

Patterns of echinoid bioerosion in two Pacific coral reef lagoons

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ABSTRACT: Echinoid populations can be major grazers on hard reef substrata and are consequently of importance in the bioerosion of coral reefs. There are no previous data on rates or patterns of bioerosion by the echinoid community in Indo-Pacific reefs. We surveyed densities of echinoid populations in 2 reef lagoons, the Tiahura section, northwest Moorea (Society Islands) and the central lagoon of Takapoto atoll (Tuamotu Islands), and determined echinoid erosion rate of the reef structure. *Echinometra mathaei* was the most numerous urchin in Tiahura (7.4 m^{-2}) followed by *Diadema savignyi* (4.8 m^{-2}), *Echinothrix diadema* (0.6 m^{-2}) and *Echinostrephus molaris* (0.2 m^{-2}). *E. mathaei* and *E. molaris* are small urchins processing small amounts of carbonate rock and the impact of their populations as bioeroders is limited at such densities, even for the numerous *E. mathaei* ($1.0 \text{ g m}^{-2} \text{ d}^{-1}$). *D. savignyi* and *E. diadema* are large (mode test diameter 55 and 60 mm respectively) and their populations consumed 9.2 and $2.2 \text{ g m}^{-2} \text{ d}^{-1}$ of hard substratum respectively. In Takapoto lagoon, the same species were present (except *E. molaris*), but densities of urchins were extremely low and echinoid bioerosion was only of importance close to lagoonal inlets ($6.2 \text{ g m}^{-2} \text{ d}^{-1}$). In situ growth of the hard reef substratum in Moorea is predominantly through growth of massive *Porites* colonies and estimated at $6 \text{ g m}^{-2} \text{ d}^{-1}$. The conclusion is that, with an echinoid bioerosion rate of $12.5 \text{ g m}^{-2} \text{ d}^{-1}$ the reef structure is being destroyed. The observed urchin densities are high for oceanic islands of the Indo-Pacific region and the possibility of a relation between human influence on the reef and urchin densities should be considered.

INTRODUCTION

The magnitude of constructive and destructive forces is a deciding factor in the fate of coral reefs. Echinoids can be major grazers on hard reef substrata (Hawkins & Lewis 1982) and as such they are important in the bioerosion of reefs. They may process as much as $9.7 \text{ kg carbonate m}^{-2} \text{ yr}^{-1}$ (Hunter 1977) and be responsible for 80 % of the total erosion of reefs (Scoffin et al. 1980). On some reefs their position has been shown to be crucial in the balance between the construction and destruction of the reef structure (Scoffin et al. 1980, Bak et al. 1984).

Such data are apparently restricted to Atlantic reefs and marginal reefs in the Pacific such as in the Galapagos Islands (Glynn et al. 1979). The data available on urchin population densities in the Indo-Pacific show a highly variable pattern with occasional high densities restricted to the continental-shelf Indo-Pacific (Birkeland 1989). In many areas (e.g. Oceania, the Great Barrier Reef) echinoids are considered not to be

very prominent and echinoid bioerosion seems to be much less significant (Ogden 1987, Sammarco 1987, Bak & Povel 1989).

It appears that in some habitats on French Polynesia reefs echinoderms, such as *Diadema* and *Echinothrix* species, can be conspicuous members of the benthos. This report presents results of a survey recording echinoid densities in different microhabitats in 2 lagoons and a short investigation of their possible impact as bioeroders on the reef structure.

MATERIAL AND METHODS

Densities of echinoid populations were recorded during October 1987 in 2 lagoons, the Tiahura section, northwest Moorea (Society Islands) and the central lagoon of Takapoto atoll (Tuamotu Islands; Fig. 1). For logistic reasons access to the reefs was limited to the daytime when urchins avoided open space and kept to crevices in and under coral heads.

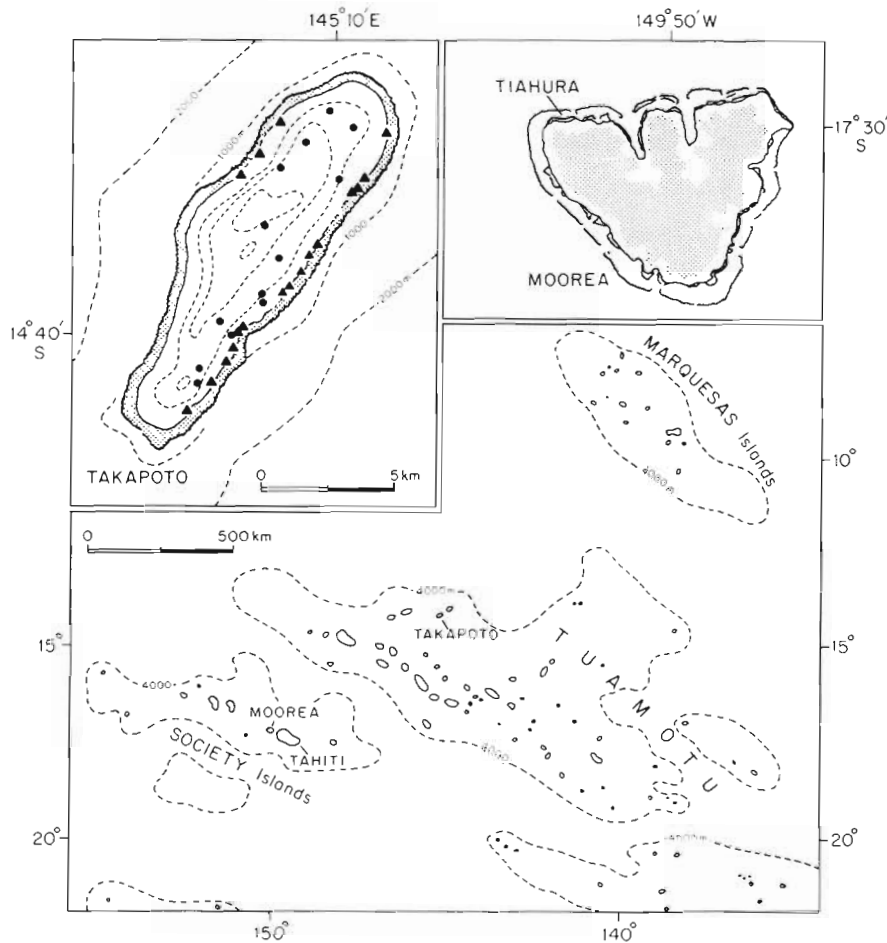


Fig. 1. Location of Moorea in the Society Islands and Takapoto in the Tuamotus. Inset of Moorea shows the Tiahura reef section. Inset of Takapoto shows position of surveyed pinnacles (●) and patch reefs (▲)

On Tiahura the study site (depth 1.5 to 2.5 m, section 8 in Fig. 5, Galzin & Pointer 1985) was dominated by isolated colonies of massive *Porites*, living or dead at different stages of destruction, separated by sand/rubble stretches. We used ten 10 m long line transects to assess cover of sand, rubble, dead and living coral colonies. Subsequently, we concentrated our efforts on diligently extracting all urchins in belt transects (50 cm wide, total length 34 m) over living and dead colonies. All urchin maximum test diameters were measured (mm). Condition of coral colonies and cover of living tissue were recorded in the 50 × 50 cm quadrats of the belt transects. From these 2 sets of data, viz. urchin density/substratum and cover of substratum, urchin densities were calculated for the area.

To assess the quantity of carbonate eroded from the reef framework by *Diadema savignyi* Michelin, *Echinothrix diadema* (Linnaeus) and *Echinometra mathaei* (de Blainville), a range of differently sized individuals ($n = 11$) of each species were collected separately outside the transects and the gut content (ash-free dry weight) of each specimen was determined. This is a measure of the minimum consumption

over a 24 h period (Glynn et al. 1979, Hawkins & Lewis 1982). *E. mathaei* lives within the close vicinity of its burrows but *D. savignyi* and *E. diadema* graze over larger areas. The source of consumed carbonate (hard substratum or loose sediment) is reflected in the composition of urchin faecal pellets (Hunter 1977, Scoffin et al. 1980). We identified and counted at least 200 pellets of each species in thin section. To prepare petrographic sections, *D. savignyi* and *E. diadema* pellets were slowly dried (35°C) and impregnated with epoxy resin (HY 951/103, Geigy, Basel). Pellets of the same diameter were mounted on glass (epoxy glue, Frencken, Weerd) and cut to a thickness of 25 µm.

Gut contents are known to vary quantitatively as well as qualitatively with urchin size (e.g. Scoffin et al. 1980). We used the significant exponential relationships between test size and gut content (*D. savignyi* $r = 0.966$, *E. diadema* $r = 0.871$, *E. mathaei* $r = 0.860$, all $p < 0.01$) to calculate the carbonate consumption for the different sizes classes. The size/frequency data recorded in the belt transects were used to obtain the mean consumption of the populations. Faecal pellets were collected in the field from random individuals.

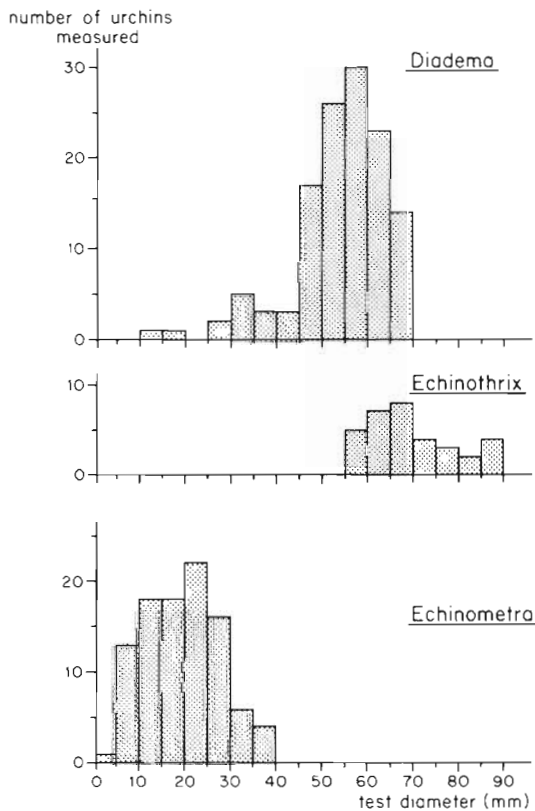


Fig. 2. Size distributions at Tiahura of *Diadema savignyi* ($n = 126$), *Echinothrix diadema* ($n = 34$), and *Echinometra mathaei* ($n = 99$)

The distribution pattern of echinoids denied a similar approach in Takapoto lagoon. Two distinct reefal habitats exist in the lagoon: isolated pinnacle reefs occur throughout, rising from deeper water (10 to 40 m) to near the surface, while small patch reefs are found shallow along the lagoonal border. We visited 13 pinnacles and 18 patch reefs to check for the presence of urchins. Whenever urchins were present their densities and cover of substratum components were recorded in 10×0.5 m wide belt transects.

RESULTS

Of the 4 urchin species present in the Tiahuaara transect [*Diadema savignyi*, *Echinometra mathaei*, *Echinothrix diadema* and *Echinostrephus molaris* (de Blainville)], the first two occurred in high densities. *D. savignyi* and *E. diadema* were found on the same substratum while *E. mathaei* and *E. molaris* showed preference for other specific microhabitats.

Diadema savignyi reached mean densities of 14.1 m^{-2} on dead/partially dead coral colonies but was absent on the remains of totally eroded colonies.

Echinothrix diadema showed the same distribution pattern at much lower densities (1.8 m^{-2}). Highest *Echinometra mathaei* densities occurred on dead colonies (38.4 m^{-2}) but *E. mathaei* was, in contrast to the former species, also common on the totally eroded flat remains of colonies (7.7 m^{-2}). *Echinostrephus molaris* occurred only on these totally eroded remains (1.7 m^{-2}). All species were uncommon on living coral colonies. Size distributions for all species (except the uncommon *E. molaris*) are shown in Fig. 2 and population densities in Table 1.

There were large differences in the quantities of carbonate in the guts of the various species. *Echinometra matthaei* is small (dissected specimens 16 to 32 mm, $\bar{x} = 24$ mm) and gut content weight was low ($\bar{x} = 0.18$ g). *Diadema savignyi* and especially *Echinothrix diadema* are very large with test size among dissected specimens up to 69 and 88 mm, respectively. Mean carbonate content of the gut was 5.2 g for *D. savignyi* and 7.4 g for *E. diadema*.

The composition of the faecal pellets indicated a hard substratum origin for the majority of the carbonate particles. In *Diadema savignyi* the ratio hard substratum/loose sediment was 67 to 33%, in *Echinothrix diadema* 52 to 48%. Combining the data on cover of bottom components, urchin population densities and size frequencies, gut content/urchin size class and origin of gut carbonate, total bioerosion for each species can be calculated. *D. savignyi* is a very common and large urchin, and the bulk of the daily reef frame erosion, $924 \text{ g } 100\text{m}^{-2}$, is caused by this species (calculation shown in Table 2). *E. diadema* is large but much less numerous (Table 1) and a similar calculation results in an erosion rate of $218 \text{ g } 100\text{m}^{-2}$. *Echinometra mathaei* is numerous but small, gut content weight is low and total bioerosion of this urchin amounts only to $102 \text{ g } 100\text{m}^{-2}$ (Table 3). The impact of *Echinostrephus molaris*, a rare species in the area, can be ignored. Consequently, the total erosion of the reef framework by echinoids is $\pm 1250 \text{ g } 100\text{m}^{-2} \text{ d}^{-1}$.

In Takapoto a very different pattern emerged. The most thorough searching did not reveal a single urchin on the pinnacles. Also coral patches along the lagoonal border proved to be devoid of echinoids, except when the patches were in the vicinity, or in the entrance, of a Hoa (shallow lagoonal inlet). However, transect surveys ($n = 6$) showed urchins to be present at low densities: *Diadema savignyi* 0.3 m^{-2} , *Echinothrix diadema* 0.9 m^{-2} and *Echinometra mathaei* 0.4 m^{-2} . Assuming the species-specific rates of reef framework erosion to be similar in Takapoto and Moorea, *D. savignyi* is daily processing $120 \text{ g } 100\text{m}^{-2}$, *E. diadema* $490 \text{ g } 100\text{m}^{-2}$ and *E. mathaei* $8 \text{ g } 100\text{m}^{-2}$. Total hard substratum erosion in this spacially restricted habitat amounts to $618 \text{ g } 100\text{m}^{-2} \text{ d}^{-1}$.

Table 1. Urchin densities per substratum component during daytime per 100 m² reef bottom at Tiahura

Bottom components	% Cover of bottom component	<i>Diadema savignyi</i>	<i>Echinothrix diadema</i>	<i>Echinometra mathaei</i>	<i>Echinostrephus molaris</i>
Coral (living surface 50–100%)	4.5	3	7	2	0
Coral (living surface 5–50%)	25.5	360	33	187	0
Coral (living surface < 5%)	12.5	121	22	480	0
Flat, eroded coral surfaces	9.0	0	3	69	15
Rubble and sediment	24.0	0	0	0	0
Fine sediment	24.5	0	0	0	0
Total urchin densities (100m ⁻²)		484	65	738	15

Table 2. *Diadema savignyi*. Daily reef-framework erosion (g 100m⁻²) at Tiahura reef

Size class ^a (mm)	Urchin density (100 m ⁻²)	Gut content (g CaCO ₃ urchin ⁻¹)	Daily content of size class	Daily erosion ^b
10–14	4	0.01	0.04	0.03
15–19	4	0.01	0.04	0.03
20–24	–	–	–	–
25–29	8	0.04	0.32	0.21
30–34	19	0.16	3.04	2.04
35–39	12	0.36	4.32	2.89
40–44	12	0.71	8.52	5.71
45–49	66	1.06	69.96	46.87
50–54	101	1.87	188.87	126.54
55–59	116	3.03	351.48	235.49
60–64	89	4.32	384.48	257.60
65–69	54	6.81	367.74	246.39
Total daily erosion (g 100 m ⁻²)				924

^a Maximum test diameter
^b 33% of pellet reworked material

Table 3. *Echinometra mathaei*. Daily reef-framework erosion (g 100m⁻²) at Tiahura reef

Size class ^a (mm)	Urchin density (100 m ⁻²)	Gut content (g CaCO ₃ urchin ⁻¹)	Daily content of size class	Daily erosion
0– 4	8	0.00	0.02	0.02
5– 9	98	0.02	1.96	1.96
10–14	136	0.05	6.80	6.80
15–19	136	0.10	13.60	13.60
20–24	166	0.16	26.56	26.56
25–29	121	0.23	27.83	27.83
30–34	45	0.31	13.95	13.95
35–39	30	0.40	12.00	12.00
Total daily erosion (g 100 m ⁻²)				102

^a Maximum test diameter

DISCUSSION

There are hardly any data available on bioerosion rates in these Indo-Pacific echinoid species. Nothing is known for *Diadema savignyi* and *Echinothrix diadema*.

Comparable to *D. savignyi* is the Atlantic species *D. antillarum*. Erosion rates are reported to vary from 0.6 to 1.4 g urchin⁻¹ d⁻¹ for this species in the Caribbean (Hunter 1977, Ogden 1977, Scoffin et al. 1980). The Pacific diadematis studied processed appreciably

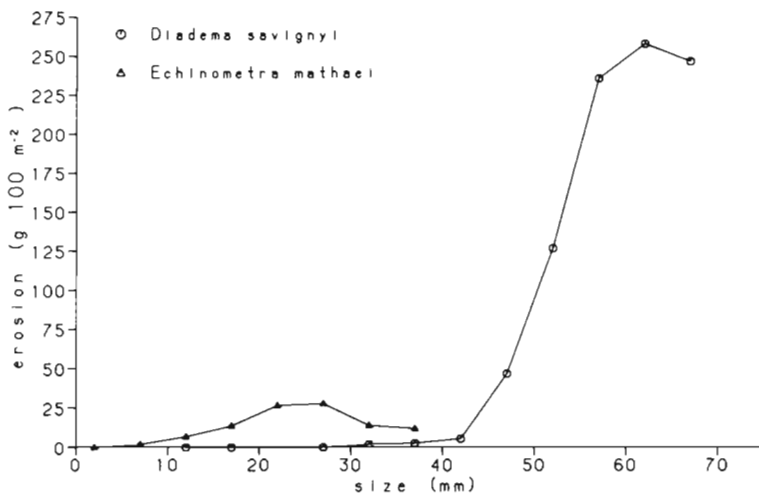


Fig. 3. *Diadema savignyi* and *Echinometra mathaei*. Daily reef-framework erosion for urchins of different size classes

higher amounts of carbonate rock, with means of 1.9 and 3.3 g urchin⁻¹ d⁻¹ respectively for *D. savignyi* and *E. diadema*. The reason appears to be that the amount of erosion per urchin is strongly related to size (Fig. 3). Our urchins were large, close to their maximum size (Ebert 1975, 1982), while mean size for Caribbean *Diadema* populations is generally smaller (e.g. Scoffin et al. 1980).

Echinometra mathaei is a modest bioeroder. Erosion rates reported for Enewetak and Hawaii (Russo 1980), 0.11 g urchin⁻¹ d⁻¹, are close to our mean 0.14 g urchin⁻¹ d⁻¹. Higher rates, e.g. 0.9 to 1.4 g (Arabian Gulf; Downing & El-Zahr 1987), can also be related to differences in size of mean test diameters of experimental individuals (means of 19.5, 19.3 and 37.1, respectively for erosion rates cited). Birkeland (1989) points out the importance of different patterns of behaviour in this urchin.

Actual echinoid erosion rate of the reef structure depends, apart from species-specific erosion rates and size distribution, on population densities. Densities of echinoids are high on Moorea compared with some other Indo-Pacific reefs (e.g. Guam, Belau: Birkeland 1984; Great Barrier Reef: Sammarco 1987; Indonesia: Bak & Povel 1989, de Beer pers. comm.) and total echinoid bioerosion, 12.5 g m⁻² d⁻¹, must be high for the region. There are, however, no comparable data available for this region.

In the Caribbean, *Diadema antillarum* was an abundant reef urchin before mass mortalities (e.g. Lessios et al. 1984) made it rare. At high densities, 9 to 23 urchins m⁻², erosion rates varied from 8 to 14.5 g m⁻² d⁻¹ (Ogden 1977, Scoffin et al. 1980, Bak et al. 1984). These values overlap the 12.5 g m⁻² d⁻¹ calculated for the Moorea reef. Highest recorded rates of echinoid reef framework destruction appear to be similar in the Indo-Pacific and Atlantic.

Do such bioerosion rates have any significance among the forces determining the fate of the reef structure? The main constructive element, in the interplay between construction and destruction, is growth of the living coral colonies (Table 4). Approximately 15% of the reef bottom at Tiahura is living coral (Table 1), predominantly massive *Porites* species. Skeletal extension rates of such colonies are 1 cm yr⁻¹ (Bak & Laane 1987) and skeletal density is about 1.4 g cm⁻³ (Hughes 1987). Consequently, in situ growth of the reef structure approximates 2100 g m⁻² yr⁻¹ or 6 g m⁻² d⁻¹. Other constructive and destructive forces, such as growth of crustose coralline algae or microexcavations, are of a smaller order of magnitude and they will partly counterbalance each other. The conclusion must be that, with a coral growth rate of 6 g m⁻² d⁻¹ and a bioerosion rate of 12.5 g m⁻² d⁻¹, the hard reef structure at Tiahura is inevitably being changed into a sandy sediment (Table 4).

Table 4. Major forces of construction/destruction at Tiahura reef

Construction	
Cover living coral ^a	15%
Linear growth ^b	1 cm yr ⁻¹
Skeletal density ^c	1.4 g cm ⁻³
Accumulation reef frame	2100 g m ⁻² yr ⁻¹
Destruction	
Bioerosion <i>Diadema savignyi</i>	9.2 g m ⁻² d ⁻¹
Bioerosion <i>Echinothrix diadema</i>	2.2 g m ⁻² d ⁻¹
Bioerosion <i>Echinometra mathaei</i>	1.0 g m ⁻² d ⁻¹
Total	12.5 g m ⁻² d ⁻¹
Echinoid bioerosion	4550 g m ⁻² yr ⁻¹

^a See Table 1
^b Bak & Laane (1987)
^c Hughes (1987)

At Takapoto the situation is quite different. Significant echinoid bioerosion, indeed occurrence of urchins, is restricted to an extremely small part of the lagoon, viz the close vicinity of lagoonal inlets. The obvious question is: what limits the distribution of the urchins? Differential recruitment and predation are the processes most likely to be involved. In an almost closed atoll such as Takapoto, water exchange between the open ocean and the lagoon is extremely limited, only 15% of the lagoonal volume being exchanged each year (Salvat & Richard 1985). Ninety-five percent of the abundant benthos consists of filter feeders – an enormous standing stock of naturally occurring and cultured molluscs (Richard 1985, Intes 1988). The energy requirements of this community are very high, sometimes in excess of supply (Intes 1988). The long residence time of lagoonal water, in combination with the great clearance capacity of the abundant filter-feeding benthos, may restrict recruitment of echinoids to the vicinity of the shallow connections to the open ocean.

There are large differences between bioerosion patterns in the lagoons, but it is obvious that high echinoid densities can be of decisive importance for the balance between construction and destruction of the reef structure. The question remains: are the urchin populations of Moorea, in view of the reported generally low urchin densities of the Indo-Pacific oceanic islands, really atypical? In the Caribbean and east African reefs human influence (e.g. overfishing) may be responsible for increased echinoid densities (Hay 1984, McClanahan & Muthiga 1988). On the Moorea reef human influence is pronounced and the possibility of a parallel relation between increasing anthropogenic stress on reefs and increased echinoid densities in the Indo-Pacific should be considered.

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