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Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons

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Summary. Large differences in community structure of sea urchins and finfish have been observed in Kenyan reef lagoons. Differences have been attributed to removal of finfish predators through human fishing activities. This study attempted to determine (i) the major sea urchin finfish predators, (ii) the effect of predation on sea-urchin community structure, and (iii) the possible effect of sea urchin increases and finfish decreases on the lagoonal substrate. Six reefs, two protected and four unprotected, were compared for differences in finfish abundance, sea urchin abundance and diversity and substrate cover, diversity and complexity. Comparisons between protected and unprotected reefs indicated that finfish populations were ca. 4 × denser in protected than unprotected reefs. Sea urchin populations were > 100 × denser and predation rates on a sea urchin, *Echinometra mathaei*, were 4 × lower in unprotected than in protected reefs. The balistidae (triggerfish) was the single sea-urchin finfish predator family which had a higher population density in protected than in unprotected reefs. Balistid density was positively correlated with predation rates on tethered *E. mathaei* ($r = 0.88$; $p < 0.025$) and negatively correlated with total sea-urchin density ($r = -0.89$; $p < 0.025$) on the six reefs. We conclude from observations that the balistids *Balistaphus undulatus* and *Rhinecanthus aculeatus* are the dominant sea-urchin predators. The sea-urchin assemblage had its greatest diversity and species richness at intermediate predation rates and low to intermediate sea-urchin densities. At low predation rates and high sea-urchin density *E. mathaei* dominated the assemblage's species composition. Preferential predation on the competitive dominant maintains the assemblage's diversity, supporting the compensatory mortality hypothesis (Connell 1978) of coral reef diversity. Protected reefs had greater cover of hard coral, calcareous and coralline algae, and greater substrate diversity and topographic complexity than unprotected reefs which had greater algal turf and sponge cover. Coral cover and topographic complexity were negatively correlated with total sea urchin density. Although experimentation is lacking, these substrate changes may be due to the switch from finfish to sea-urchins as consumers which results from overfishing of finfish. Removal of top invertebrate-eating carnivores appears to have cascading effects on the entire coral reef ecosystem.

Key words: Community structure – Coral reefs – Predation – Sea urchins – Triggerfish

The distribution and abundance of many coral reef organisms can be greatly affected by their predators (Neudecker 1979; Wellington 1982; Hay et al. 1983; Hay 1984a, b; Lewis 1986; McClanahan 1989; McClanahan and Muthiga 1989). Consequently, coral reef species composition may often reflect the organisms' predator susceptibility (Hay et al. 1983; Lewis 1986; McClanahan 1988a) although other factors such as inter-specific competition (Williams 1981; Hay and Taylor 1985; Robertson and Gaines 1986; McClanahan 1988a), planktonic settlement (Birkeland 1982; Doherty 1983), disease (Lessios et al. 1984) and physical factors (Ebert 1982) may also contribute to observed species composition. Water depth (Neudecker 1979; Wellington 1982; Hay et al. 1983, 1984a, b; Lewis 1986; McClanahan and Muthiga 1989), topographic complexity (Kohn and Leviten 1976; Shulman 1985; McClanahan 1988a) and human fishing activities (Hay 1984a; McClanahan and Muthiga 1988, 1989) can affect predators and their effective predation rates. Loss or removal of predators may cause shifts in species composition due to competitive interactions that occur in the absence of predation (Paine 1966; Carpenter 1981; Lewis 1986; Morrison 1988). These shifts in species composition and abundance may, in turn, change rates of ecological processes such as productivity (Carpenter 1985), nutrient dynamics (Wilkinson and Sammarco 1983; Wilkinson et al. 1984; Williams and

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Carpenter 1988) and the calcium carbonate balance (Ogden 1977; Birkeland 1988; McClanahan and Muthiga 1988).

Observations on southern Kenya's fringing reef suggest between reef differences in sea urchin abundance and species composition which McClanahan and Muthiga (1988) attribute to sea-urchin predator removal by human fishing activities. These authors suggest that (1) predator removal results in sea urchin population increases, (2) a reduction in predation on the sea urchin competitive dominant *Echinometra mathaei* (de Blainville) results in competitive exclusion of subordinate sea urchin species, and (3) sea urchin population increases lead to a reduction in coral cover, an increase in substrate bioerosion and a reduction in topographic complexity. McClanahan and Muthiga (1989) have demonstrated differences in predation rates between unfished Marine Parks and fished reefs and singled out finfish as the most important sea urchin predator type; these results support hypothesis 1. But, to determine cause and effect specific predators must be identified. McClanahan (1988a) has experimentally shown that *E. mathaei* competitively excludes two *Diadema* species from crevice space and is more susceptible to predation than *Diadema*, supporting hypothesis 2. This study attempts to test the validity of McClanahan and Muthigàs (1988) predictions by comparing field sites experiencing differential predation intensity on the competitive dominant.

It is difficult to conduct large scale experimental manipulations of coral reef fish species, which often occur at low densities, but the existence of Parks that exclude human fishing activities forms the basis for a loosely controlled experiment. Parks act as controls for unprotected sites where individuals of commercial species are removed. Identifying the important species removed and comparing abundance gradients of these species with other community variables helps reduce the probability of making spurious correlations and misguided interpretations. This study compares the sea-urchin fauna, finfish sea-urchin predator fauna, predation intensity on sea urchins and substrate cover and complexity between two protected and four unprotected reefs. We attempt to determine (i) the important finfish predators, (ii) their role in controlling sea urchin community structure, and (iii) the effect of sea urchin abundance and species composition on substrate complexity and cover.

Study sites

Kenya's coast south of Malindi is protected by a nearly continuous fringing reef which lies between 0.5 and 3 km offshore. Most reef lagoons are composed of coral sand and seagrass with discontinuous patches of hard corals. Within these hard substrate areas the greatest faunal diversity occurs and in many fished reef lagoons sea urchins are the most conspicuous herbivores (McClanahan and Muthiga 1988, 1989). Protected locations included the Malindi and Watamu Marine National Parks (MNP) which have been protected from fishing and shelling since 1968. Unprotected sites included Vipingo, Kanamai, Bamburi and Diani. Descriptions of Kenya's coast and these sites, except Bamburi, are in Khamala (1971), Hamilton and Brakel (1984), Crame (1986), McClanahan and Muthiga (1988) and McClanahan (1988b). Bamburi's reef lagoon is deeper (>5 m) than other sites but the field work was done close to the more shallow (<1.5 m) back reef south of the "Coral Gardens". All sites are similar in having shallow waters (< 1.5 m) at low tides and being protected from waves and strong currents. The single exception is Bamburi which, due to a channel in the reef flat, experiences strong currents during extreme spring tides.

Methods

Four general categories of measurements were made within studied reefs; these included substrate cover and complexity, sea urchin species densities, a predation experiment on the common sea urchin *Echinometra mathaei* and a finfish survey. The first three measurements were made in 1 to 3 randomly chosen sites within each reef totaling 14 sites for the entire study. Each individual site covered an area 30 m × 30 m. In each site, three parallel nylon lines separated by ca. 10 m were fastened to the substrate. Two ends and the middle of each line acted as foci for substrate and sea-urchin density measurements. Consequently, each site consisted of nine replicates for substrate and sea-urchin density measurements with the exception of one Malindi and one Bamburi site where a single line was lost. The area sampled in each reef is given in Table 1. In each reef a finfish survey was conducted. Details of each procedure follows.

The predation experiment used a technique developed and described in detail by McClanahan and Muthiga (1989). Briefly, *E. mathaei* were pierced through the test with a hypodermic needle (60 mm × 2 mm), threaded with monofilament line (0.5 mm) and tied to the sites' nylon transect lines at 1 m intervals, 10 per line totalling 30 per site. *E. mathaei* was used in this experiment because of its ubiquity, its ease of handling and because predation on it is rapid enough to be measurable in a short time period in comparison with other studied species (McClanahan 1988a). Sites were visited daily for 3 days and the presence or absence of individuals was recorded. Piercing does not induce mortality but attachment to the line restricts their movement, thus reducing their probability of finding predator refuge and increasing predation compared to untethered individuals (McClanahan and Muthiga 1989). Therefore, predation rates on tethered individuals cannot be considered the same as untethered individuals. Predation intensity was calculated from survival data of tethered individuals. Average survival time at each site was calculated by averaging the last day on which individuals were observed alive. A value of 0 by this method indicates that no individuals survived to the first day whereas a value of 3 indicates that all individuals survived the experiment's duration. Predation can account for >95% of the mortality (McClanahan and Muthiga 1989) and therefore a predation intensity measure was calculated by subtracting the average survival time from 3, the maximum survival possible. Relative predation intensity was then calculated by dividing predation intensity by 3.

Sea urchin populations were sampled in areas circumscribed by rotating a line of known length around the foci of the above mentioned nylon lines. Individuals in the created circle were identified (Clark and Rowe 1971) and counted. Densities varied by four orders of magnitude (Table 1) and therefore variable size quadrats of 2, 10 and 25 m^2 were used dependent on densities. All measurements were normalized to 10 m^2 before calculating means and diversity indices (Simpson 1949; Routledge 1979). Nonparametric rank order tests (i.e. Mann-Whitney *U*-test and Kruskal Wallis test) were used for density comparisons making changes in variance due to normalization unimportant. Species-area relationships were evaluated for each location to determine if species richness could be used as a diversity measure at the sampling intensity. An additional one hour search was undertaken on reefs to determine if additional sea urchin species were present outside of studied quadrats.

Substrate was sampled by a 1 cm × 10 m flexible line laid perpendicular to and bisected by each transect line. Surface distance under the line covered by each category: hard coral, soft coral, algal turf (microscopic filamentous algae), calcareous algae (i.e. *Halimeda*), macroalgae (i.e. *Turbinaria*, *Sargassum* and *Padina*), coralline algae, coral sand, seagrass and sponge was measured to the nearest cm and percent cover calculated. Topographic complexity was estimated by the rugosity measurement (straight line distance/bottom contour distance) using the above 10 m line. A rough measure of substrate diversity was calculated (Simpson's Index) using the above substrate classifications. Substrate variables were correlated with sea-urchin population variables.

Visual fish surveys were undertaken in each reef by placing a 100 m line ($n = 3$ to 6/site) straight across the reef lagoon, measuring a 5 m distance from the line and slowly (20 to 30 min/transect) snorkelling (without fins) parallel to the line. Fish observed within the 5 m × 100 m area were identified and the number of individuals in each potential sea urchin predator family, including the Labridae, Balistidae, Diodontidae and Lagocephalidae, was recorded. Common species from these families were identified (Smith 1965). Visibility was never less than 8 m.

In the data analysis individual sites were used for comparisons of predation, sea urchin density and diversity, coral cover and topographic complexity. Sites were pooled for comparisons between reefs and further pooled for comparisons between protected and unprotected reefs.

Results

Sea urchin density and diversity, predation (or survival), substrate cover and fish density indicate large differences between reefs (Tables 1–3). Large differences were also seen between protected (Malindi and Watamu) and unprotected (Vipingo, Kanamai, Bamburi and Diani) reefs for many measured variables (Tables 4–6). Protected

Table 1. Sea urchin densities (x ± SD) per 10 m^2, diversity (Simpson's Index), the number of sites, sample sizes and area sampled in the six reefs. Kruskal-Wallis test of difference between reefs and level of significance provided. Survival refers to the mean number of days that *Echinometra mathaei*, survived in the predation experiment NS = not significant

	Malindi	Watamu	Vipingo	Kanamai	Bamburi	Diani	Kruskal-Wallis
Sites	2	1	3	3	3	2	
Quadrats ($n =$)	15	9	27	27	24	18	
Area sampled (m^2)	375	225	270	675	420	450	
Diadema savignyi	0.0	0.0	12.9 ± 7.6	3.4 ± 4.0	6.3 ± 6.3	0.2 ± 0.5	$p<0.001$
Diadema setosum	0.0	0.0	3.7 ± 3.7	2.3 ± 1.9	0.5 ± 0.8	0.02 ± 0.9	$p<0.001$
Echinometra mathaei	0.2 ±0.3	0.2 ±0.4	32.6 ±20.7	80.6 ±53.9	10.8 ± 7.1	135.0 ±123.0	$p<0.001$
Echinostrephus molaris	0.3 ±0.4	0.1 ±0.3	1.1 ± 1.3	0.2 ± 0.3	10.7 ± 8.1	0.5 ± 0.7	$p<0.001$
Echinothrix calamaris	0.03 ±0.10	0.0	0.6 ± 0.9	0.7 ± 0.7	11.1 ± 9.1	0.3 ± 0.6	$p<0.001$
Echinothrix diadema	0.0	0.0	0.1 ± 0.3	0.0	0.4 ± 0.5	0.02 ± 0.1	$p<0.001$
Prinocidaris sp.	0.0	0.0	0.0	0.03 ± 0.11	0.0	0.0	NS
Stomopneustes variolaris	0.0	0.0	0.04 ± 0.19	0.0	0.1 ± 0.3	0.0	NS
Toxopneustes pileolus	0.0	0.04 ±0.13	0.2 ± 0.4	0.0	0.2 ± 0.4	0.02 ± 0.1	$p<0.005$
Tripneustes gratilla	0.0	0.0	8.2 ± 5.7	8.9 ± 8.2	1.3 ± 1.4	5.9 ± 8.2	$p<0.001$
Total	0.53 ±1.2	0.4 ±0.6	59.4 ±25.8	96.1 ±57.4	41.4 ±23.5	141.4 ±120.4	$p<0.001$
Echinometra mathaei							
Survival (days)	0.36 ±0.10	0.48 ±0.15	1.07 ± 0.13	2.31 ± 0.12	1.25 ± 0.13	2.32 ± 0.15	$p<0.001$
Diversity (D)	0.80	0.68	0.63	0.29	0.77	0.13	

Table 2. Water depth at low tide, topographic complexity (rugosity), the percent cover (x ± SD) of substrate categories and substrate diversity in the six locations. Sample sizes are given in Table 1. The significance level of a Kruskal-Wallis test of difference between reefs is provided

	Malindi	Watamu	Vipingo	Kanamai	Bamburi	Diani	Kruskal-Wallis
Depth, m	0.8 ± 0.3	1.1 ± 0.2	0.4 ± 0.2	0.4 ± 0.1	1.1 ± 0.3	0.6 ± 0.1	
Topographic complexity	1.37 ± 0.33	1.45 ± 0.20	1.30 ± 0.16	1.24 ± 0.18	1.23 ± 0.15	1.15 ± 0.12	$p<0.001$
Hard coral	17.6 ±12.8	30.0 ±24.7	18.1 ±13.6	12.7 ± 9.5	8.9 ± 6.9	4.6 ± 4.6	$p<0.001$
Algal turf	27.6 ±20.5	19.7 ±17.5	58.6 ±19.8	44.3 ±15.4	66.3 ±14.8	54.7 ±22.2	$p<0.001$
Calcareous algae	8.3 ± 6.3	10.3 ±10.3	0.6 ± 1.5	0.0 ± 0.0	0.0 ± 0.0	1.4 ± 3.1	$p<0.001$
Macro algae	2.4 ± 3.2	2.5 ± 2.9	2.8 ± 4.2	0.9 ± 2.4	2.4 ± 3.0	1.5 ± 1.9	$p<0.05$
Seagrass	18.1 ±22.6	28.1 ±32.9	13.8 ±14.6	31.1 ±18.9	9.2 ±15.6	31.9 ±23.0	$p<0.001$
Coralline algae	11.6 ±14.0	0.2 ± 0.7	0.04 ± 0.2	0.1 ± 0.4	2.2 ± 2.8	0.3 ± 0.7	$p<0.001$
Soft coral	1.4 ± 2.4	0.0 ± 0.0	1.9 ± 3.0	1.8 ± 3.6	3.0 ± 3.8	0.8 ± 1.2	$p<0.006$
Coral sand	14.6 ±17.0	9.1 ± 9.6	4.3 ± 7.3	10.1 ±10.1	8.2 ±10.9	4.7 ± 8.4	$p<0.02$
Sponge	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 1.1	0.1 ± 0.4	0.5 ± 1.1	0.04 ± 0.2	$p<0.008$
Substrate diversity	0.82 ± 0.0	0.78	0.59 ± 0.1	0.67 ± 0.0	0.53 ± 0.1	0.60 ± 0.0	$p=0.07$

Table 3. Sample size, total area sampled and densities (x ± SEM., #/100 m^2) of the major sea urchin predator fish families, total predator densities, total (all families) densities and a Kruskal-Wallis comparison between the six studied reefs. NS = not significant

Family	Malindi	Watumu	Vipingo	Kanamai	Bamburi	Diani	Kruskal-Wallis Test
$n=$	5	3	5	6	5	5	
Area (m^2)	2500	1500	2500	3000	2500	2500	
Labridae	11.4 ± 2.6	11.3 ± 1.9	21.2 ±3.0	8.7 ±2.7	2.6 ±0.6	4.2 ±2.0	$p<0.005$
Balistidae	0.92± 0.15	0.33± 0.07	0.08±0.05	0.03±0.03	0.12±0.08	0.04±0.04	$p<0.005$
Diodontidae	0.0 ± 0.0	0.07± 0.07	0.12±0.08	0.03±0.03	0.0 ±0.0	0.0 ±0.0	NS
Lagocephalidae	0.0 ± 0.0	0.07± 0.07	0.0 ±0.0	0.03±0.03	0.20±0.13	0.0 ±0.0	NS
Predator total	12.3 ± 2.7	11.7 ± 2.0	21.4 ±3.0	8.7 ±2.6	2.9 ±0.7	3.4 ±1.0	$p<0.001$
Total fish	117.0 ±16.6	128.7 ±18.9	59.8 ±9.1	29.8 ±5.8	29.1 ±4.1	15.1 ±8.2	$p<0.001$

Table 4. Total sea urchin densities and survival values (see methods) for protected and unprotected reefs. The significance level of a Mann-Whitney *U* test of difference between protected and unprotected reefs is provided

	Protected	Unprotected	Mann-Whitney *U* test
Sites ($n=$)	3	11	
Transects ($n=$)	24	96	
Total sea urchin density (#/10 m^2)	0.45±0.12	80.70±7.30	$p<0.001$
Survival (days)	0.40±0.08	1.68±0.07	$p<0.001$

Table 5. Topographic complexity (rugosity), the percent cover (x ± SD), and diversity of benthic organisms in protected and in unprotected locations. The significance level of a Mann-Whitney *U* test of difference between protected and unprotected reefs is provided

	Protected	Unprotected	Mann-Whitney *U* test
Sites ($n=$)	3	11	
Transects ($n=$)	24	96	
Total transect length (m)	240	960	
Topographic complexity	1.40±0.06	1.24±0.02	$p<0.004$
Hard coral	22.23±3.82	11.84±1.12	$p<0.005$
Algal turf	24.60±3.97	55.24±2.07	$p<0.001$
Calcareous algae	8.21±1.59	0.30±0.10	$p<0.001$
Macro-algae	2.45±0.62	1.92±0.32	NS
Seagrass	21.82±5.45	20.91±2.07	NS
Coralline algae	7.35±2.52	0.67±0.17	$p<0.002$
Soft coral	0.86±0.41	1.53±0.28	NS
Coral sand	12.48±3.00	6.89±0.97	$p<0.04$
Sponge	0.0 ±0.0	0.42±0.15	$p<0.03$
Diversity (D)	0.81±0.01	0.59±0.02	$p<0.02$

Table 6. Densities (x ± SEM, #/100 m^2) of the major sea urchin fish predator families and total fish (all families) between protected ($n=8$) and unprotected ($n=21$) reefs. Mann-Whitney *U*-test of significance inluded. NS = not significant

	Protected	Unprotected	Mann-Whitney *U*-test
Labridae	11.4 ± 1.7	9.2 ±1.9	NS
Balistidae	0.70± 0.14	0.07±0.12	$p<0.001$
Diodontidae	0.03± 0.03	0.04±0.02	NS
Lagocephalidae	0.03± 0.03	0.05±0.03	NS
Total predator families	12.1 ± 1.7	9.3 ±1.9	NS
Total fish	121.4 ±11.9	33.9 ±4.3	$p<0.001$

Table 7. Correlation coefficients and levels of significance of correlations between the density of the major sea urchin predator families, their total density and the total fish density (which combines predator and nonpredator families) against predation intensity and total sea urchin density. Analysis uses means for each reef ($n=6$). Due to the curvilinear distribution (see Fig. 2) Balistidae correlations were log-log transformed. NS = not significant, * = $p<0.05$, ** = $p<0.025$

Family	Labridae	Balistidae	Diodontidae	Lagocephalidae	Predator family total	Fish total
Predation intensity	0.42 NS	0.88 **	0.26 NS	0.10 NS	0.48 NS	0.89 **
Sea urchin density	−0.30 NS	−0.89 **	−0.17 NS	0.24 NS	−0.36 NS	−0.82 *

reefs had low sea urchin density, low survival of tethered individuals, low sea urchin diversity and a high density of finfish. A population density comparison of sea urchin-eating finfish families between all reefs indicated significant differences for the Labridae and Balistidae (Table 3) but for comparisons between protected and unprotected reefs only the balistids resulted in significant differences (Table 6). Balistid density was low (<1/100 m^2) even at their greatest densities.

Triggerfish density is significantly and negatively correlated with total sea urchin density, and positively correlated with predation intensity for the six reefs (Table 7; Fig. 1). Predation intensity and sea-urchin density were not significantly associated with abundance of any other

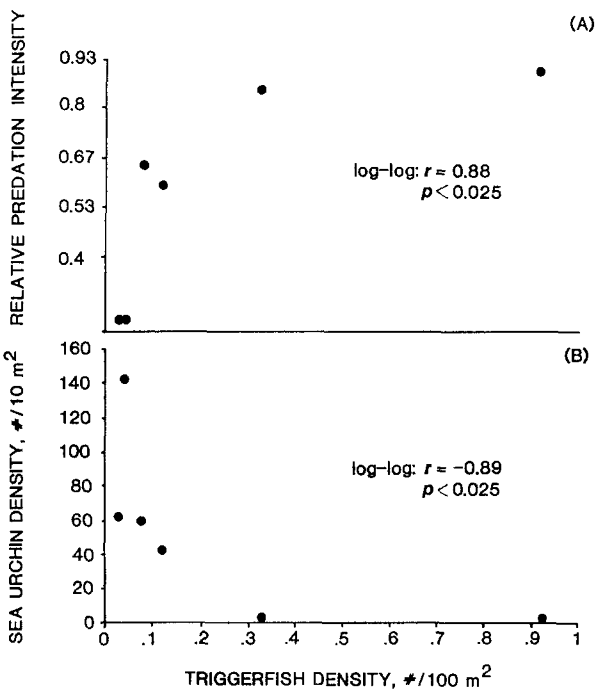

Fig. 1A and B. The relationship between triggerfish densities on six Kenyan reef lagoons and (**A**) relative predation intensity on *Echinometra mathaei* and (**B**) the total sea urchin density

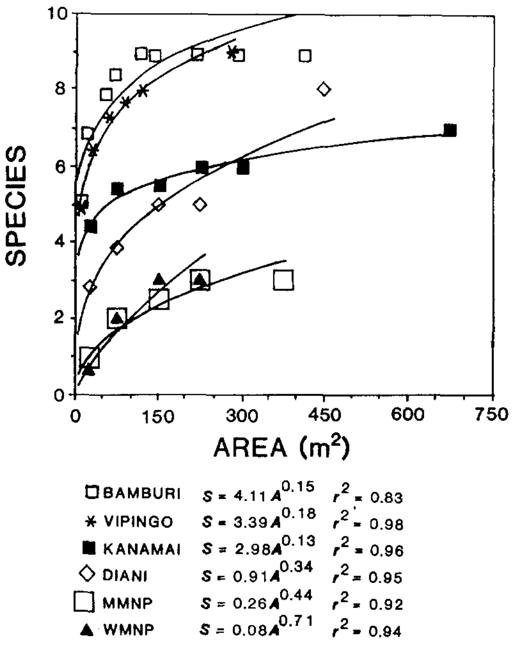

Fig. 2. Species-area curves and best-fit equations for sea urchins inhabiting reef lagoons at the six reefs sampled. MMNP and WMNP = Malindi and Watamu Marine National Parks

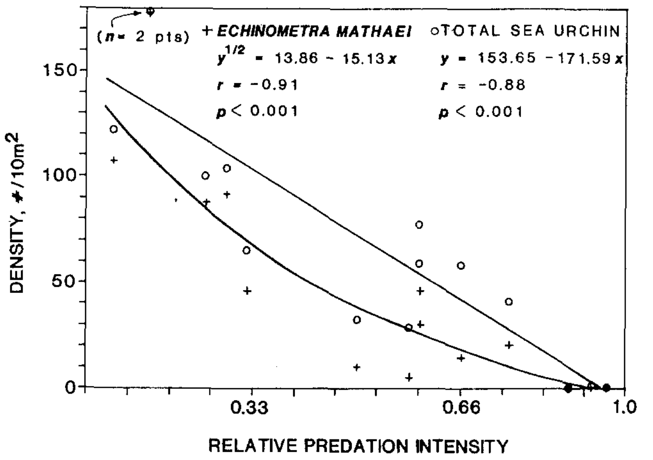

Fig. 3. Total sea urchin and *Echinometra mathaei* densities plotted against relative predation intensity at the 14 sites

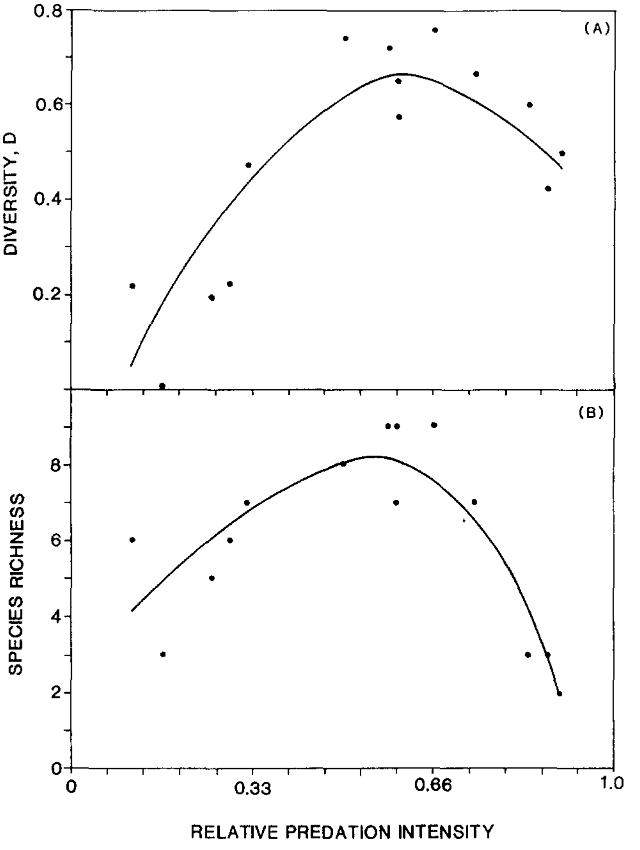

Fig. 4. (**A**) species diversity (Simpson's Index) and (**B**) species richness as a function of relative predation intensity. Hand drawn curves are included but data fit well to quadratic equations (Diversity: $y = -0.31 + 3.07x - 2.41x^2$, $r = 0.89$, $p < 0.005$; Species richness: $y = -0.238 + 35.0x - 35.53x^2$, $r = 0.85$; $p < 0.005$)

sea urchin-eating finfish families. The two most commonly (>90% of the observations) observed triggerfish were *Balistaphus undulatus* (Red-lined triggerfish) and *Rhinecanthus aculeatus* (Picasso triggerfish). *B. undulatus* was only observed in protected reefs whereas *R. aculeatus* was encountered in both protected and unprotected reefs.

The sea-urchin assemblage showed appreciable differences in species-area relationships (Fig. 2). Protected reefs had fewer species per area than unprotected reefs; these were *Echinostrephus molaris*, *Echinothrix calamaris*, *Echinometra mathaei* and a single *Toxopneustes pileolus* found in Watamu. An additional one hour search produced only one additional species, *E. calamaris*, in

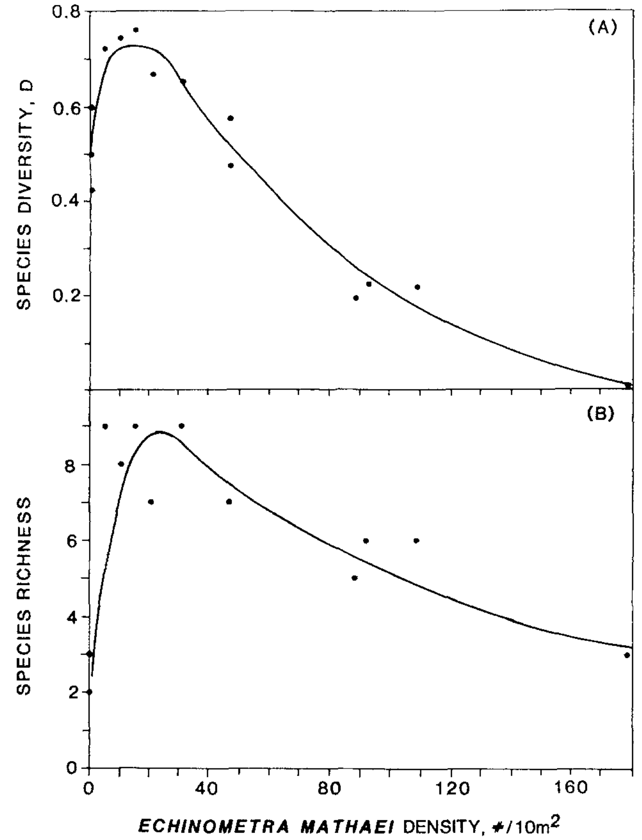

Fig. 5. (A) species diversity (Simpson's Index) and (B) species richness plotted against *Echinometra mathaei* density

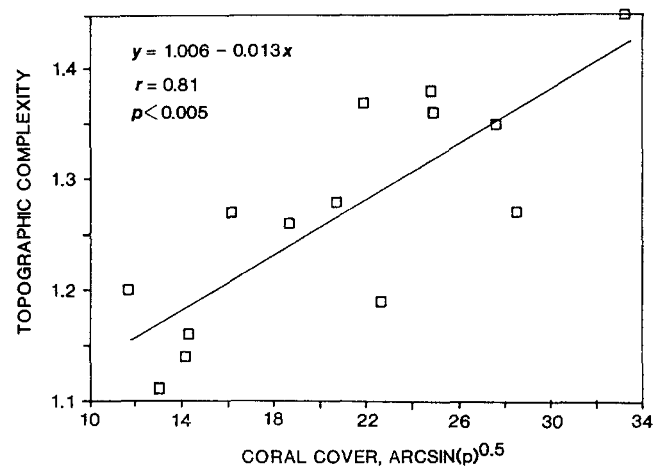

Fig. 6. Topographic complexity (rugosity = straight line distance/bottom contour distance) plotted against the arcsine transformed coral cover

Watamu. *E. mathaei* in protected reefs were typically small recruits (test length <1.5 cm). Unprotected reefs consisted of a greater diversity of species, principally *Diadema savignyi*, *D. setosum*, *Tripneustes gratilla* and *Echinothrix diadema*, species not found in protected reefs. Not all species-area curves leveled at our sampling intensity but there is sufficient spread between curves to indicate relative between-reef differences in species richness. Species richness is defined as the number of species found in each site.

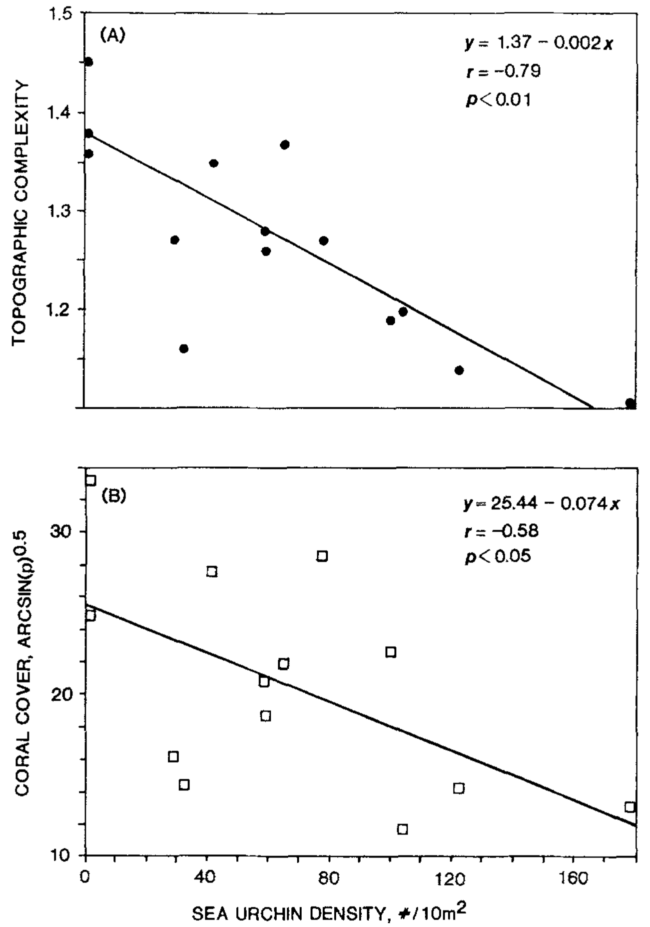

Fig. 7. (A) topographic complexity and (B) arcsine transformed coral cover plotted against the total sea urchin density

Relative predation intensity was strongly and negatively correlated with the density of *E. mathaei* and the total sea urchin density for the 14 study sites (Fig. 3). Scatter-plots of relative predation intensity and species diversity and richness indicate maximum diversity at intermediate predation intensity (Fig. 4). Species richness and diversity were significantly but weakly ($r = 0.60$, $p < 0.05$) correlated. Diversity was maximum at low to intermediate *E. mathaei* density and decreased with increasing *E. mathaei* density (Fig. 5).

Substrate variables show significant differences for all between-reef cover variables (Table 2). Variance was high for most variables suggesting patchy distributions. Protected reefs had greater topographic complexity and substrate diversity and greater cover of hard coral, calcareous and coralline algae and coral sand than unprotected reefs (Table 5). Unprotected reefs had more algal turf and sponge cover than protected reefs. Coral cover and topographic complexity were positively correlated (Fig. 6) but both were negatively correlated with total sea urchin density (Fig. 7), topographic complexity more strongly than coral cover. Correlating sea urchin density and topographic complexity using residuals from the coral cover-topographic complexity correlation produced a weak but significant correlation ($r = -0.53$; $p < 0.05$).

Discussion

Results indicate distinct differences between protected and unprotected reefs for most measured variables. Protected reefs were similar for most measured variables but unprotected reef data suggest gradients for many measured variables. A clear difference between the two reef categories is that principal consumers are finfish in protected reefs compared to sea urchins in unprotected reefs which are subject to fish and shell removal. Gastropods predate on a small percent (< 5%) of experimental sea urchins and although always representing a small fraction of predation on sea urchins they predate more frequently on sea urchins in unprotected than protected reefs (McClanahan and Muthiga 1989). Additionally, McClanahan (1989) failed to find significant differences in gastropod population densities for most commercially collected species, including potential sea urchin predators (i.e. *Cypraecassis rufa*, *Charonia tritonis* and *Cassis cornuta*), between protected and unprotected reefs. Consequently, finfish removal remains the likely cause of observed changes.

The strong negative correlation between experimental predation rates and sea urchin density (these are independent variables) suggests that predation acts as a controlling force on the sea urchin assemblage's community structure. Balistids, particularly *Balistaphus undulatus* and *Rhinecanthus aculeatus*, are the principal predators. This result supports direct observations on the consumption of experimental sea urchins in Malindi where *B. undulatus* consumed >90% of the sea urchins placed in the lagoon (McClanahan and Muthiga 1989). In protected reefs *B. undulatus* were typically observed in deeper (1 to 2 m) coral outcrop areas. Some unprotected areas contain similar habitat and therefore fishing may be the cause of their absence rather than the lack of suitable habitat.

Total finfish density correlated significantly and positively with sea urchin predation intensity and negatively with sea urchin densities. Balistids were a small part (<1.0%) of the total finfish density. Therefore, their contribution to total finfish density cannot alone account for these correlations. The majority of the additional density was contributed by scarids, acanthurids and pomacentrids. It remains possible that (i) the correlations are spurious, (ii) there is an undetermined competitive effect between sea urchins and finfish or (iii) there are other unidentified finfish predators. Data are lacking to support either hypothesis. Spurious correlations could account for the observed correlations if the total finfish population was proportional to the balistid population due to co-occurring population reductions through fishing or some other undetermined cause. Competition could not account for the correlation between total finfish density and relative predation intensity but it could account for the negative correlation between total finfish and sea urchin density. Williams (1981) has suggested that competitive interactions between pomacentrids (damselfish) and sea urchins play a role in localized sea urchin distribution patterns in the Caribbean.

The sea urchin assemblage showed differences in species composition and abundance between reefs which can largely be attributed to predation. Protected reefs had a distinct assemblage composed primarily of adult *Echinostrephus molaris* and *Echinothrix calamaris* and juvenile *E. mathaei*. The absence of other species is presumably due to high predation in these reefs. *E. molaris*, the most common species reaching adult size, may be able to persist because it inhabits deep narrow (ca. 10 cm × 3 cm) burrows (Campbell et al. 1973). The rarer *E. calamaris* has a large body size (adult test lengths are ca. 20 cm) and spines which may reduce its susceptibility to predation. The existence of *E. mathaei* recruits within protected reefs suggests that they settle from the plankton and could potentially colonize protected reefs if predators were absent. It could be argued that differences between protected and unprotected reefs are due to inherent site differences, but observations by local residents (Simpson B. and Abudi M. personal communication) suggest that *E. mathaei*, *Diadema* spp. and *Tripneustes gratilla* were previously more common on Malindi and Watamu reefs prior to and shortly after they became protected.

The existence of additional species in unprotected reefs, principally *D. savignyi*, *D. setosum* and *T. gratilla*, and increased densities of all sea urchin species can be attributed to decreased predation intensity by balistids. Yet, as predation intensity decreases *E. mathaei* becomes increasingly dominant which appears to result in competitive exclusions and localized extinctions. McClanahan (1988a) has experimentally shown that *E. mathaei* exhibits intra- and inter-specific agonistic behavior that can result in localized exclusion of the larger *Diadema* species. This same interference behavior may affect other species as well, and high *E. mathaei* settlement rates compared to that of other species (McClanahan 1988a; McClanahan personal observation) may also give it a competitive advantage.

The correspondence between intermediate predation rates and maximum diversity would appear to support Connell's (1978) nonequilibrium intermediate disturbance hypothesis. However, predator preference for the competitive dominant, *E. mathaei* (McClanahan 1988a), better supports Connell's (1978) equilibrium compensatory mortality hypothesis. Experiments, correlations and observations suggest a predictable change in the assemblage's species composition as a function of predation in the form of the hump-backed species diversity curve. This general pattern has also been found for producers such as algae (Lubchenco 1978; Carpenter 1981) and may be common for algal-coral interactions (Sammarco 1980; Lewis 1986; Morrison 1988).

Substrate variables suggest distinct and consistent differences between protected and unprotected reefs. Since the dominant grazers are herbivorous fish in the former, and sea urchins in the latter, substrate differences may be attributable to (i) a reduction in finfish, (ii) an increase in sea urchins or (iii) a combination of both changes. Determination of the precise causes requires additional experimentation. Substantial research on finfish and sea-urchin grazing indicates that substrate changes are attributable to changes in the dominant consumers. Primarily, sea urchins are major bioeroders of coral reef substrate in many regions (Ogden 1977; Glynn et al. 1979; Scoffin et al. 1980; Hutchings 1986; Downing and El-Zahr 1987; Birkeland 1988) and their bioerosion rates are at least an order of magnitude greater than those of finfish grazers such as parrotfish (Birkeland 1988). Consequently, it remains highly probable that the observed reduction in topographic complexity with increasing sea urchin density is a function of greater bioerosion rates. The greater algal turf cover and subsequent lower substrate diversity suggest that sea urchins are exposing bare calcium carbonate substrate and reducing substrate cover types such as coral and calcareous algae which are then quickly colonized by algal turf.

Data support a top-down perspective for coral reefs (Grigg et al. 1984) where species and populations are controlled by their consumers. Changes at top trophic levels may have cascading effects on lower levels. We suggest that the major change between protected and unprotected reefs is the inclusion of human predators in unprotected reefs which adds an additional consumer and trophic level to the reef. Predation on triggerfish by humans appears to have a major influence on the rest of the community. Triggerfish are neither abundant or a preferred prey of local fishermen but their removal has disproportionate consequences. Fisheries management of these reefs may be greatly simplified by focusing on the human-triggerfish interaction.

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