**BIOEROSION OF REEF-BUILDING CRUSTOSE CORALLINE ALGAE BY
ENDOLITHIC INVERTEBRATES IN AN UPWELLING-INFLUENCED REEF**

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Abstract

Coral reef growth is primarily determined by constructive and bioerosive processes acting on key reef-building organisms. Among them, corals are major contributors to the construction of reef frameworks, while crustose coralline algae (CCA) primarily take part in reef cementation. Despite the significance of CCA for reef ecology and functioning, there is very little information on CCA bioerosion rates, in particular in reefs influenced by coastal upwelling. Therefore, the aim of this study was to examine the percentage and rates of internal bioerosion by macroborer invertebrates in two dominant CCA species and to explore whether the oceanographic variability influences the nature of bioerosion in coral reefs of the Tayrona Natural National Park (Colombian Caribbean). Annual rates of gross calcium carbonate production for *Lithoplyllum cf. kaiseri* and *Porolithon antillarum* were $0.556 (\pm 0.38)$ and $0.883 (\pm 1.0)$ g $\text{CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}$ respectively, and estimates of percent area covered by macroborer boreholes showed values of 29.7 % for *L. kaiseri* and 18.0 % for *P. antillarum*. Rates of calcium carbonate removal by internal macroborers in *L. kaiseri* (0.19 ± 0.17 g $\text{CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}$) were higher than those in *P. antillarum* (0.14 ± 0.17 g $\text{CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}$). The percentage of internal bioerosion did not vary significantly across climatic/oceanographic seasons. Boreholes produced by mollusks, polychaetes, sponges and sipunculids were identified, with mollusks having the highest erosion activity. A total of 2,095 individuals of boring and opportunistic organisms were identified and grouped into 29 families (17 polychaetes, 4 mollusks, 2 sipunculids and 6 crustaceans). The composition of the macroborer invertebrate community also varied between CCA species, with higher boreholes attributed to vermetids in *L. kaiseri* than in *P. antillarum*. Although

there is no clear influence of climatic seasons on internal bioerosion, the high rates of CCA bioerosion may reduce reef consolidation in the region.

Introduction

Coral reef growth is determined by the balance between reef-building (constructive) and erosive (destructive) processes (Chave et al. 1972; Tribble et al. 1990; Rose and Risk 1985; Edinger et al. 2000; Risk et al. 2001; Vescei 2004; Reyes-Nivia 2013). Reef building functions are delivered mainly by the calcification (deposition of calcium carbonate) of hard corals and crustose coralline algae (CCA), whereas erosion is mainly caused by the activities of micro- and macroboring organisms and herbivorous grazing, as well as by physical (e.g. cyclones) and chemical (e.g. dissolution) processes (Tribollet and Payri 2001; Tribollet and Golubic 2011). Bioerosion (Neumann 1986) caused by endolithic photoautotrophs (including algae and cyanobacteria) is ubiquitous in calcium carbonate skeletons and is therefore a critical driver of carbonate reef budgets (Kiene and Hutchings 1994). The nature and dynamics of endolithic bioerosion induced by macroscopic organisms (i.e., macrobioerosion) has been extensively studied in hard corals (Perry 1996; Londoño-Cruz et al. 2003; Herpun et al. 2005; Wilson 2007), however, endolithic bioerosion has been poorly investigated in skeletons of living crustose coralline algae, which contrasts with the pivotal role CCA play in reef construction and cementation processes.

Macrobioerosion rates in hard corals vary depending on the type of bioeroder organism and the local environment. For example, clionid sponges bioerode coral skeletons at rates

between 0.3 and 1 kg of $\text{CaCO}_3\text{m}^{-2}$ year⁻¹ (Perry et al. 2012). Similar bioerosion rates have been recorded for endolithic polychaete worms such as cirratulids, eunicids, sabellids and spionids [e.g. 0.6 to 1.7 kg $\text{CaCO}_3\text{m}^{-2}$ year⁻¹ (Davies and Hutchings 1983)]. Coral skeleton located closest to shore have higher internal bioerosion rates compared to skeletons located further away from human influences (Le Grand and Fabricius 2011). Rapid settlement of bioeroder bivalves has been observed in coral blocks within the initial stages of succession in upwelling affected reefs in the Tropical Pacific (Wizemann et al. 2018). Although CCA are the second most important biomineralizing group in tropical reefs after the corals (Steneck 1986; Macintyre 1997), little is known about the rates of internal calcium carbonate loss in CCA. The pioneering work by Tribollet and Payri (2001) on the nature of internal bioerosion on the CCA *Porolithon onkodes* in Moorea, French Polynesia, showed the primary organisms contributing to internal microbioerosion were green algae of the genus *Ostreobium*, and cyanobacteria (e.g., *Mastigocoleus* and *Plectonema*). These organisms perforate the CCA skeletons at rates of 0.12 ± 0.07 g/cm⁻³ of CaCO_3 per year. Coralline algae form skeletons primarily composed of high magnesium calcite, which is a type of calcium carbonate highly susceptible to chemical dissolution and bioerosion by microboring algae (Diaz-Pulido et al. 2012), particularly when exposed to seawater with lower pH and high temperature (e.g. Reyes-Nivia et al. 2013; Diaz-Pulido et al. 2014). Given the susceptibility of CCA to ocean acidification (e.g. Anthony et al, 2008; Kuffner et al. 2008), it is critical to gather baseline information on the rates of bioerosion of CCA, particularly in coral reef environments where coralline algae play important roles in reef construction and resilience, and more specifically, in reefs affected by upwelling, where reef development is limited by oceanographic conditions.

85 Coral reefs in Santa Marta and Tayrona National Natural Park (TNNP) in the southern
86 Caribbean are influenced by a wind-induced coastal upwelling that displaces surficial
87 seawater offshore generating upwelling of cool, sub-surficial water with low temperatures
88 ($25\pm 1.6^{\circ}\text{C}$, but as low as 21°C) and high salinity (36.9 ± 0.9) (Bayraktarov et al. 2013;
89 Bayraktarov et al. 2014). Reef development in the region is reduced compared to that of
90 nearby areas not influenced by strong upwelling (e.g. Rosario Islands, ca. 200 km west
91 from TNNP). Further, calcareous algae, both red coralline algae and green siphonaceous
92 algae such as *Halimeda* are relatively rare compared to other Caribbean and Pacific reefs. It
93 has been hypothesized (Von Prahl 1985) that the upwelling phenomenon limits reef growth
94 and development, although at the same time, the upwelling may offer a refuge for corals
95 during thermal stress and subsequent bleaching (Chollett et al. 2010, Bayraktarov et al.
96 2013). Coastal shallow environments of the Tayrona region are also exposed to relatively
97 low seawater pH during the upwelling seasons (Arévalo-Martínez and Franco-Herrera
98 2008) and, although there is limited information on the variability of other carbonate
99 chemistry parameters, it is plausible that reduced saturation state of seawater with respect to
100 calcium carbonate (i.e. Ω aragonite and Ω high Mg-calcite) is also limiting reef
101 development in the area (e.g. Manzello et al. 2008). Given the low seawater pH that
102 generally characterizes upwelling systems (e.g. Manzello et al. 2008) and the above-
103 mentioned sensitivity of CCA to ocean acidification, the Tayrona region provides a unique
104 environmental setting to examine the nature and rates of bioerosion on CCA. It is also
105 likely that bioerosion rates of the carbonate skeletons of both corals and CCA are higher
106 compared to other coral reef areas (as demonstrated for areas affected by intense upwelling
107 in the Eastern Tropical Pacific, Wizemann et al. 2018 and references therein), potentially
108 explaining poor reef development in the TNNP. The lack of knowledge on the rates of

internal bioerosion of reef carbonates does not allow an assessment of its role limiting reef development in the region.

The objective of this study was to provide a detailed assessment of the rates of internal bioerosion of CCAs in reefs affected by coastal upwelling in the TNNP. Given the variety of CCA species in the TNNP reefs, we compared the rates of bioerosion caused by macroboring organisms on two CCA species: *Lithophyllum* cf. *kaiseri* and *Porolithon* cf. *antillarum*. The thallus of *L. kaiseri* is branched and presents abundant protuberances and is consequently more three-dimensional, unlike *P. antillarum*, which tends to be flat and smooth (Steneck 1985) (Fig. 1a). These two species are perhaps the most common CCA in reefs of the TNNP (e.g., Diaz-Pulido and Garzón-Ferreira 2002) and can be dominant in other Caribbean reefs (Steneck and Adey 1976).

Materials and methods

Study area

The Tayrona National Natural Park (TNNP) is located on the northern coast of Colombia and comprises a number of bays inhabited by coral reefs, seagrass beds, mangrove forests and sand plains, representing a biodiversity hotspot in the Colombian Caribbean (Garzón-Ferreira 1998). The climate in the area is governed by a dry season from December to April with presence of a seasonal upwelling system induced by strong trade winds blowing from east to west (Fajardo 1979; Andrade 2000; Andrade et al. 2003; Andrade and Barton 2005; Paramo et al. 2011) causing a drop in a seawater temperature (as low as 21°C), and pH

between 8.12 ± 0.07 and 8.11 ± 0.02 (Bayraktarov et al. 2014) (but can be as low as 7.9 ± 0.01 , Arevalo-Martinez and Franco-Herrera 2008) and increase in salinity (as high as 38) (Salzwedel and Müller 1983; Bayraktarov et al. 2013). A minor rainy (non-upwelling) season occurs from May to August and a major rainy (non-upwelling) season from September to November during which precipitations increase, trade winds dissipate, seawater temperature increases ($27-29^{\circ}\text{C}$), salinity decreases (< 34) and sediment loads are higher increasing seawater turbidity due to increased continental runoff (Salzwedel and Müller 1983; Díaz-Pulido and Garzón-Ferreira 2002). Seawater pH also increases during the rainy seasons (8.24 ± 0.12 and 8.23 ± 0.08 , Bayraktarov et al. 2014). The study was conducted at the wave-protected east side of one of the major bays of the TNNP, Gayraca Bay, during the different climatic/oceanographic seasons.

Algal collection and preparation

To assess internal skeletal bioerosion of CCA, fragments of approximately 4 cm diameter of the species *L. cf. kaiseri* [synonym of *Lithophyllum congestum* (Hernandez-Kantum et al. 2016)] and *P. antillarum* [synonym of *P. pachydermum* (Gabrielson et al. 2018)] were collected between 5 and 7 m depth using a chisel and hammer. Samples were immediately transported to the indoor laboratory (Universidad del Magdalena Planta Piloto, Taganga), where they were acclimated for 12 hours with continuous aeration and water circulation. The taxonomic identity of the algae was confirmed and fragments were cleaned of epiphytes. Fragments were embedded in epoxy (Durepoxi, Hexion Química SA, Cali, Colombia) fitted in a 6 cm² PVC ring and then placed in aquaria and stained with calcein and alizarin red for 3 h and 6 h respectively (Lewis et al. 2017). Staining was done to provide a reference point for identifying subsequent new CCA growth. Then, CCA were

taken back to the reef, placed on metal racks previously fixed to the reef floor and rings secured to the metal racks with plastic cable ties (S1). The experiment had 15 CCA fragments per species, which were left in the reef for a year and every month were gently cleaned of epiphytes and sediments.

To examine the influence of climatic/oceanographic seasons on bioerosion, additional samples (n=15 per CCA species, also embedded in epoxy within the PVC rings and fixed to existing racks) were used in each of the three climatic seasons: upwelling season 2017 (February-April), minor non-upwelling season (May to August), major non-upwelling season (September to November), with a repeat of the upwelling season in December-February 2018. A total of 120 samples were analyzed (60 per CCA species).

Internal skeletal bioerosion of CCA caused by macroorganisms was estimated using two metrics: 1) bioerosion rates, calculating the amount (g) of calcium carbonate removed from the skeleton deposited in one year, in $\text{g CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}$, and 2) calculating the percentage of calcium carbonate removed from the skeleton. To calculate the bioerosion rates, CCA samples were retrieved from the reef at the end of the experimental period (12 months), taken to the laboratory and vertical sections 5- to 7-mm thick cut using a petrographic saw. Each cut section was photographed and analyzed (digitized) using ArcMap 10.4.1 software (Fig. 1B, D). After georeferencing and adjusting each photograph to a 6- cm^2 ring in ArcMap, the total area of new growth (in each cross section) of each sample (fragment) was measured.

1- Annual rate of internal bioerosion: To measure rates of internal bioerosion we used values of gross calcium carbonate production (calcification) rate ($\text{CaCO}_3 \text{ cm}^{-2} \text{ yr}^{-1}$) and

175 subtracted the percentage of the total area bored my macroborers. To do this, we first
 176 calculated the areas of new growth of the CCA (staining protocol described earlier), which
 177 was determined by measuring the area between the stain line and the surface of the sample
 178 at the time of final collection of the algae from the reef. The alizarin red stain in *P.*
 179 *antillarum* was clearly visible in all samples; however, the alizarin stain did not work well
 180 in *L. kaiseri* fragments; therefore, we used an epifluorescence microscope to identify the
 181 calcein stain line to mark the areas of new growth. The area of new growth was used to
 182 determine the gross calcification rate of CCA, following the method by Lewis et al. (2017).
 183 In short, gross calcification rates were calculated using the fragments' marginal growth
 184 (determined using estimates of surface area of each sample using photos before deployment
 185 and after collection) and vertical extension (in cross section, from the stain line to the CCA
 186 surface, measured at the center and edge of the fragment) measurements in conjunction
 187 with skeletal density (sd) of each CCA species.

188 Mass of fragment center $M_0 = (V_0/A_0) \times sd$

189 Mass of fragment center $M_1 = \sum [(A_1 - A_0) \times V] \times sd$

190 Total mass of fragment new growth $M_3 = M_0 + M_1$

191 To estimate skeletal density we followed the method described in Davies (1989): samples
 192 were soaked in a 10% solution of commercial bleach in seawater for 24 h, buoyant-
 193 weighed, rinsed in distilled water, and dried to constant weight at 70°C. Five thalli of each
 194 CCA species were used for the skeletal density estimates. Seawater density was calculated
 195 with an inert reference object. The skeletal density was 2.115 cm³ for *P. antillarum* and
 196 2.109 g cm³ for *L. kaiseri*. The result was divided by the number of days (d) in that each

sample presented living tissue. This was then multiplied by 365 and expressed in grams per unit area per year ($\text{g CaCO}_3 \text{ cm}^{-2} \text{ yr}^{-1}$).

In each CCA section, the areas covered by boreholes caused by macroborers in the new growth area (above the staining line in a cross section) were measured (Fig. 1b) using the ArcMap software. We followed the methodology described by Bromley (1978), in which shape and size of each borehole were used to identify groups of bioeroding organisms. The results were initially expressed as percentage of bioerosion (see below, metric 2) relative to the total area of new growth. To calculate the carbonate removal rate relative to the annual CCA growth, we used the values of gross calcification rate from each sample ($\text{g CaCO}_3 \text{ cm}^{-2} \text{ yr}^{-1}$) and then subtracted the percentage of the total area bored (S2).

2- Annual percentage of internal bioerosion: To determine the percentage of internal area removed from the CCA fragment (i.e. relative proportion) by the various macro-organisms, we followed the same methodology described above for the bioerosion rates [i.e. Bromley (1978) method], but areas were standardized to percentages. Only bioeroded areas of skeleton deposited in the last year were included (i.e. from the stain line to the CCA surface).

3. Percentage of total internal bioerosion and taxonomic characterization between climatic seasons

In addition to the two bioerosion metrics described earlier, we estimated the total area of bioerosion (as percentage) by macroborers for the entire CCA substrate (not just for the new skeleton between the stain line and CCA surface) across climatic seasons. The amount of new calcium carbonate deposited between each seasonal sampling (i.e. between season

intervals) was very small and that limited our ability to accurately assess the influence of seasons on bioerosion rates. Nonetheless, the percentage of total area of bioerosion (metric 3) provided an opportunity to examine the identity of the main macroborers (invertebrates) responsible for internal bioerosive processes of the entire algal thallus and explore any potential seasonal influence on the total bioeroded area (Fig. 1b).

Taxonomic identification and abundance estimation of macroborers

To determine the taxonomic composition and abundance of the macro invertebrates present in the CCA skeletons 15 additional samples of *P. antillarum* and *L. kaiseri* each were collected in February and August 2018. After collection, samples were immediately placed in separate containers holding magnesium chloride to relax polychaete worms (George and Hartmann-Schröder 1985). In the laboratory, CCA fragments were fixed in a 10% formalin solution (Fonseca et al. 2005) and sample volume was estimated through liquid displacement (Peyrot-Clausade 1988) and standardized in dm³. For removal and identification of the invertebrates, the CCA fragments were decalcified with a solution of 5% formalin acidified with 4% nitric acid by volume, with daily replacement of the solution for seven days (Brock and Brock 1977). The bivalves were extracted using forceps to avoid dissolution of the shell (Fonseca et al. 2005). Once decalcified, extraction and counting of the macroborers was performed before being preserved in 5% formalin for subsequent taxonomic identification, which was conducted to a family level.

Statistical analyses

To compare the annual rate of internal bioerosion (metric 1) and the annual percentage of internal bioerosion (metric 2) between CCA species, a t-test for independent samples was performed after verifying normality (Shapiro-Wilk test), and homogeneity of variances

(Levene's test). To examine the influence of climatic seasons on bioerosion, we used the percentage area of total bioerosion (of the entire CCAs substrate) (metric 3) and conducted a two-way ANOVA with CCA species and seasons as fixed factors and fragments as replicates. Data were arcsine transformed to meet requirements prior to analysis (Zar 2010). Additionally, a Kruskal-Wallis test was used to compare macroborer groups for each CCA between seasons (data were not normally distributed, Shapiro-Wilks test $p < 0.05$). A non-metrical multidimensional scaling (MDS) was employed to infer if the macroborer assemblages of CCA were different between climatic seasons. Finally a Mann-Whitney test was used to analyze the abundance of macroborers between CCA. Statistical analyses were carried out using the SPSS Statistics 20 and Primer 6.

Results

The mean annual rate of gross calcium carbonate production for *L. kaiseri* was $0.556 (\pm 0.383) \text{ g cm}^{-2} \text{ year}^{-1}$, while for *P. antillarum* was $0.883 (\pm 1.0) \text{ g cm}^{-2} \text{ year}^{-1}$ (S.2), however, the difference between species was not statistically significant ($t = 0.87$, $p = 0.39$). The annual percentage of internal bioerosion of the skeleton of *L. kaiseri* deposited over one year and attributed to the macroborers was 29.7%, with the remaining 70.3% free from bioerosion. *P. antillarum* showed a lower percentage of internal bioerosion by macroboring organisms than *L. kaiseri*, with only 18.0% and the remaining 82.0 % of the skeleton free of macroboring activity (Fig. 2b, S3). The analysis revealed significant differences in percentage bioerosion between species ($t = 2.275$, $p = 0.035$).

The annual rate of gross calcium carbonate production and the respective percentages of internal bioerosion were used to estimate the annual rate of the amount of calcium carbonate removed by internal macroborers. The annual rate of internal bioerosion was modestly higher for *L. kaiseri* ($0.19 \pm 0.17 \text{ g CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}$ (34.6%)) (mean $\pm$ SE) compared to *P. antillarum* ($0.14 \pm 0.17 \text{ CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}$ (15.9%)) (Fig. 2a, S.2). The analysis, however, did not show significant differences in rates between species ($t = 0.498$, $p=0.630$).

The overall macrobioerosion pattern of the annual surface area showed that mollusks were the primary bioeroder in both CCA, removing between 95.3 % in *L. kaiseri* and 79% *P. antillarum*, followed by sponges (11.23% and 1.66% respectively). The contribution of polychaetes and sipunculids to bioerosion was negligible (Fig. 2c).

Percentage of internal bioerosion and taxonomic characterization between climatic seasons

The percentage of total area of internal bioerosion of CCA measured across climatic seasons in the TNNP (metric 3) ranged between 14.9% and 22.8% for *L. kaiseri*, and from 16.2 to 24.4 for *P. antillarum* (Fig. 3). There were no significant differences in the percentage of internal bioerosion between CCAs ($F_{1,103}=2.56$, $p=0.112$) or between seasons ($F_{3,103}=1.31$, $p=0.273$). The overall macrobioerosion pattern for each season showed that in *L. kaiseri*, mollusks were the primary bioeroder, removing between 72% and 77% of the internal surface area, followed by polychaetes (10% and 16%), sponges (4% and 10%) and, lastly, sipunculids (negligible) (Fig. 4a). There were significant differences in bioeroder groups ($X^2=180.92$, $p<0.05$); with seven pairs out of ten comparisons by Dunn's test showing significant differences, while the groups with lower percentages (sipunculids,

sponges and indeterminate) were similar. In *P. antillarum*, mollusks were also the main group responsible for internal bioerosion (between 52% and 77%), and this was followed by sponges (between 4% and 33%), polychaetes (8% and 19%) and sipunculids (4%) (Fig. 4b). There were significant differences between the percentage of bioerosion attributed to the different bioeroder groups ($X^2=121.03$ (4), $p<0.05$), with mollusks being different with the other groups, and polychaetes with sponges and sipunculids.

The multivariate (MDS) analyses used to explore the potential influence of climatic seasons on the CCA macroborer assemblage showed some variability in the major taxonomic composition of the assemblage. This variability was mainly related to the type of CCA in which the assemblage inhabits, and to a lesser extent to the climatic season. Macroborer samples from *P. antillarum* tend to occur at the bottom and left sides of the MDS plot, with samples from the minor non-upwelling season (May-Aug) well separated from the rest of the samples (S4). We found higher number of polychaetes in *P. antillarum* compared to *L. kaiseri*, particularly in this climatic season (minor non-upwelling).

Taxonomic identification and abundances of macroboring in *Porolithon antillarum* and *Lithophyllum kaiseri*

Macroborers were grouped into the categories of Annelida, Mollusca, Sipuncula and Crustacea (Fig. 5) and could only be identified to family level. The total abundance of macroborers was 2,096 ind/dm³, of which *P. antillarum* had the highest abundance with 1,150 ind/dm³ (55.1%). The polychaetes were the best represented group, with 665 individuals (14 families), followed by mollusks with 718 individuals (4 families),

sipunculids with 600 individuals (2 families) and 112 crustaceans (6 families). Mollusks were the most abundant phylum with 439 ind/dm³ (38.1%), followed by sipunculids (340 ind/dm³, 29.5%), annelids (315 ind/dm³, 27.3%) and crustaceans (57 ind/dm³, 4.9%). In *L. kaiseri*, annelids were the most abundant, with 350 ind/dm³ (37%), followed by mollusks (279 ind/dm³, 29.5%), sipunculids (261 ind/dm³, 27.5%) and crustaceans (56 ind/dm³, 6%) (Fig. 5).

For *L. congesgtum*, 18 families were identified, with the most abundant mollusks belonging to the family Vermetidae (27%, 255 ind/dm³) followed by sipunculids of the family Phascolosomatidae (23.8%, 225 ind/dm³) and polychaetes of the family Eunicidae (15.7%, 148 ind/dm³). The relative abundances of families with more than 3% were Spionidae (6.7%, 63 ind/dm³), Serpulidae (4.8%, 45 ind/dm³), Cirripedia (5%, 47 ind/dm³) and Aspidosiphonidae (3.7%, 35 ind/dm³) (Table 1). In *P. antillarum* 21 families were identified, and similar to *L. kaiseri*, mollusks, sipunculids and polychaetes were the most abundant (Vermetidae 35%, 401 ind/dm³, Phascolosomatidae 18.7%, 214 ind/dm³ and Eunicidae 11.8%, 135 ind/dm³), the family Aspidosiphonidae belonging to sipunculids was also abundant (11%, 125 ind/dm³). In regards to the annelids, the families Sabellidae (4.1%, 47 ind/dm³) and Spionidae (3%, 34 ind/dm³) had abundances greater than 3% (Table 1). There were no significant differences in abundance of bioeroder groups between CCAs (Mann-Whitney test, W=367.0, p=0.598).

Discussion

Annual rate and percentage of internal bioerosion

This is the first study to provide detailed information on internal bioerosion by macroboring organisms in reef-building crustose coralline algae. Although we found differences in the percentage of internal bioerosion between the two species of CCA considered, the rates of bioerosion were similar between species [$0.19 \text{ g CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}$ (or $1.9 \text{ kg m}^{-2} \text{ year}^{-1}$) for *Lithophyllum kaiseri* and $0.14 \text{ g CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}$ (or $1.4 \text{ kg m}^{-2} \text{ year}^{-1}$) for *Porolithon antillarum*]. This consistency in internal bioerosion rates between CCA species is due to the similar rates of gross calcium carbonate production of the two algae. The bioerosion rates reported here are comparable to those caused by boring polychaetes on coral blocks ($0.69 - 1.79 \text{ kg m}^{-2} \text{ year}^{-1}$, Davies and Hutchings 1983), but higher than rates reported for endolithic sponges in reef substrates ($<0.1 \text{ kg m}^{-2} \text{ year}^{-1}$, Perry et al. 2012), although as acknowledged by Perry et al. 2012, these values are an underestimate of the true level of sponge bioerosion due to methodological limitations. The high bioerosion activity found in the reef-building coralline algae in the PNNT may be contributing to the marginal development of coral reefs in the region. Although CCA are able to grow and cover areas of the reef substrate (e.g. Diaz-Pulido and Garzón-Ferreira 2002; Eidens et al 2014), CCA accretion rates are considerably reduced by bioerosive processes yielding a limited potential for reef growth.

The difference in the percentage of area covered by perforations (boreholes) between the species of coralline algae considered (*L. kaiseri*, 31.4%; *P. antillarum*, 18.4%) may be due to the differences in thallus morphologies. The location of the boreholes was more common on the protuberances (or “branches”) of the *L. kaiseri* crusts, and it is possible that the

branching morphology of this species facilitates the occurrence of internal macroborers. The higher three-dimensionality of the algae may provide greater substrate availability for internal macroborers compared to the smoother morphology of *P. antillarum*. There are other factors that may also influence the susceptibility of CCA species to internal calcium carbonate removal by endolithic invertebrates, for example presence of algal chemical compounds that may deter settlement of invertebrates (e.g. Ritson-Williams et al., 2014), or variable skeletal features such as density, internal structure and mineralogy (Nash et al., 2019); however, an examination of these factors is outside the scope of our study. The interaction between CCA morphology and the susceptibility to internal and external bioerosion on the persistence of CCA in the reef requires further investigation.

Influence of climatic seasons on the percentage of internal bioerosion

We did not find a clear influence of the seasonal variability in oceanographic conditions on the total percentage of internal bioerosion in the two species of CCA studied. This conclusion is at odds with what we initially expected because it has been widely documented that the variability in climatic seasons and oceanographic conditions in the region considerably influences a variety of marine biological and ecological processes. For example, macroalgal communities in the TNNP vary dramatically in species composition and abundance across the major climatic seasons, with a particular influence of upwelling enhancing macroalgal growth (Bula-Meyer 1990; Diaz-Pulido and Garzón-Ferreira 2002) and algal turf productivity (Eidens et al., 2014). Recruitment of a number of invertebrates such as sponges and barnacles (Zea 1993; Garcia and Salzwedel, 1993) also varies seasonally in the region. In our estimates of total percentage of internal bioerosion in the seasonal samples (deployed and retrieved every 3 months, metric 3), we assessed the

percentage of bioerosion in the entire skeleton and could not discriminate between bioerosion in areas of recent (i.e. deposited during the last three months) or old (i.e. deposited before the collection time) skeletal tissue. Therefore, our methodological approach did not allow us to detect a more specific signature of climatic variability on bioerosion. Wizemann et al. (2018) used dead coral fragments to assess the influence of upwelling on coral endolithic bioerosion in reefs of the Pacific coast of Costa Rica, and found that the onset of upwelling was related with enhanced carbonate bioerosion. It remains to be determined whether live corals and coralline algae follow similar trends in that region. Future studies assessing the internal bioerosion occurring only in the new skeletal tissue deposited during the specific climatic season, as well as longer-term assessments may provide insights into the importance of upwelling on internal macrobioerosion in CCA.

Taxonomic composition and abundance of macroboring organisms in CCA

The taxonomic composition of the annual and seasonal macroborer community did not vary significantly between the two species of CCA studied, with mollusks as the main macrobioeroder group, and boreholes created by sponges, polychaetes and sipunculids, were also found. These results differ with Wizemann et al. (2018) who found rapid settlement of the *Lithophaga* bivalve on dead coral substrates in upwelling areas. However, the composition of macroborer organisms, dominance and boring patterns differed between corals and CCA, with serpulids and bryozoans being the primary bioeroding groups colonizing dead coral blocks (Davis and Hutchings 1983). The presence of sponges and bivalves is evidence of a multiphase and prolonged colonization (Uchman et al. 2017),

because these organisms require more than four years to penetrate a substrate (Tribollet 2010). Corals with advanced degrees of bioerosion are characterized by the dominance of sponges in the substrate, which replace short-lived bioeroder groups such as polychaetes (Davies and Hutchings 1983; Hutchings 2008). In CCA, this progressive bioerosion may result in a continuous, gradual degradation (Freiwald and Henrich 1994), but the reasons why the nature of macrobioerosion differed considerably between corals and CCA is unclear, although this may be related to differences in skeletal characteristics such as density, porosity or mineralogy. Among the mollusks, vermetids were the primary type of macroborers found in both CCA, building their cavities close to the surface (Savazzi 1999; Savazzi 2001); thus, they are considered semi-endolithic because they dig from the surface subsequently secreting their shells (Savazzi 2001). It has been documented that the establishment of vermetid larvae is positively associated with a CCA substrate (Spotorno-Oliveira et al. 2015), which could explain its dominance in our CCA. Mytilids and Gastrochaenids mollusks were also common, and since they are long-lived organisms, their presence in the CCA may indicate long-term bioerosion (Tribollet 2011).

Polychaetes have been reported as being the most abundant group of perforating invertebrates in corals (Hutchings 1974; Davies and Hutchings 1983; Kiene 1994; Moreno-Forero et al. 1998; Hutchings 2008). In our corallines, polychaetes were also abundant but the size of their boreholes was smaller than those made by mollusks, and therefore polychaetes are considered secondary macroborers. Sipunculids were abundant and represented by families reported from corals for the Colombian Caribbean (Gómez et al. 2013). However, similar to crustaceans, the size of their boreholes is small, and thus they do not significantly affect the CCA skeleton. Because sipunculids are indicators of later

successional stages of internal bioerosion in corals (Carreiro-Silva and McClanahan, 2012),
their abundance in our CCA may suggest advanced macrobioerosion stages.

Our study demonstrates an important role of endolithic macroinvertebrates in the processes
of bioerosion in two species of tropical reef-building coralline algae. The seasonal coastal
upwelling bringing low seawater temperature and pH (Arevalo-Martinez and Franco-
Herrera 2008), together with the influence of rainy seasons with consequent runoff of
nutrients, increased sediment loads and turbidity (Bayraktarov *et al.*, 2014) can create
environmental conditions favoring high rates of bioerosion of endolithic organisms. For
example, reefs influenced by naturally acidified seawater (i.e. low seawater pH/high pCO₂)
have higher bioerosion rates than reefs exposed to higher pH levels (Barkley et al 2015;
Reyes-Nivia et al 2013). Further, living and dead coralline algae fragments exposed to low
pH experimental treatments experience high bioerosion levels caused by endolithic algae
(Diaz-Pulido et al 2012; Reyes-Nivia et al 2014, also Tribollet and Payri 2001). The
combination of oceanographic conditions, high rates of internal CCA bioerosion and
consequently reduced potential for reef cementation may contribute to the marginal
development of coral reefs in the Santa Marta and TNNP region. Specifically, low seawater
temperature and pH (and possibly low Ω aragonite and Ω high Mg-calcite), together with
high macroalgal biomass during the upwelling season combined with elevated nutrients,
increased turbidity and sediment loads during the rainy, non-upwelling seasons may be
contributing to limited reef growth. Given the critical significance of CCA for reef building
it is important to also consider other aspects of CCA bioerosion such as the contribution of
internal microbioerosion (e.g. by photoautotrophs) and external bioerosion (e.g. by

parrotfish, urchin and chiton grazing), to better understand the dynamics and contributions of other ecological processes to reef carbonate budgets.

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Figure Legends

Figure 1. Photos of the crustose coralline algae at 5-6 m depth in the Tayrona National Natural Park (TNNP), Colombian Caribbean and cross section of fragments embedded in resin. *Porolithon antillarum* (A, B) and *Lithophyllum kaiseri* (C, D). Examples of bioerosion areas (boreholes) attributed to macroboring invertebrates and their taxonomic categories (B and D).

Figure 2. A. Percentage of annual internal bioerosion relative to annual growth (gross calcification) for *Porolithon antillarum* and *Lithophyllum kaiseri*. B. Annual macrobioerosion rate ($\text{g CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}$). C. Annual percentage of internal macrobioerosion by each macroboring group. Data are means ($\pm$ SE).

Figure 3. Seasonal percentage of internal macrobioerosion for *Porolithon antillarum* and *Lithophyllum kaiseri* (mean $\pm$ SE, n=60 per CCA) at each climatic season at Gayraca bay (TNNP).

Figure 4. Proportional contribution (%) of surface area removed per by each macroboring group or organisms in A. *Lithophyllum kaiseri* and B. *Porolithon antillarum* at each climatic season at Gayraca bay (TNNP).

Figure 5. Percentage of relative abundance of the main groups of internal macroborers associated with *Lithophyllum kaiseri* and *Porolithon antillarum* (mean $\pm$ SE, n=15 samples per CCA).

Supplemental material

S1. Photo showing fragments of the crustose coralline algae *Porolithon antillarum* and *Lithophyllum kaiseri* embedded in resin within PVC disks and attached to racks fixed to the reef in Gayraca bay (TNNP) at 5 m depth.

S2. Table with values of gross calcification in $\text{g CaCo}_3 \text{ cm}^{-2} \text{ yr}^{-1}$ and percentages of bioerosion in the crustose coralline algae *Porolithon antillarum* and *Lithophyllum kaiseri*.

S3. Table with relative abundance of macroboring and percentage of bioerosion in *Porolithon antillarum* and *Lithophyllum kaiseri*.

S4. A non-metrical multidimensional scaling (MDS) results showing clustering among climatic seasons (S1 and S4: Upwelling seasons, S2: minor non-upwelling season, S3: major non-upwelling season) and the main groups of macrobioeroders for the two species of coralline algae (L: *Lithophyllum* and P: *Porolithon*).

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Fig 2.

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Fig 5.

Table 1 Abundances of macroboring families found in *Porolithon antillarum* and *Lithophyllum kaiseri*

Phylum	Family	<i>Lithophyllum kaiseri</i>		<i>Porolithon antillarum</i>		Total
		Mean abundance	Relative abundance	Mean abundance	Relative abundance	
Annelida	Cirratulidae	5.8	0.6	0.0	0.0	5.8
	Chrysopetalidae	2.9	0.3	0.0	0.0	2.9
	Eunicidae	148.7	15.7	135.5	11.8	284.2
	Hesionidae	7.9	0.8	0.0	0.0	7.9
	Neredidae	10.8	1.1	12.7	1.1	23.5
	Oeonidae	0.0	0.0	4.9	0.4	4.9
	Phyllodosidae	0.0	0.0	7.8	0.7	7.8
	Polynoidae	2.9	0.3	7.8	0.7	10.7
	Sabellidae	21.7	2.3	46.9	4.1	68.5
	Serpulidae	45.5	4.8	20.5	1.8	65.9
	Sigalionidae	2.9	0.3	12.7	1.1	15.6
	Spionidae	63.5	6.7	34.0	3.0	97.5
	Syllidae	18.8	2.0	32.1	2.8	50.8
	Terebellidae	18.8	2.0	0.0	0.0	18.8
Mollusca	Arcidae	0.0	0.0	7.8	0.7	7.8
	Gastrochaenidae	0.0	0.0	12.7	1.1	12.7
	Mytilidae	24.5	2.6	17.5	1.5	42.1
	Vermetidae	254.9	27.0	401.0	34.9	655.9
Sipuncula	Aspidosiphonidae	35.4	3.7	125.0	10.9	160.4
	Phascolosomatidae	225.2	23.8	214.7	18.7	439.9
Crustacea	Cirripedia	47.6	5.0	9.7	0.8	57.3
	Decapoda	0.0	0.0	7.8	0.7	7.8
	Gammaridae	0.0	0.0	23.4	2.0	15.6
	Gnathiidae	0.0	0.0	7.8	0.7	7.8
	Serolidae	0.0	0.0	7.8	0.7	7.8
	Penaeidae	7.9	0.8	0.0	0.0	7.9
Total		945.6	100.0	1150.1	100.0	2096