Changes in Kenyan coral reef community structure and function due to exploitation

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Changes in Kenyan coral reef community structure and function due to exploitation

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Abstract

A comparison of Kenyan reefs of different historical and observed levels of fishing exploitation showed that more exploited reef lagoons had greater sea urchin densities and sizes, fewer and smaller fish and less coral cover. In the most exploited lagoon the biomass of the burrowing sea urchin Echinometra mathaei increased five fold during the previous 15 years. An ecological study of the three most common omnivorous sea urchin species inhabiting hard substrate within these reef lagoons (E. mathaei, Diadema savignyi and D. setosum) suggests that they are ecologically separated by predation and avoid predators and competitors by occupying different size burrows or crevices within the lagoon. Predator removal through fishing activities may result in ecological release of the sea urchins and result in competitive exclusion of weaker competitors. The most exploited reef had a nearly monospecific barren of E. mathaei living outside burrows suggesting that E. mathaei may be the top competitor. Its ecological release appears to lead to a decrease in live coral cover, increased substrate bioerosion and eventually a loss of topographic complexity, species diversity, fish biomass and utilizable fisheries productivity. Data from the outer reef edge were more difficult to interpret but may indicate similar patterns. Within this area, physical stresses such as waves and currents may be a greater controlling force in regulating fishing activities and coral reef community structure.

Introduction

There is a concern in many areas of the world both temperate (Estes et al., 1978; Wharton & Mann, 1981) and tropical (Hay, 1984; Carpenter, 1984; Muthiga & McClanahan, 1987) that predator removal through fishing activities results in sea urchin population increases. The concern in temperate areas of North America is that kelp bed forests and associated fauna are being destroyed by unrestricted sea urchin feeding. In the tropics the consequences of sea urchin release are less understood but prelimi-

nary evidence suggests that high sea urchin densities may reduce coral recruitment (Sammarco, 1980) and increase bioerosion of coral reefs (Glynn et al., 1979) which could result in a loss of live coral, calcium carbonate accretion, associated faunal diversity and coral reef ecosystem services of fisheries productivity and coastal protection.

This concern prompted a preliminary study of coral reef community structure along the Kenyan coast focusing on sea urchins, their interrelationship and possible relationship with other members of the coral reef community. The authors have visited

numerous areas along the Kenyan coast including Kiunga, Lamu, Ras Tenewi, Malindi, Watamu, Vipingo, Kanamai, Mombasa, Tiwi, Diani, Msambweni and Shimoni as well as all the Marine Parks and Reserves (Fig. 1). During our visits we noticed community structure differences between reefs of similar physical structure that could often be attributed to our knowledge of their historical and present degree of protection or isolation from fishing. Within reef lagoons having hard substrate (living or dead coral) we observed that protected or remote areas generally had a high density of finfish and a low density of sea urchins, while the reverse was true in heavily fished areas. We chose two sites typifying extreme fishing conditions and a site of intermediate fishing pressure in order to quantify these observations and to develop hypotheses which might explain observed differences and the process of change.

Study sites and methods

Three sites were chosen in which community structure variables were measured and compared with our observations on other sites and our knowledge of Kenyan coral reefs over the past nine years. The Malindi Marine National Park's (MMNP) North Reef was chosen as the least exploited or unfished site, the most exploited site was the heavily populated tourist beach at Diani, and Kanamai was the intermediate site which is bordered by smaller tourist hotels and residences. Diani and Kanamai are both fringing reefs (Khamala, 1971) whereas North Reef is a platform reef (Hamilton & Brakel, 1984) but has a reef lagoon and edge similar to a fringing reef. The North Reef platform is 0.8 m above extreme low water and the lagoon is 0.9 m deep; the Diani reef platform is 0.8 m above extreme low water and the lagoon 0.6 m deep; and Kanamai is 1.4 m above extreme low water and 0.3 m deep.

Within reef lagoon and reef edge sites sea urchin density and coral cover were measured by 43–105 1 m^2 quadrats placed at 5 m intervals along land to seaward transects. Data collected on E. mathaei in Diani were compared to a study by Khamala (1971) completed 15 years previously. Random collections

of E. mathaei, Diadema savignyi and D. setosum were made and the shortest and longest test lengths of the individuals were measured with calipers. Biomass was estimated using a length-weight correlation (Muthiga & McClanahan, 1987) multiplying the average urchin weight by the density. Within each site total observable fish densities and size classes were estimated by swimming 4, 500 m^2 transects. Within Diani and Kanamai, where fish sizes were small, 4 cm size class intervals were used while 10 cm intervals were used in MMNP. Fish less than 3 cm in length were not counted. On the outer reef edge where fish transects are difficult to undertake, due to rough surf, 3 fishermen were hired to spear fish in Diani and Kanamai. Their catch was weighed and fishing time recorded in order to estimate the catch/effort as an estimate of fish abundance.

From observations we hypothesized that the three major sea urchins inhabiting hard substrate within the lagoon; E. mathaei, D. setosum and D. savignyi, are ecologically separated by their predator avoidance strategies and avoid predation and competition by utilizing different predator free space (Sih et al., 1985) associated with different size crevices. Within the Kanamai lagoon, where sea urchin species diversity is high, a preliminary study of their distribution, morphology and behavior was undertaken. These three species are omnivorous (Herring, 1972; Lawrence, 1975) and associated with hard substrate. D. savignyi and D. setosum are easily distinguishable in East Africa using the criteria of Pearse & Arch (1969). Additional sea urchin species including Echinothrix diadema, Tripneustes gratilla, Toxopnuestes pileolus, Echinostrephus molaris and Astropyga radiata inhabit reef lagoons but their densities are low and coexistence, in many instances, can be attributed to different dietary preferences (Herring, 1972). Measurements on 55 randomly chosen individuals of each species included their presence in groups, group size, test size, spine lengths, presence in burrows or crevices and burrow and crevice sizes.

Bioerosion by E. mathaei was estimated using a technique described by Glynn et al. (1979) where sediment defecation rates are assumed to equal erosion rates. This estimate, however, does not include the fact that some ingested substrate has previously
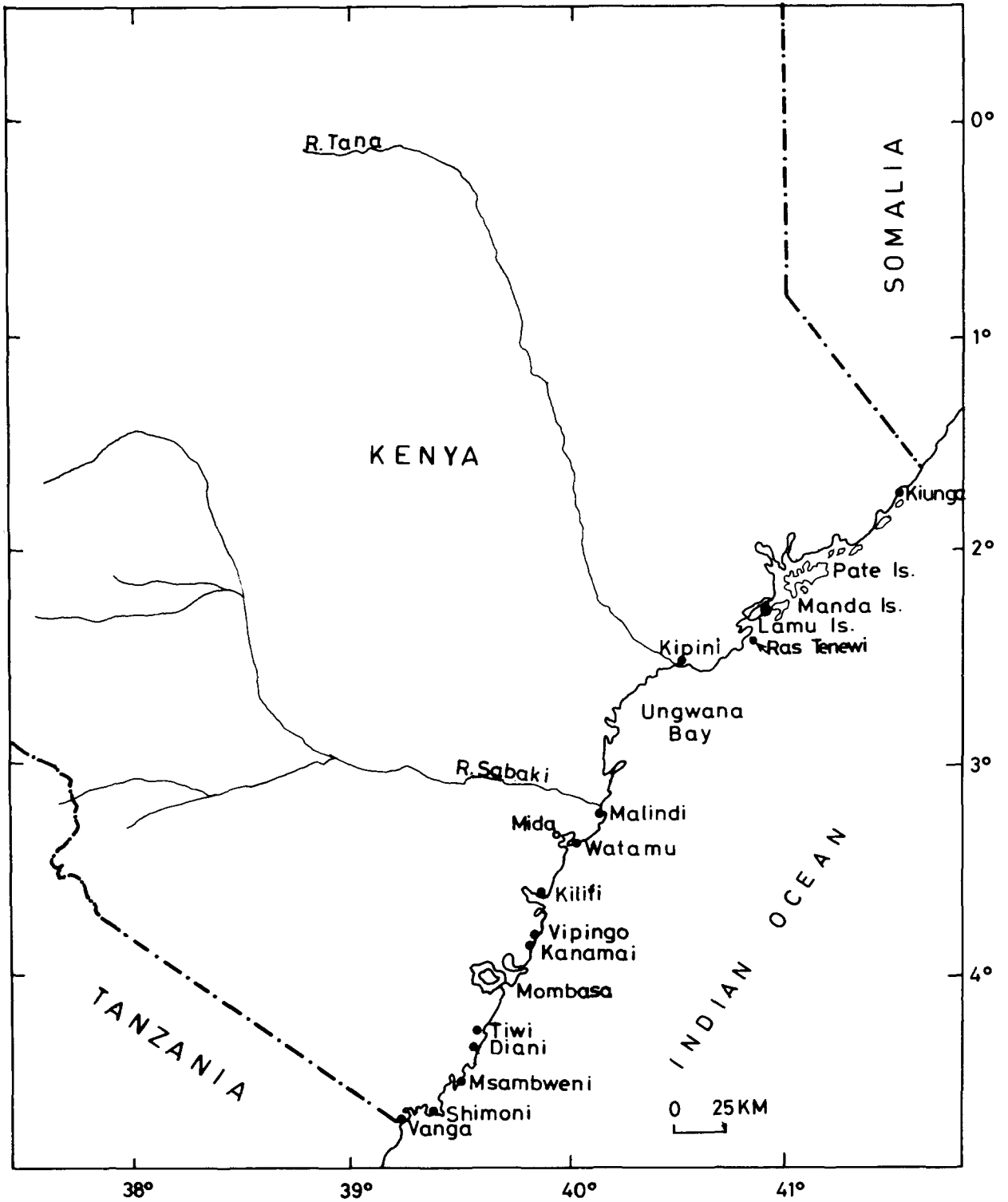
Fig. 1. Map of the Kenyan coast.

been eroded or that additional substrate is eroded by urchin spine abrasion. Thirty-four randomly chosen individuals were placed in 0.75 liters of seawater within plastic chambers for a 24 hour period. Seawater was changed every 4–6 hours. At the end of the experiment the seawater was drained, faeces were removed, dried, rinsed with a 10% hypochlorite solution (to remove organic matter), dried and weighed. The wet weight of the animal was measured and correlated with sediment weight.

Results

Within reef lagoons there were large quantitative differences in measured variables (Table 1). The Park's lagoon contains no sea urchins, high coral cover, large fish and high fish densities (Fig. 2). These parameters have remained constant since 1979 when we spent > 100 hours diving within the Park. During this time we never observed *E. mathaei* or *Diadema* within the lagoon. Abudi (personal commu-
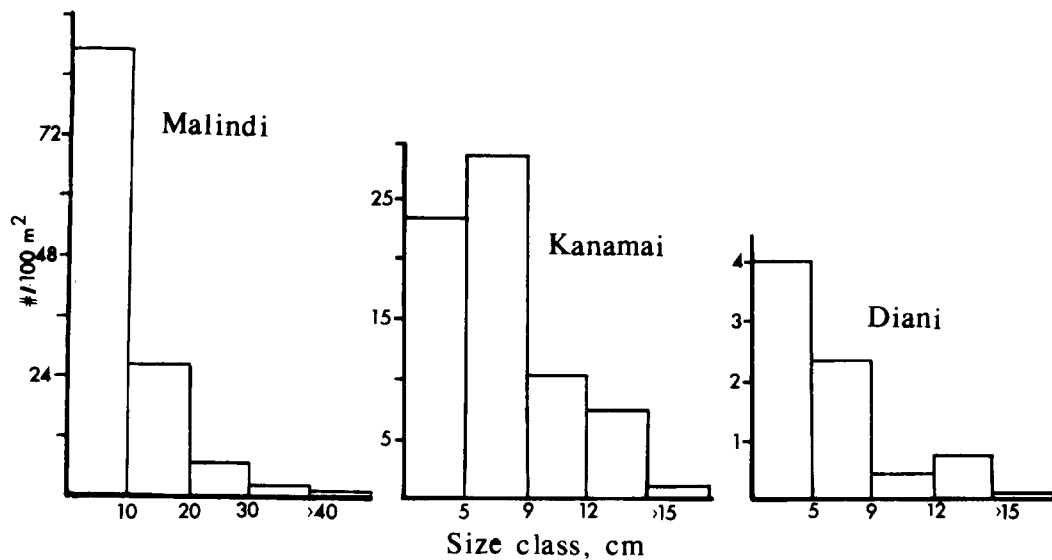

Fig. 2. Fish size frequency histograms observed at the three study sites. Note the different scales.

Table 1. *Echinometra mathaei* population and community structure data on the inner fringing reef lagoons at the Malindi Marine National Park (MMNP), Kanamai and Diani. Variance is measured as standard deviations, sample sizes are included in parenthesis and statistical significance at the end of the row (NS = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). t-tests used on populations of two and F-tests on populations greater than two.

	MMNP 1986	Kanamai 1985	Diani 1970[a]	Diani 1985
E. mathaei				
Density, #/m^2	0.0 (43)	1.2 ± 2.0 (105)	5.3 (90)	14.2 ± 15.8 (90)**
Diameter, mm	–	37.1 ± 8.0 (39)	32.7 (151)	40.8 ± 7.4 (144)
Biomass g/m^2	–	33	110	534
Burrowed, %	–	74.7 ± 32.8 (68)	–	7.3 ± 7.2 (52) ***
Diadema sp. #/m^2	0.0 (43)	0.3 (105)	–	0.0 (90)
Coral cover, %	25.1 ± 30.0 (43)	5.5 ± 13.6 (105)	–	<1 (90) ***
Fish Density,				
#/100 m^2, n = 4	124.3 ± 40.1	69.8 ± 27.0	–	7.5 ± 4.7 ***

[a]Data from Khamala (1971).
[b]Diani 1970 and 1985 significantly different ($p < 0.01$).

nication), the Park's boatman who has worked within MMNP since its inception, informed us that during the first year after the Park's inception *Diadema* were observed within the lagoon but henceforth have not been observed. Shimoni Marine National Park also has low sea urchin densities within lagoonal sites. During a 1.2 hour dive within a lagoon we counted no *E. mathaei* and 4 *Diadema*. The remote areas of northern Kenya have low sea urchin densities within lagoonal areas but reef structure and physical factors differ somewhat and comparisons may be less reliable. Kanamai's lagoon has an intermediate sea urchin density with a large fraction of the urchin biomass attributed to *Diadema*. Coral cover, fish density and fish sizes are also intermediate. Observations in Tiwi, Mombasa's North Coast, Kikambala and Vipingo suggest similar community structure and intermediate levels of fishing exploitation. Diani has the highest sea urchin density of almost exclusively *E. mathaei,* the lowest coral cover and low fish densities and small fish sizes. *Diadema* is found within this area but at densities (0.033 #/m^2, n=90) an order of magnitude lower than Kanamai. Additionally, *E. mathaei* densities, sizes and biomass in Diani have increased within the last 15 years (Muthiga & McClanahan, 1987). Most of the *E. mathaei* in Diani's lagoon are living outside burrows compared to Kanamai. No other site visited within Kenya has similarly high sea urchin densities.

Ecological characteristics of studied sea urchins (Table 2) support the hypothesis that within the lagoon the three species are ecologically separated by occupying different size burrows or crevices and have morphological and behavioral adaptations which correspond to predator avoidance strategies (Table 2) . The species form a continuum in which characteristics of spine length, crevice habitation and sociality enable species to inhabit various microspatial locations within the reef. *E. mathaei* is the smallest species, has the shortest spines and lives solitarily in burrows or crevices. *D. savignyi* has an intermediate test and spine length, is frequently found in crevices or small social groups and occasionally in the open within social groups. *D. setosum* is the largest species, has the longest spines and is most frequently found in social groups outside crevices. In Diani, the low density of *Diadema* and high density of *E. mathaei* living outside burrows suggest an ecological release of *E. mathaei* from predators and the above described niche.

Data collected on the reef edge appear more variable and more difficult to interpret. The general pattern of increasing biomass of *E. mathaei* follows the above pattern. Yet, there was no significant difference in fish catch/effort between the two studied sites. Observations suggest that within the two fished sites fish sizes and densities may not be very different but they are far less than the MMNP reef edge. Additionally, there were no significant increases in *E. mathaei* densities between Khamala's (1971) data and our 1985 data. High variability on the outer reef edge and subsequent within site differences between transects (F-test; $p < 0.05$) suggest that differences may be due to sampling different locations. *E. mathaei* is present on most reef edges within Kenya but densities are variable and more difficult to interpret in terms of the fishing intensity hypothesis.

Table 2. Ecological characteristics of the three dominant species of sea urchins inhabiting hard substrate at Kanamai. Comparisons between species for all variables are statistically significant (F-test; $p < 0.01$, n = 55).

	D. setosum	*D. savignyi*	*E. mathaei*
Spine length, cm	15.6 ± 2.9	11.3 ± 2.2	2.0 ± 0.2
Crevice or burrow width[a], cm	28.4 ± 4.6	19.8 ± 11.4	8.8 ± 9.6
Living in Crevices, %	12.7	51	80
Group size	3.0 ± 2.1	1.4 ± 0.8	1.0 ± 0.0
In groups, %	78	22	0

[a]Those individuals in areas with no crevices or crevices greater than 30 cm wide were considered in the open but 30 cm was used in the calculations.
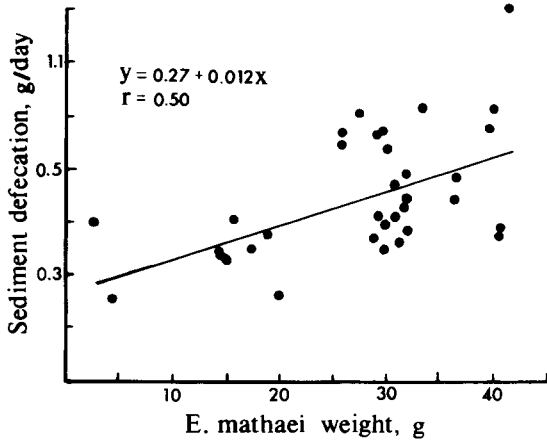
Fig. 3. Echinometra mathaei sediment defecated during 24 hours as a function of the wet weight of the individual.

The sediment defecation study indicates that a large quantity of sediment is defecated by *E. mathaei* and is proportional to the urchin's wet weight (Fig. 3). Bioerosion by *E. mathaei* in the Diani lagoon using stated assumptions is estimated at 3.8 kg/m²/yr.

Discussion

Data and our observations support general conclusions in the Caribbean about increases in sea urchin densities caused by competitor (Hay, 1984) and predator (Carpenter, 1984) reductions through fishing activities, although details may differ. Specifically,

it appears that *Echinometra* is the dominant Kenyan genus and may be the top competitor. In the Caribbean *D. antillarum* is the most abundant species (Hay, 1984) and the top competitor has not been determined (Williams, 1981). Additionally, the role of *D. antillarum* in cropping algae is emphasized within the Caribbean (Sammarco, 1982; Hay & Taylor, 1985; Carpenter, 1986) whereas we emphasize the negative consequences of high *Echinometra* bioerosion rates.

It can be argued that observed community structure differences within the lagoon result from intrinsic site differences rather than fishing activities and that observed differences are a result of pseudoreplication (Hurlbert, 1984). Yet, Stewart-Oaten *et al.* (1986) suggest that if a control and impact site diverge over time after the initiation of the impact than site differences can be attributed to the impact. In essence we have information on MMNP which can be seen as a control and Diani which can be seen as a fishing experiment site, but we lack information in Diani on prefishing conditions. Still, in Malindi we have information on fishing and post fishing conditions. Prior to the removal of fishing in MMNP sea urchins were observed and subsequently disappeared. Whereas in Diani where fishing has consistently occurred sea urchins have increased. This is supportive of the suggested hypothesis. Alternative explanations might include stochastic differences in sea urchin, fish and coral recruitment, the spread of a disease or physical differences between sites. Yet, since all sites are exposed to the same current system by relatively short distances the probability that

Table 3. Echinometra mathaei population variables, coral cover and fish catch/effort data from the outer fringing reef edges. See Table 1 for notation.

	MMNP 1986	Kanamai 1985	Diani 1970[a]	Diani 1985
E. mathaei				
Density, #/m²	0.6 ± 1.0 (76)	0.5 ± 1.3 (75)	2.6 (90)	1.7 ± 1.0 (60) *
Test diameter, mm	18.1 ± 0.7 (120)	42.5 ± 7.1 (60)	43.7 (156)	31.2 ± 6.7 (68) **
Biomass, g/m²	4.0	20.1	116	31.1
Burrowed, %	100 (30)	100 (75)	–	100 (60)
Coral cover, %	<1 (30)	3.6 ± 8.4 (75)	–	<1 (60)
Fish Catch/effort, kg/hr	–	1.5 ± 0.6 (10)	–	1.7 ± 0.7 (13)NS

[a]Data from Khamala 1971.

these factors correspond to observations on fishing intensity seem unlikely.

The ultimate intention of this study was to develop testable hypotheses about the effects of fishing on coral reef community structure and not to make conclusions. Based on our data, observations and published literature from the Caribbean we suggest the following for coral reefs within the western Indo-Pacific: i) that fishing results in sea urchin predator and competitor reductions resulting in ecological release of unutilized sea urchin species, ii) that coral cover and calcium carbonate accretion are reduced in sea urchin dominated communities compared to fish dominated communities, iii) bioerosion is greater in sea urchin dominated versus fish dominated communities and especially in *Echinometra* dominated communities, iv) predator reductions cause competitive exclusion in closely related guilds of unfished organisms and subsequently a decrease in coral reef species diversity and v) that *E. mathaei* is the top competitor in the above mentioned sea urchin guild.

Prior studies of Hay (1984) and Carpenter (1984) support the first hypothesis with respect to *D. antillarum* within the Caribbean. Hay and Taylor's (1985) data suggest that in the absence of predators, sea urchins may be able to outcompete herbivorous fish. Studies on sea urchin and fish grazing in the Caribbean suggest that at high densities sea urchins are more destructive to coral recruits (Sammarco, 1980) than fish (Birkeland, 1977). *D. antillarum* feed on live coral (Bak & van Eys, 1975) but use an optimal foraging strategy choosing fleshy algae over coral (Carpenter, 1981). Yet, at high sea urchin densities competition for food may cause sea urchins to feed more frequently on living coral. In general sea urchins appear to be less discriminate feeders than fish (Ogden & Lobel, 1978) and ingest a large quantity of sediment as part of their feeding activities. Odgen (1977) estimates that sea urchin bioerosion is an order of magnitude greater than parrot-fish bioerosion. His sea urchin estimates are close to our Diani reef measurements and are considerably higher than coral reef average calcium carbonate accretion rates of 1.0 to 1.2 kg m^{-2} yr^{-1} (Smith, 1983). This suggests a net loss of calcium carbonate substrate in sea urchin dominated reefs. However, like fish, sea urchins

crop algae and keep algae from overshadowing and outcompeting slower growing corals (Birkeland, 1977; Lewis, 1986). It should be pointed out that sea urchin removal experiments (Ogden et al., 1973; Sammarco, 1982; Hay & Taylor, 1985) do not necessarily test hypotheses 2 and 3 as these sites may already have reduced fish biomass due to fishing (Hay, 1984) and although sea urchin removal may increase fish grazing (Hay & Taylor, 1985) it probably does not return fish biomass to prefishing conditions and cannot be considered a natural (unfished) fish dominated community. Examples of the keystone effect in maintaining species diversity caused by carnivorous fish has yet to be documented for coral reef fish or sea urchin guilds but remains a likely mechanism contributing to coral reef diversity (Paine, 1966). Grunbaum et al. (1978) show that *Echinometra* has strong intraspecific competitive interactions. At high sea urchin densities territorial behavior may give it a competitive advantage over the more social *Diadema*.

We suggest that the Diani site represents an ecological community approaching a new equilibrium caused by fishing activities. *E. mathaei* feeding and spine abrasion activities appear to have reduced a community of high coral cover, calcium carbonate accretion, and species diversity to one of high calcium carbonate degradation, a reduction in topographic complexity, species diversity and ultimately the coral reef's utilizable fisheries productivity. *E. mathaei* conversion of hard to soft substrate may self-limit itself unless it is able to thrive on seagrass associated with soft substrate.

The degree to which this model applies to the outer reef edge is of great interest as the reef edge is the shore's protective barrier from the physical forces of waves and currents. We suggest that wave energy will limit *Echinometra* populations to some extent but predator reductions will also result in population increases, albeit smaller than within lagoons. A loss of calcium carbonate accretion and subsequent reductions in reef height could have a drastic effect on lagoonal beaches and associated economic investments. It is therefore urgent that these hypotheses receive testing within lagoon and reef edge sites throughout the Indo-Pacific.

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