Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs

Timothy R. McClanahan [1] and Nyawira A. Muthiga [2]

[1]*Friends World College, East African Centre, Machakos, Kenya;* [1]*Center for Wetlands, University of Florida, Gainesville, Florida, U.S.A.;* [2]*Kenya Marine and Fisheries Research Institute, Mombasa, Kenya*

Abstract: Rates and factors affecting predation on the omnivorous burrowing sea urchin *Echinometra mathaei* (de Blainville) were studied on four Kenyan coral reefs, two with a history of heavy fishing and two protected from fishing. Three hypotheses concerning predation were tested; these were that predation should be lower (1) on fished reefs compared to unfished reefs, (2) in shallower water and therefore between sites within reefs as a function of water depth and (3) with increasing sea urchin body size. Results support the above hypotheses with fishing being the most important variable followed by depth and individual body size. Finfish accounted for 90%, asteroids 5% and gastropods 5% of the predation which suggests that the removal of finfish is more important than shelling in restricting *E. mathaei* populations. Depth was less important within fished sites than the protected site where very small differences in depth corresponded to increases in predation. Reef flat sites consistently had the lowest predation rates which accounts for *E. mathaei* natural (unfished) distribution on reef flats. Fishing pressure leads to a reduction in predators which allows *E. mathaei* to increase its density and expand its distribution to deeper areas. As *E. mathaei* is a major bioeroder of coral reefs we suggest that bioerosion is higher and at greater depths on heavily fished reefs.

Key words: Coral reef; *Echinometra*; Intertidal benthic ecology; Overfishing; Predation; Sea urchin; Shelling

INTRODUCTION

Predation is often assumed to be an important process affecting the organization of coral reef ecosystems (Connell, 1978), but little experimental work has been completed to support this hypothesis (Sih et al., 1985). Additionally, studies of herbivory have been more common (Ogden et al., 1973; Sammarco et al., 1974a; Carpenter, 1981; Hay et al., 1983; Hay, 1984a,b) than carnivory on coral reefs (Keller, 1983), apart from coral predation studies (Bak & van Eys, 1975; Glynn et al., 1979; Sammarco, 1980; Wellington, 1982; Moran, 1986). In this study, we present an experimental method for measuring relative predation rates using sea urchins and test some commonly stated hypotheses concerning predation.

The primary concern of this study was to determine the causes of observed sea urchin population increases on Kenyan coral reefs over time (Muthiga & McClanahan, 1987)

Correspondence address: T.R. McClanahan, Center for Wetlands, University of Florida, Gainesville, FL 32611, U.S.A.

and between reefs of differing fishing pressure (McClanahan & Muthiga, 1988). As in the Caribbean (Carpenter, 1984; Hay, 1984a) and temperate areas (Estes et al., 1978; Wharton & Mann, 1981), we hypothesized that sea urchin population increases are caused by predator reductions due to overfishing. This hypothesis is based on observed changes in community structure as a function of subjective observations on fishing intensity (McClanahan & Muthiga, 1988). Yet, unless experimentally tested other alternative factors which are known to affect marine invertebrate distribution, such as differential recruitment (Birkeland, 1982; Ebert, 1983), competition (Williams, 1981; Hay, 1984a; Hay & Taylor, 1985), disease (Bak et al., 1984; Lessios et al., 1984; Miller, 1985), water flow, food availability (Russo, 1977) and surf intensity (Ebert, 1983), cannot be discounted.

Research focused on *Echinometra mathaei* (de Blainville), which is a ubiquitous burrowing omnivore (Herring, 1972; Lawrence, 1975) distributed throughout the Indo–Pacific (Clark, 1976; Ebert, 1983). *E. mathaei* distribution is generally restricted to shallow waters (0.5–1.5 m above datum in Kenya) on reef flats (Khamala, 1971), the top of coral outcrops in reef lagoons (Russo, 1980) and back reef rocky shores (Ruwa, 1984). Yet, in some heavily fished reefs their distribution expands into deeper reef lagoon areas (Muthiga & McClanahan, 1987; McClanahan & Muthiga, 1988).

Based on our previous studies and general factors, such as body size and water depth, believed to affect predation (Connell, 1972) we tested the following three hypotheses about predation on sea urchins. These were that (1) predation rates on sea urchins should be lower on the heavily fished versus unfished reefs, (2) predation on sea urchins should increase with water depth and therefore should differ between sites within reefs as a function of depth and (3) predation should decrease with increasing individual body size.

STUDY SITES AND METHODS

Four locations along Kenya's coast were chosen for their similarity in reef structure and differences in levels of exploitation (Fig. 1). Two protected sites included the Malindi Marine National Park's (MNP) North Reef and Watamu MNP "Coral Gardens", which have been protected since 1968 from fishing and shelling activities, Kanamai which adjoins a residential and recreational area with a few small tourist hotels and Diani a highly developed tourist beach. From our subjective observations over the previous 10 yr, Kanamai and Diani beach are heavily fished but until recently Diani more intensely than Kanamai. Some additional experimental work was done in Vipingo, which is more sparsely inhabited than the other two fished sites and therefore, from our observations, less heavily fished. Fishing techniques used within unprotected sites include seining, spear-fishing, line-fishing and traps.

Visual fish censuses (500 m², $n = 6 \cdot \text{site}^{-1}$) were undertaken within the reef lagoons during low tides. A 100-m line transect was established by snorkelling without fins

within the shallow (< 2.5 m) coral and hard substrate areas. A distance of 5 m was measured from the line and the observer maintained this distance while counting all observable fish. At a random interval, the 5 m distance was checked to maintain its accuracy. Movements while establishing the line transect and snorkelling were slow
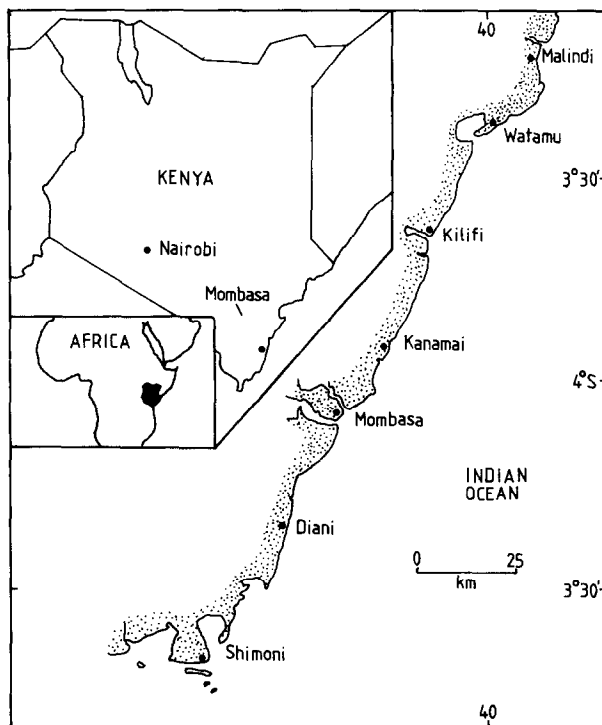

Fig. 1. Map of study site locations along the Kenyan coast.

($\approx$ 20–30 min · transect^{-1}) in order not to disturb the fish. Water clarity was never < 8 m. Total fish numbers and potential sea urchin predator families including Labridae, Balistidae, Diodontidae and Lagocephalidae were counted. The Balistidae, Lago- cephalidae and Diodontidae are often cryptic hiding within burrows and crevices. Undersampling may have occurred but the error is probably greater within the Parks where increased topographic complexity allows more hiding places. No research on sea urchin predators has been undertaken within this region and therefore these censuses are only indicative of potential predators and predation rates.

All sites except Watamu MNP are similar in terms of waves and current action. Sampling was undertaken during the north east monsoons when wave energy and current speeds are low (McClanahan, 1988). Descriptions of these locations and Kenya's coast are included in Khamala (1971), Hamilton & Brakel (1984), Crame (1986) and McClanahan (1988). Briefly, all reefs except Watamu MNP have a seaward

reef edge (RE) exposed to waves at low tide, a reef flat (RF) exposed during most neap and all spring tides and a shallow reef lagoon (RL). The Watamu reef flat is lower (<0.3 m above datum) than the other sites, rarely exposed except on extreme low tides, and experiences greater wave and current activity. Tides in Kenya have a 4-m tidal range and a 3.2-m mean spring tide range (Brakel, 1980).

Predation was studied by tethering intermediate size *Echinometra mathaei* (Table I) to nylon transect lines using a tagging method modified from Ebert (1965). Sea urchins were perforated through the ventral and dorsal sections of the test with a hypodermic needle and threaded with monofilament line (0.5 mm). Nine to 11 sea urchins were attached at 2-m intervals onto 18–22-m transect lines. Within each of the reef edge, reef flat, and reef lagoon sites three transect lines were laid perpendicular to shore (Table I) except in Watamu MNP where only the reef lagoon site was studied due to rough conditions on the reef flat and edge sites. Transects within reef edge sites were placed below the surf zone ($<$MLWS) to avoid the effects of waves (Table I). All transects were laid within similar hard substrate or coral dominated areas, but unavoidably some sections of the lines passed over seagrass and soft substrate.

Since *E. mathaei* were small and at low densities within Park locations (McClanahan & Muthiga, 1988) sea urchins were collected outside the Parks and transported (<1.5 h) in buckets with a portable aerator. This reduced the probability of differences in test sizes occurring for comparisons between Parks and unprotected sites. The test width of each experimental individual was measured with calipers to the nearest millimeter, depth and time were taken, and the depth of each individual calculated in relation to datum (Kenya Ports Authority, 1986). Transects were visited every 24 h for a 3-day period. Collections of randomly selected *E. mathaei* were made within Malindi, Kanamai and Diani reef flats and average test sizes measured [(long + short axis) $\cdot 2^{-1}$] with calipers to the nearest 0.5 mm for test size frequency comparisons.

The above experimental procedure was repeated twice at each location between September 1986 and April 1988 during spring tides except at the Malindi MNP reef edge where nine transect lines were laid only once and Watamu MNP where the reef lagoon was studied only once. During the first sampling period observations on predation and test condition were made in order to determine predators and their effect on sea urchin tests. Observed predators frequently included various species of triggerfish *Balistaphus undulatus* (Mungo Park), *Rhinecanthus aculeatus* (Linnaeus) and *Rhinecanthus rectangulus* Schneider and occasionally the gastropod *Cypraecassis rufa* (Linnaeus) and the asteroids *Culcita schmideliana* (Retzius) and *Protoreaster lincki* (de Blainville). During the interval between the two sampling periods we undertook aquarium trials on the three invertebrate species. Individuals ($n = 4$) were placed within separate salt-water aquariums for periods of 5–19 days together with the sea urchins *Echinometra mathaei*, *Tripneustes gratilla* (Linnaeus) and *Diadema setosum* (Leske) (4 ind $\cdot$ species^{-1}) to determine their prey preference, predation rates and sea urchin test condition after predation. Based on field and laboratory observation we were able to determine three predator types based on test condition. These categories were then used within the second

TABLE I

Height in relation to datum of the sampling sites ($\bar{x} \pm$ SEM), sea urchin test size ($\bar{x} \pm$ SEM) and total sea urchin and transect sample sizes used in the data analysis on reef edges (RE), reef flats (RF) and reef lagoons (RL) for the three locations.

| | Unfished | | | | Fished | | | | | |
| | Malindi | | | Watamu | Kanamai | | | Diani | | |
	RE	RF	RL	RL	RE	RF	RL	RE	RF	RL
Height (m)	-1.5	0.6	-1.17	-1.13	-0.16	0.97	1.06	-0.32	0.3	0.07
	±0.14	±0.01	±0.07	±0.03	±0.04	±0.01	±0.01	±0.04	±0.03	±0.02
Test size (mm)	34.9	34.8	35.5	50.74	36.3	38.6	38.5	40.0	40.4	40.8
	±0.57	±0.51	±0.44	±1.01	±0.50	±0.67	±0.73	±0.82	±0.68	±0.81
Total (n)	93	60	58	27	58	43	50	34	47	58
Transect (n)	9	6	6	3	6	4	4	4	4	5

sampling interval. The categories used were: (1) missing tests and broken tests without the Aristotle's lantern indicated predation by finfish; (2) tests with a single perforation in the test, periproct or peristome indicated predation by a gastropod, probably *Cypraecassis rufa*; and (3) an intact bleached test missing spines or missing the Aristotle's lantern but with an unbroken test indicated predation by an asteroid probably *Culcita schmideliana*. Ninety-five percent of the observations fit within these categories and there were no indications of other predator types such as crabs or shorebirds. The additional mortality, ($<5\%$) may have been caused by tagging or other undetermined factors. Transect lines removed by fishermen and deaths due to undetermined causes were removed from the data analysis.

A series of experiments were designed to determine the effects of tagging, leakage of coelomic fluids, removing sea urchins from their burrows and to test the validity of the assumption that missing tests were a result of finfish predation. To determine the effect of tagging on mortality, two field and one laboratory experiment were undertaken. Within the Kanamai and Vipingo lagoons sea urchins were tagged ($n = 40$) and placed in a double-walled wire mesh (2.5 cm) predator exclusion cage along with additional untagged control sea urchins. The lab experiment consisted of transporting, tagging and placing individuals within saltwater aquariums along with untagged controls. Individuals were visited every day for 3 days, body condition and mortality were noted. Two experiments were undertaken to determine if coelomic fluid leakage influenced predation rates. After tagging, sea urchins ($n = 50$) were kept for 2 months within aquariums (while fed on *Ulva*) and the Vipingo reef lagoon to observe repair of the damaged tests. After 3–4 days, the holes created from the hypodermic needle were covered with a membranous tissue but the calcium carbonate tests never repaired during the 2-month period. Two experiments in Vipingo compared predation on individuals with repaired tests (>4 days after tagging) and individuals tagged at the initiation of the experiment. One group was kept within aquariums for 14 days and the other within a protected area of the Vipingo lagoon for 5 days. Repaired ($n = 30$) and recently tagged sea urchins ($n = 30$) were placed on alternating transect lines at >10-m intervals. An additional group ($n = 30$) was removed from their burrows, tagged and replaced within their burrows. All groups were visited every 24 h for 3 days. Due to the difficulty of obtaining live, healthy fish predators for aquarium experiments the final experiment consisted of observations on tagged sea urchins ($n = 40$) within the Malindi MNP lagoon using scuba for 1 h and 45 min. Species feeding on these sea urchins and the sea urchin's test condition were noted after predation. The site was visited the following day to determine the presence or absence of sea urchin tests after predation.

In the data analysis, average survival rates were calculated for each transect, site and location. The last surviving day of each experimental *E. mathaei* was recorded and used as the unit of measure. The total length of the experiment was 3 days and therefore 100% survival would produce a mean of 3 days whereas 100% mortality during the 1st day would produce a mean survival rate of 0 days. Predation was then calculated as the total length of the experiment (3 days) minus the survival rate. Mann–Whitney U tests or

Kruskal–Wallis tests were used to test for differences in survival within and between transects, sites and reefs. Survival rates were plotted and regressed against *E. mathaei* densities collected by McClanahan & Muthiga (1988) and this study where densities were calculated from 40–120 1-m^2 quadrats established within the site locations. Additionally, survival rates were correlated with depth in relation to datum and test size.

RESULTS

Parks had the greatest aggregate fish, wrass and triggerfish densities followed by Kanamai and lastly Diani (Table II). Of the potential sea urchin predators, triggerfish differed the most, being nearly 20 times more dense in Parks ($0.58 \pm 0.12 \cdot 100$ m^{-2}, $\pm$ SEM, $n = 12$) than unprotected areas ($0.03 \pm 0.02 \cdot 100$ m^{-2}; Mann–Whitney U test,

TABLE II

Fish densities per 100 m^2 ($\bar{x} \pm$ SEM) from transects (500 m^2, $n = 6$) within the four lagoons. Kruskal–Wallis comparison, NS = not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Family	Malindi	Watamu	Kanamai	Diani	Kruskal–Wallis test
Labridae	10.63 ± 2.35	8.63 ± 1.54	8.66 ± 2.65	3.57 ± 0.88	*
Balistidae	0.9 ± 0.13	0.27 ± 0.07	0.03 ± 0.03	0.03 ± 0.03	***
Diodontidae	0.0 ± 0.0	0.03 ± 0.03	0.03 ± 0.03	0.0 ± 0.0	NS
Lagocephalidae	0.0 ± 0.0	0.07 ± 0.07	0.03 ± 0.03	0.03 ± 0.03	NS
Others[1]	89.3 ± 13.8	77.5 ± 20.0	21.1 ± 5.0	10.23 ± 2.41	***
Total	101.8 ± 14.9	84.9 ± 21.1	29.8 ± 5.8	19.73 ± 8.4	**

[1] Principally includes the pomacentridae, chaetodontidae, scaridae, lutjanidae, siganidae and holocentridae.

$P < 0.001$). Wrasses were also denser ($P < 0.01$) within Parks ($9.6 \pm 1.4 \cdot 100$ m^{-2}, $\bar{x} \pm$ SEM) compared to unprotected areas ($6.11 \pm 1.5 \cdot 100$ m^{-2}) but differences were not as great as triggerfish. Fish sizes also follow the above pattern (McClanahan & Muthiga, 1988).

TABLE III

The percentage survival and sample sizes (in brackets) for tagged and untagged control sea urchins excluded from predators for a 3-day period. Two field experiments and one lab experiment are included. NS = not significant.

Experiment	Tagged	Controls	P
Field exp. 1	97.5 (40)	100 (30)	NS
Field exp. 2	100 (40)	100 (40)	NS
Aquarium exp.	100 (46)	100 (49)	NS
Total	99.2 (126)	100 (119)	NS

Tagging appears to have little effect on sea urchin survival (Table III). One of the 126 tagged animals died during the 3-day experiment. Additionally, the leakage of coelomic fluid appeared unimportant in affecting predation (Table IV) but animals restricted

TABLE IV

Results of predation experiments within the Vipingo lagoon to determine the effect of coelomic fluid leakage and burrow habitation on predation rates. Results are the survival rates ($\bar{x} \pm$ SEM, $n = 30$) in days for a 3-day period for sea urchins with damaged and repaired tests. One group's tests were repaired while in the field for 5 days and the other while in aquariums for 14 days. NS = not significant.

	Repaired	Damaged	P
Field	0.70 ± 0.22	0.73 ± 0.22	NS
Aquarium	0.17 ± 0.08	0.73 ± 0.20	NS[1]
Burrowed	–	2.70 ± 0.14[2]	

[1] $P = 0.56$. [2] Mann–Whitney U test comparison between burrowed and unburrowed sea urchins significant at $P < 0.001$.

outside burrows had significantly ($P < 0.0001$) lower survival than those inhabiting burrows. During the 1-h-and-45-min dive within the Malindi MNP lagoon predation was observed on 11 of the 40 experimental animals. Ten were eaten by five *Balistaphus undulatus* individuals and one by a large (30–40 cm) wrass (*Halichores* spp.). The following day all tests of eaten sea urchins were missing, as well as 26 of the other experimental individuals. We observed that *Balistaphus undulatus* did not always remove the tests from the transect lines but smaller wrasses often picked apart the remaining carcasses.

TABLE V

Average *Echinometra mathaei* survival rate in days ($\bar{x} \pm$ SEM) for a 3-day period within the three locations, sites and totals. Kruskal–Wallis test of significance between sites and locations. NS = not significant, $* = P < 0.05$, $** = P < 0.01$, $*** = P < 0.001$.

	Reef edge	Reef flat	Reef lagoon	Location totals	Kruskal–Wallis
Malindi	0.13 ± 0.04	0.95 ± 0.12	0.09 ± 0.06	0.35 ± 0.05	$30.1***$
Watamu	–	–	0.48 ± 0.15	0.48 ± 0.15	–
Kanamai	1.40 ± 0.17	1.84 ± 0.20	1.78 ± 0.20	1.64 ± 0.11	3.1 NS
Diani	1.12 ± 0.08	1.83 ± 0.20	2.41 ± 0.15	1.90 ± 0.11	$15.6***$
Site totals	0.71 ± 0.08	1.48 ± 0.10	1.28 ± 0.10	1.13 ± 0.06	$26.0***$
Kruskal–Wallis	$37.7***$	$17.6***$	$71.6***$	$120.9***$	

Survival rates within the three locations and sites (Table V) show highly significant differences for most comparisons. The Malindi and Watamu MNP had the highest predation rate which can almost exclusively be attributed to finfish (Table VI). Predation within the Malindi MNP reef edge and reef lagoon were similarly high with the

lowest rates on the reef flat. The average survival rate within the lagoon by this method was 2 h and 10 min and by the direct observation method 3 h and 10 min which affirms the accuracy of the experimental method. Intersite differences in predation can be attributed to depth (Fig. 2a; Tables VIII, IX) as small increases in depth corresponded to increases in predation.
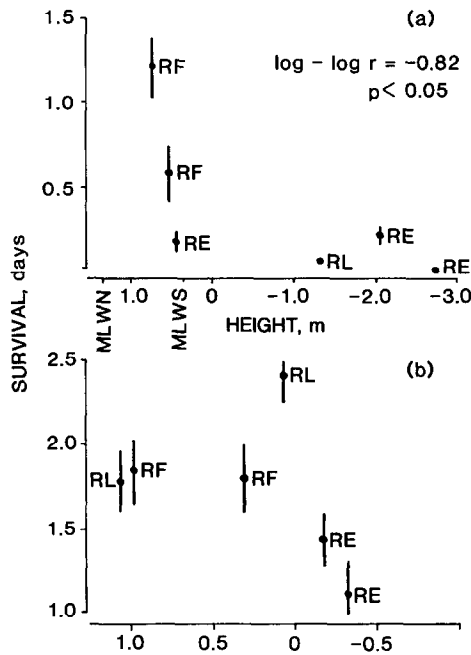

Fig. 2. Predation rates as a function of reef heights in relation to datum within the (a) Malindi Marine National Park and (b) the fished Kanamai and Diani sites for reef flat (RF), reef edge (RE) and reef lagoons (RL). Bars represent one standard error. MLWN = mean low water neap and MLWS = mean low water spring.

Kanamai and Diani (fished reefs) had lower predation rates than Parks within all three sites. Predation within reef edge and reef flats were similar in Kanamai and Diani but reef lagoons differed with predation being lowest within the Diani reef lagoon and subsequently the whole reef. Predation in relation to depth, although significant in fished reefs (Fig. 2b; Tables VIII, IX), was less important than within Malindi. Predation was largely due to finfish within fished sites but there was an increase in the relative importance of invertebrate predators (Table VI). This can probably be attributed to the gastropod *Cypraecassis rufa* and the asteroid *Culcita schmideliana* which were observed consuming experimental sea urchins.

The aquarium trials (Table VII) indicate that *Cypraecassis rufa* is a more effective sea urchin predator than the asteroids but both have low predation rates. *Protoreaster lincki* did not feed on any individuals within the aquariums.

TABLE VI

Mortality and predator types determined during the second sampling interval by test condition for the three sites, locations and totals. Missing tests are assumed to be predated on by fish. Undetermined causes are deaths occurring by means other than predation. Numbers in parentheses are percentages where undetermined and total eaten categories are percentages of the total sample size and other classifications are percentages of the total eaten category. See Table I for notation.

	Malindi				Watamu	Kanamai			
	RE	RF	RL	Total	RL	RE	RF	RL	Total
Sample size	103	30	30	163	27	29	30	30	89
Undetermined	0(0)	1(3.3)	0(0)	1(0.6)	1(3.7)	0(0)	6(20)	0(0)	6(6.7)
Total eaten	103(100)	29(96.7)	30(100)	162(99.4)	25(92.6)	15(52)	11(56.7)	16(53.3)	48(53.9)
Missing test	103(100)	26(89.7)	30(100)	159(98.1)	15(60.0)	10(66.7)	2(11.8)	4(25.0)	16(33.3)
Observed fish	0(0)	1(3.4)	0(0)	1(0.6)	8(32.0)	4(27.7)	2(11.8)	7(43.8)	13(27.1)
Total fish	103(100)	27(93.1)	30(100)	160(98.8)	23(92)	14(93.3)	4(23.5)	11(68.8)	29(60.4)
Gastropoda	0(0)	0(0)	0(0)	0(0)	0(0)	1(6.7)	7(41.2)	1(0)	9(18.8)
Asteroidea	0(0)	2(6.9)	0(0)	2(1.2)	2(8.0)	0(0)	0(0)	4(25.0)	4(18.2)
Total invert.	0(0)	2(6.9)	0(0)	2(1.2)	2(8.0)	1(6.7)	7(41.2)	5(31.3)	13(27.1)

Variability within sites (Table X) suggests that differences in transect placement within sites and times were sometimes significant within reef edges and flats. Predation appeared to be particularly patchy on reef edges. However, differences within sites were not as great as differences between sites and locations. Predation appears to be lower if individuals were able to find crevices, in seagrass beds compared to coral outcrop areas, and in areas with greater surf activity.

The relationship between test size and survival, although significant for some sites, locations and totals, appears to be the least important of the measured variables (Tables VIII, IX) and, at most, explains only 6% of the total variation. The experimental design did not select for high variability in test sizes and therefore one would not expect strong correlations. Test size appears to be most important within reef lagoons. *E. mathaei* test size frequency histograms (Fig. 3) of individuals inhabiting reef flats indicate that the unprotected reef flats have larger test sizes than the Malindi MNP. Additionally, the Malindi *E. mathaei* test size distribution is positively skewed suggesting that predation

TABLE VII

Daily predation rates ($\bar{x} \pm$ SEM) for the gastropod *Cypraecassis rufa* ($n = 4$) and the asteroid *Culcita schmideliana* ($n = 4$) on three different sea urchin species (*Echinometra mathaei*, *Tripneustes gratilla* and *Diadema setosum*) cohabiting aquariums ($n = 4$ ind·species^{-1}).

Prey	*Cypraecassis rufa*	*Culcita schmideliana*
E. mathaei	0.29 ± 0.12	0.07 ± 0.05
T. gratilla	0.35 ± 0.17	0.08 ± 0.08
D. setosum	0.0 ± 0.0	0.0 ± 0.0
Total	0.55 ± 0.21	0.14 ± 0.22

	Diani				Site total		
RE	RF	RL	Total	RE	RF	RL	Total
29	31	28	88	161	91	115	367
5(17.2)	3(9.7)	0(0)	8(9.1)	5(3.1)	10(11)	1(0.9)	15(4.1)
22(75.9)	18(58.1)	11(39.3)	51(58.0)	140(87.0)	64(70.3)	82(71.3)	286(77.9)
7(31.8)	15(83.3)	10(90.9)	32(62.7)	120(85.7)	43(67.2)	59(72.0)	222(77.6)
8(36.4)	2(11.1)	0(0)	10(19.6)	12(8.6)	5(7.8)	15(18.3)	32(11.2)
15(68.2)	17(94.4)	10(90.9)	42(82.4)	132(94.3)	48(75.0)	74(90.2)	254(88.8)
3(13.6)	0(0)	0(0)	3(5.9)	4(2.9)	7(10.9)	1(1.2)	12(4.2)
4(8.3)	1(5.6)	1(9.0)	6(11.8)	4(2.9)	3(1.6)	7(8.5)	14(4.9)
7(31.8)	1(5.6)	1(9.0)	9(17.6)	8(5.7)	10(15.6)	9(10.9)	26(9.1)

is a dominant force affecting *E. mathaei* body sizes. Finally, predation rates within study sites appear to be a good predictor of *E. mathaei* densities regardless of sites or locations (Fig. 4).

A complicating factor must be considered due to sampling variation between reefs. Although we suggest that differences between Parks and fished reefs are due to fishing activities, the Park's aggregate sampling was at a slightly greater depth (Table I) than fished reefs which could account for differences. Yet, if one considers the Malindi reef flat data collected at 0.6 m above datum, which had a survival rate of 0.95 ± 0.12 ($\pm$ SEM) days ($n = 60$), one can see that this predation rate is higher than any site within fished reefs regardless of depth.

DISCUSSION

The method appears to be useful for testing hypotheses about predation and data is supportive of stated hypotheses. The tagging technique as concluded by Ebert (1965) appears to have little detrimental effect on the sea urchins. Yet, predation rates are relative because the technique restricts individuals outside burrows which appears to be a sea urchin predator avoidance strategy (Bernstein et al., 1981; Carpenter, 1984; McClanahan, 1988). On Kenyan reefs *Echinometra mathaei* are found both in and outside burrows and this appears to be a function of their density and predation intensity on the various reefs (McClanahan & Muthiga, 1988). Our personal observation is that triggerfish and *Cypraecassis rufa* are capable of feeding on sea urchins within burrows but not as effectively as when they are outside burrows. Ninety-five percent of the mortality could be attributed to predators but the additional undetermined

TABLE VIII

Correlation coefficients and levels of significance for correlations between survival and height in relation to datum and sea urchin test size for the three locations, sites and totals. See Tables I and II for notation.

	Malindi				Watamu	Kanamai				Diani				Site total			
	RE	RF	RL	Total	RL	RE	RF	RL	Total	RE	RF	RL	Total	RE	RF	RL	Total
Height	0.14 NS	0.00 NS	−0.02 NS	0.40 ***	−0.22 NS	−0.09 NS	0.10 NS	−0.01 NS	0.12 NS	−0.06 NS	0.30 *	0.16 NS	0.25 **	0.30 ***	0.13 NS	0.51 ***	0.41 ***
Test Size	0.04 NS	0.10 NS	0.19 NS	0.06 NS	0.28 NS	0.11 NS	0.11 NS	0.38 **	0.25 ***	0.30 NS	−0.06 NS	0.26 *	0.17 *	0.26 ***	0.20 *	0.20 **	0.24 ***

TABLE IX

Regression equation coefficients, their standard error of the means and correlation coefficients for regressions between survival (y) and *Echinometra mathaei* average test size and their reef height position in relationship to datum for the three locations. Reef lagoon data does not include the Watamu site data.

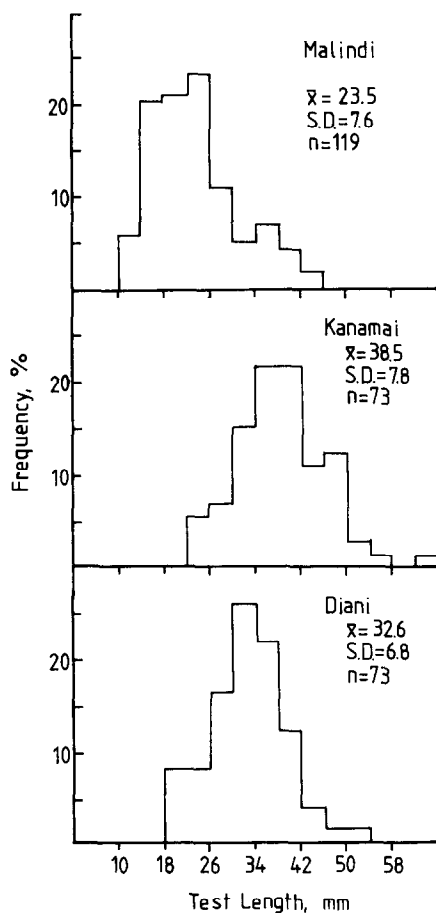|	Survival vs. test size		
	Reef edge	Reef flat	Reef lagoon
n	185	150	166
Equation	$y = -1.68 + 0.066x$	$y = -0.41 + 0.050x$	$y = -3.46 + 0.127x$
SEM	0.67 0.018	0.78 0.020	0.71 0.018
r	0.26	0.20	0.48
	Survival vs. reef height		
Equation	$y = 0.95 + 0.281x$	NS	$y = 1.46 + 0.747x$
SEM	0.10 0.067		0.10 0.103
r	0.30		0.49

Fig. 3. *Echinometra mathaei* average test size [(short + long axis)$\cdot 2^{-1}$] frequency histograms for populations inhabiting reef flats within three of the studied locations.

TABLE X

Comparison of survival between transects within sites. Kruskal–Wallis statistic and level of significance are presented. NS = not significant, * = $P < 0.05$, *** = $P < 0.001$.

	Reef edge	Reef flat	Reef lagoon
Malindi	7.44 NS	10.23 NS	0.46 NS
Watamu	–	–	0.13 NS
Kanamai	12.88*	4.72 NS	2.12 NS
Diani	18.41***	10.04*	9.45 NS
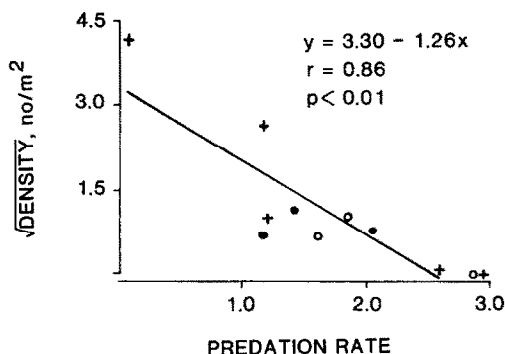
Fig. 4. Density of *Echinometra mathaei* as a function of predation rates calculated as the total length of the experiment (3 days)–survival (days). Locations within the reefs are symbolized as: +, reef lagoon; ●, reef flat; and ○, reef edge.

mortality, highest on reef flats and edges, may be due to tagging combined with other physical stresses such as surf on the reef edge and water temperature and salinity fluctuations on the reef flat.

The most prominent difference in predation is between the protected and fished sites. We attribute this difference to predator removal within fished areas. Fishermen catch a variety of edible finfish which feed on sea urchins. As well, the gastropod *Cypraecassis rufa* is heavily collected and sold for its ornamental value. Results suggest that fishing rather than shelling is more important in affecting sea urchin populations as finfish predators are more effective than invertebrate predators. Triggerfish, which appear to be the most important sea urchin predators, are claimed to be poisonous (Smith, 1965; Carcasson, 1977) but are commonly eaten in Kenya once their poisonous skins are removed (T. R. McClanahan, pers. obs.), although they are not a prefered fish (R. K. Ruwa, pers. comm.). Wrasses are a popular local fish. Although not frequently observed feeding on experimental sea urchins, many wrasses may feed on smaller recruits rather than the adult sizes used in this study. Species from the Diodontidae and the asteroid *Protoreaster lincki* are dried and sold as ornaments. Species from the Lagocephalidae and the asteroid *Culcita schmideliana* are probably the least harvested predators and

may therefore be relatively more important on heavily fished reefs. The reason that unharvested species have not responded to restrict sea urchin population increases remains obscure. There may be other limitations such as high postsettlement mortality (Shulman & Ogden, 1987) which restrict their population expansion or prey preferences which affect their feeding rates on *E. mathaei*. Differences within reefs may also be attributed to fishing pressure or natural variation in predator abundance. Lagoons showed the greatest between site variation and from our observations they appear to be more susceptible to overfishing due to their closeness to shore and calm conditions in comparison to reef edge sites (McClanahan & Muthiga, 1988).

Echinometra mathaei natural (unfished) distribution in Kenya is limited to locations between 0.5 and 1.5 m above datum (Ruwa, 1984). The upper limit is presumably due to desiccation but the lower limit is probably due to predation. This is supported by the rapid increase in predation with increasing depth within Malindi MNP. From our data and observations *Cypraecassis rufa* can feed on *E. mathaei* on the highest reef flats. We also observe the balistids *Rhinecanthus aculeatus* and *Rhinecanthus rectangulus* living in cracks and sea urchin burrows on reef flats during low tides at heights not > 1 m above datum but usually < 0.5 m above datum. Below spring mean low water (0.3 m above datum), the predator guild diversity increases further to include species from Ostracoidei, other Ballistoidei, Labridae and Asteroidea. Negative geotrophism in *E. mathaei* and other sea urchins (Binyon, 1972) may be a predator avoidance strategy.

The diversity of predators suggests that no single species is responsible for controlling *E. mathaei* distribution but is rather a combined effect of many predators. Yet, our observations and data suggest that the balistids *Rhinecanthus aculeatus*, *R. rectangulus* and *Balistaphus undulatus* may be the most important predators of *E. mathaei* and may be considered keystone species within their respective habitats. From observations on many Kenyan reefs (McClanahan & Muthiga, 1988) these three species occupy different areas across the reef. Seaward reef edges are most frequently inhabited by *R. rectangulus* and leeward edges by *R. aculeatus* while *B. undulatus* is most common in calmer deeper lagoons. These species distribution, feeding and behavioral patterns require additional research.

Within this study, predation seems to be the single most important factor controlling *Echinometra mathaei* distribution. Russo (1977) found a positive association between *E. mathaei* densities and water flow which he suggested increases algal drift and subsequently *E. mathaei* food resources. Yet, increased water flow might also reduce predator abundance and their feeding rates and therefore these results are ambiguous. The patchy distribution of *E. mathaei* on reef edges (Muthiga & McClanahan, 1987) may, in part, be due to variable predation within these locations which, in turn, may be affected by surf and current activity. Lewis & Storey (1984) show that surf may act as a stress on *Echinometra* but wave action may also reduce predation and therefore be beneficial to *Echinometra* populations. Observations in Kenya suggest that *E. mathaei* is most frequently restricted to wave swept areas on back reef rocky shores and reef flats within reefs not subjected to heavy fishing. Muthiga & McClanahan (1987) found a

positive association between *E. mathaei* densities and hard substrate in Diani. We suggest that if predators are reduced *E. mathaei* will expand its distribution on hard substrate utilizing algae associated with hard substrate. In these instances *E. mathaei* may be able to expand its distribution until other food, space or competition limits are reached. Because *E. mathaei* has high planktonic settlement rates and is more susceptible to predation than other common sea urchin species (McClanahan, 1988) we suggest that, within this region, it can be used as an indicator species of predation intensity on invertebrates and overfishing.

The increasing size of an individual has been suggested as a form of predatory escape for marine invertebrates (Connell, 1972; Vermeij, 1972) and our results are consistent with this observation. Smaller individuals are more susceptible to predation by a larger number of species and therefore survival increases with size. Models based on a constant mortality for sea urchins and other intertidal invertebrates (Ebert, 1973, 1981) may be overly simplistic. Additionally, changes in body size between closely related species may be a predator escape adaptation over evolutionary time (McClanahan, 1988).

Fishing may have a major effect on coral reef community structure and as recognized by Hay (1984a), community organization cannot be seen independently of fishing intensity. Additionally, as *E. mathaei* is a major bioeroder on coral reefs (Russo, 1980; Hutchings, 1986; Downing & El-Zahr, 1987) bioerosion may be related to fishing intensity. Therefore, beach and shoreline protection provided by coral reefs may be affected by over-exploitation of coral reef fisheries.

REFERENCES

Bak, R. P. M. & G. Van Eys, 1975. Predation of a sea urchin *Diadema antillarum* on living coral. *Oecologia (Berlin)*, Vol. 20, pp. 111–115.
Bak, R. P. M., M. E. J. Carpay & E. D. De Ruyter Van Steveninck, 1984. Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curacao. *Mar. Ecol. Prog. Ser.*, Vol. 17, pp. 105–108.
Bernstein, B. B., B. E. Williams & K. H. Mann, 1981. The role of behavioral responses to predators in modifying urchins (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. *Mar. Biol.*, Vol. 63, pp. 39–49.
Binyon, J., 1972. *Physiology of echinoderms*. Pergamon Press, Oxford, 246 pp.
Birkeland, C., 1982. Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). *Mar. Biol.*, Vol. 69, pp. 175–185.

Brakel, W.H., 1980. Tidal patterns on the East African coast and their implication for the littoral biota. In, *Proceedings of the Symposium on the Coastal and Marine Environment of the Red Sea, Gulf of Aden and Tropical Western Indian Ocean*, Red Sea & Gulf of Aden Environmental Programme, Jeddah, Saudi Arabia, UNESCO/ALESCO, pp. 403–408.

Carcasson, R.H., 1977. *A field guide to the coral reef fishes of the Indian and West Pacific Oceans*. Collins, London, 320 pp.

Carpenter, R.C., 1981. Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *J. Mar. Res.*, Vol. 39, pp. 749–765.

Carpenter, R.C., 1984. Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. *Mar. Biol.*, Vol. 82, pp. 101–108.

Clark, A.M., 1976. Echinoderms of coral reefs. In, *Biology and geology of coral reefs*, edited by O.A. Jones & R. Endean, Academic Press, New York, pp. 99–123.

Connell, J.H., 1972. Community interaction on marine rocky intertidal shores. *Annu. Rev. Ecol. Syst.*, Vol. 31, pp. 169–192.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science*, Vol. 199, pp. 1302–1310.

Crame, A.J., 1986. Late Pleistocene molluscan assemblages from the coral reefs of the Kenyan coast. *Coral Reefs*, Vol. 4, pp. 183–196.

Downing, N. & C.R. El-Zahr, 1987. Gut evacuation and filling rates in the rock-boring sea urchin, *Echinometra mathaei*. *Bull. Mar. Sci.*, Vol. 41, pp. 579–584.

Ebert, T.A., 1965. A technique for the individual marking of sea urchins. *Ecology*, Vol. 46, pp. 193–194.

Ebert, T.A., 1973. Estimating growth and mortality rates from size data. *Oecologia (Berlin)*, Vol. 11, pp. 281–298.

Ebert, T.A., 1981. Estimating mortality from growth parameters and a size distribution when recruitment is periodic. *Limnol. Oceanogr.*, Vol. 26, pp. 764–769.

Ebert, T.A., 1982. Longevity, life history, and relative body wall size in sea urchins. *Ecol. Monogr.*, Vol. 52, pp. 353–394.

Ebert, T.A., 1983. Recruitment in echinoderms. In, *Echinoderm studies*, edited by J.M. Lawrence & M. Jangoux, A.A. Balkema Press, Rotterdam, The Netherlands. pp. 169–203.

Estes, J.A., N.S. Smith & J.F. Palmisano, 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology*, Vol. 59, pp. 822–833.

Glynn, P.W., G.M. Wellington & C. Birkeland, 1979. Coral reef growth in the Galapagos: limitation by sea urchins. *Science*, Vol. 203, pp. 47–49.

Hamilton, H.G.H. & W.H. Brakel, 1984. Structure and coral fauna of East African reefs. *Bull. Mar. Sci.*, Vol. 34, pp. 248–266.

Hay, M.E., T. Colburn & D. Downing, 1983. Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia (Berlin)*, Vol. 58, pp. 299–308.

Hay, M.E., 1984a. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology*, Vol. 65, pp. 446–454.

Hay, M.E., 1984b. Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia (Berlin)*, Vol. 64, pp. 396–407.

Hay, M.E. & P.R. Taylor, 1985. Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia (Berlin)*, Vol. 65, pp. 591–598.

Herring, P.J., 1972. Observations on the distribution and feeding habits of some littoral echinoids from Zanzibar. *J. Nat. Hist.*, Vol. 6, pp. 169–175.

Hutchings, P.A., 1986. Biological destruction of coral reefs: a review. *Coral Reefs*, Vol. 4, pp. 239–252.

Keller, B.D., 1983. Coexistence of sea urchins in seagrass meadows: an experimental analysis of competition and predation. *Ecology*, Vol. 64, pp. 1581–1598.

Kenya Ports Authority, 1986. *Tide tables for East African ports*. Rodwell Press, Mombasa, Kenya.

Khamala, C.P.M., 1971. Ecology of *Echinometra mathaei* (Echinoidea: Echinodermata) at Diani Beach, Kenya. *Mar. Biol.*, Vol. 2, pp. 167–172.

Lawrence, J.M., 1975. On the relationship between marine plants and sea urchins. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 13, pp. 313–386.

Lessios, H.A., D.R. Robertson & J.D. Cubit, 1984. Spread of *Diadema* mass mortality through the Caribbean. *Science*, Vol. 226, pp. 335–337.

Lewis, J.B. & G.S. Storey, 1984. Differences in morphology and life history traits of the echinoid *Echinometra lucunter* from different habitats. *Mar. Ecol. Prog. Ser.*, Vol. 15, pp. 207–211.

McClanahan, T.R., 1988. Seasonality in East Africa's coastal waters. *Mar. Ecol. Prog. Ser.*, Vol. 44, pp. 191–199.

McClanahan, T.R., 1988. Coexistence in a sea urchin guild and its implications to coral reef diversity and degradation. *Oecologia (Berlin)*, Vol. 77, pp. 210–218.

McClanahan, T.R. & N.A. Muthiga, 1988. Changes in Kenyan coral reef community structure and function due to exploitation. *Hydrobiologia*, Vol. 166, pp. 269–276.

Miller, R.J., 1985. Succession in sea urchin and seaweed abundance in Nova Scotia, Canada. *Mar. Biol.*, Vol. 84, pp. 275–286.

Moran, P.J., 1986. The *Acanthaster* phenomenon. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 24, pp. 379–480.

Muthiga, N.A. & T.R. McClanahan, 1987. Population changes of a sea urchin (*Echinometra mathaei*) on an exploited fringing reef. *Afr. J. Ecol.*, Vol. 25, pp. 1–8.

Ogden, J.C., R.A. Brown & N. Salesky, 1973. Grazing by the echinoid *Diadema antillarum* Phillippi: formation of halos around West Indian patch reefs. *Science*, Vol. 182, pp. 715–717.

Paine, R.T., 1966. Food web complexity and species diversity. *Am. Nat.*, Vol. 100, pp. 65–75.

Paine, R.T., 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)*, Vol. 15, pp. 93–120.

Russo, A.R., 1977. Water flow and the distribution and abundance of echinoids (Genus *Echinometra*) on an Hawaiian reef. *Aust. J. Mar. Freshwater Res.*, Vol. 28, pp. 693–702.

Russo, A.R., 1980. Bioerosion by two rock boring echinoids (*Echinometra mathaei* and *Echinostrephus aciculatus*) on Enewetak Atoll, Marshall Islands. *J. Mar. Res.*, Vol. 38, pp. 99–110.

Ruwa, R.K., 1984. Invertebrate faunal zonation on rocky shores around Mombasa, Kenya. *Kenya J. Sci. Tech. Ser. B.*, Vol. 5, pp. 49–65.

Sammarco, P.W., 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *J. Exp. Mar. Biol. Ecol.*, Vol. 45, pp. 245–272.

Sammarco, P.W., J.S. Levinton & J.C. Ogden, 1974. Grazing and control of coral reef community structure by *Diadema antillarum* (Philippi) (Echinodermata : Echinoidea): a preliminary study. *J. Mar. Res.*, Vol. 32, pp. 47–53.

Shulman, M.J. & J.C. Ogden, 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Mar. Ecol. Prog. Ser.*, Vol. 39, pp. 233–242.

Sih, A., P. Crowley, M. McPeek, J. Petranka & K. Strohmeier, 1985. Predation, competition and prey communities. *Annu. Rev. Ecol. Syst.*, Vol. 16, pp. 269–311.

Smith, J.L.B., 1965. *The sea fishes of southern Africa*. Central News Agency, South Africa.

Vermeij, G.J., 1972. Intraspecific shore-level size gradients in intertidal molluscs. *Ecology*, Vol. 53, pp. 693–700.

Wellington, G.M., 1982. Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. *Ecol. Monogr.*, Vol. 52, pp. 223–241.

Wharton, W.G. & K.H. Mann, 1981. Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia. *Can. J. Fish. Aquat. Sci.*, Vol. 38, pp. 1339–1349.

Williams, A.H., 1981. An analysis of competitive interactions in a patchy back-reef environment. *Ecology*, Vol. 62, pp. 1107–1120.