Boring worms (Sipuncula and Annelida: Polychaeta): their early impact on Eastern Tropical Pacific coral reefs

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ABSTRACT: The form, condition, and survival of coral reefs depends on the balance between construction and destruction. Natural processes such as bioerosion can cause this balance to lean towards destruction, threatening these ecosystems. Polychaetes and sipunculids are members of the boring community; however, knowledge of their identity and role in the bioerosive process and their capacity to remove calcium carbonate ($CaCO_3$) in the coral reefs of the Eastern Tropical Pacific (ETP) is scarce. To tackle this problem, 5 experimental units of *Pocillopora* spp. branches were deployed in 4 reef zones (back-reef, reef-flat, reef-front, reef-slope) at 2 reefs (La Azufrada, Playa Blanca) for 2 time periods (P1: 6 mo, P2: 9 mo; n = 80) in Gorgona National Natural Park, Colombia. All worms (polychaetes and sipunculids) were identified and net removal and bioerosion rate were determined. In total, 137 worms were found: 64.2% in La Azufrada and 35.8% in Playa Blanca. There were no significant effects of reef, reef-zone, or duration of exposure (6 vs. 9 mo) for either net removal of $CaCO_3$ or bioerosion rate. Irrespective of reef or exposure duration, average net removal was 0.022 and 0.027 g during P1 and P2, and 0.032 and 0.018 g at La Azufrada and Playa Blanca, respectively. Average bioerosion rate, also irrespective of reef or exposure duration, was 2.553 and 2.011 g kg^{-1} yr^{-1} for P1 and P2, and 2.839 and 1.807 g kg^{-1} yr^{-1} at La Azufrada and Playa Blanca, respectively. The trend between periods was opposite for net removal and bioerosion rate, which indicates a decelerating impact of worms on the coral substrate as time passes. We suggest that, regardless of the small size of the boring worms, their role in $CaCO_3$ removal is very important. The information provided here — species involved and amounts removed — is key in understanding the bioerosion process in ETP coral reefs.

KEY WORDS: Bioerosion · $CaCO_3$ removal · Colombian Pacific · Gorgona Island

1. INTRODUCTION

The current form, condition, and maintenance in time (survival) of coral reefs are determined by the balance of constructive and destructive processes. This balance is the outcome of biological, physical, and chemical factors interacting together, and it can vary spatially (within and between reefs) and temporally (Londoño-Cruz et al. 2003, Hutchings et al. 2005, Hutchings 2011, Alvarado et al. 2017). When substrate destruction is caused by live organisms, it is known as bioerosion, and this process can account for most of the substrate removal, either at the surface (bioabrasion) or inside (bioboring) of calcium carbonate ($CaCO_3$) substrates (Hallock 1988, Londoño-Cruz et al. 2003, Hutchings et al. 2005, Alvarado et al. 2017). Polychaetes and sipunculids are among the most common boring organisms, being dominant at times in richness and abundance. These animals recruit via pelagic or benthic larvae; the differential availability of worm larvae in time is reflected in the abundance and composition of the community of borers colonizing available substrate (Hutchings 1981, 1986, Enochs 2012).

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Depending on the type of erosion these worms cause, they can be categorized as borers (when they break out and remove the calcareous substrate) or nestlers (they do not bore, but use vacant crevices to dwell in or on the substrate) (Hutchings 1981, Davies & Hutchings 1983). Although the boring mechanism is not yet fully understood, a combination of physical (substrate abrasion by hooks and spines in sipunculids and by chaetae and mandibles in polychaetes) and chemical (substrate dissolution by substances produced in glands or papillae) processes has been proposed (Hutchings 1981, 2011, Fonseca et al. 2006, Alvarado et al. 2017).

To date, the boring polychaetes are included in the families Spionidae, Eunicidae, Lumbrineridae, Dorvilleidae, Sabellidae, and Cirratulidae (Blake 1969, Hutchings 2011). For sipunculids, the boring species belong to the Aspidosiphonidae and Phascolosomatidae families (Alvarado et al. 2017). It has been stated that these worms, at least polychaetes, are early colonizers of available coral substrates (Hutchings 1986, 2008, 2011), so to understand their contribution to coral substrate removal, it is worth assessing relatively new (younger than 1 yr) available substrates. In later stages of the process, at least in the area of interest, these animals are replaced by mussels (Londoño-Cruz et al. 2003).

At normal levels, bioerosion might benefit coral reefs through increased asexual reproduction of branching corals and augmenting available surface area for recruitment, increasing biodiversity (Hutchings 1986, Hallock 1988, Alvarado et al. 2017, Davidson et al. 2018). However, at high levels, bioerosion can drastically affect reef stability and diminish reef heterogeneity, threatening the whole ecosystem (Hutchings 1986, Hallock 1988, Glynn 1990, Davidson et al. 2018). This, in turn, might severely impede the capacity of coral reefs to provide ecosystem services (e.g. food security, tourism, shore protection), causing a cascade of social, economic, and ecological problems (Pari et al. 2002, Hutchings et al. 2005, Hoegh-Guldberg et al. 2007). Different types of perturbations (ecological, environmental, and anthropogenic), for instance eutrophication (which increases phytoplankton and macro-algae biomass, food for bioeroders) and ocean water acidification (which weakens the strength of corals and diminishes production of $CaCO_3$), have contributed to increased bioerosion and the continuous deterioration of reef framework (Hoegh-Guldberg et al. 2007, Baker et al. 2008, Decarlo et al. 2015, Enochs et al. 2016, Davidson et al. 2018), with concomitant deterioration of the whole ecosystem. Hence, it is important to assess this process, especially in poorly known marginal coral reefs.

Different studies carried out in Eastern Tropical Pacific (ETP) coral reefs have contributed to knowledge of their ecology, zoogeography, and species composition (Glynn 1990, 1994, Cortés 1992, Vargas-Ángel et al. 2001, Zapata 2001, Cantera et al. 2003, Londoño-Cruz et al. 2003, Zapata & Vargas-Ángel 2003, Toro-Farmer et al. 2004, Fonseca et al. 2006, Enochs 2012, Alvarado et al. 2017, Glynn et al. 2017). However, studies on coral bioerosion and its effects, especially bioboring, in the Colombian ETP are scarce and focus mainly on boring bivalves, their effects, and taxonomic identification (Cantera & Contreras 1988, Cantera et al. 2003, Londoño-Cruz et al. 2003). There is, therefore, a need to assess the boring rates of understudied bioeroding taxa, such as ecologically important annelid and sipunculid species. Determining the species involved in the process can be learned by sampling natural substrates; however, knowing their contribution to $CaCO_3$ removal is not possible with this approximation because the time since infestation is normally unknown. To overcome this problem, many authors have used experimental substrates of different origin, including molded substrates from native coral species (Tribollet et al. 2002, Londoño-Cruz et al. 2003). Hence, the main purpose of this research was to provide information on the species of worms (polychaetes and sipunculids) and their contribution to coral reef bioerosion, using artificial substrates in 2 reefs located in the Gorgona National Natural Park (Colombian Pacific).

2. MATERIALS AND METHODS

2.1. Study area

Gorgona Island (2.9689° N, 78.1819° W; Fig. 1), about 30 km offshore of the Colombian coast, is part of the Gorgona National Natural Park, a well-known site for conservation and research that is listed in the Green List areas of the IUCN. Along with Coco Island (Costa Rica), Coiba Island (Panamá), the Galápagos Islands (Ecuador), and Malpelo Island (Colombia), this area constitutes the ETP Marine Corridor (CMAR). Gorgona, along with Gorgonilla (a small islet), is the largest insular territory (about 13.2 km²) on the Pacific coast of Colombia (Zapata 2001, Giraldo 2012). While within-year (seasonal) variation in climatic and oceanographic conditions at Gorgona is influenced by the latitudinal displacement of the Intertropical Convergence Zone (ITCZ; Rodríguez-

Fig. 1. Gorgona Island (Colombia) in the Eastern Tropical Pacific, showing the study sites of La Azufrada and Playa Blanca reefs on the lee side of the island

Rubio et al. 2003, Giraldo et al. 2008), inter-annual variation is primarily determined by strong El Niño–Southern Oscillation (ENSO) events (Poveda et al. 2006). Average annual precipitation reaches 8000 mm yr^{-1} and freshwater inflow (rain, runoff, and discharges from permanent creeks) is therefore high. This results in low salinity and a high concentration of suspended solids. The tidal range is large, reaching up to 5 m (von Prahl & Erhardt 1985, Zapata 2001, Giraldo et al. 2008). Because of these marginal environmental conditions, Gorgona's coral reefs are modestly developed (maximum framework thickness of 8 m; Glynn et al. 1982); nonetheless, they are considered one of the most diverse and best developed coral reef formations in the ETP, and the most developed reef system in the Colombian Pacific (Zapata 2001, Zapata & Vargas-Ángel 2003, Giraldo et al. 2008). Gorgona's coral reefs exhibit low coral species diversity and are dominated by branching corals of the genus *Pocillopora* (von Prahl & Erhardt 1985, Zapata 2001).

The most developed reefs at Gorgona are La Azufrada and Playa Blanca reefs, located on the lee of the island (Zapata 2001, Giraldo et al. 2008). La Azufrada is the largest continuous reef (~1000 ×

90–250 m), followed by Playa Blanca, which is split into 2 patches separated by a sandy trench ~100 m width. The north patch is smaller (~240 × 40 m) than the south (~900 × 60–230 m). On Playa Blanca and La Azufrada reefs, 4 distinct reef zones can be distinguished: back-reef, reef-flat, reef-front, and reef-slope (Zapata & Morales 1997, Zapata 2001). These reef zones are distinguished mainly by coral cover, substrate composition, and depth. The back-reef, separated from the shore by the navigation channel, is composed mainly of loose coral colonies; turbidity there is normally high. The reef-flat has a live coral cover close to 50%. Both the back-reef and reef-flat are sub-aerially exposed during extreme low tides, causing coral bleaching and mortality in extreme events every few years (Castrillón-Cifuentes et al. 2017). The reef-front is densely packed with coral colonies and live coral cover is much higher, reaching up to 90%. The reef-slope is narrow and composed mostly of loose and tumbled coral colonies; this is the deepest zone of the reefs (~3 m at low tide).

2.2. Field methods

Branches of *Pocillopora* spp. with no signs of bioerosion, recently broken from their colonies under natural conditions, were collected from La Azufrada and Playa Blanca reefs. These branches were taken to the lab, the live tissue washed off when present, and then they were shaped into similar-sized cylinder-like structures (cylinders), using a handheld grinder. All cylinders were weighed in triplicate to the nearest ±0.0001 g with an OHAUS (Pioneer, PA313) balance. Each cylinder was drilled at one of the ends to anchor a 1.59 mm diameter stainless steel L-shaped rod, using epoxy resin. Larger (6.35 mm diameter × 2 m long) stainless steel rods were hammered in advance into the reef framework, leaving about 50 cm extended above the reef bottom. The cylinders were tied (using cable ties) to this portion of the rod (1 cylinder rod^{-1}) (Fig. 2). This way, only bioborers (e.g. mollusks, worms) recruited into the cylinders. Sea urchins were unable to climb the anchor rod, and fishes were never seen to be attracted to the cylinders (at least during our visits), nor were fish bite scars detected on any of the cylinders. Five cylinders were randomly deployed along each reef zone and left on the reef for either 6 (P1) or 9 (P2) months, for a total of 80 cylinders (5 cylinders × 4 reef zones × 2 periods × 2 reefs). The initial average (±SE) weight of the cylinders was 16.5 ± 0.32 g. All cylinders were deployed the same day (11 February 2016). Once the exposure period ended

Fig. 2. Experimental setting showing (A) a freshly deployed coral cylinder, (B) a cylinder after about 7 mo underwater, and (C) a retrieved cylinder with fouling removed (borer holes — here from bivalves — are easily seen)

(i.e. P1 and P2), each cylinder allocated to a given period was collected, stored in a plastic container with 10% formalin and taken to the lab.

2.3. Lab methods

All fouling was removed from the cylinder surface in an attempt to recover, as best as possible, the original surface. This was performed using metallic instruments under a stereomicroscope. After that, each cylinder was carefully fragmented using locking pliers in a manner which minimized the loss of $CaCO_3$. All boring fauna was removed for analysis; for abundance calculations, only complete worms and fragments with the head of the worm were considered. For $CaCO_3$ removal calculations, all animals (i.e. complete worms and worm fragments) were considered. After fragmentation, remaining coral chips were dried and weighed in triplicate to the nearest ±0.0001 g. The difference between initial and final weight (net removal) is the weight of the substrate (i.e. $CaCO_3$) removed by boring organisms (W_S). All borers (i.e. mollusks, worms, and acrothoracican cirripeds) found in each cylinder were also (wet) weighed (W_b). To estimate the relative contribution of worms to substrate removal, these were weighed separately (W_w) and a proportion between these 2 values (W_w/W_b) was calculated. Since it is almost impossible to calculate the exact amount of $CaCO_3$ removed by each individual directly (i.e. the weight of the $CaCO_3$ that was removed from each hole), we used the weight of the boring worms (polychaetes and sipunculids) as a proxy for the amount of $CaCO_3$ removed, so we assumed W_b equivalent to W_S. In order to calculate the amount of substrate removed by worms, we multiplied this weight (W_S) by the proportion (Eq. 1). Net removal (NR, in g) was converted into a bioerosion rate using the initial cylinder weight and the duration of exposure. This rate is expressed in g kg^{-1} yr^{-1}:

$$\text{NR CaCO}_3 = \frac{W_w}{W_b} \times W_S \qquad (1)$$

2.4. Data analysis

The net removal and bioerosion rate data did not fulfill the normality and homoscedasticity assumptions required for parametric tests. Therefore, a randomization test (10 000 permutations) was implemented with reef (2 levels), reef zone (4 levels), and exposure period (2 levels) as predictive factors. As no significant statistical effects were found, no additional analyses were necessary. However, we present all descriptive statistics: percentages for abundance and richness data and averages and deviations for $CaCO_3$ removal. All statistical analyses were performed to a significance level of $\alpha = 0.05$ using R v.3.5.1 (R Core Team 2018).

3. RESULTS

3.1. General abundance/richness

Of the 80 cylinders originally deployed, 64 were recovered: 33 from P1 and 31 from P2; 30 cylinders were recovered from La Azufrada and 34 from Playa Blanca reefs. The average (±SE) initial weight of the recovered cylinders was 18.1 ± 0.68 g. From the cylinders, a total of 137 worms were found, allocated into 9 (19 species) and 2 (4 species) families of polychaetes and sipunculids, respectively (Table 1). Of the worms, 64.2% were found in La Azufrada and 35.6% in Playa Blanca. Regarding reef zones, worms were more abundant in the reef-front (38%) and less so in the reef-flat (18.2%). The temporal comparison showed an increasing trend, with the number of individuals growing from 44.5% in P1 to 55.5% in P2. Polychaetes were, in general, 4.5 times more abundant than sipunculids, and this tendency was more evident during P1 when polychaetes were 11.2 times more abundant than sipunculids. In P2, sipunculid

Table 1. Abundance of families of polychaete and sipunculid boring worms found during the 2 exposure periods (P1: 6 mo; P2: 9 mo) at each coral reef (LA: La Azufrada; PB: Playa Blanca) at Gorgona Island, Colombia

| Species | Abundance | | | |
| | LA | | PB | |
	P1	P2	P1	P2
Polychaetes				
Cirratulidae				
Cirratulidae sp.	0	1	0	0
Dodecaceria laddi	1	0	0	0
Timarete luxuriosa	2	0	0	0
Dorvilleidae				
Dorvillea rubra	5	7	2	4
Eunicidae				
Eunice cedroensis	2	0	0	0
Lysidice ninetta	0	0	2	1
Palola paloloides	0	1	0	0
Sabellidae				
Euratella salmacidis	0	0	2	0
Spionidae				
Dipolydora commensalis	7	0	0	4
Flabelligeridae				
Semiodera cariboum	3	0	0	0
Nereididae				
Eunereis sp.	0	1	0	0
Syllidae				
Parasphaerosyllis malimalii	13	11	2	12
Syllis gracilis	14	3	0	8
Syllis prolifera	0	0	1	0
Terebellidae				
Polycirrus sp.	0	3	0	0
Sipunculids				
Aspidosiphonidae				
Aspidosiphon (*Aspidosiphon*) cf. *elegans*	1	1	0	8
Phascolosomatidae				
Phascolosoma (*Fisherana*) sp.	1	2	0	1
Phascolosoma (*Phascolosoma*) cf. *nigrescens*	0	1	0	0
Phascolosoma (*Phascolosoma*) cf. *perlucens*	2	6	1	1

abundance increased and polychaetes (which had the same abundance in both periods) were only 2.8 times more abundant than sipunculids. The highest species richness of worms (16 species of polychates and sipunculids) was found in La Azufrada, compared to 10 species in Playa Blanca. Temporal variation was not evident, with 14 species during P1 and 13 during P2. As for reef zones, richness was highest in the reef-slope (12 species), followed by the reef-front (9), the reef-flat (8), and the back-reef (7).

Worms were divided into true-borers (or borers) (Blake 1969, Hutchings 2011, Alvarado et al. 2017) and nestlers (not reported as borers previously). Of the 9 polychaete families, Cirratulidae, Dorvilleidae, Eunicidae, and Sabellidae have been reported as true borers, while the remaining families are considered nestlers. Interestingly, one family (Syllidae) of this group was the most common (46.7%) of all collected polychaetes. Sipunculids, considered borers, were less abundant and belonged to the families Aspidosiphonidae and Phascolosomatidae.

Nestlers were more abundant in La Azufrada (67.6%) than in Playa Blanca (32.4%). Regarding reef zones, the highest abundance was found in the reef-front (45.1%), followed by the reef-slope (26.8%), reef-flat (15.5%), and back-reef (12.7%). These worms were slightly more abundant during P2 (53.5%) than P1 (46.5%). Borers, on the other hand, were also more abundant in La Azufrada (60.6%) than Playa Blanca (39.4%), and their abundance was highest in the reef-front (30.3%), followed by the back-reef (25.8%), reef-slope (22.7%), and reef-flat (21.2%). These worms were more abundant during P2 (57.6%) than P1 (42.4%).

3.2. CaCO$_3$ removal

CaCO$_3$ removal data (net removal and bioerosion rate) corresponded to the combined effect of polychaetes and sipunculids. Nevertheless, the relative contribution of polychaetes, sipunculids, and fragments of both to this process is reported in an effort to provide more specific information on each group. This information must be considered with caution, however, given that the small size of the organisms found could result in a large error in individual weight measurements. Net removal and bioerosion rate (Fig. 3) were not affected by any predictive factor in the randomization test (Table 2) (i.e. reef, reef zone or exposure period). However, average net removal increased by 19.6% in 3 mo. In addition, this rate was 1.8 times greater in La Azufrada than in Playa Blanca and, for reef zone, it was highest in the reef-slope and lowest in the reef-front (Table 3). On the other hand, bioerosion rates (g kg^{-1} yr^{-1}) showed the same pattern for both reefs (i.e. 1.6 times faster rates in La Azufrada than in Playa Blanca) and reef zones (i.e. fastest in the reef-slope and slowest in the reef-front); however, the temporal trend was reversed, with the rate being 1.27 times faster during P1 than P2 (Table 3).

4. DISCUSSION

Cryptic organisms, including numerous predatory and scavenging species that dwell in cavities as well as endolithic borers, are very common in coral reefs.
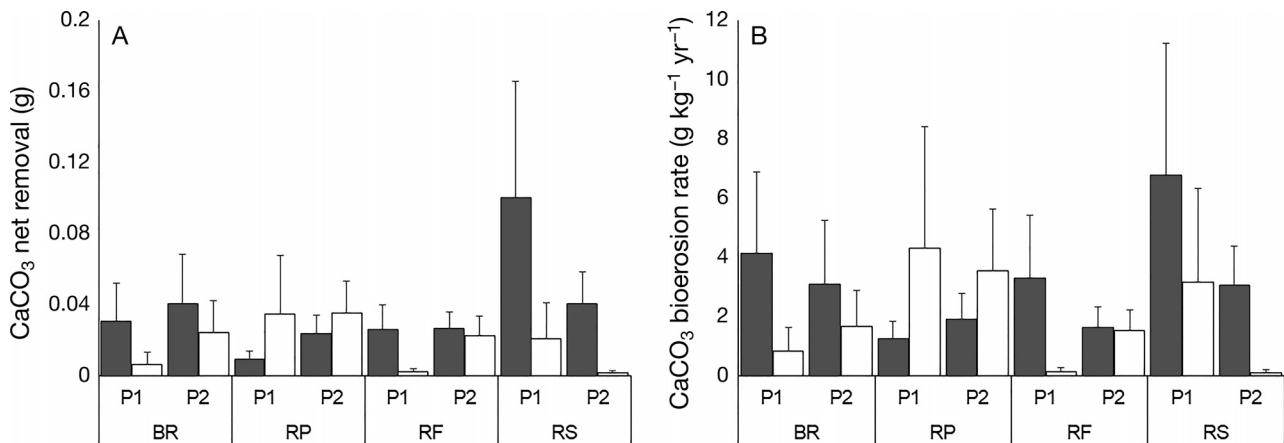
Fig. 3. Average (±SE) (A) net removal and (B) bioerosion rate of calcium carbonate by boring worms (polychaetes and sipunculids) in 2 different periods of exposure (P1: 6 mo; P2: 9: mo) along the reef zones (BR: back-reef; RP: reef-flat; RF: reef-front; RS: reef-slope) of La Azufrada (grey) and Playa Blanca (white) reefs at Gorgona Island, Colombia

Table 2. Results of the randomization test (10 000 permutations) for the net removal (g) and bioerosion rate (g kg^{-1} yr^{-1}) of calcium carbonate caused by boring worms (polychaetes and sipunculids) at La Azufrada and Playa Blanca reefs, Gorgona Island, Colombia

Factor	df	Net removal		Bioerosion rate	
		F	p	F	p
Reef	1	2.335	0.141	1.158	0.293
Reef zone	3	0.450	0.720	0.375	0.782
Exposure period	1	0.202	0.656	0.315	0.585
Reef × reef zone	3	2.323	0.085	1.552	0.205
Reef × exposure period	1	0.204	0.667	0.245	0.626
Reef zone × exposure period	3	1.229	0.308	0.609	0.627
Reef × reef zone × exposure period	3	0.316	0.815	0.256	0.852

Table 3. Average (±SD) net removal and bioerosion rate of calcium carbonate caused by boring worms (polychaetes and sipunculids) at La Azufrada (LA) and Playa Blanca (PB) reefs, Gorgona Island, Colombia, during Period 1 (P1; 6 mo) and Period 2 (P2; 9 mo) at each reef zone (BR: back-reef; RP: reef-flat; RF: reef-front; RS: reef-slope). The relative contribution by polychaetes (P), sipunculids (S), and worm fragments (F) to net removal and bioerosion rate are shown as percentages of the average value

Factor	Net removal (g)					Bioerosion rate (g kg^{-1} yr^{-1})				
	Average	SD	%P	%S	%F	Average	SD	%P	%S	%F
Reef										
LA	0.032	0.041	28.4	29.1	42.5	2.839	3.540	28.3	26.1	45.6
PB	0.018	0.033	11.3	30.2	58.5	1.807	3.779	10.6	23.8	65.6
Exposure period										
P1	0.022	0.041	27.5	8.9	63.6	2.553	4.478	24.3	8.9	66.8
P2	0.027	0.033	16.7	47.9	35.4	2.011	2.616	16.3	47.0	36.7
Reef zone										
BR	0.025	0.042	7.0	64.0	29.0	2.332	3.771	10.2	54.3	35.5
RP	0.024	0.035	14.2	27.6	58.2	2.603	4.245	14.9	22.5	62.6
RF	0.018	0.021	31.4	6.0	62.5	1.558	2.319	32.3	4.7	62.9
RS	0.033	0.052	40.2	8.0	51.9	2.962	4.665	33.2	6.3	60.5

Due to this hidden life style, accurate knowledge about their diversity, abundance, and ecology is scarce; such is the case for many polychaete and sipunculid species (Díaz-Castañeda et al. 2005, Glynn & Enochs 2010). These common inhabitants of coral reefs increase biodiversity but may also contribute to reef framework erosion (Hutchings 1986). It is necessary to recognize their morphology and habitat preferences as well as their relationship to the substrate (e.g. borers or nestlers; Rice & Macintyre 1982, Hutchings 2008, 2011). This knowledge will allow us to interpret the role each group may have in the bioerosive process. For instance, the family Syllidae, although reported as dominant in hard substrates, is not considered a borer but it has been suggested that some of these species (nestlers) may use burrows made by borers (Capa et al. 2001a,b). However, other authors (e.g. Dharmaraj et al. 1987) have reported species of this family boring calcareous substrates (i.e. pearl oysters). A common finding in this study,

that individuals of this family were found dwelling in burrows that almost perfectly fit their bodies, would suggest that they are making their own burrows (i.e. boring); however, more species-specific research in this aspect is needed to clearly state if these polychaetes are or are not true borers. In addition, the high abundance of individuals of this family could be due to their reproductive process involving high larvae output, as many epitokes were found in the burrows along with the worms. Regarding sipunculids, a similar study by Cantera et al. (2003) found that the most common genus in Gorgona was *Aspidosiphon* (family Aspidosiphonidae). In this study, the most abundant family was Phascolosomatidae, which has species that are cosmopolitan (Fonseca et al. 2006) and common dwellers of grooves and burrows of coral reefs (Rice & Macintyre 1982, Cantera et al. 2003). A possible explanation for the difference with Cantera et al. (2003) is that they collected colonies (dead and alive) lying on the bottom, while in this study the cylinders were set above the bottom. Experimental design — apart from ecological (e.g. recruitment strategy) and temporal (there is a time gap between studies of at least 12–13 yr) changes in e.g. species composition and distribution — might be responsible for the differences found in sipunculid species composition between both studies. In any case, it is worth noting that the prevalence of boring worms (polychaetes and sipunculids) within ETP coral reef substrates is relatively low compared to other areas of the world (Londoño-Cruz et al. 2003, Alvarado et al. 2017).

4.1. CaCO$_3$ removal

CaCO$_3$ removal from dead substrates by borers depends on substrate hardness (density) and availability (amount) (Hutchings 1986, 2011). The rate at which it is removed is highly affected by the timing (when the substrate becomes available) and duration of exposure (Hutchings & Peyrot-Clausade 2002, Londoño-Cruz et al. 2003, Osorno et al. 2005), as this rate tends to increase as boring communities mature and exposure periods increase (Hutchings 2008, 2011). Although a longer exposure period means a higher chance for larval settlement and theoretically a more eroded substrate (which in turn becomes easier to colonize), the bioerosion rate was higher during the shorter exposure period. This could be the result of worms removing more substrate when they are growing than when they reach larger sizes (Londoño-Cruz et al. 2003); once worms achieve maxi-

mum sizes, the bioerosion rate seems to decelerate. On the other hand, net removal was higher during the longer exposure period; this is expected since a longer period may allow for a higher chance of borers to colonize, and is supported by there being 1.4 times more boring worms after P2 than after P1.

The lack of significant statistical differences in CaCO$_3$ removal between reefs, reef zones or exposure periods might be because (1) these reefs were under very similar environmental conditions; (2) the depth range was relatively narrow, and although there was a marked and clear zonation in terms of coral cover and structure complexity, depth as such did not affect borer community composition and structure; and (3) the width (i.e. distance between backreef and reef-slope) was relatively narrow; hence the larval pool might be shared. Similar results have been found previously (Cantera et al. 2003, Londoño-Cruz et al. 2003). Despite the similarities in environmental and ecological conditions between these 2 reefs, some specific features, like heavy sediment loads, can vary spatially and differentially affect the amount of CaCO$_3$ removed by certain borers (Londoño-Cruz et al. 2003). For example, Playa Blanca receives around 293 g m^{-2} d^{-1} of total dissolved solids from a permanent creek, while La Azufrada only receives 95 g m^{-2} d^{-1} (Blanco 2009). This might be one of the reasons why, although not statistically different, CaCO$_3$ removal was higher in La Azufrada. Furthermore, several authors have argued that conditions particular to reef zones may affect the composition and abundance of the borer community (Hutchings 1981, 1986, Rice & Macintyre 1982, Cantera et al. 2003). It has been proposed that corals increase in density as distance from shore increases (Sammarco & Risk 1990), perhaps due to increased wave energy (Rice & Macintyre 1982, Davies & Hutchings 1983, Hutchings 1986, Cantera et al. 2003, but see Warme 1970) rendering harder (and safer) coral substrates. In addition, offshore zones are likely to receive more nutrients from currents than inshore zones (Macintyre et al. 1992, Reaka-Kudla et al. 1996, Glynn 1997, Wellington et al. 2001), which in turn might be reflected in more food (e.g. plankton or organic deposits) for borers. Therefore, it can be proposed that offshore zones might be more attractive to borers. Although there were no significant differences between zones in terms of CaCO$_3$ net removal or bioerosion rate, the outer zone (i.e. the reef-slope) always showed the highest values; so our results support the previous reasoning. In addition, it has been shown that fouling promotes the settlement of borers by serving as a refuge while they finish metamorpho-

sis (Hutchings 2011). The reef-slope showed the highest dead coral cover and it was clear that the cylinders exposed in this zone showed the highest fouling cover.

Finally, Hutchings (2008) argued that $CaCO_3$ removal by worms is normally underestimated due to their small sizes. Their low weight makes it highly likely that measurement errors may arise, generating difficulties in determining the true effect that these organisms have on $CaCO_3$ removal. In addition, some polychaete species have short life cycles (from weeks to months) (Hutchings 2008), so generations may have come and gone during the experimentation period. Therefore, many worms may have affected the substrate and disappeared from it, so when calculating the $CaCO_3$ removal, these worms were not considered. Furthermore, it has been proposed that in productive, low pH, and ENSO-influenced waters (like at Gorgona), boring bivalves are more common, and this is true in the ETP where they are responsible for the majority of $CaCO_3$ removal (Alvarado et al. 2017). Additional results from this study show that $CaCO_3$ removal by bivalves was 111 times larger than that of worms. However, it is worth mentioning that polychaetes have a heavy impact on $CaCO_3$ removal in other parts of the world (Hutchings 1981, Peyrot-Clausade et al. 1995) and that sipunculids from the family Aspidosiphonidae are considered to be large contributors to coral bioerosion in the ETP (Alvarado et al. 2017). In this study, sipunculids increased in number and size as time passed, so it is plausible to think that their relative contribution to $CaCO_3$ removal may increase with time. In conclusion, worm bioerosion seems to be very small in the ETP compared to other groups of boring invertebrates (e.g. bivalves). However, the role of these animals seems to be very important since (1) they weaken the substrate in which they bore and (2) might also attract larger predators that can break off large fragments of the coral substrate.

4.2. Conclusions

The similarity we found in net removal and bioerosion rates of $CaCO_3$ by boring worms (polychaetes and sipunculids) across zones and reefs at Gorgona Island was probably due to the short distance that separates La Azufrada and Playa Blanca coral reefs, as these reefs are likely subject to similar environmental conditions. Regardless of the lack of statistical significance in the results of this study, there is a highly suggestive effect of time on net removal and

bioerosion rates. Increasing the experimental duration would likely bring any significant differences to light as boring communities mature and change through time. Finally, this is the first time that the identity of the species of worms performing bioerosion (polychaetes and sipunculids), many of which are new records, has been reported and their direct effect on coral bioerosion assessed for coral reefs of the ETP.

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