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Echinoid Bioerosion as a Major Structuring Force of Red Sea Coral Reefs

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Abstract. Echinoid bioerosion is ecologically important as a limiting factor for reef growth. *Diadema setosum* and *Echinometra mathaei* are the most abundant sea urchins in the Gulf of Eilat, Red Sea. Bioerosion by these urchins was estimated from field experiments with urchins placed in underwater chambers. A novel methodology was developed for measuring the $CaCO_3$ content of fecal pellets and total gut contents. This method is based on measurement of the amount of gas formed by total acidification of a mixed sample. The population density of the urchins was determined for the reef flat (depth 0.6–1 m) and the reef slope (depth 6–8 m). *D. setosum,* which erodes 310 mg individual^{-1} d^{-1}, is much less abundant on the reef flat (0.1 individuals m^{-2}) than on the reef slope (6.4 individuals m^{-2}). In contrast, *E. mathaei,* which erodes 120 mg individual^{-1} d^{-1}, is more dominant on the reef flat (10.5 individuals m^{-2}) than on the reef slope (3.7 individuals m^{-2}). We estimate that echinoid bioerosion converts to carbonate sediments 7%–11% of the total reef flat calcification and 13%–22% of the total reef slope calcification. These findings emphasize the importance of echinoid bioerosion as a structuring force in the coral reef, and its potential importance to the dynamics of reef development. However, they imply that some previous studies may have overestimated the role of echinoid bioerosion, thus possibly underestimating internal bioerosion.

Introduction

The hardness of the teeth of echinoids gives them the ability to scrape or bore into hard carbonate substrates and to ingest calcareous plants (Klinger and Lawrence, 1985). Sea urchins were reported to be very important hard-substrate bioeroders in coral reefs (*e.g.,* Hunter, 1977; Glynn *et al.,* 1979; Trudgill *et al.,* 1987; Bak, 1990), scraping the surface in the process of grazing (Lawrence and Sammarco, 1982). Echinoid bioerosion is considered ecologically important as a limiting factor for reef growth (Glynn *et al.,* 1979), and also has a profound effect on community composition through the control of newly settled coral spat (Sammarco, 1980, 1982).

Reported rates of bioerosion by echinoids are usually in the range of 3–9 kg m^{-2} y^{-1}, depending on the species, intensity of grazing, and population density. Stearn and Scoffin (1977) report a rate of about 9 kg m^{-2} y^{-1} for *Diadema antillarum* in the Caribbean. However, Hunter (1977), who recorded almost the same rate (9.7 kg m^{-2} y^{-1}) for the same species at the same locality, claims that only about 60% of the amount of $CaCO_3$ found in the digestive system of the urchins represents the transformation of hard substrate to sediment, the rest being reworked sediment. Many authors stress the importance of sediment production by echinoids. Glynn *et al.* (1979) found that almost the entire gut content of sea urchins in the Galapagos was composed of particulate carbonate: 30%–40% (weight) was coral skeleton grains; 40%–50% was coralline algae fragments. Hoskin and Reed (1984) measured sediment production of more than 3 kg m^{-2} y^{-1} by *Echinometra lucunter* on Little Bahama Bank.

Among the sea urchins in the northern Gulf of Eilat, *Diadema setosum* and *Echinometra mathaei* are the most abundant (Benayahu and Loya, 1977). Available data on the rate of bioerosion by *E. mathaei* imply a maximum rate of 0.008 kg m^{-2} y^{-1} in Enewetak (Russo, 1980) and 0.4 kg m^{-2} y^{-1} in Moorea (Bak, 1990). The population density of this species in Eilat is similar to that in Moorea. In the northern Gulf of Eilat, bioerosion by echinoids is therefore expected to play a major role in the destruction

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of the reef framework and its conversion to carbonate sediments.

This study aims at (1) quantifying the bioerosion activity of sea urchins in Eilat coral reefs and (2) comparing the results with known rates of reef construction in this area (Barnes and Lazar, 1993).

Materials and Methods

Sea urchins studied in the experiments (both *Diadema setosum* and *Echinometra mathaei*) were collected by scuba diving at the Nature Reserve Reef (NRR), Eilat, Red Sea, at a depth of 4–6 m. Collection was at dawn, when the urchins have completed their nocturnal grazing activity. Seven to ten urchins were put into each of the experimental acrylic chambers (Fig. 1), and the first tube was attached for fecal-pellet collection. The chambers were transferred underwater to the area in front of the H. Steinitz Marine Biology Laboratory (MBL), where they were set at a depth of 4 m. Experiments lasted for 10–10.5 h, and the collection tubes were replaced every 2.5–3 h. Tubes were immediately transferred to the laboratory and stored at 4°C until analyzed (2–12 h later).

Prior to analysis, samples were inspected and any urchin spine was removed. The samples were then homogenized and weighed. Subsamples of 50–100 mg (wet weight) from the homogenate were placed in a 30-ml vessel, along with 1 ml H_2O (to facilitate the reaction) and a tiny plastic cup containing 150 μl concentrated HCl. A cover was screwed on the top and the vessel was sealed. The vessel was then tilted slightly so that the acid cup would tip over, spilling the acid. The acid was then mixed with the sample by gently rotating the vessel. A complete acidification of the sample created CO_2 gas. The CO_2 pressure was read by a 4-digit voltmeter connected to the vessel through a pressure sensor and an analog-to-digital signal convertor. The amount of $CaCO_3$ in the sample is proportional to the measured CO_2 pressure. The apparatus was calibrated with dry aragonite prepared from bleached coral skeletons; its linear range was approximately 0–40 mg $CaCO_3$ (corresponding to pressures of about 1–1.3 atmospheres). This method is much easier and faster than the one formerly used (*e.g.*, Russo, 1980; Scoffin *et al.*, 1980; McClanahan and Kurtis, 1991), which involves several rinse-dry cycles of collection filters.

To estimate the net bioerosion of the reef, the $CaCO_3$ content of fecal pellets of the sea urchins was corrected for reworked $CaCO_3$ particles trapped in the algal turf upon which the urchins graze. Reworked carbonate sediments cannot be considered bioerosion of primary hard-reef substrate, because they were recycled by resuspension. A correction factor was estimated from experiments with "control" urchins grazing on epilithic algae that grow on

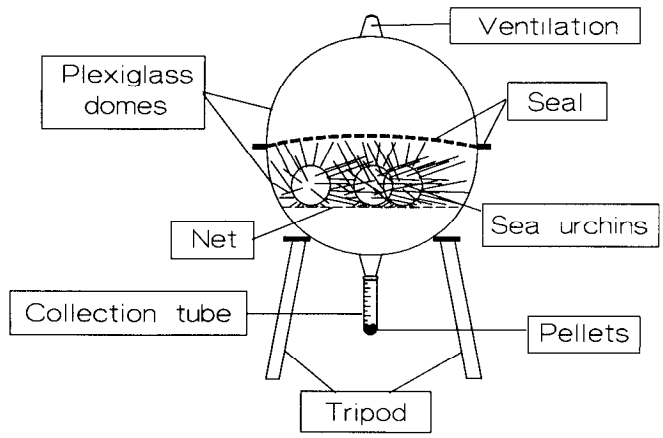

Figure 1. Schematic presentation of the underwater experimental chambers. The urchins were placed on a plastic mesh (*ca.* 1 cm). At each sampling time (every 2.5–3 h) the collection tube was replaced. Following each sampling, the top dome was removed for about 10 s, and gentle currents were created manually to ensure sufficient water replenishment.

granite-pebble talus and beachrocks, located about 100–300 m south of the NRR. The carbonate particles in this area were transported by either currents or wind and are therefore recycled detrital carbonate. Due to limitations imposed by the Nature Reserves Authority, there is only one control group for each species.

Several groups of sea urchins (corresponding to experimental groups kept together in an experimental chamber) were dissected, and total soft tissue was analyzed for $CaCO_3$ content by the method described above. Data were used to calculate the residence time of $CaCO_3$ in the alimentary tract of sea urchins, by dividing the total amount of $CaCO_3$ present at the beginning of the experiment (fecal contents + alimentary tract contents) by the $CaCO_3$ defecation rate. Height and diameter of the test and of Aristotle's lantern were measured for each dissected urchin.

The population density of sea urchins in two distinct reef zones, (1) the reef flat (depth 0.6–1 m) and (2) the reef slope (depth 6–8 m), was determined by belt transects (10×1 m^2). Transect censuses were done at night, after the urchins were fully active, by scuba diving. The total area counted was 80 m^2 for *D. setosum* and 100 m^2 for *E. mathaei*.

Results

Figure 2 shows the percent $CaCO_3$ found in the alimentary tract of *Diadema setosum* collected from three types of substrate: (1) calcareous reef rock, (2) talus of large granite pebbles, and (3) coarse-grain beachrock composed mainly of igneous rock grains with carbonate (high-Mg calcite) cement. The gut contents of urchins from the reef contained about three times more $CaCO_3$ than that of urchins from the granite pebbles and beachrock.

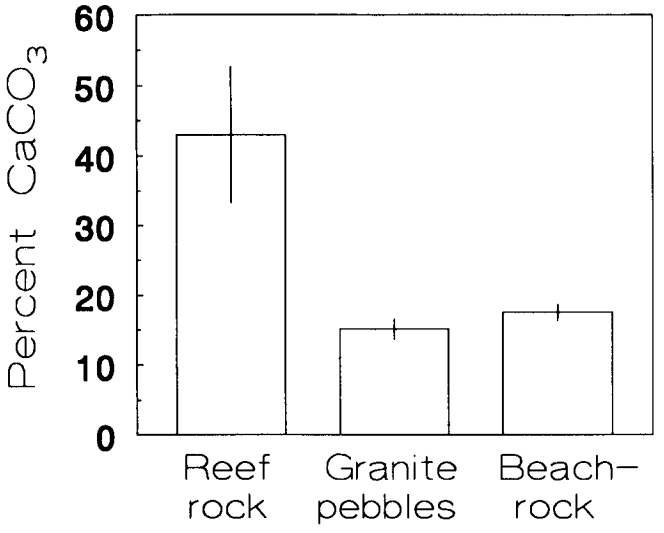

Figure 2. Percent $CaCO_3$ in gut contents of *Diadema setosum* collected from different substrates: calcareous reef rock, granite pebbles, and beachrock. Data represent average ±SD of 10, 5, and 5 urchins, respectively.

The results of feces collection experiments for *D. setosum* and *E. mathaei* are given in Figure 3 and Table I. The $CaCO_3$ defecation rates are the slopes of linear regression lines in Figure 3. Note that lines in the figure do not intersect at the origin. This is due to the exceptionally high amount of $CaCO_3$ collected at the end of the first time interval. The anomalously high defecation rate measured for the first time interval was probably a result of disturbance during the transfer of the experimental chambers from the site of urchin collection to the experimental area, and is therefore considered to be an artifact. The "control" urchins, which were collected on the granite pebbles or the beachrock near the experimental area (thus being less disturbed), showed no change in defecation rate. Consequently, the results of the first time interval were not used for calculating the defecation rate. The average rate of $CaCO_3$ defecation for *D. setosum* is 24.6 ± 8.4 mg individual^{-1} h^{-1} for the experimental groups and 11.7 mg individual^{-1} h^{-1} for the control. $CaCO_3$ defecation rate for *E. mathaei* is 5.3 ± 2.1 mg individual^{-1} h^{-1} for the experimental groups and 0.25 mg individual^{-1} h^{-1} for the control.

Table II summarizes the physical parameters of *D. setosum* and *E. mathaei* and their distribution on the reef. Test diameter and height of *D. setosum* are 1.3 and 1.5 times (respectively) larger than the corresponding parameters of *E. mathaei*. Consequently, the test volume of *D. setosum* is computed to be 2.7 times larger. The distributions of *D. setosum* and *E. mathaei* in the studied reef zones are markedly different. Whereas *D. setosum* is most abundant over the reef slope, *E. mathaei* dominates the reef flat.

Discussion

Each of the experimental groups, in both species studied, defecated $CaCO_3$ at a relatively constant rate (r^2 values of the regression slopes are noted in Fig. 3). Despite the similarity of the slopes, however, the intersects vary widely (especially for *D. setosum*, Fig. 3A). This may be attributed to different "stress reactions" to the transport from the Nature Reserve to the MBL. The duration of the anomalously high defecation rate is probably variable, but seems to range between 0.5 h and 2.5 h. The lines describing $CaCO_3$ defecation of all experimental groups for which the first collection tube was replaced after 2.5 h or more (all *D. setosum* groups and *E. mathaei* groups I and II, Table I) are typified by very high r^2 values (Fig. 3), reflecting constant rates. The three *E. mathaei* groups, for

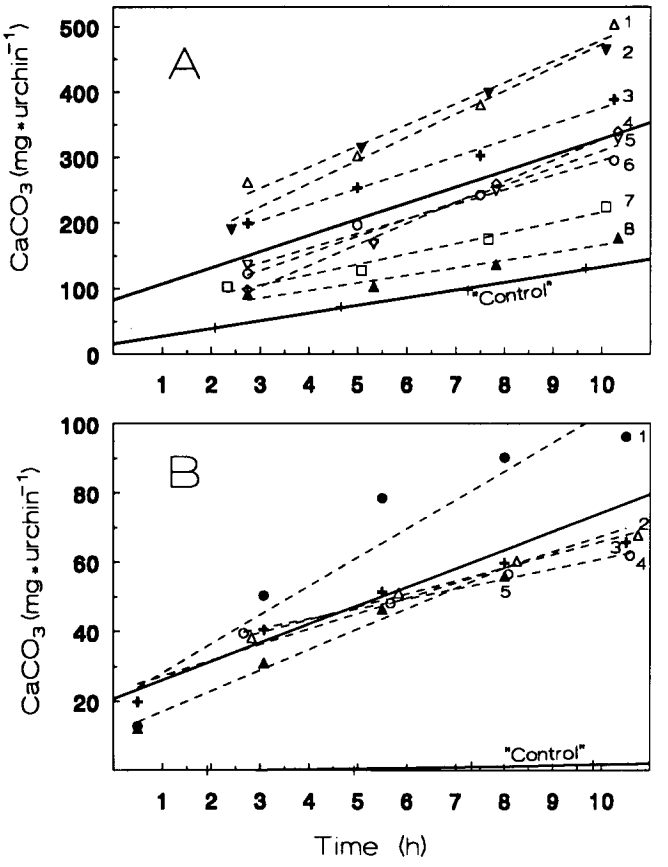

Figure 3. Cumulative amount of $CaCO_3$ in fecal pellets collected from the underwater experimental chambers for (A) *Diadema setosum* and (B) *Echinometra mathaei*. In each part: dashed lines represent each experimental group; top solid line represents data combined from all experimental groups; bottom solid line represents the "control" group. Linear curves were fitted by regression analysis. Slopes and r^2 values for individual lines are as follows. (A): (1) 32.4, 0.94; (2) 35.5, 0.96; (3) 24.7, 0.98; (4) 32.1, 0.98; (5) 26.1, 0.94; (6) 22.4, 0.96; (7) 15.9, 0.94; (8) 11.5, 0.90; (combined data) 24.6, 0.41; ("Control") 11.7; 0.98. (B): (1) 8.3, 0.81; (2) 3.8, 0.98; (3) 4.5, 0.88; (4) 2.9, 0.98; (5) 5.9, 0.96; (combined data) 5.3, 0.69; ("control") 0.25, 0.74. Note that the *y*-axis scale is five times smaller for *E. mathaei* than for *D. setosum*.

Table I

Results of 10-h feces collection experiments (data represent one experimental group except where noted[a])

Species	$CaCO_3$ (mg)		Gut evacuation (%)	Gut turnover rate (d^{-1})
	Defecated	Remaining in gut		
Diadema setosum	296	603	33 (±1)[a]	0.75
Echinometra mathaei	67	38	64	1.5

[a] The SD was calculated together with two additional experimental groups dissected and analyzed (results not shown).

Table II

Physical parameters and population densities of the echinoids Diadema setosum *and* Echinometra mathaei *in the Eilat Nature Reserve reef (values represent the average ± 1 standard deviation)*

Species	Physical parameters (mm)				Population density (urchin m^{-2})[a]	
	Test		Aristotle's lantern			
	Diameter	Height	Diameter	Height	Reef slope	Reef flat
Diadema setosum	30.1 ± 7.6 $n = 50$	17.3 ± 4.9 $n = 50$	11.2 ± 2.7 $n = 50$	14.8 ± 3.4 $n = 50$	6.4 ± 3.1 (60)	0.1 ± 0.3 (20)
Echinometra mathaei	23.1 ± 4.5 $n = 20$	11.9 ± 2.2 $n = 20$	7.0 ± 1.1 $n = 20$	8.8 ± 1.6 $n = 20$	3.7 ± 3.3 (60)	10.5 ± 5.6 (40)

[a] Numbers in parentheses are the total area (in square meters) censused by belt transects.

Table III

Estimates of echinoid bioerosion rates

Species	Bioerosion (g individual^{-1} d^{-1})	Population density (individual m^{-2})	Locality	Method		Reference
				$CaCO_3$ measurement	Correction for reworked sediments	
Diadema antillarum	1.070	23	Barbados	Acidification of total gut contents (weight difference)	No correction	Stearn and Scoffin, 1977
	1.160	23	Barbados	Unpublished data from C.M. Hawkins	Petrographic sections	Hunter, 1977
	0.630 ± 0.040	23	Barbados	Acidification of total gut contents (weight difference)	Petrographic sections	Scoffin *et al.*, 1980
Diadema savignvi	1.920	4.8	Moorea	Ash-free dry weight of total gut contents	Petrographic sections	Bak, 1990
Diadema setosum	0.310 ± 0.200	Reef flat 0.1 ± 0.3 Reef slope 6.4 ± 3.1	Eilat	Acidification of excreted fecal pellets (CO_2 pressure measurement)	According to urchins from a noncarbonate substrate	This study
Echinometra mathaei	0.140	0.16	Enewetak	Acidification of total gut contents (weight difference)	Based on 20% reworked sediment—unpublished calculations by Peterson	Russo, 1980
	0.120	7.4	Moorea	Ash-free dry weight of total gut contents	No correction	Bak, 1990
	0.120 ± 0.050	Reef flat 10.5 ± 5.6 Reef slope 3.7 ± 3.3	Eilat	Acidification of excreted fecal pellets (CO_2 pressure measurement)	According to urchins from a noncarbonate substrate	This study

which the first collection tube was replaced after 0.5 h, show somewhat lower r^2 values, and the defecation rate declines a little. The implications of this decrease for further calculations are discussed below.

The rate of bioerosion is calculated separately for each zone on the reef, by multiplying the average $CaCO_3$ defecation rate per individual by the population density in the reef-zone of interest. Total urchin bioerosion was calculated to be approximately 0.5 kg $CaCO_3$ m^{-2} y^{-1} on the reef flat and 0.9 kg $CaCO_3$ m^{-2} y^{-1} on the reef slope (Fig. 4). Typical reef accretion (calcification rate) in this area is approximately 4–7 kg $CaCO_3$ m^{-2} y^{-1} (Barnes and Lazar, 1993). The bioerosion activity of sea urchins alone, therefore, counteracts only about 7%-11% of the total calcification on the reef flat, and 13%-22% of that on the reef slope. The effect of echinoid bioerosion in the two reef zones studied is depicted in Figure 4, emphasizing the relative importance of each sea urchin species in each zone.

E. mathaei clearly erodes much less $CaCO_3$ per individual than does *D. setosum* (Fig. 3, Table I). Consequently *E. mathaei* is responsible for only about 18% of the echinoid bioerosion on the reef slope (Fig. 4), although it constitutes nearly 40% of the urchin population there (Table II). On the other hand, it is responsible for over 97% of echinoid bioerosion on the reef flat, where it is much more abundant than *D. setosum* (Table II). The smaller size of *E. mathaei* and its stronger attachment to the substrate probably enable this urchin to dominate the reef flat, which is typified by high-energy wave and current action.

Considerable differences exist between estimates of echinoid bioerosion (Table III). It is, therefore, interesting to compare the methods by which these estimates were obtained. Many authors (*e.g.*, Scoffin *et al.*, 1980; Bak, 1990) have used total $CaCO_3$ gut content of dissected urchins as an estimate for daily erosion. Besides being a rather destructive method (all studied urchins are killed), it may yield erroneous results. Sea urchins of different size classes, or of different species, may have profoundly different gut contents, but their gut turnover rates may vary just as much. Thus, urchins having larger gut contents do not necessarily ingest more food and $CaCO_3$ per unit time. Markedly different gut turnover rates were calculated for the two species studied here (Table I). The faster turnover rate of *E. mathaei* might be accounted for if a smaller space was occupied by the intestine within the test. Although its Aristotle's lantern is relatively smaller (*D. setosum* has a 2.7 times larger test and a 4.7 times larger lantern, see Table II), the absolute volume left for soft tissue is still about 2.7 times smaller in *E. mathaei*. This may limit the ability of the intestine to expand.

Estimation of the rate of $CaCO_3$ ingestion from measurements of $CaCO_3$ in collected fecal pellets is based on the assumption of a gross "steady state" regarding gut

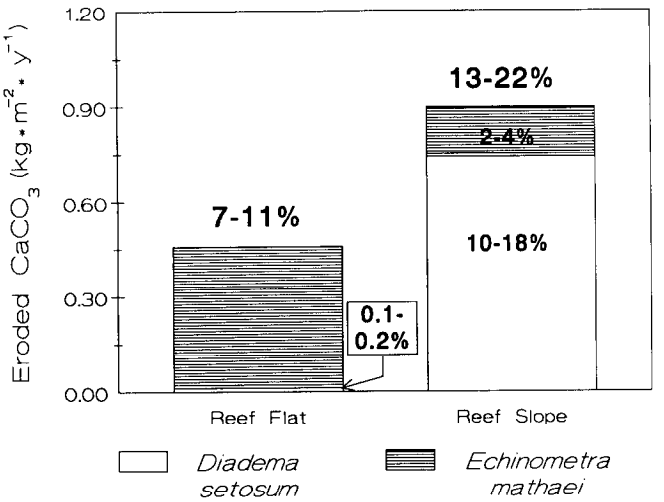

Figure 4. Bioerosion by *Diadema setosum* and *Echinometra mathaei* in two reef zones in Eilat, Red Sea. Open and hatched areas of each bar represent the proportion of reef calcification that is eroded by each urchin species. The total fraction of reef accretion eroded by these echinoids is shown above the bars. Note that urchin bioerosion on the reef flat is almost exclusively due to the activity of *E. mathaei*, whereas most of the urchin bioersion on the reef slope is due to *D. setosum* activity.

contents. Such an assumption is widely accepted (*e.g.*, McLean, 1967; Glynn, 1979; McClanahan and Kurtis, 1991). Whereas fecal-pellet collections record true values for urchins of all sizes and species, dissections may overestimate bioerosion by very large urchins with low gut turnover rates, such as *D. setosum*. This may partially account for Bak's (1990) high estimates for echinoid bioerosion in Moorea: *Diadema savignyi*, with an average test diameter of 54 ± 10 mm (calculated from data presented by Bak), is responsible for about 75% of the bioerosion there.

Knowing the amount of $CaCO_3$ that passes through the digestive system of a sea urchin, one still has to correct for the amount of $CaCO_3$ that is derived from reworked sediments. Kendrick (1991) reports 200–1800 g of sediment (dry weight) trapped in 1 m^2 of algal turf. Uncorrected high estimates of echinoid bioerosion have been published (*e.g.*, Lewis, 1964) with the notion that correction is desirable (Stearn and Scoffin, 1977). Hunter (1977) and Bak (1990) used thin-section microscopy to differentiate between $CaCO_3$ particles directly eroded by the urchin and reworked material. This technique requires considerable work for slide preparation and examination. In our study the correction was more easily obtained by comparing the amount of $CaCO_3$ measured for urchins grazing on reef rock with the amount in urchins grazing on igneous rock and beachrock (see Fig. 2). The proximity of the two sites and the prevailing current regime result in transportation of suspended particles between these

sites, exposing "reef" and "control" urchins to similar amounts of reworked $CaCO_3$.

An important part of our experimental design is the timing and duration of the experiments. To avoid interruption of the urchins' dial biological rhythms, all experiments were carried out during the day, when the urchins are inactive. Calculation of daily bioerosion was based on the assumption that defecation rate is constant throughout day and night. This condition is probably well met by the urchins, which show very constant defecation rates throughout the experiments (Fig. 3), despite the gradual emptying of the gut. The substantial amount of $CaCO_3$ remaining in the gut at the end of the experiment (Table I) also supports the assumption of a constant rate of defecation. These observations contradict a suggestion made by Lawrence and Hughes-Games (1972) that these nocturnally feeding echinoids might have higher defecation rates at night. However, even if defecation were twice as fast during nighttime feeding, our estimated rate of bioerosion (Fig. 4) would not change much. In such a case, bioerosion by echinoids would be about 0.6 kg m^{-2} y^{-1} on the reef flat (9%–15% of reef accretion) and about 1.2 kg m^{-2} y^{-1} on the reef slope (17%–29% of reef accretion).

Evidently, the overall effect of echinoid bioerosion on the reef framework in the study area is of considerable importance. Our results emphasize the already acknowledged importance of bioerosion as a structuring force in coral reef areas. However, they imply that some previous studies may have overestimated the impact of echinoid bioerosion. Concurrently, the role played by other erosion forces, including internal bioerosion and physical erosion (mainly on the reef flat), was possibly underestimated. Erosion by agents other than echinoids probably plays a central role in the area studied in the present research, as indicated by a 70%–90% discrepancy between reef accretion and echinoid bioerosion. Our conclusions thus call for follow-up investigations to evaluate the relative importance of other major reef bioeroders in the Red Sea. Such studies should provide important complementary information on the overall importance of bioerosion in this area.

Acknowledgments

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