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Bioerosion by two rock boring echinoids
(Echinometra mathaei and Echinostrephus aciculatus)
on Enewetak Atoll, Marshall Islands

by Anthony R. Russo

ABSTRACT

Bioerosion can be important to the configuration and destruction of coral reefs. Echinoids as grazers and burrowers can contribute significantly to coral reef erosion. Studies done on the turnover of gut contents of the two major burrowing echinoids on Enewetak atoll (Echinometra mathaei and Echinostrephus aciculatus) show a range of total CaCO$_3$ erosion by both species from 80-325 g m$^{-2}$y$^{-1}$. An estimated total of 4000 g m$^{-2}$y$^{-1}$ of CaCO$_3$ is produced annually on Enewetak. In this case, echinoids on Enewetak can contribute from 2 to 8% of the total bioerosion on the atoll. Echinoids may be considered important bioeroders when compared with other organisms; the sponge Cliona, for example, a major bioeroder, can destroy as much as 25% of the total annual CaCO$_3$ production on Enewetak. The daily mean erosion rates per individual (g d$^{-1}$ urchin$^{-1}$) range from 0.1 to 0.2 for E. mathaei and 0.2 to 0.4 for E. aciculatus.

1. Introduction

In 1966 Neumann used the term bioerosion to describe the destruction and removal of calcareous substrata by boring and rasping organisms. Since then there has been extensive work done on bioerosion, mainly in tropical marine environments related to the importance of bioerosion in sedimentary calcium carbonate budgets (Moore and Shedd, 1977; Smith, 1973; and Stearn et al., 1977) and production of sedimentary particles (Futterer, 1974). Quantitative studies are important not only to gain an understanding of coral reef carbonate budgets and sedimentology but also to estimate the relative importance of bioerosion to purely physical and chemical erosion processes. Physical erosion by waves and currents is considered the most important destructive factor on coral reefs but recent studies have shown that bioerosion can be significant in breaking down carbonate substrata. Among the most important bioeroders are microboring algae and fungi (Perkins and Halsey, 1971), sipunculids (Rice, 1969; Cutler, 1968; Williams and Margolis, 1974), sponges

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(Cobb, 1969; Futterer, 1974; Rutzler and Reiger, 1973; Rutzler, 1975), and fish (Bardach, 1961; Randall, 1974; Ogden, 1977 and Frydl, 1977). Boring sponges can contribute up to 25% of the total erosion of the substratum on Enewetak (Smith, 1973) and are considered major eroders on most coral reefs (Rutzler, 1975). North (1954) and Hodgkin (1962) were among the first to investigate the erosion activities of gastropod mollusks. Taylor and Way (1976) reported on the erosive activities of chitons on Aldabra atoll and estimated that although their individual erosion rates can be substantial, the total destruction by these animals is minimal due to their low population densities. Sea urchins were not considered major eroders of substrata until Lewis (1964) and McLean (1967) published their work on some of the major burrowing and rasping echinoids.

In this study, an attempt is made to gain more information on the erosive activities of two burrowing echinoids *Echinometra mathaei* (Blainville) and *Echinostrephus aciculatus* (Agassiz) on Enewetak atoll. *E. mathaei* is a well-known burrowing urchin whose ecology has been described by several workers (Kelso, 1970; Russo, 1977). The distribution, abundance, and behavior of this echinoid has also been extensively studied by other workers in Japan (Shigei, 1973 and Yanagisawa, 1974) and by Khamala (1971) in Kenya. The effect of echinoids of the genus *Echinometra* as agents of calcium carbonate degradation has been investigated by Shinn (in Hughes and Keij, 1973) and by Ogden (1977). On the other hand, there is very little literature on the ecology and bioerosion activities of *Echinostrephus*. Shigei (1973) reported on the distribution, abundance, and substratum preference of this species in Japan.

*Echinometra* is abundant in high energy shallow water habitats such as reef platforms, coral heads, and algal ridges. *E. mathaei* is a cosmopolitan sedentary species found in many subtropical and tropical Pacific environments usually burrowed into potholes and crevices (Mortensen, 1943). Its depth range is from the intertidal to approximately 10-15 meters below MLW. This species occupies deeper habitats, especially in Hawaii, but tends to be rare below 15 m (Kelso, 1970). *Echinostrephus aciculatus* has essentially the same distribution as *E. mathaei* but its depth range appears to be greater. I have seen this species as deep as 40 meters off the seaward slope of Enewetak atoll.

### 2. Description of study sites

Enewetak atoll is located at approximately 11° 30' North and 162° 15' East in the Marshall Islands in the North Pacific. It includes approximately 40 coral islands which encircle a lagoon 32 km wide by 40 km long. The sites for this study were chosen off the island of Enewetak in the southeastern part of the atoll. On the lagoon side of Enewetak island a coral knoll (located off the northern tip of Enewetak south of Medren island) was chosen as one site. This knoll, approximately 400 m² in area, projects from its base at a depth of 6 m to within ½ m of the surface
in some places. Approximately 90% of the knoll is covered with live coral. The second and third sites are on a lithified limestone intertidal reef platform on the seaward side of Enewetak about 80-150 m north of the Mid-Pacific Marine Laboratory. The inner reef site and outer reef site are 50 m and 100 m from shore respectively. The substratum is the same at both platform sites and these areas are continuously covered with water 50 to 200 cm deep, depending on tidal conditions. There are a few live scattered coral heads (Genus: *Pocillopora* and *Porites*) on the reef platform; live coral cover was estimated to be less than 1%. Holothurians (*Holothuria atra*) abound at the outer reef site. Echinoids at both reef sites are densest in dead coral heads but are also found inhabiting burrows in the reef platform. There is vigorous water movement at the outer reef site due to constant wave action.

3. Methods and materials

Using line transects 50 m in length and random 1m² quadrat sampling, the density (Nos/m²) of both species of urchin and diameters of their tests were measured at each site. Vernier calipers were used to measure diameters. Analysis of variance techniques were used to determine any significant differences in mean values of these parameters between sites. The presence or absence of each species was recorded and Cole's (1949) index of association was used to determine any interspecific association between the two species. In order to determine erosion rates of CaCO₃ by the two species, specimens were removed from the field. The echinoids were carefully left intact in their burrows as coral heads were fragmented into small sections with hammer and chisel and placed in running seawater aquaria. Twenty to thirty urchins of each species ranging from 0.5-5.0 cm in test diameter were removed from their burrows for gut analysis and their diameters measured with vernier calipers. To extract the gut of an urchin, the test was broken by opening needle nosed pliers set around the Aristotles’ lantern. The gut material was removed and placed on 10 cm Whatman glass filters, rinsed with distilled water for 30 seconds by suctioning the water through the filter. The filters were dried in an oven at 80°C for 8 hours. Eight hours is sufficient time for complete drying. After weighing, the filters were saturated with 0.1N HCl, dried and rinsed. After another drying, they were weighed. The difference in initial and final weighings is an estimate of CaCO₃ in the gut. Ogden (1977) in a study of bioerosion by *E. lucunter* estimated a gut turnover of 1 time per 24 hours based on work done on the grazing echinoid *Diadema antillarum* by Lewis (1964). I obtained a gross estimate of the turnover of gut contents by monitoring three mean sized urchins of each species continuously for 8 hours. The urchins were placed in small aquaria with clean seawater. Fecal pellets were collected and placed on Whatman filters, rinsed with distilled water and dried at 80°C for 8 hours. After drying, the filters were weighed and saturated with 0.1N HCl. The filters were dried, rinsed and dried again. The final rinse is neces-
102  
Journal of Marine Research  

Table 1. Urchin bioerosion erosion rates.

<table>
<thead>
<tr>
<th>Environment</th>
<th>Species</th>
<th>Density (nos./m²)</th>
<th>% Frequency</th>
<th>Mean Size (cm)</th>
<th>S²</th>
<th>N Sample Size</th>
<th>Mean Erosion** (g/d per urchin)</th>
<th>Total CaCO₃ Erosion g/m²/y</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coral knoll</td>
<td><em>E. mathaei</em></td>
<td>0.16</td>
<td>14.5</td>
<td>2.20</td>
<td>.56</td>
<td>40</td>
<td>.1338</td>
<td>8.0</td>
</tr>
<tr>
<td></td>
<td><em>E. aciculatus</em></td>
<td>0.50</td>
<td>24.0</td>
<td>2.40</td>
<td>.61</td>
<td>120</td>
<td>.3990</td>
<td>73.0</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>81.0</td>
</tr>
<tr>
<td>Inner reef</td>
<td><em>E. mathaei</em></td>
<td>6.50</td>
<td>80.0</td>
<td>1.90</td>
<td>.3</td>
<td>200</td>
<td>.1083</td>
<td>257.0</td>
</tr>
<tr>
<td>Platform</td>
<td><em>E. aciculatus</em></td>
<td>1.05</td>
<td>33.3</td>
<td>1.80</td>
<td>.28</td>
<td>54</td>
<td>.1771</td>
<td>68.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>325.0</td>
</tr>
<tr>
<td>Outer reef</td>
<td><em>E. mathaei</em></td>
<td>1.75</td>
<td>53.0</td>
<td>1.95</td>
<td>.25</td>
<td>58</td>
<td>.113</td>
<td>72.0</td>
</tr>
<tr>
<td>Platform</td>
<td><em>E. aciculatus</em></td>
<td>0.66</td>
<td>34.3</td>
<td>1.68</td>
<td>.21</td>
<td>21</td>
<td>.1505</td>
<td>36.0</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>108.0</td>
</tr>
</tbody>
</table>

* % Frequency = \( \frac{\text{No. of quadrats with species} \times x}{\text{Total no. of quadrats}} \times 100 \)

** Mean erosion (\( e \)) = \( \frac{\Sigma eidi}{\Sigma di} \)

\( e_i = \text{Size specific erosion rate} \)

\( d_i = \text{Urchin diameter ranging from 0.5-5 cm} \)

sary to remove any precipitated CaCl₂. The difference in weight is an estimate of total CaCO₃ in the feces. This procedure has many serious drawbacks which prevent it from being used to directly calculate a daily rate of CaCO₃ passage through the gut. Fecal pellets of *Echinometra* and *Echinostrephus* are small and difficult to collect. The rate of excretion may depend on circadian feeding patterns and a 24-hour observation period would be better than an 8-hour one. However, the breakdown time of the fecal pellets is short. During one full day of observation, pellets become soft and break up after 6-7 hours. It is very difficult, with limited time and facilities, to collect pellets from enough urchins over 24-hour periods for statistical validity. By extrapolating the mean weight of CaCO₃ in the feces produced in 8 hours to a daily rate, a gross estimate of gut turnover (times/day) is calculated by dividing this daily rate by the CaCO₃ weight determined by gut analysis for a mean sized urchin. The author feels that this is better than assuming a rate of turnover based on observations of a nonburrowing urchin of a different family. Timing the passage of dyed food through the gut with Nile sulphate (Lewis, 1964) is virtually impossible with *E. mathaei* and *E. aciculatus* as the urchins are fixed to their substratum and feed mostly on drift algae washed into their burrows.

4. Results

Cole’s index of association showed a significant positive association at the 99%
confidence level between *Echinometra mathaei* and *Echinostrephus aciculatus* in both the lagoon and reef platform habitats. The probability of finding them together in a random sample is significantly greater than would be expected if their distribution were independent of each other’s presence. Table 1 is a summary of the density and size distributions of both species in the three environments. The densities were significantly different between the lagoon and reef platform but not between the inner and outer reef platform itself. The erosion rates of both species varied curvilinearly with size as shown in Figure 1. A weighted mean erosion rate was calculated for each species and each habitat (Table 1). These rates may be conservative since it was assumed that all ingested carbonate was newly eroded. The turnover of total gut content was estimated to be 1-1½ times per day for *E. mathaei* and 2-2½ times per day for *E. aciculatus*. The total percent by weight of CaCO$_3$ in the feces is approximately 60-65% for both species. An estimate of quality differences in fecal content was not attempted in this study.

5. Discussion

The interspecific association between *E. mathaei* and *E. aciculatus* on Enewetak atoll is significantly positive indicating possible similar ecological requirements by the two species. The two species are found together more often than would be expected if they were distributed at random. They may persist together and may be
isolated ecologically due to their different habits of burrow construction and feeding. The burrows of *E. mathaei* are extremely irregular whereas those of *E. aciculatus* are strikingly cylindrical. The burrows of *E. mathaei* are usually not made by a single urchin and are occupied as a pre-formed crevice. The almost perfect cylindrical burrow of *E. aciculatus* implies the complete construction by a single individual since the urchin remains in its burrow throughout its life. The spines below the ambitus in this species are normally short and worn and they increase the diameter of the burrow by spine abrasion and the depth by the rasping of their Aristotle’s lantern (Edmundson, 1946). *E. mathaei* normally feeds on drifting algae which falls into its burrows (Kelso, 1970; Russo, 1977). There is little spine movement by this species even when disturbed although *E. mathaei* has been observed to move within and around its burrow (Abbott, 1974). It seems to remain sedentary in areas where water flow is vigorous (Russo, 1977). Already made burrows are more likely to be inhabited by this species than partly formed ones since they may afford protection against excessive water currents especially on seaward reef platforms.

In some populations of the Atlantic echinoid *E. lucunter* agonistic behavior may be significant in the defense of protected living space and access to food supply since this species lives in dense aggregations in wave-swept areas (Grünbaum et al., 1978). Preliminary investigation (Ogden, unpublished) of burrow defense in *E. mathaei* on the Kona Coast of Hawaii has shown that this species will evict conspecific intruders from its burrows. In the Virgin Islands, the rock boring echinoid *E. lucunter* displays territorial defense of its burrows (Grünbaum et al., 1978). Territorial behavior was not observed in this study. Russo (1977) speculates that competition over long periods of time for larval settling sites in high density areas may lead to a restricted number of burrows being formed by *Echinometra* in Hawaii. In comparison, *E. aciculatus* normally constructs a burrow two to three times deeper than its own body thickness and uses its delicately fine spines to trap floating detritus. As it grows, it continues to construct a deeper and wider burrow. Most of the CaCO₃ removed by this species probably occurs during burrow enlargement. When disturbed, this urchin recedes into its burrow completely.

The density (nos/m²) of both species of urchin is greatest at the inner reef platform site; the density of *E. mathaei* being almost four times greater here than on the coral knoll. On the knoll *E. aciculatus* was more abundant than *E. mathaei*; the reverse is true on the reef platform. The higher densities of *E. mathaei* on the reef platform are consistent with other studies (Russo, 1977 and Khamala, 1971) which have shown that *Echinometra* is very abundant where water flow is vigorous. The mean test diameters, of both species, are greater on the calmer coral knoll environment suggesting a possible inverse relationship between density and growth. The lower mean size in areas of higher population densities may be reflecting the result of competitive interaction for space and food resources by both species. Differences in the maturity of *E. aciculatus* is reported to be a function of food supply in
Japanese waters (Kobayashi and Tokioka, 1976). The differences in mean size between the two areas may also be due to differential mortality.

Results show that *E. aciculatus* passes almost two times more CaCO$_3$ through its gut per day than does *E. mathaei* for the same size class. However, because of the higher relative abundance of the *E. mathaei* the total CaCO$_3$ eroded by this species (g m$^{-2}$ y$^{-1}$) is much greater than *E. aciculatus* on the reef platform (Table 1). Also, due to the greater combined densities of *E. mathaei* and *E. aciculatus* on the inner reef platform, this environment undergoes the greatest total bioerosion by echinoids. On the knoll site an estimated 80 g m$^{-2}$ y$^{-1}$ of CaCO$_3$ is removed by both species while on the reef platform the erosion is four times greater (325 g m$^{-2}$ y$^{-1}$). Smith (1973) reports a total of 4000 g m$^{-2}$ y$^{-1}$ of CaCO$_3$ produced annually on Enewetak. In this case echinoids on the platform can erode from 2 to 8% of the total annual carbonate produced on the atoll. A study on the bioerosion by the sea urchin *Diadema antillarum*, a grazer, on a Caribbean reef shows a maximum value of 9000 g m$^{-2}$ y$^{-1}$ of calcium carbonate removed by this species (Stearn *et al.*, 1977) with a density estimated at 23 urchins per m$^2$. The bioerosion by *Diadema* alone equals the total annual production of CaCO$_3$ on the reef (Stearn *et al.*, 1977). Frydl (1977) reports the bioerosion of CaCO$_3$ by parrotfish to be approximately 54 g m$^{-2}$ y$^{-1}$ in the tropical Atlantic and Bardach (1961) reports 230 g m$^{-2}$ y$^{-1}$ eroded by these fish on Bermuda reefs. As much as 20,000 g CaCO$_3$ m$^{-2}$ y$^{-1}$ is eroded on Bermuda reefs by sponges alone (Neumann, 1966). Smith (1973) reports 1000 g CaCO$_3$ m$^{-2}$ y$^{-1}$ destroyed by sponges on Enewetak atoll. At Heron Island in the Pacific the chiton *Acanthozostera gemmata* erodes up to 20 g m$^{-2}$ y$^{-1}$ per individual and littorine snails up to 2 g m$^{-2}$ y$^{-1}$ per individual (McLean, 1974). Although the densities (nos/m$^2$) of echinoids are relatively low on Enewetak reefs, they may be considered important bioeroders when compared with other organisms. Results of this study show a mean erosion rate from 0.10-0.20 g d$^{-1}$ of CaCO$_3$ removed per individual for *E. mathaei* and from 0.20 to 0.40 g d$^{-1}$ for *E. aciculatus*. In a study of *E. mathaei* in the Persian Gulf Shinn (in Hughes and Keij, 1973) reported the daily erosion rate to be 0.50 g d$^{-1}$ per urchin. Ogden (1977) recorded an annual erosion rate of 3.9 kg m$^{-2}$ y$^{-1}$ for urchins (*E. lucunter*) with densities up to 100 per m$^2$. This is equivalent to about 0.107 g d$^{-1}$ urchin$^{-1}$ which is comparable to the results of this study for *E. mathaei*. The size specific erosion rates for both species are shown in Figure 1. In bioerosion studies it is important to report both density and mean size since total CaCO$_3$ removal is dependent on both parameters. Differences in reported erosion rates per individual may reflect differences in the size range of the echinoids observed since daily erosion rates increase geometrically with test diameter.

In calculating daily erosion rates, it was assumed: 1) that all carbonate scraped was freshly eroded and ingested, 2) that 20% of the ingested carbonate rock was *in situ* sediment. Peterson (1973) calculated that 4/5 of the sediment ingested by the
grazer *Diadema antillarum* on Caribbean reefs is newly scraped sediment. There may be substantial error inherent in extrapolating the daily erosion rates of *E. mathaei* in all cases to a yearly rate since *E. mathaei* may be sedentary in certain environments (Ogden, 1977; Russo, 1977), and motile in others (Grünbaum et al., 1978). *E. mathaei* seems to remain sedentary as long as its food supply is sufficient (Kelso, 1970; Russo, 1977). I have observed starved *E. mathaei* leave their burrows at night to graze the glass sides of their aquaria. Khamala (1971) reports that *E. mathaei* remains in its burrow in the intertidal but will forage at night close to its burrow in the subtidal. In the case of *E. aciculatus* an extrapolation of daily erosion rates to yearly ones is more feasible since this species remains in its burrow its entire lifetime and removes a relatively large volume of carbonate rock mainly for burrow construction (personal observation). This burrowing strategy may contribute to the apparent faster turnover rate of CaCO$_3$ of this species since *E. mathaei* occupies already formed pits and removes the majority of CaCO$_3$ while feeding and less in burrow construction. Assimilation efficiencies may be different for the two species. This was not determined in this study.

Erosion rates by various echinoids in different locations are shown in Table 2. Erosion by echinoids can be substantial, depending on their abundance (nos/m$^2$) and their size distribution. On low latitude tropic reefs echinoids are less important to sediment production and bioerosion than sponges (Smith, 1973; Rutzler and Reiger, 1973). In the Hawaiian Islands on the northern periphery of the coral reef belt, echinoids, especially *Echinometra*, can become important. A recent study (Russo, 1977) has shown that population densities of *E. mathaei* and *E. oblonga* can reach values as high as 100-150 individuals per m$^2$. If Enewetak erosion rates for *E. mathaei* are used for the populations of echinoids on typical Hawaiian algae reefs, a gross estimate of from 0.5 to 30 kg m$^{-2}$ of substratum would be removed per year, depending on population densities. Annual CaCO$_3$ production on seaward reef environments in Hawaii are within the range of those reported for Enewetak (4 kgm$^{-2}$ y$^{-1}$). (Dr. Steve Smith, Dept. of Oceanography, University of Hawaii, personal communication) Stearn et al. (1977) report a production rate of 9 kg CaCO$_3$ m$^{-2}$ y$^{-1}$ on Caribbean reefs. On Hawaiian reefs where population densities are higher, the average size of *Echinometra* is large (Russo, 1977) and therefore the erosion of CaCO$_3$ may exceed its production. In this case, echinoids are major bioeroders and can supersede sponges in importance as vectors for the control of reef growth. On Enewetak echinoids seem to play an important but minor role in controlling reef configurations.

When total bioerosion by all organisms is considered, previous conceptions about the control of reef growth must be altered. Up to recent times, physical and chemical erosion were considered the major determinant factors in shaping reefs and in the production of sediment. In light of recent studies on bioerosion, this conception may need to be reviewed since bioerosion may be, in some cases, more important than
Table 2. Rates of erosion of carbonate substrata by echinoids.

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Population density or biomass</th>
<th>Mass removed/urchin Kg/urchin/y</th>
<th>Substratum</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Long spined urchin</td>
<td>Virgin Is.</td>
<td>9 indiv./m²</td>
<td>4.6</td>
<td>.5</td>
<td>Coral reef</td>
</tr>
<tr>
<td><em>Diadema antillarum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Ogden (1977)</td>
</tr>
<tr>
<td>Rock borer</td>
<td>Virgin Is.</td>
<td>100 indiv./m²</td>
<td>3.9</td>
<td>.039</td>
<td>Algal ridge</td>
</tr>
<tr>
<td><em>Echinometra lucunter</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Ogden (1977)</td>
</tr>
<tr>
<td>Rock borer</td>
<td>Barbados</td>
<td></td>
<td></td>
<td>.025</td>
<td>Beach rock</td>
</tr>
<tr>
<td><em>Echinometra lucunter</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>McLean (1967)</td>
</tr>
<tr>
<td>Rock borer</td>
<td>Bermuda</td>
<td>25 indiv./m²</td>
<td>7.0</td>
<td>.28</td>
<td>Eolianite</td>
</tr>
<tr>
<td><em>Echinometra lucunter</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Hunt (1969)</td>
</tr>
<tr>
<td>Rock borer</td>
<td>Persian Gulf</td>
<td></td>
<td></td>
<td>.183</td>
<td>Dead <em>Acropora</em></td>
</tr>
<tr>
<td><em>Echinometra lucunter</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Shinn (in Hughes et al. 1973)</td>
</tr>
<tr>
<td>Rock borer</td>
<td>Enewetak</td>
<td>2-7 indiv./m²</td>
<td>.070-.260</td>
<td>.04</td>
<td>Lithified limestone</td>
</tr>
<tr>
<td><em>Echinostrephus aciculatus</em></td>
<td>Enewetak</td>
<td>0.16 indiv./m²</td>
<td>.008</td>
<td>.045</td>
<td>Coral knoll</td>
</tr>
<tr>
<td><em>Echinostrephus aciculatus</em></td>
<td>Enewetak</td>
<td>1.05 indiv./m²</td>
<td>.036-.067</td>
<td>.063</td>
<td>Lithified limestone platform</td>
</tr>
<tr>
<td>Rock borer</td>
<td>Hawaii</td>
<td>12-100 indiv./m²</td>
<td>.5-30</td>
<td>.04-.3</td>
<td>Limestone veneer on basalt platform</td>
</tr>
<tr>
<td><em>Echinostrephus aciculatus</em></td>
<td>Hawaii</td>
<td>12-100 indiv./m²</td>
<td>.5-30</td>
<td>.04-.3</td>
<td>Limestone veneer on basalt platform</td>
</tr>
</tbody>
</table>

* Erosion rates extrapolated from Enewetak study.
physical erosion by waves and currents in contributing to reef configuration and destruction.

The ecology of echinoids on a coral reef can affect reef geology in two ways. Firstly, grazing echinoids, in feeding on calcareous and noncalcareous algae, inhibit the buildup of extensive algae mats, especially on shallow lagoon floors. Algae cementation is one of the most important lithification processes in shallow water limestone production (Chilingar et al., 1967). Without echinoid grazing, reef growth through algae cementation may increase substantially. Secondly, in the process of feeding and burrowing by echinoids, reef limestone is broken down. This material is then added to the pool of unconsolidated sediment, some of which eventually undergoes submarine lithification and diagenesis (Seibold et al., 1973). In the Persian Gulf, calcareous material blown into the lagoons from exposed areas by winds must add finer material to the sediment. The inner lagoon near shore sand is produced in situ by bioerosion (Evans et al., 1973). On the inner parts of the lagoon floor, settling of sediment may take place and subaqueous cementation may be fairly extensive. This occurs when the sediment immediately beneath the surface of the lagoon floor is stable (being bound by a thin layer of algae) and then cementation occurs (Evans et al., 1973). These processes of diagenesis and cementation when measured and compared to bioerosion can, in part, lead to an assessment of long-term net growth or destruction of a reef. If physical erosion is minimal when averaged annually, then the production of new CaCO₃ substrata by submarine lithification and coral productivity can be balanced against total bioerosion.

6. Summary

The two rock boring echinoids Echinometra mathaei (Blainville) and Echinochroocidus aciculatus (Agassiz) live in positive association on Enewetak atoll. They are found together in the intertidal and subtidal zone more than would be expected if their distributions were random. Together they are estimated to remove 80 g m⁻² y⁻¹ on lagoon coral knolls and 325 g m⁻² y⁻¹ on the seaward reef platforms off Enewetak island. E. aciculatus turns over its gut content approximately twice as fast as E. mathaei. Individual mean erosion rates (g d⁻¹) for the former species were consistently higher in all habitats studied than for the latter. Echinoids on Enewetak atoll can erode from 8-33% of the amount of CaCO₃ estimated to be removed by sponges which are considered major bioeroders on the tropical reefs. This represents from 2-8% of the total amount of CaCO₃ production on Enewetak atoll (Smith, 1973). This combined with other bioerosion can be significant in determining reef configuration and growth. From the estimates presented here, bioerosion may be a geologically significant factor in the production of sediment on Enewetak. Estimates of echinoid erosion in other areas (Table 2) show that sea urchin grazing and burrowing can produce, conservatively, 4-7 kg/m²/y of CaCO₃ sediment. As it grows, the coral reef framework encorporates the eroded sediment
in voids produced by physical and biological erosion (Stearn et al., 1977). Diagenesis within the reef crevices creates new hard limestone substrata (Chilingar et al., 1967). If reef building is in equilibrium, this process, along with coral skeletal production, must balance total erosion of the reef complex by physical and biological factors.

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