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Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables

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Abstract. Two aspects of erosion by sea urchins (Echinoidea) in coral reef habitats are: the direct passage of reef framework material through the gut and the indirect effects through the weakening of the reef structure. Urchin bioerosion can equal or exceed reef carbonate production. The impact of urchins on reefs depends on three variables: species type, test size and population density. Large differences in bioerosion by urchins of the same test size occur between different species. Size differences between species in a sea urchin community, as well as size differences within a species along a reef, can be significant. Bioerosion per urchin increases enormously with size. Changes in population density, through time and space, result in significant changes in bioerosion. It is demonstrated how the interaction of these variables determines in-situ sea urchin bioerosion.

Introduction

In the interplay between constructive and destructive forces in reef-building, bioerosion plays a major rôle: In fact the outcome of this interaction may decide the fate of the reef structure (Stearn et al. 1977; Scoffin et al. 1980; Lessios 1988; Bak et al. 1984; Glynn et al. 1979; Bak 1990). A variety of organisms are involved in bioerosive processes and a group frequently listed is the sea urchins (Echinoidea). A large group of sea urchins, the irregular echinoids, are not engaged in bioerosion. They live on soft bottoms and feed as sediment ingestors. The regular echinoids are the dominating urchins in coral reefs. They can erode hard substratum indirectly through weakening their structural environment, causing parts to become dislodged in storms, and directly through their feeding behaviour. Regular urchins employ four sources of food: attached/drifted plants, encrusting/excavating organisms, sessile organisms, and detritus. The last three categories of food especially are accessed using a strong, agile and somewhat protractile

chewing apparatus, which is responsible for the scraping erosion caused by grazing on hard substrata.

In contemporary reefs, a limited number of species are capable of grazing/abrading the carbonate reef substrata and are commonly reported to be of importance in bioerosion. In the Atlantic, important species are: *Diadema antillarum* Philippi, and *Echinometra lucunter* (Linnaeus) (Abbott 1974; Ogden 1976; Scoffin et al. 1980; Carpenter 1988). In the Indo-Pacific *Eucidaris thouarsii* (Valenciennes), *Diadema savignyi* Michelin, *D. setosum* (Leske), *Echinothrix calamaris* (Pallas), *E. diadema* (Linnaeus), *Echinometra mathaei* (de Blainville), and *Echinostrephus molaris* (de Blainville) have been mentioned as important bioeroders (Glynn and Wellington 1983; McClanahan and Muthiga 1988; Bak 1990). At least two of these species, *Diadema antillarum* and *Eucidaris thouarsii*, feed on the non-living component of the reef framework as well as on living coral surfaces (Bak and van Eys 1975; Carpenter 1981; Glynn and Wellington 1983).

Bioerosion by urchins has many aspects. One significant aspect of urchin bioerosion, though not treated here, has major biological and geological effects. This includes all abrasive activities, including spine abrasion, which results in the forming of cavities and burrows. In the same category are all effects resulting from urchin abrasive activity, such as the dislodgement of large massive coral colonies after storms have weakened the bases of coral colonies. Echinoid bioerosion in this report is limited to the erosion caused by the feeding activities of the organisms. This short study incorporates the literature, supplemented with unpublished data collected by the author, to address the questions: how important is sea urchin bioerosion in the context of reef construction/destruction, and, what are the important variables in sea urchin bioerosion?

How important is sea urchin bioerosion?

How important is urchin bioerosion compared with the total bioerosion? Unfortunately, the activities of the dif-

ferent groups of bioeroders have rarely been assessed on one reef, but where they have been studied, echinoids played a major role. Table 1 shows total bioerosion from the activities of three groups of organisms, parrot fish (Scaridae), excavating sponges (mainly Clionidae), and sea urchins (*Diadema antillarum*), on two Caribbean fringing reefs. Sea urchins played a major role on each reef since more than 75% of the total bioerosion was attributed to their feeding behaviour.

Table 1. Echinoid erosion as percentage of total bioerosion ($\text{g m}^{-2} \text{d}^{-1}$)

	Echinoid (%)	Total (g)	Source
Barbados	79.4	18.7	Scoffin et al. 1980
Curacao	87.8	9.0	Bak et al. 1984

Table 2. Gross production estimates of reefs versus estimated rates of echinoid bioerosion

Gross prod ($\text{kg m}^{-2} \text{y}^{-1}$)	Echinoid bioerosion ($\text{kg m}^{-2} \text{y}^{-1}$)	Source
1–10*		Chave et al. 1972
1–2		Smith and Harrison 1977
5.2		Land 1979
15**		Stearn et al. 1977
9	5.8	Scoffin et al. 1980
3.4–8.0		Glynn and Wellington 1983
3.0	2.9	Bak et al. 1984
2.1	4.6	Bak 1990
0–5.78 (1.21***)		Hubbard et al. 1990
	8.5	Ogden 1977

* 100% cover, ** excluding sandy area, *** average

Table 3. Echinoid erosion as percentage of gross production ($\text{g m}^{-2} \text{d}^{-1}$)

	Echinoid (%)	Gross prod.	Source
Barbados	47	24.7–31.2	Scoffin et al. 1980
Curacao	96	8.2	Bak et al. 1984
Galapagos	5–100	9.3–21.9	Glynn and Wellington 1983
Moorea	216	5.6	Bak 1990

Table 4. Erosion rates ($\text{g m}^{-2} \text{d}^{-1}$) for groups of excavating and scraping animals in reef environments

Locality	Polychaetes	Sponges	Echinoids	Scarids	Source
Caribbean					
St. Croix			23.3		Ogden 1977
Panama				1.3	Ogden 1977
Barbados		3.8	14.8	0.1	Scoffin et al. 1980
Curacao		0.5	7.9		Bak et al. 1984
Bonaire				1.4–19.2	Bruggeman personal communication
Pacific					
Moorea			12.5		Bak 1990
GBR	0.9–13.2				Hutchings and Bamber 1985

The importance of echinoid bioerosion is evident by comparing it with a gross carbonate production. Estimates of gross production on reefs generally vary with three variables: coral cover, coral species and growth rate (the last two being interrelated). Values of gross production range from zero (no cover, Hubbard et al. 1990) to $10\text{--}15 \text{ kg m}^{-2} \text{y}^{-1}$ (100% cover, Chave et al. 1972; Stearn et al. 1977), but generally are $1\text{--}4 \text{ kg m}^{-2} \text{y}^{-1}$ (Table 2). Records of sea urchin bioerosion are in the same range and it appears that urchin bioerosion can sometimes equal or exceed reef carbonate production.

A much more accurate picture is obtained if we compare echinoid bioerosion with gross production on the same reef. This comparison has been made in widely separate localities: the Caribbean, the central and the eastern Pacific. In all cases echinoid erosion was an extremely important factor in the carbonate budget (Table 3). A substantial part of the gross production can be eroded. In some cases the balance between reef construction and destruction was negative because the rate of reef framework destruction was higher than that of framework formation. When sea urchin erosion rates are compared with such figures for other groups of bioeroding organisms (Table 4), urchin erosion is considerable. This is the case even though other organisms, e.g. parrot fishes in the shallow reef of Bonaire (Bruggeman personal communication), can make very substantial contributions.

What are the important factors in echinoid bioerosion?

Urchin communities on reefs vary in species composition, in size frequency distributions, and in densities. The importance of a factor such as density seems obvious, as well as the possible consequence of the taxonomic composition of an echinoid community. Even so, there are very few data on the quantitative impacts of different densities of different urchin species in the same reef habitat. Similarly, the significance of sea urchin size frequency distribution in reef bioerosion processes has only rarely been described (e.g. Scoffin et al. 1980). Interaction of these three variables in the same reef habitat in quantitative terms has never been quantified. I studied bioerosion of a mixed community of echinoids, consisting of *Diadema savignyi*, *Echinothrix diadema* and *Echinometra mathaei*, in a reef at Tiahura on the island of Moorea, French Polynesia. The depth of the study site was 1.5 to 2.5 m, (see Galzin and Pointer 1985);

for details on measuring urchin densities, population size frequencies and bioerosion see Bak (1990).

First, there are important differences in species. Quantitative differences in bioerosion between two species of urchins, *E. mathaei* and *D. savignyi*, in the same size class are shown in Fig. 1. *E. mathaei* individuals eroded more material than *D. savignyi* of the same size in all but the largest *E. mathaei* size class (test diameter 35–39 mm, Fig. 1a). When larger individual *D. savignyi* erosion rates are compared with the larger individuals of *E. diadema* there is also a small difference (Fig. 1b) but it is difficult to say if these are universal characteristics of the species, since no other data sets are available.

The next variable to assess is size. Two aspects are important, differences in size between species and differences in size between populations of the same species. The data from Moorea (Fig. 2a) clearly show the difference in size between the small species *E. mathaei* and the large *D. savignyi*. In addition, mean size and size frequency of populations can vary significantly within a species. The

Fig. 1. Bioerosion of sea urchins (expressed as bioerosion urchin⁻¹ day⁻¹) in different test size categories. **a** *Echinometra mathaei* (—■—) and *Diadema savignyi* (—□—); **b** *E. mathaei*, (—■—), *Diadema savignyi* (—□—) and *Echinothrix diadema* (—◆—)

Fig. 2. **a** Size frequency of populations of three species of sea urchins *Echinometra mathaei* (—◆—), *Diadema savignyi* (—■—) and *Echinothrix diadema* (—□—) in Moorea ($n = 99$, 126 and 34 respectively, location Tiahura). **b** Size frequency of three populations of *Diadema antillarum* at three sites on the south coast of Curaçao: Carmabi Buoy Three ($n = 482$; —■—), Carmabi Buoy Zero ($n = 527$; —□—), Awa di Oostpunt ($n = 508$; —◆—)

test size in three populations of *D. antillarum* was measured occurring at shallow depths (< 10 m) along the south coast of Curaçao (Bak and van Eys unpublished) and the data show that there are considerable differences in size frequency between the populations (Fig. 2b). Most obvious is the difference between the large animals of the Awa population and the smaller ones of the Carmabi buoys, but the difference between all three populations was significant (Kolmogorov-Smirnov two sample test on the three density functions, all comparisons $P < 0.0001$). Such variation in size is possibly related to factors such as food availability (Levitan 1988).

These large differences in size frequency of populations have significant consequences for sea urchin bioerosion. Figure 1 indicates, apart from the differences between the species, the increase in bioerosive potential with increasing size in each urchin. Within each species larger animals are much more effective as bioeroders. Data on the mean bioerosion rates of *Echinometra* species support this relationship (Table 5). In populations with a test size of about 30–40 mm mean erosion rates are 5 to 10 times higher as in populations with mean tests half that size.

Table 5. Mean test size (mm) and mean erosion rates in *Echinometra* (g urchin⁻¹ d⁻¹) at a range of localities

	Size	Erosion	Source
<i>E. mathaei</i>			
Hawaii	19.5	0.11	Russo 1980
Moorea	19.3	0.14	Bak 1990
Arabian Gulf	37.1	0.9–1.4	Downing and El-Zahr 1987
Kenya	40.8	0.7	McClanahan and Muthiga 1988
<i>E. lucunter</i>			
St. Croix	30.0	0.12	Ogden 1977

Fig. 3. Total bioerosion of each of three species of sea urchins (expressed as bioerosion of all urchins present day⁻¹) *Echinometra mathaei* (□), *Diadema savignyi* (■), and *Echinothrix diadema* (▨), in Moorea ($n = 99, 126$ and 3 respectively, location Tiahura)

Finally, the density of urchin populations is also an important variable. There are large differences in spatial densities within species at all scales. The smallest scale at which density differences can be demonstrated, a few metres, has no significance for bioerosion. Urchins operate on a larger scale in the process of bioerosion. There are also variations in density with depth, over tens of metres and along coasts, on scales of hundreds of metres or kilometres (Table 3 Birkeland 1989). Urchin density ranges from less than one to more than ten per square metre. Variations in time also occur. In 1974 we measured densities in shallow *D. antillarum* populations of 12.5 and 11.3 urchins m⁻² at two sites on the south coast of Curaçao (Bak and van Eys unpublished). In 1983 these densities were 2.9 and 4.2 urchins m⁻², respectively (Bak et al. 1984). Events such as sea urchin mass mortalities result in significant decreases in density and as a result, bioerosion and foraging processes are significantly altered (de Ruyter van Steveninck and Bak 1986; Carpenter 1985; Hughes et al. 1985).

The major question is how these variables, taxonomic identity, test size and population density, interact. Interaction is demonstrated by the results of the Moorea study (Fig. 3). When urchins are in the same size class, *Echinometra* (per urchin) has more impact as a bioeroder than *Diadema* (Fig. 1a). This is a species specific characteristic. The impact of *Echinometra* was enhanced because its density was nearly twice that of *Diadema*, 7.4 versus 4.8 urchins m⁻². Nevertheless, because the *Diadema* were

much larger in size, the *Diadema* population has a much larger impact as a bioeroder than the *Echinometra* population (Fig. 3). The third important urchin at the site, *Echinothrix*, had a very large test size. However, density was relatively low and consequently total bioerosion caused by the population was low. The effect of high density and large test size was shown by the *Diadema* population. It was by far the most important urchin in terms of bioerosion (Fig. 3).

In conclusion, sea urchin bioerosion appears to be a major factor determining the fate of the reef structure and is a significant component in the carbonate budget. In conclusion, it has been shown that a simple model where bioerosion B:

$$B = (n_1 \times sp_1)(n_2 \times sp_2) \cdots (n_i \times sp_i)$$

in which n_i is urchin density in each size class i and sp_i is species specific bioerosion in size class i , can be used to quantify the impact of urchin bioerosion. The impact of the three variables was demonstrated through analysis of urchin bioerosion on coral reefs of Moorea, French Polynesia.

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