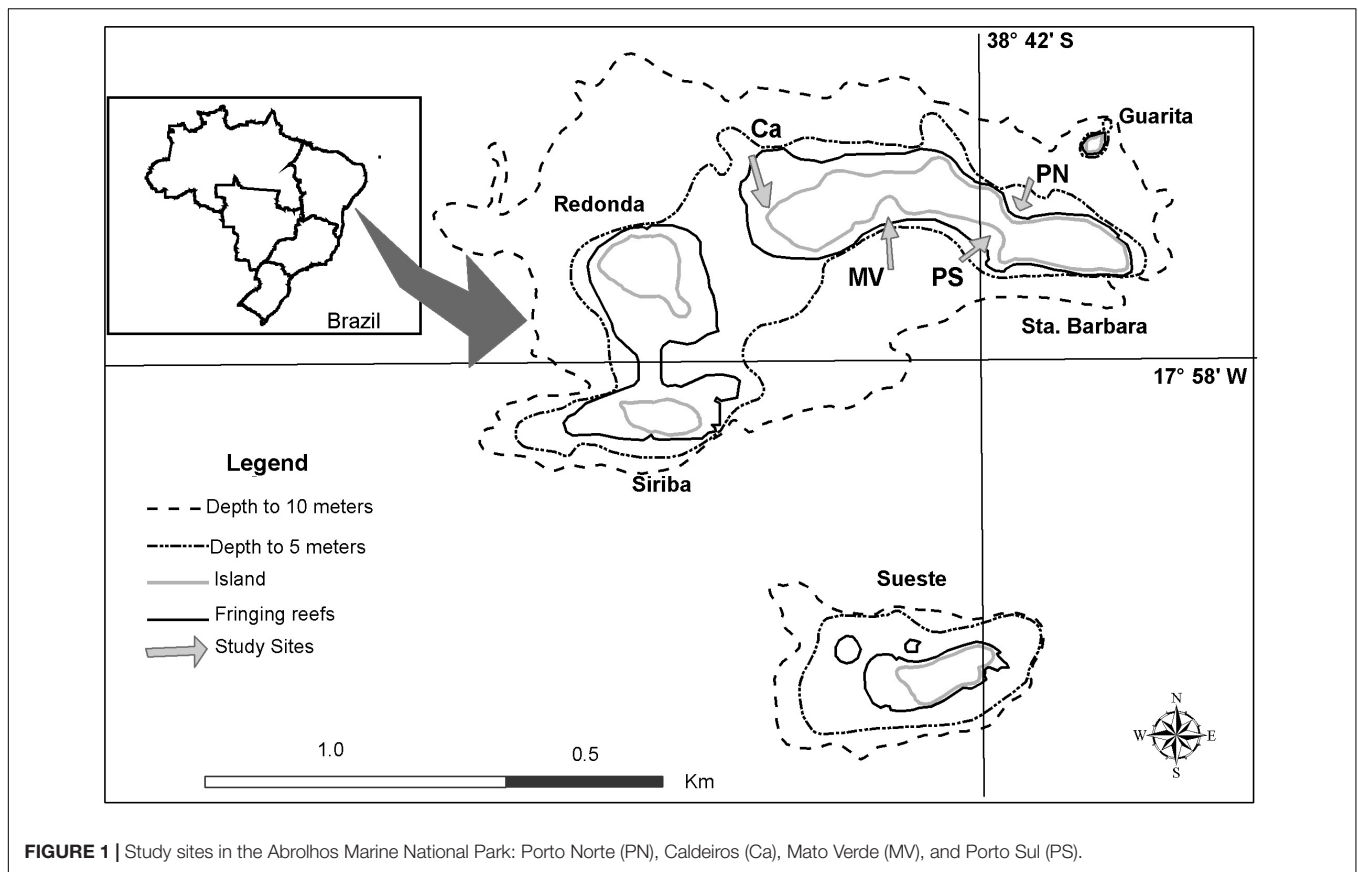
Colonization

The colonization of CCA and erect seaweeds was followed at all study sites, 10 replicate disks made of epoxy (Tubolit), 75 mm diameter, were fixed by epoxy to the substratum at each study site. After 3 months each disk was recovered and stored in a plastic bag with formalin solution (4% in seawater). The cover of colonizing seaweeds was analyzed using a Petri dish marked with 47 random points, placed on the surface of each disk. Seaweeds were separated in functional form groups (Littler and Littler, 1984; Steneck and Dethier, 1994) and also identified to species level when possible. Sorted samples were oven dried at 60°C for 72 h until their mass was constant (not changing with time).

Colonizing seaweeds can be limited by herbivores such as parrotfishes (Labridae: Scarini), that are able to excavate calcified thalli with their fused teeth (Steneck, 1986).

Growth Rates

Growth was compared between two CCA, *L. stictaeforme* and *P. onkodes*. CCA were collected with a hammer and chisel and shaped by cutting pliers to obtain 20 mm diameter and 3 ml volume disks. A single disk naturally free of epiphytes



was fixed onto an epoxy disk of 30 mm diameter (for each crustose coralline species, $n = 10$ per location). Disks of both CCA species were interspersed, fixed to the reef with epoxy and left for the same period as colonization disks. The initial and final sizes of CCA were estimated by averaging two perpendicular diameters measured with calipers. The formula used to calculate the marginal relative growth rate (RGR) was:

$$\text{RGR} = (\ln D_t - \ln D_0) / t$$

which is based on the difference between the logarithms of final and initial average diameter (D) over time (t), following recommendations of Kain (1987). *L. stictaeforme* also had thickness (vertical) growth measured but in *P. onkodes* only marginal (horizontal) growth was measured as it was considered that vertical growth was not sufficient to be detected in this species during such a short deployment time. CCA species were identified following Tâmega et al. (2014).

Productivity

To estimate the competence of the two most abundant CCA species under different irradiance levels, oxygen produced by CCA through net photosynthesis was measured at different levels of light intensities naturally found at each habitat. The irradiance at each site was measured with a Li-Cor light meter (LI-1000) linked to a terrestrial and submersible sensor to estimate the percentage of incident irradiance reduced by the water column.

In the field, the irradiance was measured at midday hours in the summer on sunny days. The light levels of habitats were reproduced in the laboratory by 4, 6, or 10 fluorescent lamps (daylight, 20 watts each), and in the field by shading with 1 or 3 layers of black plastic grids, with 3 mm mesh diameter.

Fragments of the two species of CCA were collected and cleaned of epiphytes with brush and forceps. Seawater was filtered through coarse filter paper in the field or by Millipore 0.47 μm pore and sterilized at boiling point to fill 300 ml BOD bottles. Seaweed samples of standard size (diameter 20 mm) and volume of 3 ml were distributed among clear BOD bottles (with or without shades) to measure O_2 production. One clear BOD bottle with only seawater was used as an initial reference for O_2 production. Number of replicates varied between 8 and 12, in the laboratory and field experiments, respectively. In the laboratory experiments, CCA samples were acclimated to light levels lower than the ones found at the reef base, 2 weeks prior to the experiments. Dissolved oxygen readings were measured by a sensor with a stirrer linked to an oximeter (YSI 5000). Net photosynthesis was calculated to estimate primary productivity using the modified formula of Thomas (1988):

$$\text{Net photosynthesis} = [(\text{BOD bottle} - \text{initial bottle})] / \text{incubation time}$$

At the end of experiments, CCA were decalcified by a solution of 10% nitric acid and oven dried at 60°C to adjust

O₂ production readings to sample weight. Incubation time (4 h) was previously tested and showed no difference from either 2 or 6 h, though shorter times resulted in negative readings at some light levels. Pigment concentration of CCA species was assumed to be similar because only sunlit specimens were used in experiments. Nutrients and carbon depletion did not interfere with results. Similar levels of nitrate, phosphate, and alkalinity between incubated samples and surrounding seawater were found for *P. onkodes* after 4 h of incubation (pers. comm. S. M. Ribeiro). Levels of irradiance used in field tests corresponded to ones mentioned for CCA in shallow reefs (Littler and Littler, 1984), being close to saturated photosynthesis (623 and 408 $\mu\text{mol m}^{-2} \text{s}^{-1}$), photo-inhibition (1093 and 716 $\mu\text{mol m}^{-2} \text{s}^{-1}$), or to levels below those that might limit photosynthesis (218 and 143 $\mu\text{mol m}^{-2} \text{s}^{-1}$). In the laboratory, irradiance levels corresponded to those found at the reef base and within cryptic habitats (218, 107, and 68 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Statistical Analysis

Variance homogeneity was tested using Cochran's test before performing analysis of variance (ANOVA) and, when necessary, data were transformed (Underwood, 1997). Uni or bi-factorial orthogonal ANOVAs were used to test differences between treatments in experiments. Multiple comparison of means was performed using Tukey's test.

RESULTS

Colonization

The most common erect seaweeds found on colonization disks were filamentous algae (*Cladophora dalmatica*, *Sphacelaria tribuloides*, *Polysiphonia scopulorum*, *Ceramium byssoides*), foliose algae (*Enteromorpha flexuosa*, *Padina gymnospora*, *Colpomenia sinuosa*, *Dictyota ciliolata*, *Dictyota mertensii*, *Dictyota menstrualis*), non-calcareous crusts (cyanobacteria, crusts) and calcareous coralline crusts.

The abundance of coralline crusts was different among sites independent of seasons (Figures 2A,B). These groups of algae were abundant at all sites, except Caldeiros. Foliose algae showed similar distribution pattern. A significant interaction between seasons and sites was found for filamentous algae and non-calcareous crusts (Figures 2A,B, ANOVA $F = 2.99$; $p \leq 0.05$ and $F = 2.99$; $p \leq 0.05$, respectively). The filamentous algae were abundant in almost all sites during both seasons, except in Caldeiros (ANOVA $p \leq 0.0001$ and $p \leq 0.01$). In contrast, non-calcareous crusts were more abundant in Caldeiros in both seasons (ANOVA $p \leq 0.0001$ and $p \leq 0.0001$).

A significant interaction was observed for biomass of colonizing algae between sites and seasons (Figures 3A,B and Table 1). Total biomass was different among sites in summer and in winter (ANOVA $F = 5.68$; $p \leq 0.05$ and $F = 7.11$; $p \leq 0.001$, respectively). There was less biomass on Caldeiros than on most sites in summer and higher biomass in Porto Sul than on most sites in winter. In relation to total cover of algae, there were no significant interactions or differences in colonization among sites

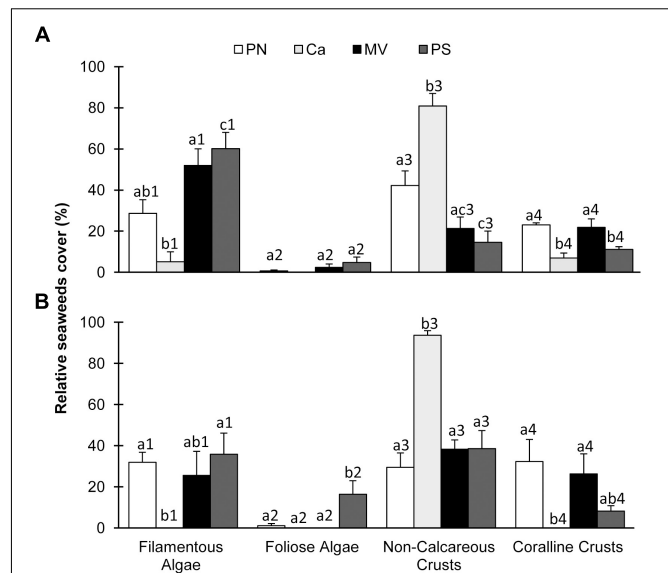


FIGURE 2 | Seaweeds cover at study sites on reef edge, in summer (A) and winter (B). Means \pm standard error. Different letters above bars indicate significant differences among means detected by Tukey's test ($p < 0.05$).

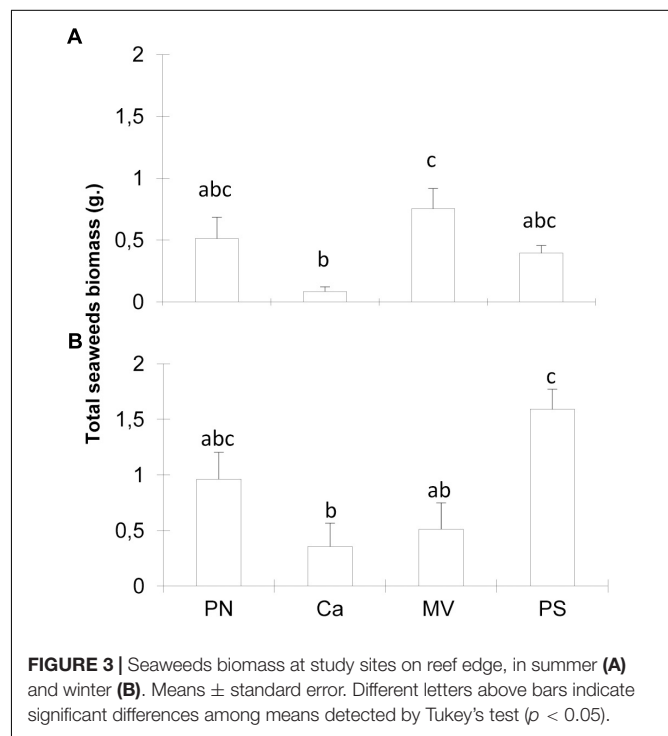


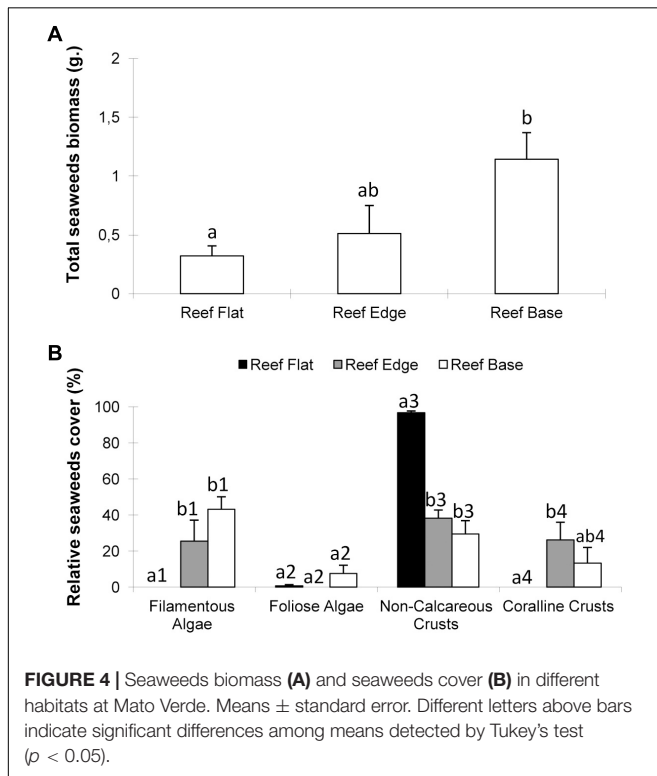
FIGURE 3 | Seaweeds biomass at study sites on reef edge, in summer (A) and winter (B). Means \pm standard error. Different letters above bars indicate significant differences among means detected by Tukey's test ($p < 0.05$).

or seasons, in summer the total cover ranged from 90 to 97%, and in winter from 90 to 99%.

There was a significant difference in the total macroalgal biomass among habitats (Figure 4A, $F = 4.85$, $p \leq 0.05$), which was higher at the reef base and lower at both reef flat and edge. Similarly, total algae cover did not differ significantly among reef habitats (ANOVA $F = 0.65$; $p > 0.05$). In relation

TABLE 1 | Analysis of variance for algae colonization in relation to total cover and total biomass in study sites in summer and winter ($n = 8$).

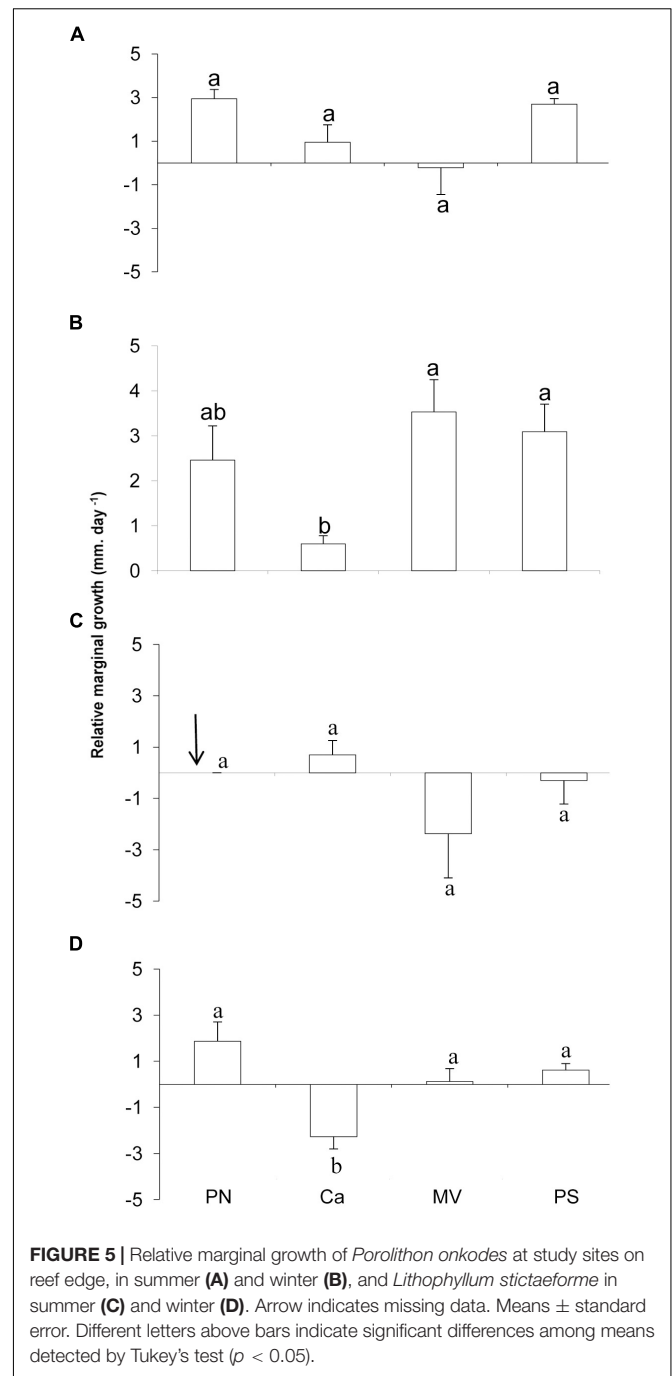
	Source	df	MS	F	P-value
Cover	Seasons	1	0.84	0.01	$P > 0.05$
	Sites	3	11.16	0.17	$p > 0.05$
	Interaction	3	151.74	2.39	$p > 0.05$
	Error	40	63.24		
Biomass	Seasons	1	1.62	11.59	$p \leq 0.001$
	Sites	3	1.89	13.52	$p \leq 0.0001$
	Interaction	3	1.42	10.16	$p \leq 0.0001$
	Error	40	0.14		



to algae functional groups, coralline crusts were present at the reef base and edge, but absent on the reef flat (Figure 4B, ANOVA $F = 5.37$; $p \leq 0.01$). Filamentous algae were abundant at the reef base and edge and absent on the reef flat (ANOVA $F = 10.74$; $p \leq 0.001$). Foliose algae were present only at the reef base (ANOVA $F = 3.38$; $p \leq 0.05$). Non-calcareous crusts were abundant in all habitats, and were dominant at the reef flat (ANOVA $F = 38.56$; $p \leq 0.0001$).

Growth Rates

The absolute marginal growth ranged from 0.01 to 0.28 mm for *P. onkodes* and 0.01 to 0.13 mm for *L. stictaeforme*. The vertical growth of this second species varied from 0.02 to 0.23 mm. Marginal relative growth of *P. onkodes* between seasons and among sites though was not significantly different, a small growth was observed at Caldeiros in winter (Figures 5A,B and Table 2). Marginal relative growth of *L. stictaeforme*, had a strong



significant interaction among sites and seasons, growth was negative in Caldeiros differing from all other sites only in winter, (Figures 5C,D and Table 2). Comparing seasons in Caldeiros, growth was positive in summer and negative in winter (ANOVA $F = 30.35$; $p \leq 0.001$). In Mato Verde and Porto Sul growth was negative in summer and positive in winter, but differences between seasons were not significant (ANOVA $F = 2.10$; $p > 0.05$ and $F = 1.70$; $p > 0.05$, respectively). In summer growth could not be measured at Porto Norte because samples were lost due to strong wave surge.

TABLE 2 | Analysis of variance for marginal growth rate of *Porolithon onkodes* and *Lithophyllum stictaeforme* and vertical growth of *L. stictaeforme* in study sites in summer and winter.

	Source	df	MS	F	P-value
<i>P. onkodes</i> (marginal growth)	Season	1	3.49×10^{-6}	1.18	$p > 0.05$
	Sites	3	4.39×10^{-6}	1.48	$p > 0.05$
	Interaction	3	6.49×10^{-6}	2.19	$p > 0.05$
	Error	24	2.96×10^{-6}		
<i>L. stictaeforme</i> (marginal growth)	Season	1	8.98×10^{-7}	0.23	$p > 0.05$
	Sites	2	4.34×10^{-6}	1.14	$p > 0.05$
	Interaction	2	1.96×10^{-5}	5.16	$p \leq 0.01$
	Error	18	3.80×10^{-6}		
<i>L. stictaeforme</i> (vertical growth)	Season	1	0.0002	9.73	$p \leq 0.05$
	Sites	2	4.61×10^{-5}	2.10	$p > 0.05$
	Interaction	2	0.0001	7.67	$p \leq 0.05$
	Error	18	2.19×10^{-5}		

Relative growth rates (RGRs) calculated from differences in initial and final \log_e of average diameters over time ($n = 4$). Mean squares are exponential numbers ($MS \times 10^{-4}$).

Vertical growth rate of *L. stictaeforme* showed a similar pattern as marginal growth with a significant interaction among seasons and sites. Again Caldeiros showed different growth rates from all other sites but only in winter. (Figures 6A,B and Table 2). In Caldeiros, there was a positive growth in summer and negative in winter. (ANOVA $F = 60.77$; $p \leq 0.001$). In Mato Verde and Porto Sul there was no significant difference between summer and winter (respectively, ANOVA $F = 1.49$; $p > 0.05$ and $F = 0.81$; $p > 0.05$).

Comparing marginal relative growth among habitats there was a significant difference for *P. onkodes* (Figure 7A, ANOVA $F = 11.76$; $p \leq 0.001$), being higher on the reef edge and reef base and zero on reef flat. However, *L. stictaeforme*, had an inconspicuous marginal growth on both edge and base and zero on the reef flat, so differences was not significant among habitats. (Figure 7B, ANOVA $F = 0.008$; $p > 0.05$). There was also no significant difference in vertical growth for *L. stictaeforme* among habitats (ANOVA $F = 0.67$; $p > 0.05$), since growth was negative on both edge and base and zero on the reef flat. Epiphyte algae overgrew some coralline crusts but this cover was not enough to interfere with their growth in any habitat.

Productivity

The maximum irradiance measured was $1975 \mu\text{mol m}^{-2} \text{s}^{-1}$ on the reef flat, $1125 \mu\text{mol m}^{-2} \text{s}^{-1}$ on the reef edge and $869 \mu\text{mol m}^{-2} \text{s}^{-1}$ on the reef base, at midday on a sunny day in summer. Considering light attenuation of 56% by water column on a spring tide, irradiance on reef base could reach as low as $105 \mu\text{mol m}^{-2} \text{s}^{-1}$ in late afternoon. Under the

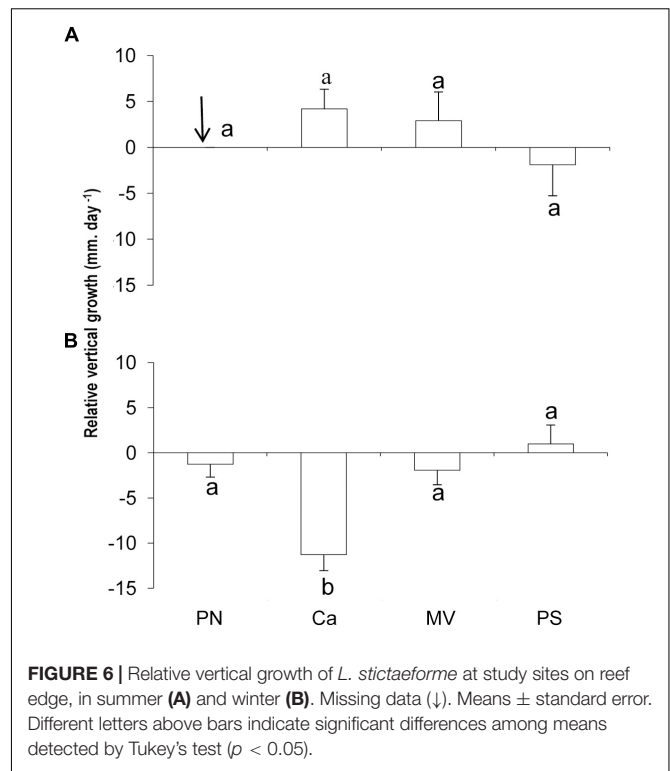


FIGURE 6 | Relative vertical growth of *L. stictaeforme* at study sites on reef edge, in summer (A) and winter (B). Missing data (↓). Means \pm standard error. Different letters above bars indicate significant differences among means detected by Tukey's test ($p < 0.05$).

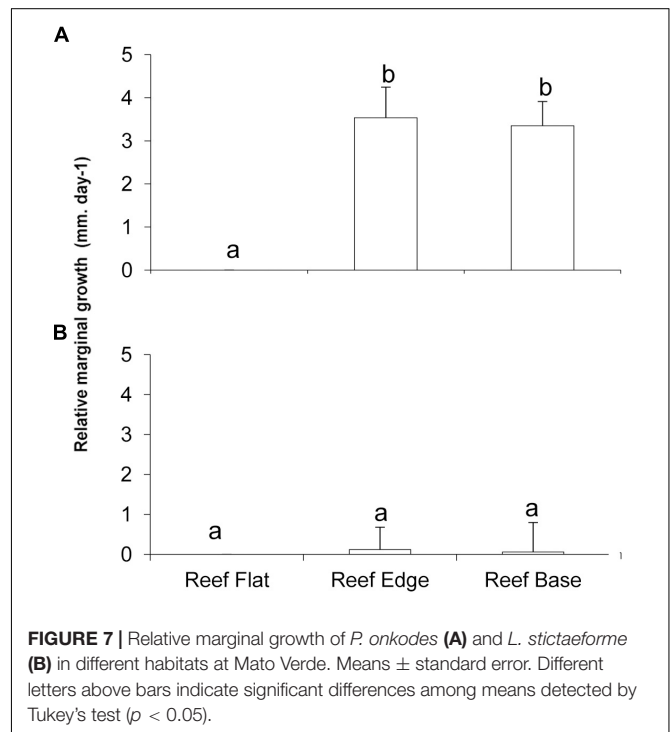
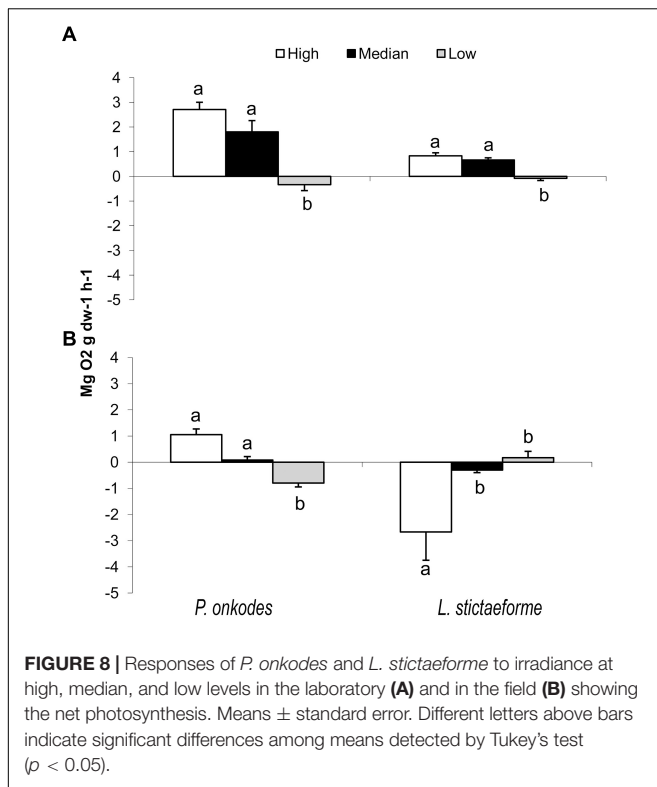


FIGURE 7 | Relative marginal growth of *P. onkodes* (A) and *L. stictaeforme* (B) in different habitats at Mato Verde. Means \pm standard error. Different letters above bars indicate significant differences among means detected by Tukey's test ($p < 0.05$).

conditions of low irradiance simulated in the laboratory, it was observed that crustose coralline species presented significant differences at the three levels tested ($218, 107, \text{ and } 68 \mu\text{mol m}^{-2} \text{s}^{-1}$), O_2 production being greater for *P. onkodes* than *L. stictaeforme* (Figure 8A, ANOVA $F = 7.81$; $p \leq 0.005$ and



$F = 19.42$; $p \leq 0.0001$, respectively). In contrast, exposure to the lowest irradiance level, $68 \mu\text{mol m}^{-2} \text{s}^{-1}$, resulted in negative production in both species (Figure 8A).

In the field, irradiance effects on oxygen produced by *P. onkodes* presented significant difference among levels, being positive at 1093 (high), 623 (median), and negative at 218 (low light level) $\mu\text{mol m}^{-2} \text{s}^{-1}$, (Figure 8B, ANOVA $F = 30.75$; $p \leq 0.0001$). In contrast, *L. stictaeforme* exposed to equivalent irradiance levels, had a negative O₂ production under high irradiances of 716 and $408 \mu\text{mol m}^{-2} \text{s}^{-1}$ and positive under the lowest one of $143 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 8B, ANOVA $F = 4.79$; $p \leq 0.05$).

DISCUSSION

Colonization

In the Abrolhos Archipelago shallow reefs are mainly dominated by the CCA *P. onkodes* and *L. stictaeforme* (Figueiredo and Steneck, 2002; Tâmega and Figueiredo, 2007; Tâmega et al., 2014; Amado-Filho et al., 2018). However, during early stages of colonization erect seaweeds may smother coralline crusts. Filamentous algae generally are small in size, being less than 5 mm in height, and have low biomass (Steneck and Watling, 1982; Hackney et al., 1989), so their proliferation in summer may contribute little to final biomass, unless they form dense turfs. Nevertheless, filamentous algae were abundant colonizers covering reef edges of most sites, except during winter in Caldeiros. This absence may be related to competition by

preemption of space (Olson and Lubchenco, 1990) by the non-calcareous crusts as these crusts are thinner and might have faster growth when compared to thick CCA (Dethier, 1994). Though the non-calcareous crusts were common early colonizers in all sites and seasons they were not common on the mature reef communities. These crusts occur seasonally during the development of communities but may be less successful than other fast growing ephemeral algae that may shade or sweep the substratum (Dethier, 1981). The CCA are long living crusts and are more resistant than non-calcareous crusts to consumption by grazers (Steneck and Dethier, 1994) and generally dominate in environments under moderate herbivore pressure (Steneck and Watling, 1982; Hackney et al., 1989; Figueiredo, 1997). However, intense herbivory could result in an inversion of this pattern in favor of non-calcareous crusts, which have faster growth (Steneck et al., 1991). In relation to the dominant algae groups, the colonization patterns found generally agreed with those found by others in Abrolhos' reef communities. Algae turf is one of the most abundant functional groups, ranging from 15 to 80% cover in both early colonization and in mature reef communities (Figueiredo, 1997; Villaça and Pitombo, 1997; Tâmega and Figueiredo, 2007).

Biomass of colonizing algae was higher on the reef base and edge than on the reef flat. The base and edge were covered by filamentous, foliose, non-calcareous crusts, and CCA. The absence of filamentous algae on reef flats may be related to the inability of their propagules to support prolonged desiccation during low tide, as diurnal low tides are more frequent in autumn and winter (Hackney et al., 1989). Species of *Polysiphonia* can lose 25% of water in its thallus in only 1 or 2 h and 75 up to 90% in longer periods when exposed to air (Kain and Norton, 1990). Foliose algae were present only on the reef base, which may act as a refuge from high hydrodynamic conditions as these algae are easily removed by wave action (Norton, 1991) and as refuge for fishes (mainly Acanthuridae and Labridae: Scarini) that is reduced when depth increases (Steneck, 1997; Figueiredo and Steneck, 2002; Tâmega and Figueiredo, 2007).

Coralline crusts colonized reef edges and bases but did not grow on the reef flat, similar to non-calcareous crusts. Despite both crustose groups being able to survive most disturbances (Dethier, 1994; Steneck and Dethier, 1994), coralline crusts are easily bleached when exposed to air although they can be protected from high light intensities by epiphyte cover (Figueiredo et al., 2000). The success of CCA depends not only on the capacity of recruits to resist disturbance, but also on their ability to occupy space through marginal vegetative growth.

Growth Rates

The absolute marginal growth of *P. onkodes* and *L. stictaeforme* ranged from 0.01 to 0.28 mm and 0.01 to 0.13 mm per day, respectively, the vertical growth being 0.023 to 0.23 mm per day for the latter species. These values were close to daily rates found for the first species in the Brazilian reef: Abrolhos (0.02 to 0.17 mm, Figueiredo, 1997); Rocas Atoll (0.01 to 0.05 mm, Villas-Bôas et al., 2005), and other reef forming species in the Caribbean region (0.07 mm for *P. onkodes* and 0.07–0.12 mm for *Neogonioliton megacarpum* in Adey and Vassar, 1975), but were

higher than those found in Pacific reefs (*P. onkodes* 0.02 mm, Matsuda, 1989). Coralline crust growth is comparatively slower in temperate environments (0.02 to 0.04 mm, Huvé *appud* Adey, 1970; Leukart, 1994). However, studies elsewhere have based their estimates of growth on small individuals during early colonization and thus, they proportionally detected greater marginal extension rates.

In general, marginal growth of *P. onkodes* crusts was positive at all sites in both seasons, except in Mato Verde in summer. Cover of epiphytic algae, especially non-calcareous crusts may have influenced crustose coralline growth because they were abundant when growth was reduced or absent. In contrast, marginal growth of *L. stictaeforme* crusts were negative or absent in most sites in both seasons, but significantly higher in Caldeiros in summer. This result can also be related to epiphytic cover mainly by non-calcareous crusts and articulated calcareous algae. Comparing reef habitats, lateral growth of *P. onkodes* was positive on the reef edge and base, but zero on the reef flat, which could be explained by desiccation plus high epiphytic cover of non-calcareous crusts. The minute or imperceptible marginal growth of *L. stictaeforme* might also have resulted from desiccation and epiphytes, which out-competed coralline crusts on the reef flats.

Lithophyllum stictaeforme develops well at depths around 0.3 to 4 m in regions where wave action is greater (Steneck and Adey, 1976). In shallow habitats, protected from waves, the CCA need herbivores to remove epiphytes, especially turf algae (Steneck, 1997), which may limit their growth (Williams and Carpenter, 1990; Figueiredo et al., 2000). The mechanism of sloughing epithelial cells to remove epiphytes (e.g., Masaki et al., 1984; Keats et al., 1997) is efficient in less productive environments, such as under canopies (Figueiredo et al., 1997) and probably in cryptic environments and at great depths (Steneck, 1997). In the sites at the Abrolhos, it was observed that epiphytic seaweeds were drastically reduced on *P. onkodes* on the reef edge and base, where herbivorous fishes are more frequently seen (Figueiredo and Steneck, 2002; Tâmega et al., 2016). However, epiphytes proliferated on *L. stictaeforme* in all habitats, probably because branches of these algae protect epiphytes against potential herbivory by acanthurids. In contrast, the vertical growth of *L. stictaeforme* was negative on the reef base and edge probably due to herbivory by parrotfishes, which are more adapted to consume branches and large portions of coralline crusts. The ramified forms of *L. stictaeforme* attract these fishes, resulting in a drastic loss of biomass (Steneck and Adey, 1976). Preliminary experiments with transplants of *L. stictaeforme* in Abrolhos demonstrated high consumption rates (40 to 80% of its branches to 12 h, unpublished data). Studies demonstrated that tropical seaweeds could survive and grow following ingestion by surgeonfishes and parrotfishes in the Caribbean (Vermeij et al., 2013) and Brazil (Tâmega et al., 2016), suggesting that these fishes contribute to the dispersion of seaweeds on reefs.

Productivity

In the laboratory *P. onkodes* usually responded better than *L. stictaeforme* under low irradiance, but under $68 \mu\text{mol m}^{-2} \text{s}^{-1}$

both species showed negative net O_2 production, which indicates that this level is beneath their compensation point (Bessell-Browne et al., 2017). In the field *P. onkodes* was more productive under irradiance levels up to $623 \mu\text{mol m}^{-2} \text{s}^{-1}$, but in contrast to the lab, showed negative growth when exposed to $218 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Lithophyllum stictaeforme responded positively, as expected, to equivalent levels of irradiance ($143 \mu\text{mol m}^{-2} \text{s}^{-1}$), but was photo-inhibited under irradiance up to $408 \mu\text{mol m}^{-2} \text{s}^{-1}$. The encrusting coralline algae *P. onkodes* not only grew better but was also more productive in environments subjected to high irradiance, when compared to *L. stictaeforme*.

Deposited sediments can limit incident light. Sediments are more easily trapped among turf algae than among other erect macroalgal thalli. In fact, sediments on disks tended to accumulate more on the reef base, where filamentous turfs are more abundant than on the reef flat (unpublished data). According to Fabricius and De'ath (2001), sedimentation increases even more with a slight reef slope, resulting in a decrease of CCA abundance. Filamentous turfs that trap sediments might also cause damage to the encrusting coralline algae because sediments create an anoxic area over the epithelial cells, suffocating these crusts (Connell and Slatyer, 1977; Kendrick, 1991; Steneck, 1997). Crustose corallines were as abundant on the reef edge as on the reef base, thus it was assumed that the deposition of sediments trapped by erect seaweeds was too low to affect CCA.

On the reef edge, crusts of *P. onkodes* are twice as abundant as branched *L. stictaeforme* (Tâmega and Figueiredo, 2007), which is apparently more common in cryptic habitats, such as reef crevices. In all experiments, flat crusts of *P. onkodes* responded better than branched crusts of *L. stictaeforme* to high irradiances, showing marginal growth rates up to four times faster in sunlit areas. In fact, fused branches of *L. stictaeforme* may indicate photoinhibition of branch tips exposed directly to sunlight (Littler and Littler, 2000). Competition for space between these coralline crusts might be regulated not only by their intrinsic capacity to grow and respond to different light conditions, but also by their resistance to herbivores. It has been shown that *L. stictaeforme* is more likely to be consumed by Labridae: Scarini (Steneck and Adey, 1976); when transplanted to the reef edge the consumption was about 50 to 60% in the study area (unpublished data).

CONCLUSION

In summary, although there exist differences in biological limits between CCA, *L. stictaeforme* coexists with *P. onkodes* in habitats with high light intensity probably due to self-shading by its dense branches. *L. stictaeforme* showed high abundance only in cryptic reef habitats, such as crevices and beneath reefs with negative slopes. *P. onkodes* grew faster and was more productive under high light levels. Therefore, *P. onkodes* can be regarded as a plant adapted to high light environments and *L. stictaeforme* adapted to low light ones, where saturations levels are around 500 and $150 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Lüning, 1990). These CCA are highly dependent on light, as has been demonstrated

for CCA in tropical and temperate environments (Adey, 1970; Leukart, 1994).

Coralline crusts were not the most common algae among early colonizers, rather filamentous turfs and non-calcareous crusts dominated the studied reefs. They are, however, usually more abundant in mature communities, possibly because of their greater resistance to disturbances (Steneck and Dethier, 1994). Changes in community structure in coral reefs are highly determined by a continuous gradient of grazing intensity (Hackney et al., 1989; Williams and Carpenter, 1990). Herbivory of coralline crusts in Abrolhos was lower (up to 10% of fish bite marks, unpublished data) when compared to former studies (up to 40% of fish bite marks, Figueiredo, 1997). Parrotfishes are one of the most important and abundant herbivorous fish families on tropical reefs (Steneck, 1988) and form shoals with large individuals in the Abrolhos Archipelago (Ferreira and Gonçalves, 1999, 2006). In Abrolhos, *Scarus trispinosus*, one of the most abundant scarinae, has been reported to forage intensely on CCA (Ferreira and Gonçalves, 1999, 2006; Tâmega et al., 2016). We suggest that branches of *L. stictaeforme* might be preferentially consumed (Steneck and Adey, 1976) because its protruding branches seemed to attract herbivorous fishes (field observations), thus explaining the higher abundance of *L. stictaeforme* in reef refuges and its rarity on reef edges and flats. Parrotfishes are the only

fish group able to excavate CCA (Steneck, 1983, 1986), but articulated calcareous, filamentous algae and a large amount of detritus are also important items in their diet (Ferreira and Gonçalves, 2006).

AUTHOR CONTRIBUTIONS

FT and MF conceived the study, conducted the analysis, and wrote the manuscript.

ACKNOWLEDGMENTS

We would like to thank the staff of the National Marine Park of Abrolhos who supported field work, Abrolhos Turismo for helping with boat transportation, Tubolit for providing epoxy putty, and the Brazilian Navy for their hospitality. Instituto Brasileiro do Meio Ambiente – IBAMA issued a research license IBAMA 026/2000 for collecting samples. We are also grateful to Gary Andrew Kendrick from University of Western Australia for improving the English version and for their important comments. Comments and suggestions from the Editor NS and two reviewers improved the early version of the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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