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Bioerosion of coral reefs—A chemical approach

Abstract—We measured total alkalinity changes as a direct clue to the rate and mechanism (chemical or mechanical) of boring of the bivalve *Lithophaga lessepsiana* in colonies of the coral *Stylophora pistillata*, the most abundant coral-borer association in the reefs of the northern Gulf of Elat (Aqaba), Red Sea. Our experiments included comparison between total alkalinity measurements of seawater surrounding colonies of *S. pistillata* free of *L. lessepsiana* and colonies infected with it. It is suggested that *L. lessepsiana* is able to redissolve chemically up to 40% of the $CaCO_3$ deposited by *S. pistillata*.

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Buildup of the primary framework on coral reefs is accompanied by continuous biological, physical, and chemical destruction. The net rate of $CaCO_3$ deposition on the reef is the sum of these processes (MacGeachy and Stearn 1976). Biological weathering, or bioerosion (Neumann 1966), destroys and removes the calcareous substrate by the direct boring or rasping action of organisms.

Boring organisms, rather than rasping organisms, have a significant effect on the mechanical stability of the reef framework,

since they remove material from the interior. The mechanisms by which marine organisms burrow into hard substrates have been the subject of considerable research (Yonge 1955, 1971; Fang and Shen 1988). Quantitative data on bioerosion rates in reef environments are rather scarce (Neumann 1966; MacGeachy and Stearn 1976; Kobluk and Risk 1977; Tudhope and Risk 1985; Hutchings 1986). Most of the research has been aimed at the clionid sponges (Neumann 1966; MacGeachy 1977; Hutchings 1986), and little information is available on the role of worms, barnacles, and bivalves.

The boring bivalve *Lithophaga* is an important borer on the reefs of Isla del Caño (Costa Rica), Isla Uva (Panama) (Scott and Risk 1988), and on the reefs of the Gulf of Elat (Aqaba), Red Sea (Fishelson 1973; Loya 1982). In the Gulf of Elat about 15 coral species are infected by this bivalve (Loya unpubl. results). Among them, *Stylophora pistillata* shows the greatest infestation: typically 300–600 *Lithophaga lessepsiana* bore into a medium-sized (30-cm diam) colony (Loya 1982). *S. pistillata* composes ~20% of the reef framework in the northern part of the gulf (Loya 1972), and an estimate of its bioerosional rate and mechanism is extremely relevant.

The mode of penetration into calcareous substrates differs among bivalve species. Boring by lithophagid bivalve molluscs is believed to occur through chemical dissolution of coral substrate (e.g. *see* Jaccarini et al. 1968; Bolognani Fantin and Bolognani 1979; Morton and Scott 1980) or a combination of chemical and mechanical abrasion (e.g. *see* Soliman 1969). Fang and Shen (1988) suggested that *Lithophaga nigra* is a mechanical and not a chemical borer. They attributed an observed pH decrease in artificial burrows of *L. nigra* to excretion of metabolic CO_2 rather than to excretion of a strong acid. The pH decrease that they observed is capable, however, of reducing aragonite saturation state to a level at which it will dissolve. Thus, pH provides only indirect evidence for $CaCO_3$ dissolution or precipitation, and a direct estimate is needed to determine the boring mechanism.

Here we suggest measurement of total alkalinity (A_T) in the seawater surrounding corals as direct evidence of a boring mechanism. A_T change over time, which has been widely used to estimate growth rates of coral reefs (e.g. *see* Smith 1973; Barnes et al. 1976), can potentially quantify the rates of construction (skeletogenesis) vs. destruction (bioerosion) of living corals bored by any chemical borer.

The operational definition of A_T is the number of equivalents of strong acid added to the sample in order to reach the H_2CO_3 endpoint (Stumm and Morgan 1981). A_T in normal oxygenated seawater is expressed by

$$A_T = m_{HCO_3^-} + 2m_{CO_3^{2-}} + m_{B(OH)_4^-} + m_{OH^-} - m_{H^+} \quad (1)$$

where $m_i n^-$ denotes the molal concentration of species i having a charge of n^-. An important characteristic of A_T is its conservative behavior, i.e. the ratio A_T : salinity is constant. Nonconservative A_T changes in normal oxygenated seawater are almost exclusively due to $CaCO_3$ precipitation or dissolution (Stumm and Morgan 1981). Thus, after normalization to salinity, A_T increases by 2 equivalents per mole of $CaCO_3$ dissolved. Precipitation decreases A_T by the same amount (Eq. 1).

A_T is slightly affected by other nonconservative processes, i.e. changes of NO_3^- concentration. Aerobic oxidation of average oceanic organic matter by respiration produces nitric acid (e.g. *see* Redfield et al. 1963):

$$[(CH_2O)_{106}\cdot(NH_3)_{16}\cdot H_3PO_4] + 138O_{2(aq)} \rightarrow 106CO_2 + 16H^+ + 16NO_3^- + H_3PO_4 + 122H_2O. \quad (2)$$

Nitrate regeneration within the skeleton of the coral *Porites lobata* was observed by Risk and Müller (1983). Nitric acid decreases ("titrates") the alkalinity because hydrogen ions combine with anions of weak acids and neutralize them. Thus, respiration lowers A_T by the amount of NO_3^- produced:

$$A_T = A_{T(i)} - m_{NO_3^-} = m_{HCO_3^-} + 2m_{CO_3^{2-}} + m_{B(OH)_4^-} + m_{OH^-} - m_{H^+} \quad (3)$$

where $A_{T(i)}$ denotes the A_T before respiration takes place. Consumption of NO_3^- by primary production (the opposite of Eq. 2) will increase A_T. The overall change in A_T

by primary production-respiration, according to Eq. 2, is 16/106 or ~15% of the CO_2 change due to these processes.

The present study applies A_T to measure chemical boring rates in coralline aragonite. If *L. lessepsiana* is a chemical borer, then dissolution of coralline aragonite will increase the A_T of the surrounding seawater due to addition of $Ca(HCO_3)_2$ to the water. If the mode of penetration is mechanical, however, then only particulate aragonite will be produced and A_T will remain constant.

Two colonies of *S. pistillata* were collected in front of the Heinz Steinitz Marine Laboratory (Gulf of Elat). One was heavily infected (infected colony—IC) with boring *L. lessepsiana* and the other was free of borers (noninfected colony—NC). Our discussion is based only on the experimental results from these two colonies.

After an acclimation period of 1 d in a tank supplied with running seawater, each colony was transferred to an aquarium containing 10 liters of freshly collected seawater. The aquaria were kept open in the laboratory and were illuminated continuously with fluorescent light and aerated with fresh outdoor air. During each sampling period, water samples were taken from each aquarium with a 60-ml plastic syringe and collected in 60-ml glass bottles. Eighty milliliters of water were removed during each sampling period; 20 ml were used to rinse the syringe and the sample bottle and the rest was stored at 4°C until the alkalinity titration.

Three days after this experiment, the colonies were returned to running seawater and maintained there for 9 d. Then, the corals were placed under a strong jet of seawater until they were completely cleaned of their tissue (bleached) as inspected with a binocular microscope. During this process the boring clams in IC closed their valves and appeared unharmed. After an acclimation period of 1 d, the clams extended their paired siphons out of the burrows and exhibited normal behavior. The bleached colonies were placed again in the aquaria, and the experiment was repeated.

Computerized alkalinity titration, modified and improved from Ben-Yaakov et al. (1982) and Lazar et al. (1983), was used in the study. The sample was filtered through a 0.45-μm Millipore membrane filter. About 15 g (avg weighing SD was 0.001 g) of the filtrate were weighed directly in the titration vessel (Radiometer model 956-176) and placed in a covered, Radiometer model TTA 80 titration assembly. The samples were titrated with 0.25 N HCl (BDH concd volumetric solution). Two types of measuring device were used to measure the potential of the pH electrochemical cell (glass electrode Radiometer model G2040C and K4040 reference electrode): a very high input impedance differential amplifier with an A/D converter (AD/7550), and a Radiometer model PHM 84 pH meter with an analog output. The digital signal of the pH electrode was fed to an IBM PC-XT equipped with a digital I/O card (PPI 8255) via an interface-controller. The analog output of the pH meter was fed to the computer via a Data Translation model DT 2801 single board analog and digital I/O system. The acid was delivered by a Radiometer ABU 80 autoburette controlled by the PC via the I/O devices. Complete system control for the DT 2801 was provided by software written in ASYST (Macmillan). The PPI 8255 was controlled by software written in TURBO PASCAL (Borland). The average SD between duplicate titrations estimated from 200 seawater samples was 0.8 μeq kg^{-1}.

Salinity changes during the experiment were monitored by Br^- concentration. Bromine was analyzed by ion chromatography with a Dionex 2010 (typical SD of 0.75%).

The surface areas of the colonies were determined by breaking them into subcylindrical pieces with a cutter. The length (l) and two diameters (the largest and the smallest), to the nearest 0.1 mm, of each piece were taken with a caliper. The radius (r) of the cylinder was calculated as half the average of the two diameters. Two types of cuttings were produced: fragments cut on both sides and tips of branches having one cut only. The surface area of fragment type 1 is given by $2\pi rl$ and the area of type 2 is estimated by $2\pi r(l + \frac{1}{2}r)$. Replicate surface area determinations showed an average SD of 3%.

Alkalinities were calculated from the titration data with a modified Gran method

Table 1. Analytical results from the experiment with living colonies. Surface areas are 875 ± 26 and 1,330 ± 40 cm² for NC and IC respectively.

Jun 1988	Time	NC A_T (μeq kg⁻¹)	IC A_T (μeq kg⁻¹)	Br^- (mg kg⁻¹)
9	1245	2,452	2,460	75.1
	1435	2,430	2,435	—
	1505	2,424	2,429	—
	1635	2,413	2,404	—
	1835	2,367	2,379	—
	2400	2,261	2,314	—
10	0900	2,177	2,232	—
	1945	2,017	2,052	76.3
11	1050	1,813	1,828	—
	1510	1,776	1,784	—
	2100	1,703	1,693	78.9
12	0830	1,599	1,605	79.9

Table 2. As Table 1, but with bleached colonies.

Jun 1988	Time	NC A_T (μeq kg⁻¹)	IC A_T (μeq kg⁻¹)	Br^- (mg kg⁻¹)
21	1340	2,445	2,464	75.2
	1440	2,437	2,458	—
	1640	2,428	2,468	—
	1925	2,436	2,510	—
	2150	2,445	2,599	—
	2350	2,457	2,627	—
22	0830	2,466	2,720	—
	1130	2,514	2,770	—
	1340	2,547	2,785	76.0
	1740	2,539	2,834	—
	2050	2,534	2,838	—
23	0745	2,577	2,922	—
	1130	2,575	2,949	76.9

(Gran 1952). The ratio $A_T : E_{Br}$ was used to correct A_T for the degree of evaporation (E_{Br}) of the aquaria seawater, where E_{Br} is defined by:

$$E_{Br} = Br^-/Br^-_{(sw)} \quad (4)$$

and Br^- and $Br^-_{(sw)}$ denote bromine concentrations in the sample and "mean" seawater (Stumm and Morgan 1981). Br^- values for samples in which it was not determined (*see Tables 1, 2*) were interpolated linearly.

The experiments with living (Table 1 and Fig. 1A) and bleached corals (Table 2 and Fig. 2A) reflected A_T changes due to coralline aragonite precipitation and dissolution in the aquaria. Comparison between colonies was provided via normalized alkalinity data, where $A_{T(gain)}$ (Figs. 1B, 2B) is defined as:

$$A_{T(gain)} = d \times V_a \times [A_T \times E_{Br}/E_{Br(i)} - A_{T(i)}]/A_{coral} \quad (5)$$

where $A_{T(gain)}$ is excess alkalinity gained due to aragonite dissolution from the beginning of the experiment to any particular sampling point per unit of area of coral in μeq cm⁻², d the density of the aquarium seawater in kg liter⁻¹, V_a the volume of the aquarium at this particular point in liters, $E_{Br(i)}$ the initial degree of evaporation (~1.16), $A_{T(i)}$ the initial A_T in μeq kg⁻¹, and A_{coral} the surface area of the colony in cm². Positive $A_{T(gain)}$ means dissolution of $CaCO_3$ and negative $A_{T(gain)}$ represents precipitation of $CaCO_3$.

The integrated rates of $CaCO_3$ dissolution or precipitation were calculated by dividing $A_{T(gain)}$ by the time (t) passed from the beginning of the experiment to a particular

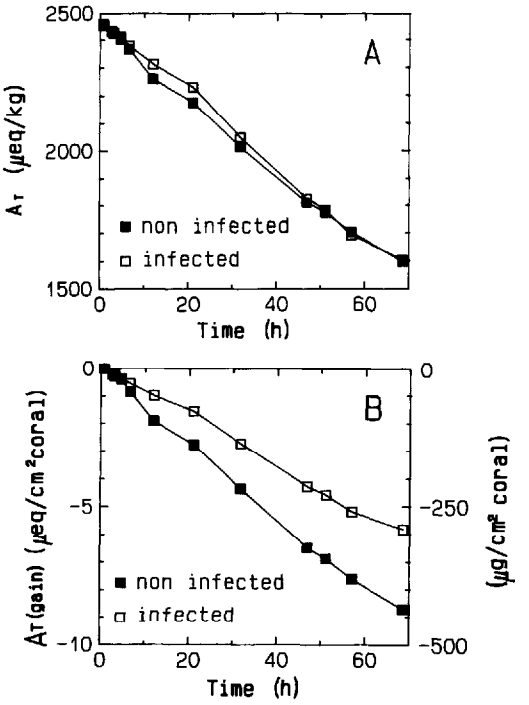

Fig. 1. Alkalinity and $CaCO_3$ weight as a function of incubation time for the live corals experiment. A—A_T curve. B—$A_{T(gain)}$ curve, the weight of $CaCO_3$ per unit area of coral is shown on the right. Analytical error is smaller than the symbol size.

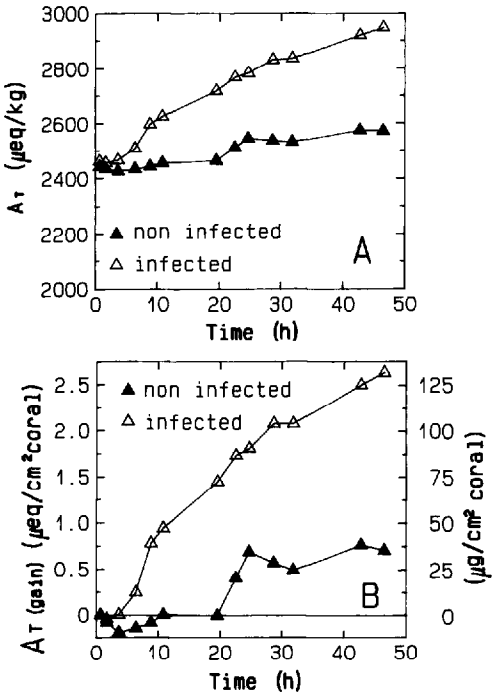

Fig. 2. As Fig. 1, but for the bleached corals experiment.

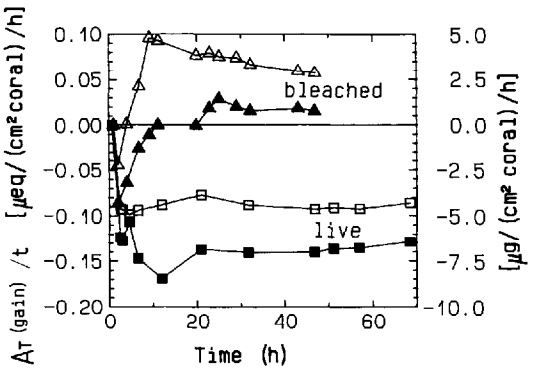

Fig. 3. Apparent aragonite deposition rate (negative part) and dissolution rate (positive part) vs. incubation time. Live IC—□; bleached IC—△; live NC—■; bleached NC—▲. To eliminate most of the noise in the derivative calculation, each sampling point was divided by the total time passed from the beginning of the experiment, instead of the time interval between two consecutive points. This type of derivative calculation introduces some artifacts: the derivative value is not zero when the signal does not change with time, and the derivative of linear trend which does not pass through the origin is not constant, but decreases slowly.

sampling point. Plots of this rate vs. time are given in Fig. 3.

In the live corals experiment, NC and IC behaved similarly and reflected an A_T drop of ~60% from the original value (Fig. 1A). $A_{T(gain)}$ is negative throughout the experiment with the live corals (Fig. 1B), indicating net deposition of skeletal aragonite. Due to the continuous illumination, almost no diurnal growth pattern was observed. NC deposited ~150 μg cm^{-2} more aragonite than IC at the end of the experiment. Net deposition rate of skeleton for NC thus is higher than that of IC.

In the bleached corals experiment, A_T and $A_{T(gain)}$ curves showed a substantial alkalinity increase in the aquarium with IC, in contrast to a small change for NC (Fig. 2). The large positive $A_{T(gain)}$ values recorded in the aquarium with IC (Fig. 2B) clearly demonstrate that *L. lessepsiana* is able to dissolve coralline aragonite. The amount of aragonite bioeroded chemically at the end of the experiment is ~100 μg cm^{-2} higher than that of NC. The exact process of aragonite dissolution by *Lithophaga* is still much debated, however, in the literature. Numerous papers have demonstrated the presence of acid glands in *Lithophaga* (Yonge 1955; Morton and Scott 1980 and references cited there), but none has described the chemical component that was secreted. Histochemical analyses of the glands identified few components that can act as Ca^{2+} chelators—a neutral mucoprotein (Jaccarini et al. 1968) and lipoproteic components with acidic groups (Bolognani Fantin and Bolognani 1979). Aragonite dissolution caused by the activity of these components will result in the observed A_T increase.

Another common acidic component probably present in the burrow is metabolic CO_2. It was demonstrated experimentally that metabolic CO_2 caused a significant pH decrease in artificial burrows of *L. nigra* (Fang and Shen 1988). We suggest that this CO_2 can dissolve $CaCO_3$ via the reaction:

$$CO_{2(aq)} + H_2O + CaCO_{3(s)} \rightarrow Ca^{2+} + 2HCO_3^-. \quad (6)$$

Thus, for every mole of CO_2 reacted with aragonite, the A_T of the solution increases by 2 equivalents.

The drop in $A_{T(gain)}$ at the beginning of the experiment with NC (Fig. 2B) is probably due to precipitation of aragonite. This inorganic deposition may be triggered by introduction of the bleached coral to the aquarium seawater, which is supersaturated with respect to aragonite (Lazar et al. 1983). Lazar et al. (1983) demonstrated an A_T decrease upon addition of excess coralline aragonite powder to Gulf of Elat surface seawater. Similarly, the exposed coral surface serves as a $CaCO_3$ deposition site, although it is less efficient than the powder, due to a smaller area : volume ratio. Therefore, one would expect $A_{T(gain)}$ to remain somewhat negative throughout the experiment. The experiment with NC also exhibited A_T increase, however (Fig. 2B); this increase probably is due to local dissolution of aragonite in places where some remaining organic matter has oxidized microbially. In the case of organic matter oxidation in contact with solid carbonate, Eq. 2 will take the form

$$[(CH_2O)_{106}\cdot(NH_3)_{16}\cdot H_3PO_4] + 106CaCO_{3(s)} + 138O_{2(aq)} \rightarrow 106Ca^{2+} + 212HCO_3^- + 16H^+ + 16NO_3^- + H_3PO_4 + 16H_2O. \quad (7)$$

According to Eq. 7, each mole of total CO_2 gained due to "organic matter" oxidation produces maximally (212–16) : 106 = 1.85 equivalents of A_T due to aragonite dissolution. The actual change in A_T is most probably smaller than that, because the solution is supersaturated with respect to aragonite (Lazar et al. 1983). Therefore, CO_2 will locally lower the degree of saturation before any dissolution takes place. An alternative explanation for the observed A_T increase could be boring by endolithic algae (Kobluk and Risk 1977; Tudhope and Risk 1985). Their photosynthetic activity could cause an increase of A_T according to the inverse of Eq. 2. It was shown by Bellamy and Risk (1982), however, that live *S. pistillata* from the Great Barrier Reef is only sparsely infested by boring algae. The same observation was made by Y.L. on *S. pistillata* from the Gulf of Elat. Thus, A_T increase due to the activity of boring algae is probably minor. Moreover, the trivial amount of endolithic algae present in our experiment will produce a similar photosynthetic signal (per unit coral area) for both (NC and IC) colonies. That area cover of endolithic algae is probably uniform for corals older than ~2 yr is suggested from the experiments of Tudhope and Risk (1985). Therefore the difference in $A_{T(gain)}$ between IC and NC is probably due to dissolution only. The $A_{T(gain)}$ of ~0 μeq cm^{-2} at the beginning of the experiment with IC can be explained as a balance between inorganic aragonite precipitation due to supersaturation and dissolution of coralline aragonite by the boring clams.

Table 3. Calculated potential growth rate (P) of the investigated colonies. The numbers for G and D are averages of the data points that plot on the lines and reflect small changes in rate (Fig. 3).

	NC	IC	
	μg (cm^2 coral)$^{-1}$ h^{-1}		n*
Net growth rate (G)	6.8±0.8	4.5±0.3	11
Dissolution rate (D)	0.72±0.47	3.6±0.5	8
$P = G + D$	7.5±1.2	8.1±0.8	

* Number of data points taken for calculating averages.

The plots of growth and dissolution rates (Fig. 3) show that both experiments reached relatively constant rates after ~10 h. This steadiness permits calculation of the average net growth and dissolution rates (Table 3). It is reassuring that the potential growth rate (P) calculated for both colonies (Table 3) was comparable, averaging 7.8±1.0 μg (cm^2 coral)$^{-1}$ h^{-1}. This similarity implies that the skeletal density of a heavily infected coral colony should be substantially smaller than that of a noninfected colony of the same age. The effect of burrows on skeletal density was demonstrated by Scott and Risk (1988) in their table 1, which reflects a significant negative correlation between the percentage of material removed by *Lithophaga* and the skeletal density of *P. lobata*.

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