ELSEVIER

Biological Conservation 89 (1999) 161–182

BIOLOGICAL CONSERVATION

The effects of marine parks and fishing on coral reefs of northern Tanzania

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Received 20 February 1998; received in revised form 7 September 1998; accepted 14 October 1998

Abstract

The macrobenthic (coral, algae, and sea urchins) and fish communities in 15 back-reef sites on the patch and rock-island reefs of southern Kenya and northern Tanzania (~250 km of coastline) were studied in order to (1) test an overfishing model developed in Kenya's fringing reef (McClanahan, 1995a, A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. Ecol. Model. 80, 1–19.), (2) develop a baseline of information on Tanzanian coral reef ecosystems, and (3) determine if some of the government gazetted but unprotected marine reserves were still deserving of protective management. The overfishing model was tested by comparing five sites in two fully protected reefs—one in southern Kenya (Kisite Marine National Park) and the other in Zanzibar (Chumbe Island Coral Park)—with 10 sites in eight fished reefs, and by comparing coral surveys conducted in reefs off of Dar es Salaam in 1974 with present-day studies. These comparisons suggest that fishing is primarily reducing the abundance of angelfish, butterflyfish, parrotfish, scavengers, surgeonfish, and triggerfish groups while some species of small-bodied damselfish and wrasse appear to have benefited. The total fish wet weight estimate was 3.5 times higher in protected than unprotected sites. Sea urchin abundance was six times higher, and predation rates on tethered sea urchin *Echinometra mathaei* were two times lower, in unprotected compared to protected sites. This is largely attributable to the reduction of the red-lined triggerfish *Balistapus undulatus* and other sea urchin predators by fishing. Loss of coral cover and changes in coral generic composition had occurred in four of the five sites visited in the Dar es Salaam area after the 22-year period. There was no evidence for species losses. One site appeared to be severely damaged over this time. Some reefs were dominated by fleshy brown algae, such as *Sargassum* and *Dictyota*, which may result from a loss of grazers and coral cover. Reduced fishing effort, elimination of destructive gear (dynamite and beach seines), protection of vulnerable species and, in some cases, sea urchin reductions could rectify the problems of overfishing. Despite the damage, the gazetted but unprotected reefs of Mbudya and Bongoyo still have high potential as marine protected areas due to the persistence of species and reef structure.

Keywords: Coral reefs; East Africa; Fishing; Indirect effects; Marine protected areas; Predation; Sea urchins

1. Introduction

Coral reef biologists and geologists agree that fishing is one of the biggest human-induced factors affecting the ecology and diversity of coral reefs (Ginsburg, 1993; Polunin and Roberts, 1996; Birkeland, 1997). The specific effects that fishing has on coral-reef ecology has been the focus of a number of recent studies (Koslow et al., 1988; Samoilys, 1988; Russ and Alcala, 1989; McClanahan and Shafir, 1990; Russ, 1991; Polunin and Roberts, 1993; Grigg, 1994; Russ and Alcala, 1994; Watson and Ormond, 1994; Jennings and Polunin, 1995, 1996a; Jennings et al., 1995, 1996; McClanahan and Obura, 1995; Roberts, 1995; McClanahan and Kaunda-Arara, 1996; Watson et al., 1996; 1997; Ohman et al. 1997). Fishing may have little effect on the fish community other than to reduce overall numbers and wet weights of target species but other studies implicate fishing in dramatic shifts in the ecological structure of the reef community (Hughes, 1994; McClanahan, 1995a) as well as localized species losses (Russ and Alcala, 1989; McClanahan, 1994; McClanahan and Obura, 1996; Jennings et al., 1995, 1996). The environmental and habitat factors that affect fish populations are also of considerable debate and critical to predicting

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0006-3207/99/$ - see front matter
PII: S0006-3207(98)00123-2

population changes under different types of management (Sale, 1991). Studies from different regions, habitats, gear uses, and levels of effort are required in order to determine how these factors interact and change the ecology of fishing grounds (Jennings and Lock, 1996).

A general conceptual and simulation model of overfishing effects has been developed for East African reefs (McClanahan, 1995a; McClanahan and Obura, 1995; Jennings and Lock, 1996). This model is based on comparisons between protected and unprotected areas of Kenya's fringing reef (McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990; McClanahan, 1994; 1995a), the recovery of a heavily fished reef (McClanahan and Mutere, 1994; McClanahan and Obura, 1995) and large-scale sea urchin reduction experiments (McClanahan et al., 1994; 1996). Model and field studies suggest that reefs can move between various ecological states dependent on the numbers and choices of fishermen (Hughes, 1994; McClanahan, 1995a; Jennings and Polunin, 1996b). For example, in Kenya, harvesting of fishes, which prey on invertebrates, is predicted to cause increases in invertebrate populations such as sea urchins that can result in losses of some grazing fishes and other feeding groups, and number of fish species. This change is attributable to direct effects of fishing and indirect effects of competition with sea urchins (McClanahan et al., 1994, 1996). Coral can also be damaged by certain fishing techniques (McClanahan et al., 1996). In some cases, when sea urchins either die from diseases or have poor recruitment into the area, reefs can become dominated by fleshy algae that can outcompete hard corals for light and space in the absence of fish grazers (Hughes, 1994; McClanahan et al., 1996). Changes in the dominant grazers are also associated with changes in ecological processes such as the calcium carbonate balance of coral reefs (Birkeland, 1988; McClanahan, 1995a). High sea urchin abundance is associated with a high erosion rate of coral reef substratum and low topographic complexity of reefs (McClanahan and Shafir, 1990; Eakin, 1996) and, therefore, high sea urchin abundance may have long-term detrimental effects on the structure and ecology of these reefs and eventually fisheries production (McClanahan and Obura, 1995; Jennings and Polunin, 1996b).

In East Africa, field studies of fishing and its direct and indirect ecological consequences have largely been confined to Kenya's fringing reefs (Samoilys, 1988; McClanahan and Shafir, 1990; McClanahan and Obura, 1995; Watson et al., 1996; 1997) with some recent work completed on the patch reefs of southern Kenya (Watson and Ormond, 1994; Watson et al., 1997). Reports of the status of Tanzanian fisheries and coral reefs are largely anecdotal but grim as fishing effort has doubled in < 20 years (Fig. 1) and a number of destructive methods are commonly used. Previous reports imply that many of Tanzanian reefs have been

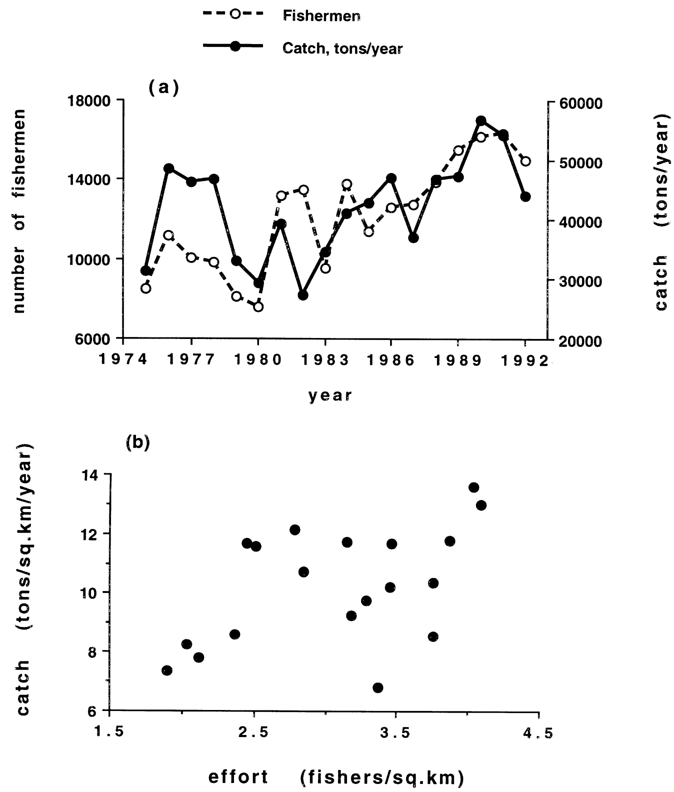

Fig. 1. Changes in fishing pressure as (a) existing data on the changes in the numbers of fishermen and vessels in mainland Tanzania (1975 to 1993) and (b) the fishing effort–yield relationships over this period. Effort–yield relationships based on the estimated area of the major fishery as 4500 km^2 (an 800 km coastline with fishing to 5 km from shore). Data from the Tanzanian Fisheries Department.

extensively damaged by dynamite fishing (UNEP, 1989; Bryceson et al., 1990). Further, fisheries yields are beyond their maximum sustainable limits (Ngoile et al., 1988). These reports are difficult to confirm or rigorously test because of the lack of long-term data on coral reefs and the existence of multiple unfished reefs required for comparison. A more recent compilation of fisheries data (Fig. 1) does not, however, suggest fishing beyond maximum sustained yields but, rather, a temporary drop in catches during the early 1980s and a very variable catch over time. The Tanzanian government established eight marine protected areas in 1975 but none has received protective management. They have been heavily used as fishing grounds, and it has been suggested that they are no longer worthy of attempts at protective management (UNEP, 1989; Gaudian et al., 1995).

Because of the lack of quantitative data on many Tanzanian reefs this study was undertaken to test the overfishing model developed in Kenya's fringing reef on Tanzanian patch reefs. This was acheived by (a) comparing two protected reefs in southern Kenya (Kisite Marine National Park) and northern Tanzania [Chumbe Island Coral Park (CHICOP)] with a number of fished patch reefs in northern Tanzania, and (b) comparing coral surveys conducted in reefs off of Dar es Salaam in 1974 (Hamilton, 1975; Hamilton and Brakel, 1984) with present-day studies. Secondly, we wanted to acquire a baseline of information on coral reefs of northern Tanzanian to determine their ecological status. Thirdly, we wished to determine if some of the previously gazetted but unprotected marine protected areas are in sufficiently good ecological condition to recover quickly and be retained as marine protected areas. Below we present results of studies on the macrobenthic and fish fauna from 15 sites in southern Kenya and northern Tanzania in which five sites were fully protected while 10 experienced unregulated use (Fig. 2).

2. Methods

2.1. Study sites

Coral reefs in offshore waters of southern-most Kenya and northern Tanzania have a complicated structure where living reefs circumscribe rock islands and submerged patch reefs (Fig. 2). Although there are

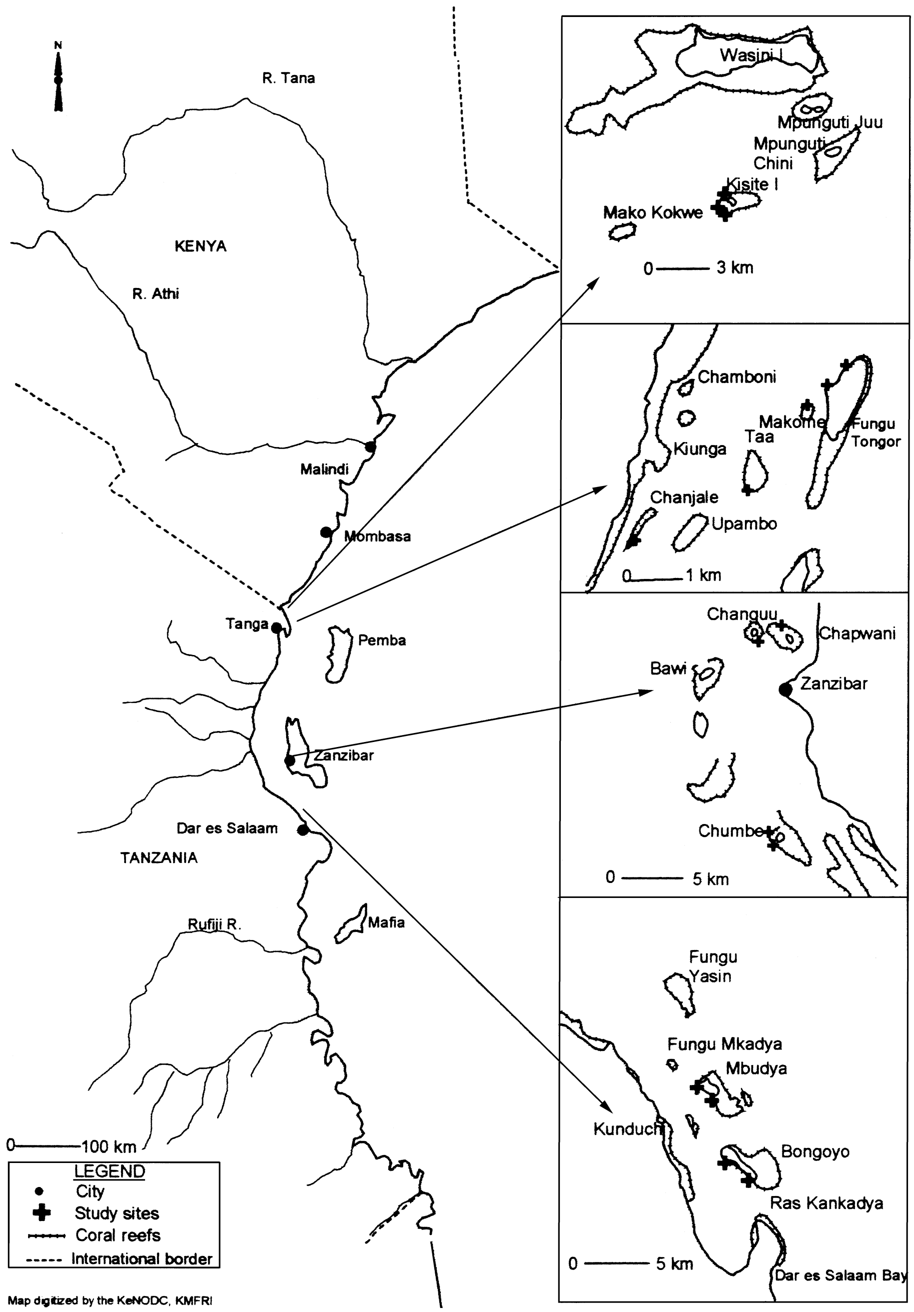

Fig. 2. Map of the coral reefs in the East African region and the studied reefs. Crosses denote the location of the study sites.

five functioning marine protected areas along the East African coastal waters only two exist on patch-reef formations—Kisite Marine National Park (MNP) on the Kenyan–Tanzanian border and Chumbe Island Coral Park (CHICOP) on Zanzibar island. Both parks are regularly patrolled to exclude fishing, Kisite MNP since 1974 and CHICOP since 1991. The Kisite park area is ca. 10 km^2 while the CHICOP area is a stretch of reef ca 500 m long. Within Kisite MNP we studied three sites and in CHICOP two sites chosen to maximize the full spatial variability of these protected areas. The fished sites in northern Tanzania included four patch reefs in the Tanga-Pangani region, four back-reef sites in the Mbudya and Bongoyo patch-reef islands, and two sites in Changuu and Chapwani patch reef islands situated off Zanzibar town.

Two of the fished sites Mbudya and Bongoyo were surveyed by Hamilton (1975) in 1974 and were established as marine reserves in 1975. Another marine reserve and survey site of Hamilton (1975), Fungu Yasini, was visited but no data were collected from this site. All sites consisted of areas with corals of ca. 100 m$\times$30 m in which transects were randomly placed. Sites were shallow (0.5–2.5 m deep) and located in the calm back-reef areas.

2.2. Field measurements

2.2.1. Benthic substrate

Measurements included quantitative studies of the cover benthic macrobiota populations, sea urchin populations, and fish communities. Attached benthic communities were studied by the line-intercept method using seven to 24 (but usually nine) 10 m line transects per site. Cover of benthic marcrobiota under the line > 3 cm in length were classified into nine categories (hard coral, soft coral, algal turf, coralline algae, calcareous algae, fleshy algae, seagrass, sand, and sponge) and their lengths were measured to the nearest centimetre (McClanahan and Shafir, 1990). Hard coral and fleshy algae were further identified to the genus with the exception that branching and massive *Porites* and *Galaxea fascicularis* and *G. clavus* were distinguished. These groups were distinguished because they are different ecologically—massive *Porites* and *G. clavus* being major reef builders while branching *Porites* (mostly *P. nigrescens*) and *G. fascicularis* are early-successional species. From these measurements the percentage cover of the various categories was calculated for each reef. A diversity index was calculated for corals and sea urchins using the following form of the Simpson's Index ($D = 1 - \Sigma p_i^2$) such that diversity increases with increasing D (Magurran, 1988).

In order to determine the number of coral genera, on a scale larger than permitted by line transects, a search-sampling technique (McClanahan and Muthiga, 1992) was completed at the studied reefs. The observer swam haphazardly along the shallow reef sites for 20 min and recorded the time taken to observe the first individual of a coral genera. This was repeated five times at each reef. From these data cumulative genera-search plots were created to estimate the number of genera in each reef.

2.2.2. Sea urchins

Sea urchins were identified to species and counted in nine haphazardly placed 10 m^2 plots per site. The wet weight of each species was estimated by multiplying the population densities by an average wet weight per species from specimens collected off the Mbudya and Bongoyo reefs (Appendix). Total sea urchin wet weight was estimated by summing the wet weights of each species.

A tethering experiment measuring predation on the rock-boring sea urchin *Echinometra mathaei* was completed in each site (McClanahan and Muthiga, 1989). To initiate the predation experiment, 30 *E. mathaei* were pierced with a hypodermic needle, a monofilament line was threaded through their body and tied to a nylon lines fastened to the bottom at each site. Broken tests or body walls indicated death by a predator (McClanahan and Muthiga, 1989; McClanahan, 1995b). The number of surviving *E. mathaei* was recorded each day for three days and the average survival was calculated for each site and normalized to a 0 to 1 scale—0 corresponding to no predation-induced mortality and 1 with all predation-induced mortality occurring on the first day. Animals dying from causes other than predation were eliminated from the analysis.

2.2.3. Fish

Fish communities were quantified using two methods in two 5 m $\times$ 100 m belt transects per site (McClanahan, 1994; McClanahan and Kaunda-Arrara, 1996). The first method was used to estimate the wet weight of fish while the second method was used to determine the numbers of species. Wet-weight estimates were made by classifying each individual encountered in the transect to the family, estimating its length, and placing it into 10 cm size-class intervals. No individuals < 3 cm in length were recorded. The three closely related families of Haemulidae, Lethrinidae and Lutjanidae were pooled into a single group named scavengers. Wet weights per family were estimated from length–weight correlations established from measurements of the common species in each family (McClanahan et al., 1996). This method was not accurate for the small and cryptic species but obtains reasonable estimates of fish wet weights because the larger and more exposed species make up, by far, the largest fraction of the total fish weight.

A second, more accurate, method used a discrete-group sampling (DGS) method where one to three families were sampled with each pass through the belt transect and the line is passed four times to sample eight families (angelfish = Pomacanthidae, butterflyfish = Chaetodontidae, damselfish = Pomacentridae, parrotfish = Scaridae, pufferfish = Diodontidae, surgeonfish = Acanthuridae, triggerfish = Balistidae and wrasses = Labridae; these groups are among the families with the most species of typical coral-reef fishes, see McClanahan, 1994 for more details). Using this method, the number of individuals per species and the number of species per transect were calculated and species–area relationships were determined by combining line–transect data.

Data are presented for each site and a one-way ANOVA statistical comparisons made for differences between protected and unprotected sites based on site averages (i.e. five protected and 10 unprotected replicates). Data were tested for normality and homogeneity of variance. Data were normally distributed but in some cases variances were not equal. In these instances we used Welch's ANOVA, which does not assume homogeneity of variance, and also the nonparametric Wilcoxon test if the Welch's test produced marginal significance levels (i.e. $0.04 < p < 0.10$) (Sall and Lehman, 1996). We also performed cluster analyses using the centroid method on the faunal assemblage data of corals, fleshy macroalgae, sea urchins and fish (Sall and Lehman, 1996). We make only qualitative comparisons with the coral surveys of Hamilton (1975) in Fungu Yasini, Mbudya and Bongoyo, as he did not complete quantitative line transects but rather diagrammed the cover and species of coral on each reef profile. Hamilton (1975) presented very accurate maps of his locations and, therefore, our quantitative transects were placed very close to his qualitative profiles.

3. Results

3.1. The benthic community

Hard coral cover (37%) and algal turf cover (35%) were the dominant benthic cover types in all reefs followed by fleshy algae, sand, soft coral, coralline algae, and sponge [Table 1(a)]. Calcareous algae *Halimeda* spp. and the usually common seagrasses such as *Thalassia hemprichii* and *Thalassadendron ciliatum* were very uncommon in these shallow back-reef crest habitats. Although coral cover was 20% lower in unprotected than protected reefs there were no statistically significant differences found between protected and unprotected sites with the exception of there being more sand cover in protected sites. There were, however, large differences in the dominance and composition of coral genera at the studied sites [Table A1(b)]. Some sites were dominated by *Galaxea clavus*, others by foliaceous *Montipora*, branching and massive *Porites* (mostly *P. nigrescens* and *P. lutea* respectively), *Pavona* and *Acropora*. The sites in Bongoyo were unique in having a high dominance of *Galaxea fascicularis* at one site and *Fungia* at another.

Most sites had high diversity, but a few sites, with a high dominance of one of the above genera, had lower diversity [Table A1(b)], but dominance and diversity were not clearly related to management [Fig. 3(a)]. Protected reefs did cluster together along with three unprotected sites which all had moderate abundance of *Galaxea clavus*, *Acropora* spp. and *Porites nigrescens* [Fig. 3(a), Table A1(b)]. There were similarities in the number of genera encountered among regions by the search-sampling method for up to 100 min of searching (Fig. 4). Each region had between 30 and 35 genera of coral in these shallow-water sites. Kisite MNP sites may have had slightly higher within-site genera diversity (at 20 min of sampling) but this small difference was not maintained at greater levels of sampling.

Fleshy algae were also highly variable among sites [Table 1(b) and A1(c)]. The fleshy brown algae *Sargassum*, *Turbinaria* and *Dictyota* were the most abundant genera but very uncommon in the Dar es Salaam and Zanzibar town islands area. Two protected sites, Kisite 1 and Chumbe 1, had a high abundance of *Sargassum* as did a number of sites in the Tanga region and these sites clustered as outliers to a central cluster of sites with low fleshy macroalgal cover [Fig. 3(b)]. High variability among regions produced high levels of variance for comparisons between protected and unprotected reefs such that none of the differences were statistically significant—despite there being about twice as much *Sargassum* in unprotected than protected reefs. The relationship between hard coral and fleshy algae cover was also highly variable and suggests some limitations of coral abundance by algal abundance but a highly variable relationship (Fig. 5).

3.2. Comparison with Hamilton's 1974 reef profile studies

Five sites described by Hamilton in 1974 were visited in 1996 and at four of these sites we completed quantitative transects (Mbudya and Bongoyo 1 and 2). Hamilton's descriptions are qualitative profile diagrams showing the zonation patterns of corals and includes a series of black and white photographs of corals in the field. Diagrams and photographs give a good description that allows us to compare our quantitative data with fair accuracy.

Hamilton describes the Fungu Mkadya reef as having a fore reef dominated by *Acropora hyacinthus* which was "not profusely developed" in 1974 and leeward slope dominated by *Galaxea clavus* with *Echinopora lamellosa* and *Acropora hyacinthus* colonies at the base of the slope. Despite extensive searching we found very low cover by coral (< 10%) but a high cover of algal turf (> 85%) growing on consolidated rubble, and large

Table 1
Comparison of the studied mean (S.D.) parameters of (a) gross substrate cover, (b) fleshy macroalgae, (c) sea urchins, their diversity and predation rates on the tethered *Echinometra mathaei*, and (d) fish abundance for protected and unprotected reefs. Includes an ANOVA comparison between proteced and unprotected reefs, *F*-value and level of significance

(a) Gross substrate categories

	Hard Coral	Turf algae	Fleshy algae	Coralline crustose algae	Sand	Soft coral	Seagrass	Sponge	Calcareous algae (*Halimeda*)
Protected	39.74	32.72	6.04	5.05	12.10	4.26	0.00	0.16	0.22
($n=5$)	(22.91)	(18.70)	(7.24)	(2.45)	(4.48)	(3.73)	(0.00)	(0.18)	(0.45)
Unprotected	31.69	39.27	12.28	8.61	2.97	3.86	1.06	0.27	0.04
($n=10$)	(13.90)	(8.40)	(15.17)	(6.63)	(3.28)	(2.18)	(2.18)	(0.23)	(0.07)
%Difference	−20.27	20.01	103.41	70.37	−75.45	−9.42		73.97	−81.47
ANOVA									
F-value	0.68	0.84	0.73	1.30	19.29	0.23	1.13	0.96	0.76
Significance	N.S.	N.S.	N.S.	N.S.	0.000	N.S.	N.S.	N.S.	N.S.

(b) Fleshy algae categories by genus

	Sargassum	*Turbinaria*	*Dictyota*	*Hypnea*	*Dictyospheria*	*Haliptylon*	*Pocockiella*	*Padina*	*Lyngbya*
Protected	55.9	7.5	1.8	0.0	0.0	0.0	0.0	0.0	0.0
($n=5$)	(72.9)	(7.9)	(3.9)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Unprotected	86.5	7.7	9.0	2.8	1.5	0.7	0.5	0.5	0.2
($n=10$)	(119.5)	(18.8)	(14.4)	(4.2)	(2.4)	(2.1)	(1.5)	(1.2)	(0.7)
%Difference	54.8	2.0	412.1						
ANOVA									
F-value	0.27	0.0	2.2	2.11	1.83	0.48	0.48	0.74	0.48
Significance	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

N.S. = not significant.

Table 1 (*Continued*)

(c) Sea urchin wet weight (kg/ha) by species, their diversity and the predation index on tethered *Echinometra mathaei*

	Diadema savignyi	*Echinothrix diadema*	*Diadema setosum*	*Tripneustes gratilla*	*Echinothrix calamaris*	*Echinometra mathei*	*Echinostrephus molaris*	*Toxopneustes pileolus*	All urchins	Diversity $D=$	Species richness	Predation index
Protected	46.8	147.7	397.2	0.0	1.5	13.9	5.2	1.1	613.4	0.42	3.80	0.69
($n=5$)	(52.2)	(165.2)	(663.6)	(0.0)	(2.2)	(19.7)	(9.5)	(2.5)	(573.0)	(0.34)	(1.30)	(0.23)
Unprotected	1493.6	1058.1	859.1	87.0	18.5	5.1	2.7	4.4	3528.5	0.29	3.90	0.32
($n=10$)	(1899.4)	(1352.4)	(1540.9)	(265.5)	(30.4)	(8.3)	(5.6)	(14.1)	(2325.2)	(0.21)	(1.85)	(0.16)
%Difference	3092.6	616.5	116.3		1161.4	−63.3	−48.4	300.0	475.3	−30.8	2.6	−53.1
ANOVA												
F-value	5.79	4.4	0.40	0.52	3.1	0.9	0.43	0.27	14.01	0.87	0.01	13.40
Significance	0.04	0.07	N.S	N.S.			N.S.	N.S.	0.003	N.S.	N.S.	0.0028

(d) Fish wet weight (kg/ha) by family

Sites	Acanthuridae	Balistidae	Chaetodontidae	Labridae	Lutjanidae	Mullidae	Pomacanthidae	Pomacentridae	Scaridae	Siganidae	Others	Total
Protected	116.1	14.4	33.7	43.5	133.0	9.2	20.3	78.2	247.6	2.1	106.4	806.0
($n=5$)	(60.1)	(8.0)	(26.9)	(15.1)	(156.1)	(13.8)	(15.7)	(28.0)	(192.6)	(2.7)	(90.2)	(291.1)
Unprotected	32.4	0.1	10.5	33.4	12.6	1.7	3.1	75.6	29.3	1.5	30.1	230.3
($n=10$)	(24.5)	(0.3)	(6.4)	(17.4)	(11.6)	(3.2)	(2.9)	(24.1)	(30.7)	(1.8)	(22.1)	(64.6)
%Difference	−72.1	−99.4	−68.8	−23.1	−90.5	−81.2	−85.0	−3.3	−88.2	−28.0	−71.8	−71.4
ANOVA												
F-value	8.89	15.95	3.64	1.20	2.96	1.43	6.0	0.03	6.34	0.25	3.47	19.1
Significance	0.03	0.02	N.S.		N.S.	N.S.	0.07		0.07		N.S.	0.01
Wilcoxon			0.02		0.02		0.002		0.005		0.04	

numbers of *Echinothrix diadema* and *Diadema savignyi* sea urchins grazing on the turf and consolidated rubble. Because coral cover was low there was little clear evidence of zonation but the dead skeletons of *Galaxea clavus* were common on the leeward side and live *Acropora* was sparsely distributed on the fore reef.

Comparison of the Mbudya sites indicates the least change since Hamilton's survey but there were notable differences in the back reef crests he described (Profiles 6 and 7) and photographed (Plates 3.1 and 3.2). He described one reef crest (Profile 6) as having a "very dense coverage of cespitose colonies of *Acropora* of several species" and his photographs suggest coral cover > 70% and a low population density of sea urchins (none observed in the two photographs). In 1996, at the same site, we measured 28% hard coral cover and found that *Montipora* was the dominant genus with *Acropora* contributing only 30% of this hard coral cover. We recorded sea urchin wet weights of 5500 kg/ha in 1996 (it would have been extremely difficult to photograph this reef without a sea urchin in the picture). Our second site in Mbudya 2 had a very high coral cover (70%) and seemed to be similar to the descriptions provided by Hamilton.

Comparison of the three Bongoyo reef profiles (Hamilton, 1975: Profiles 9, 10 and 11 and photographs 8.1, 8.2, 9.1 and 9.2) with our transect studies suggest large changes in the coral community since 1974. The 1974 study describes a very high cover (> 70%) of *Acropora hyacinthus* and *A. formosa* on the reef crest, few sea urchins (none in four pictures), and, in the reef slopes, dominance by either *Galaxea clavus* or *Acropora formosa*. Our 1996 survey shows only 28–36% hard coral cover on the reef crest and a much lower dominance of *Acropora* than found in 1974. *Galaxea clavus*, which was and still is dominant on the reef slope, was also very common on the reef crest as were *Galaxea fascicularis* and species of *Fungia*. Sea urchins were very abundant—ranging from 5730 to 6610 kg/ha [Tables 1(c) and A1(d)].

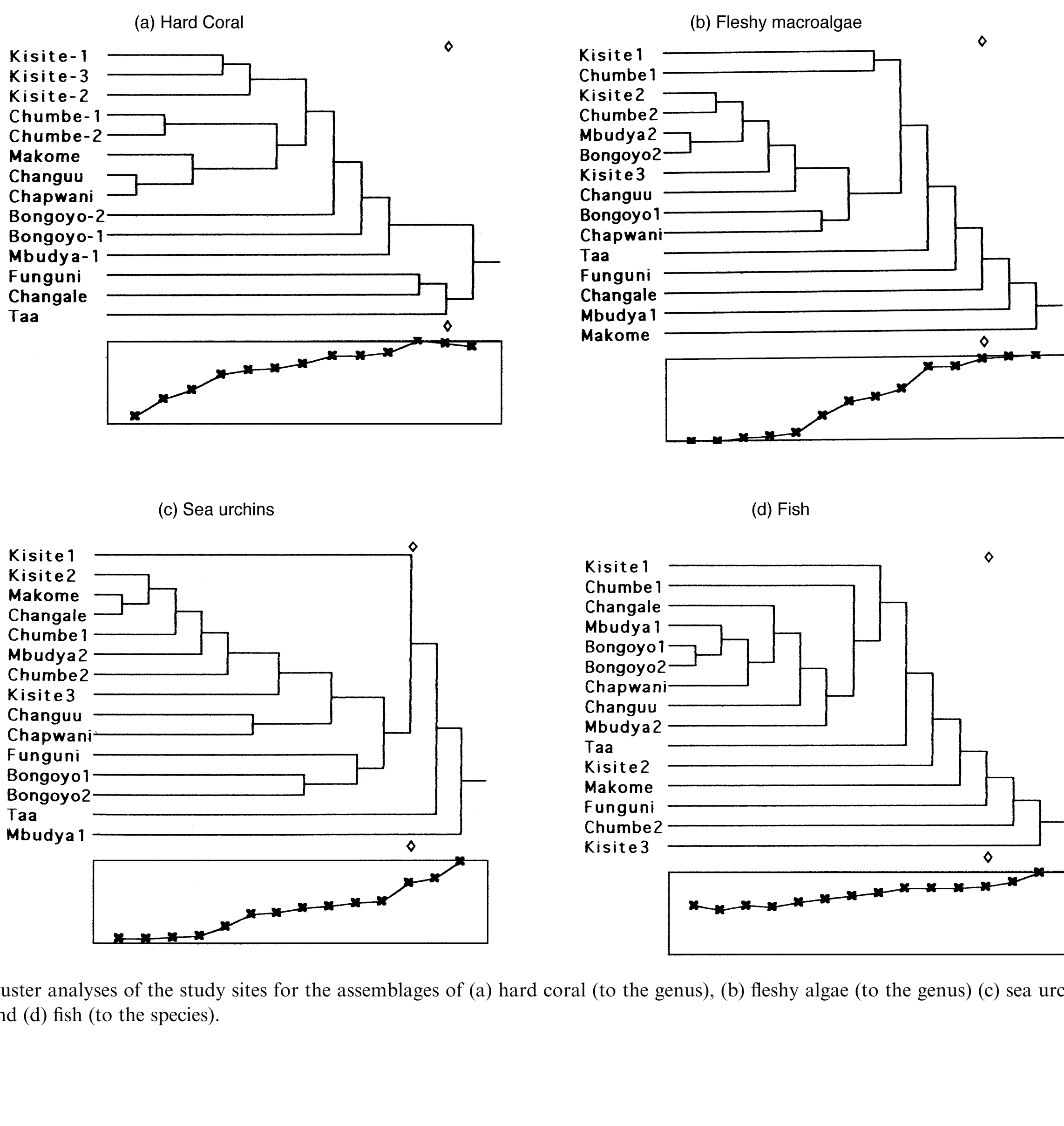

Fig. 3. Cluster analyses of the study sites for the assemblages of (a) hard coral (to the genus), (b) fleshy algae (to the genus) (c) sea urchins (to the species) and (d) fish (to the species).

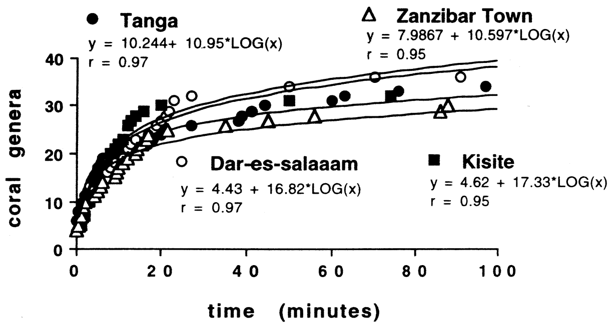

Fig. 4. Cumulative number of coral genera found as a function of the time spent searching in each of the four regions.

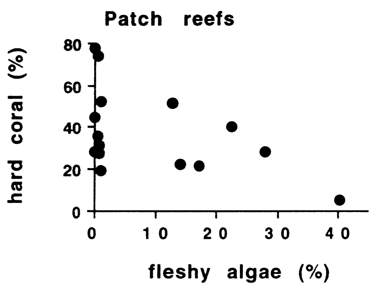

Fig. 5. Relationship between fleshy brown and red algae and the abundance of hard coral in the 15 studied sites.

3.3. The sea urchin assemblage and predation

Sea urchin wet-weight estimates on these reefs varied greatly from 78 to 6609 kg/ha [Tables 1(c) and A1(d)]. Wet-weight estimates in the protected sites were about one sixth (613 kg/ha) those of the unprotected sites (3528 kg/ha) while species diversity and predation rates were about two times higher in protected than unprotected reefs ($p < 0.01$). Predation was very uniform among the three protected sites in Kisite MNP—ranging from 0.82 to 0.88, and to a lesser extent in the newer and smaller CHICOP reef (0.38–0.52), while highly variable in unprotected sites—ranging from 0.05 to 0.56. The two dominant species and the total sea urchin abundance were statistically more abundant in unprotected than protected reefs [Table 1(c)].

The relationship between predation intensity and sea urchin wet weight was negative but highly variable [Fig. 6a]. Scatter plots of the relation between the predation index and the abundance of the dominant predator, *Balistapus undulatus*, indicate low abundance and variance in sea urchin abundance at high levels of predators and predation but very high variance at the low levels of predators and predation (Fig. 7). Despite high variation in the abundance of sea urchins the predation index was closely correlated with the abundance of *B. undulatus* [Fig. 7a].

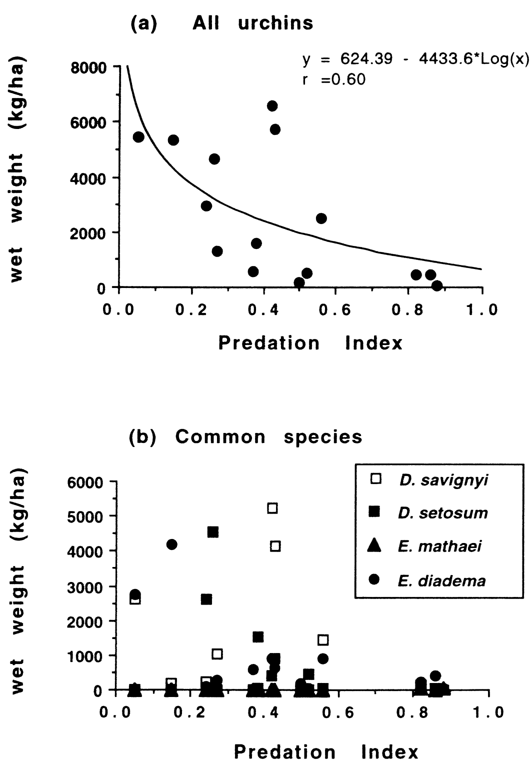

Fig. 6. Relationships between predation intensity and (a) total sea urchin abundance and (b) the three most common species (*Diadema savignyi*, *Diadema setosum* and *Echinothrix diadema*) and the rock-boring sea urchin *Echinometra mathaei*.

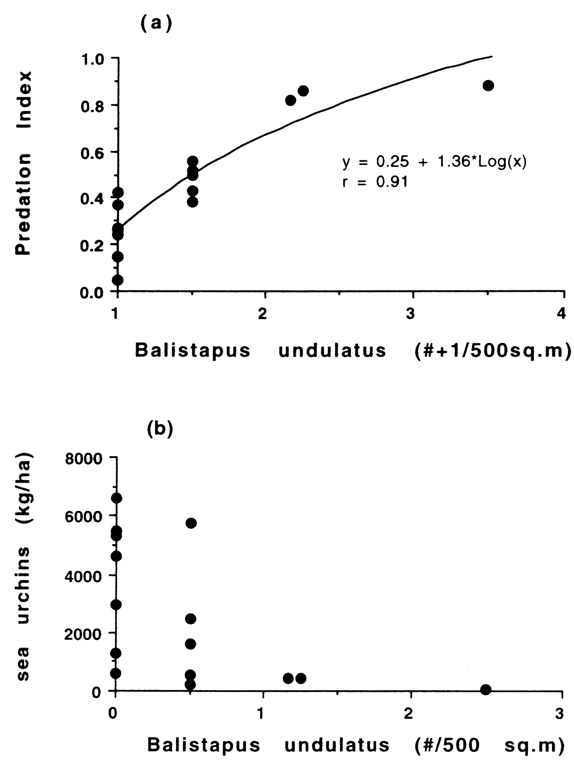

Fig. 7. The relationship between red-lined triggerfish *Balistapus undulatus* and (a) the predation index and (b) the abundance of sea urchins in the 15 studied reefs.

The dominant sea urchin species in these reefs were *Diadema savignyi* and *Echinothrix diadema* while most other species were patchily distributed and not abundant [Table 1(c); Fig. 6(b)]. Sites clustered by the degree of dominance of the common species at the study sites with sites of high abundance clustering as outliers on a central cluster of sites with few sea urchins [Fig. 3(c)]. *Echinothrix diadema* appears to have a negative exponential relationship with predation while *D. savignyi* has a scattered or, perhaps, hump-shaped relationship with predation. *Echinometra mathaei*, which is usually the most dominant sea urchin species in Kenya's fringing reef and closely correlated with predation rates in those reefs (McClanahan and Shafir, 1990),was uncommon in the subtidal patch reefs we studied and showed no relationship with our measure of predation.

3.4. The fish fauna

Estimates of fish wet weights in these reefs varied from 167 to 1091 kg/ha with protected sites having around 3.5 times more fish biomass than the unprotected reefs [$p < 0.01$; Table 1(d)]. By wet weight estimates, the most abundant groups in the protected reefs were the herbivorous parrotfishes and surgeonfishes (~247 and 161 kg/ha respectively) and scavengers (~190 kg/ha; includes Lethrinidae, Lutjanidae, and Haemulidae). The wet weights of these groups along with the triggerfish, angelfish and butterflyfish were significantly lower ($p < 0.05$) in unprotected compared to protected sites. Wrasses, goatfish, damselfish and rabbitfish did not display differences in wet weights by this sampling method. The more accurate DGS sampling method for calculating numbers of individuals and species shows, however, that there were 77% more individual damselfishes and 11% more wrasses in the unprotected compared to protected reefs (Table 2).

A comparison of the density of individual species between protected and unprotected reefs sampled by the DGS method showed statistically significant differences ($p < 0.07$) in 27 of the 134 sampled species, distributed in all families. Differences were highly significant ($p < 0.01$) for *Scarus sordidus*, *Naso annulatus*, *Chaetoodon guttatissimus*, *Balistapus undulatus*, and *Suflamen chrysopterus*. Twenty seven of these significant differences were losses, and the only gain was for *Plectroglyphidodon lacrymatus* (Table 3). There was, however, no distinct clustering of the fish fauna based on management except that these sites were outliers to a central cluster of sites dominated by damselfish and wrasses and a lower abundance of the commercial species [Fig. 3(d)].

The density and cumulative numbers of species also reflected similar changes in the fish fauna. There were 34–95% reductions in the numbers of species per transect in unprotected compared to protected sites among

Table 2
Number of individuals and species per 500 m^2 belt transects determined from the discrete-group sampling method. Data summarized by protection and region. The *F*-value and level of significance from the ANOVA comparison of differences among regions and protection are given[a]

	Protected				Unprotected						Difference	ANOVA	
	Kisite		Chumbe		Dar es Salaam		Tanga-Pangani		Zanzibar-Town				
	x	S.D.	x	S.D	x	S.D.	x	S.D.	x	S.D	%	*F*-value	Significance
Species/500 m²													
Acanthuridae	6.8	2.1	5.5	2.4	2.3	1.2	3.4	2.3	0.8	1.0	−65.5	13.51	*
Balistidae	2.0	1.0	0.8	0.5	0.1	0.4	0.3	0.5	0.0	0.0	−90.9	6.92	+
Chaetodontidae	3.4	1.4	3.5	1.0	2.6	1.9	1.6	0.9	2.5	1.0	−34.5	8.44	+
Diodontidae	0.2	0.4	0.0	0.0	0.0	0.0	0.1	0.4	0.0	0.0	−55.6	0.35	N.S.
Labridae	10.9	3.1	13.5	1.9	12.6	2.4	14.8	3.2	10.3	3.9	2.9	0.03	N.S.
Pomacanthidae	0.8	0.4	2.5	1.7	0.3	0.5	1.3	0.9	0.5	0.6	−59.0	1.59	N.S.
Pomacentridae	9.8	3.9	15.8	2.2	14.8	2.9	12.5	4.1	10.5	3.9	−1.3	0.00	N.S.
Scaridae	6.5	1.4	8.3	1.0	2.5	1.5	3.6	2.4	3.0	2.0	−58.8	31.20	*
Total	40.1	9.4	49.8	5.7	35.1	5.2	38.6	12.4	27.5	9.9	−24.9	4.03	N.S.
Density, number/500m²													
Acanthuridae	75.5	25.6	16.3	9.3	10.8	9.3	30.4	20.7	1.0	1.4	−69.4	1.66	N.S.
Balistidae	5.1	4.3	0.8	0.5	0.1	0.4	0.3	0.5	0.0	0.0	−95.7	2.98	N.S.
Chaetodontidae	7.9	3.3	19.3	13.2	9.9	9.9	3.5	2.1	4.5	4.4	−56.1	2.36	N.S.
Diodontidae	0.3	0.7	0.0	0.0	0.0	0.0	0.1	0.4	0.0	0.0	−73.3	0.80	N.S.
Labridae	87.0	36.1	70.0	6.0	112.8	57.8	115.4	54.3	35.3	22.3	11.8	0.07	N.S.
Pomacanthidae	2.6	2.6	4.5	0.6	0.4	0.7	6.1	5.8	0.5	0.6	−33.9	0.22	N.S.
Pomacentridae	136.8	135.9	317.3	98.5	609.0	268.6	417.9	229.4	179.8	115.9	77.2	1.02	N.S.
Scaridae (Adult)	35.5	12.2	34.5	12.4	7.3	7.5	35.0	42.9	6.3	7.2	−53.8	2.40	N.S.
Scaridae (Juveniles)	0.0	0.0	0.0	0.0	0.0	0.0	30.3	41.1	0.0	0.0		0.60	N.S.

[a] N.S. = not significant, + = $p < 0.07$, * = $p < 0.05$, ** = $p < 0.01$.

Table 3
Population densities (no. per 500 m^2) of the studied fish species in the three regions. The *F*-value and level of significance from the one-way ANOVA comparison of differences among protection are given

Species	Protected		Unprotected		Difference %	ANOVA	
	Mean	s.e.m.	Mean	s.e.m.		*F*-value	Significance
Acanthuridae							
Ctenochaetus striatus	10.83	4.17	8.72	3.55	−19.49	0.14	N.S.
Acanthurus nigrofuscus	13.75	5.80	3.17	2.65	−76.97	3.66	+
Naso annulatus	13.10	4.61	0.11	0.11	−99.15	15.25	**
Zebrasoma scopas	4.17	1.61	3.17	1.48	−24.00	0.19	N.S.
Ctenochaetus strigosus	4.07	1.79	1.33	0.71	−67.21	2.86	N.S.
Acanthurus leucosternon	2.27	0.84	0.56	0.28	−75.49	5.70	*
Acanthurus tennenti	1.77	0.94	0.00	0.00	−100.00	6.84	*
Acanthurus triostegus	1.68	1.34	0.00	0.00	−100.00	3.04	N.S.
Zebrasoma veliferum	0.58	0.36	0.39	0.12	−33.33	0.36	N.S.
Paracanthurus hepatus	0.63	0.63	0.00	0.17	−100.00	1.93	N.S.
Acanthurus dussumieri	0.35	0.35	0.06	0.06	−84.13	1.25	N.S.
Acanthurus nigricauda	0.08	0.05	0.17	0.17	100.00	0.13	N.S.
Naso lituratus	0.25	0.16	0.00	0.00	−100.00	4.82	*
Acanthurus xanthopterus	0.05	0.05	0.17	0.60	233.33	0.50	N.S.
Naso unicornis	0.03	0.03	0.00	0.00	−100.00	1.93	N.S.
Balistidae							
Sufflamen chrysopterus	1.65	0.73	0.00	0.17	−100.00	9.81	**
Balistapus undulatus	1.18	0.37	0.17	0.08	−85.92	12.57	**
Rhinecanthus aculeatus	0.33	0.33	0.00	0.00	−100.00	1.93	N.S.
Pseudobalistes fuscus	0.13	0.13	0.00	0.00	−100.00	1.93	N.S.
Balistoides viridescens	0.03	0.03	0.00	0.00	−100.00	1.93	N.S.
Chaetodontidae							
Chaetodon trifasciatus	7.37	3.58	2.60	1.28	−64.71	2.44	N.S.
Chaetodon trifascialis	4.22	2.44	1.05	0.45	−75.10	3.18	+
Chaetodon auriga	1.37	0.49	1.25	0.54	−8.54	0.02	N.S.
Chaetodon kleinii	0.20	0.20	0.65	0.37	225.00	0.68	N.S.
Chaetodon guttatissimus	0.83	0.35	0.00	0.10	−100.00	12.60	**
Chaetodon zanzibarensis	0.27	0.19	0.30	0.20	12.50	0.01	N.S.
Chaetodon lunula	0.05	0.05	0.40	0.21	700.00	1.34	N.S.
Chaetodon xanthocephalus	0.38	0.16	0.05	0.07	−86.96	6.44	*
Chaetodon falcula	0.33	0.19	0.00	0.00	−100.00	6.67	*
Chaetodon melannotus	0.03	0.03	0.15	0.13	350.00	0.56	N.S.
Diodontidae							
Diodon hystrix	0.13	0.13	0.00	0.00	−100.00	2.17	N.S.
Diodon liturosus	0.03	0.03	0.05	0.05	50.00	0.05	N.S.
Labridae							
Thalassoma amblycephalum	38.13	14.97	23.70	7.54	−37.85	0.94	N.S.
Thalassoma hebraicum	13.52	3.50	21.35	4.19	57.95	1.79	N.S.
Gomphosus caeruleus	8.43	1.64	10.80	2.12	28.06	0.54	N.S.
Labroides dimidiatus	6.58	2.27	11.70	2.23	77.72	2.57	N.S.
Thalassoma hardwicke	6.40	1.76	6.00	3.33	−6.25	0.01	N.S.
Stethojulis albovittata	5.88	1.48	4.30	1.02	−26.91	0.85	N.S.
Labrichthys unilineatus	4.75	2.71	2.65	1.34	−44.21	0.62	N.S.
Halichoeres hortulanus	2.68	1.06	3.75	1.59	39.75	0.21	N.S.
Pseudocheilinus hexataenia	4.02	1.61	2.40	0.81	−40.25	1.19	N.S.
Hemigymnus melapterus	0.60	0.36	1.65	0.75	175.00	0.95	N.S.
Anampses meleagrides	1.55	0.78	0.65	0.33	−58.06	1.88	N.S.
Thalassoma lunare	0.20	0.12	1.95	1.31	875.00	0.85	N.S.
Cheilinus oxycephalus	0.00	0.00	1.45	0.55		2.48	N.S.
Anampses twistii	0.40	0.10	1.00	0.31	150.00	1.39	N.S.
Anampses caeruleopunctatus	0.77	0.28	0.45	0.27	−41.30	0.53	N.S.
Cheilinus trilobatus	0.10	0.10	1.05	0.40	950.00	2.62	N.S.
Cheilio inermis	0.18	0.15	0.90	0.53	390.91	0.88	N.S.

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Table 3 (*Continued*)

Species	Protected		Unprotected		Difference %	ANOVA	
	Mean	s.e.m.	Mean	s.e.m.		*F*-value	Significance
Coris caudimacula	0.15	0.10	0.90	0.50	500.00	1.08	N.S.
Bodianus axillaris	0.67	0.24	0.35	0.17	−47.50	1.18	N.S.
Hemigymnus fasciatus	0.58	0.20	0.20	0.15	−65.71	4.53	+
Coris formosa	0.27	0.17	0.40	0.21	50.00	0.17	N.S.
Labroides bicolor	0.37	0.10	0.30	1.43	−18.18	0.08	N.S.
Halichoeres marginatus	0.00	0.00	0.55	0.45		0.72	N.S.
Cheilinus fasciatus	0.00	0.00	0.50	0.24		2.17	N.S.
Halichoeres scapularis	0.30	0.30	0.20	0.15	−33.33	0.11	N.S.
Stethojulis strigiventer	0.00	0.00	0.45	0.36		1.07	N.S.
Novaculichthys taeniourus	0.10	0.10	0.30	0.26	200.00	0.75	N.S.
Epibulus insidiator	0.05	0.05	0.30	0.25	500.00	0.48	N.S.
Coris gaimard africana	0.22	0.12	0.05	0.05	−76.92	2.29	N.S.
Cirrhalabrus exquisitus	0.00	0.00	0.15	0.15		0.48	N.S.
Halichoeres nebulosus	0.00	0.00	0.10	0.10		0.48	N.S.
Hologymnosus doliatus	0.10	0.07	0.00	0.00	−100.00	4.88	*
Coris aygula	0.07	0.07	0.00	0.05	−100.00	2.17	N.S.
Hologymnosus annulatus	0.00	0.00	0.05	0.15		0.48	N.S.
Cheilinus diagrammus	0.00	0.00	0.00	0.00		0.00	N.S.
Cheilinus mentalis	0.00	0.00	0.00	0.45		0.00	N.S.
Pomacanthidae							
Centropyge multispinis	2.80	0.34	2.10	1.27	−25.00	0.15	N.S.
Pomacanthus semicirculatus	0.20	0.12	0.75	0.59	275.00	0.41	N.S.
Pygoplites diacanthus	0.10	0.10	0.15	0.11	50.00	0.09	N.S.
Pomacanthus chrysurus	0.10	0.10	0.00	0.00	−100.00	2.17	N.S.
Pomacentridae							
Chromis viridis	97.55	66.72	69.35	26.76	−28.91	0.22	N.S.
Pomacentrus sulfureus	87.53	60.28	14.35	4.97	−83.61	3.11	N.S.
Neopomacentrus azysron	26.00	16.00	74.85	53.49	187.88	0.40	N.S.
Plectroglyphidodon lacrymatus	16.65	2.67	83.75	23.29	403.00	3.96	+
Chromis dimidiata	40.83	21.29	28.30	19.63	−30.69	0.16	N.S.
Dascyllus aruanus	2.30	2.18	47.65	31.61	1971.74	0.99	N.S.
Stegastes nigricans	13.70	13.33	34.50	22.57	151.82	0.38	N.S.
Chrysiptera unimaculata	11.62	7.62	34.25	9.73	194.84	2.20	N.S.
Chromis ternatensis	33.55	23.80	7.50	6.67	−77.65	1.92	N.S.
Chromis nigrura	26.97	12.59	7.80	4.81	−71.08	3.04	N.S.
Abudefduf sexfasciatus	18.67	17.09	8.20	2.18	−56.07	0.76	N.S.
Plectroglyphidodon dickii	16.33	5.49	7.60	3.49	−53.47	2.00	N.S.
Dascyllus trimaculatus	2.40	1.94	19.45	11.62	710.42	1.04	N.S.
Abudefduf vaigiensis	8.40	8.28	6.60	3.92	−21.43	0.05	N.S.
Pomacentrus caeruleus	3.17	1.66	11.50	9.85	263.16	0.35	N.S.
Amphiprion akallopisos	3.97	3.04	7.40	2.89	86.55	0.56	N.S.
Chromis weberi	1.15	0.80	9.75	5.85	747.83	1.04	N.S.
Abudefduf sparoides	4.03	3.99	4.30	1.98	6.61	0.00	N.S.
Pomacentrus pavo	2.00	2.00	4.60	3.07	130.00	0.32	N.S.
Amphiprion allardi	0.93	0.31	4.60	3.80	392.86	0.86	N.S.
Stegastes lividus	0.00	0.00	4.50	2.99		1.07	N.S.
Neoglyphidodon melas	1.60	1.12	2.50	1.03	56.25	0.32	N.S.
Dascyllus carneus	0.13	0.13	2.75	0.15	1962.50	0.49	N.S.
Pomacentrus baenschi	1.27	0.94	0.65	0.47	−48.68	0.58	N.S.
Amblyglyphidodon leucogaster	0.65	0.53	1.10	1.22	69.23	0.16	N.S.
Plectroglyphidodon johnstonianus	1.00	0.65	0.10	15.39	−90.00	3.94	+
Chrysiptera biocellata	0.63	0.45	0.00	0.05	−100.00	4.21	+
Pomacentrus pulcherrimus	0.33	0.19	0.00	1.40	−100.00	6.67	*
Dascyllus reticulatus	0.27	0.27	0.00	0.70	−100.00	2.17	N.S.
Stegastes fasciolatus	0.00	0.00	0.25	0.25		0.48	N.S.
Abudefduf melanopus	0.13	0.10	0.00	0.00	−100.00	4.08	+
Chrysiptera leucopoma	0.10	0.10	0.00	5.40	−100.00	2.17	N.S.
Chrysiptera glauca	0.00	0.00	0.05	0.00		0.48	N.S.

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Table 3 (*Continued*)

Species	Protected		Unprotected		Difference %	ANOVA	
	Mean	s.e.m.	Mean	s.e.m.		*F*-value	Significance
Scaridae							
Scarus sordidus	17.38	2.38	2.83	0.82	−83.70	50.48	**
Scarus frenatus	4.80	1.23	1.50	0.52	−68.75	8.26	*
Scarus niger	3.48	1.73	1.28	0.62	−63.32	2.18	N.S.
Scarus ghobban	1.23	0.95	1.17	0.88	−5.41	0.00	N.S.
Scarus russelii	1.87	0.97	0.11	0.07	−94.05	6.18	*
Scarus scaber	0.90	0.68	0.89	0.89	−1.23	0.00	N.S.
Scarus rubroviolaceus	1.45	0.72	0.22	0.22	−84.67	4.15	+
Calotomus carolinus	0.35	0.23	1.17	0.61	233.33	0.93	N.S.
Scarus gibbus	1.18	0.55	0.33	0.22	−71.83	2.93	N.S.
Hipposcarus harid	0.92	0.38	0.06	0.06	−93.94	9.19	*
Scarus falcipinnis	0.67	0.26	0.17	0.12	−75.00	4.04	+
Cetoscarus bicolor	0.42	0.20	0.17	0.12	−60.00	1.31	N.S.
Scarus viridifucatus	0.40	0.29	0.00	0.00	−100.00	3.63	+
Scarus atrilunula	0.37	0.26	0.00	0.00	−100.00	3.83	+
Scarus tricolor	0.13	0.13	0.11	0.11	−16.67	0.02	N.S.
Leptoscarus vaigiensis	0.00	0.00		0.06	0.06	0.54	N.S.

N.S. = not significant, + = $p < 0.07$, * = $p < 0.05$, ** = $p < 0.01$. The percentage difference between protected and unprotected reefs is also given

the butterfly, parrot, surgeon, and triggerfishes but 12–77% increases for the more species-rich and small-bodied damselfish and wrasse families (Table 2). Consequently, overall there was a statistically insignificant 25% decrease in species density between protected and unprotected reefs at the scale of 500 m^2. Plots of cumulative numbers of species, combining sites into the protected and unprotected categories further reflect these differences at the small scale but many of these differences in species numbers were not evident at the larger scale of 1 ha (Fig. 8).

4. Discussion

4.1. Fishing effects on East African patch reefs

The role of fishing on patch-reef ecology was studied by (1) comparing the macrobenthic and fish communities in 10 fished sites with five sites in two marine parks, and (2) by comparing five heavily fished reefs after a 22-year period in an area where fishing effort has approximately doubled over this time (Fig. 1). Both of these methods of study present some difficulties in making firm conclusions about the effects of fishing on reef ecology but we believe that the combination of spatial and temporal comparisons, even with their individual shortcomings, produces a reasonable picture of the ecological changes associated with moderate fishing. The best comparison of protected and unprotected areas should include several protected areas in order to reduce errors associated with pseudoreplication (Underwood, 1994). In the case of East African patch or island reefs, only two fully protected marine park exists which made additional replication of protected areas impossible. In order to reduce possible pseudoreplication errors we sampled a large amount of the existing variability in the two marine protected areas. This does not, however, suffice if there are some unique properties about these two reefs as a whole that would produce unfair comparisons. There are, however, notable physical differences between Kisite and CHICOP which make this possibility less likely. The comparison of five Dar es Salaam reef sites over time is weakened by a lack of quantitative data from the 1974 study as well as the limited focus on corals. We relied on map locations, reef profile diagrams, black and white photographs, and the authors description for comparisons. This is probably sufficient to document the most obvious changes. Below are some of the effects that we suggest are supported by these temporal and spatial comparisons as well as comparisons with the better-studied fringing reefs of Kenya.

Fishing, in this study, as in many other recent coral-reef studies has reduced the total wet weight of fish on fished reefs but the effects were not the same for all groups and some of the effects may not be due to the direct effects of fishing. The direct effects of fishing are probably most responsible for the lowered abundance of angelfish, scavengers, surgeonfish, and triggerfish in unprotected reefs. Lower abundance of some species of parrotfishes, and perhaps some surgeonfish species, may be the direct effect of fishing itself combined with the indirect effect of competition with sea urchins (Hay and Taylor, 1985; McClanahan et al., 1994, 1996). Other studies have shown decreases, no change and increases in herbivorous fish with increased fishing intensity

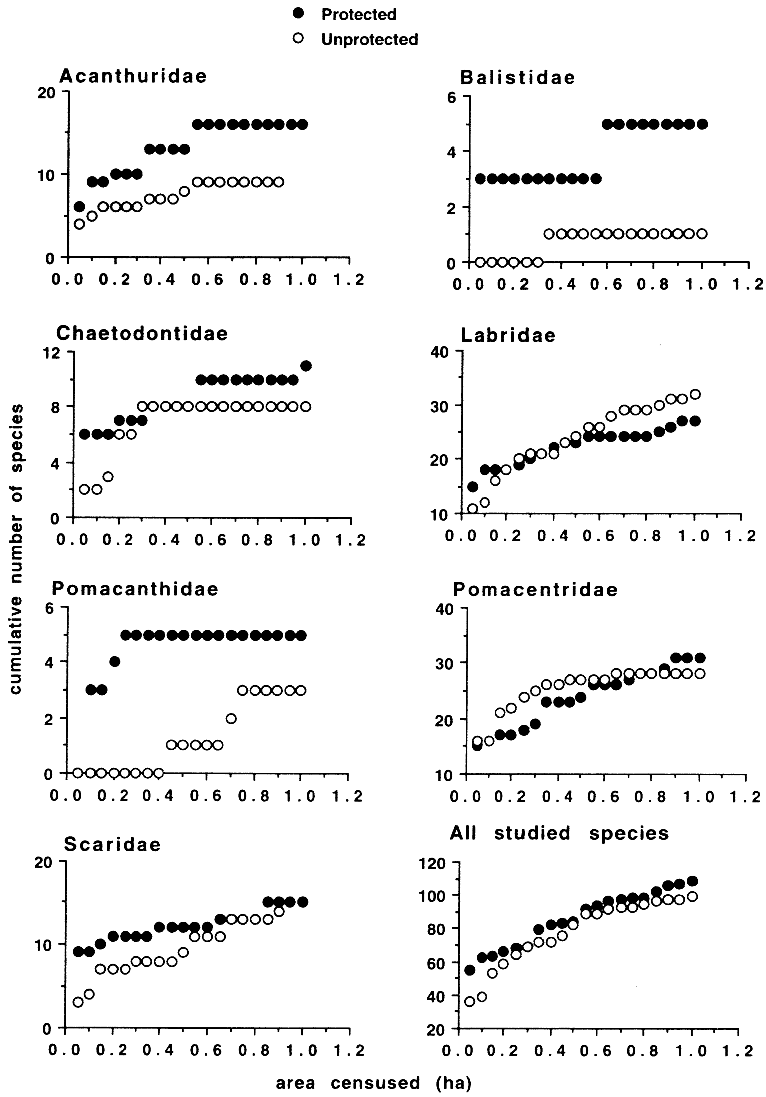

Fig. 8. Species-area relationships for the studied fish families and total sampled fauna comparing protected and unprotected reefs.

(Koslow et al., 1988; Russ and Alcala, 1989; Jennings et al., 1995; Roberts, 1995; Jennings and Polunin, 1996a). Where sea urchins are not abundant or controlled by fish predators, a number of responses are possible depending on the level of fishing and choices of the fisherfolk (for example see McClanahan, 1995a). There is also evidence from sea urchin reduction studies that snappers (Lutjanidae) and emperors (Lethrinidae) can be reduced by high sea urchin abundance but the cause is not well understood (McClanahan et al., 1996).

Increases in the numbers of individuals and species of damselfishes and wrasses in unprotected reefs is likely to be an indirect effect of fishing. A number of studies including this one have found increases in some small-bodied wrasses with increased fishing (Russ and Alcala, 1989; McClanahan, 1994; Jennings and Lock, 1996). These families of fish contain species with small body sizes that may experience ecological release with the loss of larger and more fishing-susceptible predators and, perhaps, competitors. Russ and Alcala (1989) attribute an increase in wrasse numbers in fished reefs to greater rubble in their fished sites while McClanahan (1994) suggests that it is the fusiform species that can escape through nets that show population increases.

The loss of triggerfish, particularly *Balistapus undulatus*, reduced rates of predation on sea urchins; increased sea urchin abundance appears to be one of the major consequences of fishing in East Africa—occurring in both fringing and patch reefs (McClanahan and Shafir, 1990; Watson and Ormond, 1994), but with some unique characteristics in each environment. Evidence to support this conclusion include the more abundant *B. undulatus*, higher predation rates on tethered sea urchins, and fewer sea urchins in the protected compared to unprotected reefs as well as direct observation on predation in the marine protected areas (McClanahan, 1995b). There was also evidence for increased sea urchin abundance in the Dar es Salaam reefs since 1974 associated with a doubling in fishing intensity The relationship between *B. undulatus* and predation on tethered sea urchins was, however, much stronger than with sea urchin abundance, particularly at the low levels of predators and predation. This suggests that, at low levels of predators, factors other than predation and *B. undulatus* abundance are controlling sea urchin abundance. Previous field studies suggest that *B. undulatus* is an aggressive species that can dominate baited sites and may, therefore, be a species very susceptible to fishing (McClanahan, 1995b; unpublished data). In the absence of *B. undulatus* some wrasses (species in the genus *Coris* and *Cheilinus*) and emperors (*Lethrinus mahensa*, *L. xanthochilus* and others) may occupy the sea urchin predator niche (McClanahan, 1995b) but these species appear less effective at controlling sea urchin populations.

In the studied patch reefs the sea urchins *Diadema savignyi*, *D. setosum*, and *Echinothrix diadema* were highest in unprotected reefs. This contrasts with Kenya's fringing reef where *Echinometra mathaei* is the dominant sea urchin and closely controlled by predation (McClanahan and Shafir, 1990). Differences in dominance between habitats is not clear but the larger bodied *Diadema* and *Echinothrix* may be more tolerant than the small-bodied *E. mathaei* to physical disturbances and open substrate that are probably greater in patch than fringing reefs, but this explanation remains speculative.

In general, the model of coral reef degradation developed in Kenya's fringing reefs has some predictive power for patch and rock-island reefs, as described above, except that there appears to be more species and population variability in the patch than fringing reefs which produces less predictable clustering of sites based on management when using species or genera-level groupings (Fig. 3). This may be attributable to either lowered levels of fishing in these patch compared to fringing reefs, and therefore fewer differences between reefs based on management, or, perhaps, that the smaller size of these reefs causes them to be more influenced by stochastic recruitment rather than biological interactions. Ault and Johnson (1998) studied the population dynamics of damselfish on small patch and continuous reefs and found higher population variability in the patch than the fringing reef environment and attributed this to differences in the size and connectivity of habitats. The factors of fishing intensity and reef size are difficult to tease apart as smaller and sparsely distributed reefs can spread out fishing effort while fringing reefs compress fishing into the calm lagoons behind fringing reefs and encourages fisherfolk without large or seaworthy boats.

Losses of coral abundance and diversity were not evident from the comparison of protected and unprotected reefs but there was evidence for losses and compositional changes in the Dar es Salaam reefs over the past 22 years. The difference in findings may reflect the different initial conditions of the reefs and the effects of physical disturbance on coral abundance. The Mbudya and Bongoyo sites were the most protected from physical disturbances and probably have a higher potential for maximum coral cover because of low wave disturbance. There is evidence, however, that disturbance directly by fishing, and perhaps by sea urchins and territorial damselfish has reduced the abundance and changed the generic composition of corals in four of the five visited sites—the least changed site (Mbudya 2) being the most wave-protected site. The most wave-exposed site visited in the Dar es Salaam area, Fungu Mkadya, has lost most live hard coral cover and the remaining calcium carbonate skeletons are now being grazed and eroded by sea urchins. These observations suggest that the damaging effects of fishing can be difficult to distinguish from natural physical disturbances like waves. Moreover, the effect of high physical disturbance combined with fishing may produce an additive or interactive force that can damage corals, associated species, and retard recovery.

A few of the reefs in the Tanga-Pangani area had a high cover of fleshy algae that may reflect reduced grazing intensity on these reefs. Sea urchin abundance was variable among these reefs and the relationship between fleshy algae and sea urchin abundance was not strong. One site in particular, Funguni, had both high sea urchin and fleshy algae abundance, but low coral cover. This may be attributable to the high bottom contour complexity of this site. High complexity may provide sufficient space for sea urchins and their grazing lawns, while fleshy algae dominates in sites where sea urchins cannot or do not graze. Competition with fleshy algae, grazing sea urchins, and damage from dynamite or fishing nets probably kept coral cover low at this site. The interactions between physical disturbance, fleshy algae, coral, and sea urchins is complex and requires additional experimental and field studies before they will be better understood.

4.2. Ecological status and conservation of northern Tanzanian coral reefs and protected areas

Fishing appears to be having some predictable and detrimental changes in the ecology of studied patch reefs but the damage on most of the visited reefs was not so severe that species of coral and fish were lost. Reef damage by fishing is most evident for the total abundance of fish and for some important grazing and invertebrate-feeding species. Corals appears to be least effected by fishing although there appeared to be some loss of coral cover and species composition changes in Mbudya 1, Bongoyo 1, Fungu Mkadya, and Funguni. This result is surprising in that unregulated dynamite fishing and pull seines, and their damage to coral has been the focus of past conservation concerns (UNEP, 1989). Dynamite fishing is, however, expensive, unacceptable in some fishing communities, and therefore used frugally and often secretively. Dynamite fishing is often focused on abundant and schooling fishes in offshore waters or reefs where detection or competition with other fishing methods is reduced. Nonetheless, dynamite damage was evident at some visited reefs by the existence of circular craters of 1 to 2 m radius among living coral and explosives may be largely responsible for the poor condition of Fungu Mkadya and Funguni reefs. Overall, however, these craters were rarely so common at our study sites that coral was eliminated over large areas (Fungu Mkadya and Funguni being exceptions). Fished reefs were in poor enough condition that they could benefit from fisheries management but not so poor that they could not recover if given some protective management. Consequently, we would encourage both increased fisheries management to reduce effort and destructive methods, the revitalization of the marine protected areas, and efforts to reduce the harvest of *B. undulatus* and some of the most affected species, such as in the genus *Scarus*.

Acknowledgements

Research was supported by the Pew Scholars in the Environment Program grant to The Wildlife Conservation Society and the US State Department's International Coral Reef Initiative (Principal Investigator—R.N. Ginsburg). Institutional support was provided by University of Dar es Salaam Institute of Marine Science, Chumbe Island Coral Park, Kunduchi Fisheries and Training Institute, Tanzanian Fisheries Department, Tanga Coastal Conservation and Development Program (IUCN), and Kenya Wildlife Service. For assistance with logistics we are grateful to J. Francis, C. Horrill, A. Nikundiwe, D. Obura, and S. Reidemiller in Tanzania and the Wardens of the Kisite MNP in Kenya.

Appendix A

Table 4
Summary statistics of the mean (S.D.) values of the (a) percent gross substrate categories, (b) relative abundance of hard coral cover, (c) dominant algal genera (cm/10 m), (d) sea urchin parameters of density (no. per 10m^2) and wet weight (kg/ha) and (e) fish wet weights (kg/ha) for each of the 15 studied sites

(a) Gross substrate categories

Reef sites	Hard Coral	Turf algae	Fleshy algae	Coralline algae	Sand	Soft coral	Seagrass	Sponge	Calcareous algae
Protected Reef									
Kisite 1	22.10	44.64	14.00	5.67	10.03	3.44	0.00	0.13	0.00
($n=20$)	(15.24)	(14.16)	(9.32)	(5.44)	(10.12)	(4.06)	(0.00)	(0.40)	(0.00)
Kisite 2	31.66	41.57	0.65	3.21	14.16	8.74	0.00	0.00	0.00
($n=24$)	(28.99)	(30.03)	(1.28)	(4.12)	(17.83)	(8.02)	(0.00)	(0.00)	(0.00)
Kisite 3	19.41	51.80	0.98	1.86	18.44	7.51	0.00	0.00	0.00
($n=24$)	(24.70)	(21.99)	(1.30)	(2.33)	(15.35)	(7.83)	(0.00)	(0.00)	(0.00)
Chumbe 1	51.61	16.06	13.94	7.53	11.31	0.32	0.00	0.42	0.07
($n=9$)	(20.34)	(13.67)	(21.38)	(4.44)	(9.09)	(0.64)	(0.00)	(0.68)	(0.22)
Chumbe 2	73.94	9.53	0.61	7.00	6.53	1.28	0.00	0.24	1.03
($n=9$)	(9.02)	(6.40)	(1.10)	(3.66)	(5.49)	(2.55)	(0.00)	(0.30)	(2.06)
Unprotected reefs									
Tanga-Pangani area									
Funguni	5.03	36.82	40.30	7.18	1.61	2.11	6.62	0.34	0.00
($n=9$)	(4.95)	(13.72)	(8.57)	(3.55)	(1.81)	(2.42)	(8.06)	(0.53)	(0.00)
Makome	28.61	33.08	28.06	6.86	0.00	3.26	0.00	0.00	0.13
($n=9$)	(27.21)	(17.17)	(16.72)	(4.94)	(0.00)	(5.01)	(0.00)	(0.00)	(0.38)
Taa	21.32	45.93	17.01	2.03	8.37	2.91	1.84	0.52	0.07
($n=9$)	(11.02)	(7.47)	(9.05)	(2.11)	(8.00)	(3.00)	(3.19)	(1.03)	(0.22)
Changale	40.68	25.20	22.24	4.25	0.98	6.38	0.00	0.27	0.00
($n=7$)	(11.38)	(11.43)	(13.16)	(2.82)	(1.69)	(5.16)	(0.00)	(0.72)	(0.00)
Dar es Salaam–Kunduchi									
Mbudya 1	27.75	45.19	0.89	24.87	0.00	0.92	0.22	0.00	0.17
($n=11$)	(10.30)	(17.35)	(1.19)	(19.15)	(0.00)	(1.13)	(0.73)	(0.00)	(0.56)
Mbudya 2	77.77	10.64	0.00	7.73	0.16	0.32	3.16	0.21	0.00
S.D.	(19.07)	(15.15)	(0.00)	(9.61)	(0.51)	(0.70)	(9.98)	(0.48)	(0.00)
Bongoyo 1	36.00	51.84	0.60	8.17	0.55	2.33	0.00	0.50	0.00
($n=10$)	(14.06)	(14.14)	(1.13)	(5.40)	(1.25)	(2.31)	(0.00)	(0.81)	(0.00)
Bongoyo 2	28.78	43.48	0.00	11.15	7.67	7.82	0.81	0.29	0.00
	(14.95)	(16.14)	(0.00)	(16.28)	(9.67)	(8.87)	(2.57)	(0.72)	(0.00)
Zanzibar–town islands									
Changuu	44.69	40.64	0.05	5.10	5.22	4.30	0.00	0.00	0.00
($n=9$)	(21.94)	(18.47)	(0.15)	(6.82)	(7.71)	(4.45)	(0.00)	(0.00)	(0.00)
Chapwani	52.32	31.21	1.36	7.89	2.33	4.68	0.00	0.56	0.00
($n=9$)	(8.93)	(8.46)	(1.27)	(3.65)	(3.51)	(7.35)	(0.00)	(0.85)	(0.00)

Table 4 (*Continued*)

(b) Dominant cover of the coral genera and subgenera presented as percentage cover of the hard corals. Ordered from most to least abundant from right to left

Genera/species	*Galaxea astreata*	*Acropora*	*Porites*, branching	*Montipora*	*Porites*, massive	*Galaxea fascicularis*	*Fungia*	*Pocillopora*	*Millepora*	*Echinopora*	*Hydnophora*	*Seriatopora*	*Platygyra*	*Favites*	*Pavona*
Protected reefs															
Kisite 1	3.6	13.6	40.9	2.6	14.3	1.3	0.4	3.1	0.9	1.6	1.2	7.2	1.1	1.6	0
Kisite 2	9.2	3.2	61.5	13.8	0.4	0.2	0.7	0.6	1	5	0.7	2	0.4	0.1	0
Kisite 3	57.3	3.1	19.4	2.7	1	0.4	1.8	1.5	0.2	3.5	0.5	5.3	0.3	0.8	0
Chumbe 1	2	65.5	6.4	0.1	9	0	3.2	0	2.5	0	0	0.3	0.1	0	0
Chumbe 2	2	43.1	18.1	6.2	15.9	0	0.2	0.6	2.9	0	0.6	0.2	0	0.1	0.4
Unprotected Tanga-Pangani															
Funguni	6.7	9.1	1.7	30	15.3	0	0	12.3	6.5	0	7.8	0	1.7	4.8	0
Makome	90	1	7	0	0	0	0	1.3	0	0	0.2	0	0	0	0
Taa	1.3	1.6	4.6	0.9	71	0	0.3	2.2	6.4	0.7	0.8	0	3.2	2.8	0.5
Changale	0	3.8	14.1	43.1	1.9	3.9	0	1.5	5.9	2.2	4.9	0	5.4	2.2	0.4
Dar es Salaam															
Mbudya 1	0	29.5	6.6	43.1	0.2	1.3	5.8	2.3	0	2.4	0	0	0	0.2	4.4
Bongoyo 1	22.4	12.2	2.7	9.1	3.7	33.1	4	3	0.6	1.3	0.4	0	0.5	0.1	2.5
Bongoyo 2	23.1	22.2	1	2.1	0.7	10.4	29.6	0.7	0.4	1.3	0.4	0.4	2.2	0	0
Zanzibar															
Changuu	35.7	10.6	2	0.3	4.3	0	1.7	0.7	0.2	0	0.5	0	0.3	0	0
Chapwani	32.6	4	1.8	0	1.5	0	0.7	0	0.2	0.1	0	0	0	0	0

(c) Fleshy macroalgae by genus

Reef sites	*Sargassum*	*Turbinaria*	*Dictyota*	*Hypnea*	*Dictyospheria*	*Haliptylon*	*Pocockiella*	*Padina*	*Lyngbya*
Protected Reef									
Kisite 1	137.4	21.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(*n* = 20)	(103.3)	(18.6)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Kisite 2	0.8	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
n = 24	(2.0)	(5.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Kisite 3	5.1	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(*n* = 24)	(7.6)	(14.4)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Chumbe 1	134.0	5.0	8.8	0.0	0.0	0.0	0.0	0.0	0.0
n = 9	(211.5)	(7.6)	(11.9)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Chumbe 2	2.2	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(*n* = 9)	(4.4)	(9.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Unprotected reefs									
Tanga-Pangani Funguni	300.9	60.7	32.3	6.2	4.4	0.0	0.0	0.3	0.0
(*n* = 9)	(115.8)	(43.6)	(51.8)	(17.6)	(6.4)	(0.0)	(0.0)	(1.0)	(0.0)
Makome	253.8	3.7	6.3	0.0	4.8	0.0	0.0	0.0	2.1
(*n* = 9)	(153.7)	(6.4)	(10.0)	(0.0)	(8.1)	(0.0)	(0.0)	(0.0)	(6.3)
Taa	168.0	6.0	12.7	0.0	0.0	0.0	0.0	4.0	0.0

Table 4 (*Continued*)

Reef sites	*Sargassum*	*Turbinaria*	*Dictyota*	*Hypnea*	*Dictyospheria*	*Haliptylon*	*Pocockiella*	*Padina*	*Lyngbya*
($n=9$)	(97.5)	(7.9)	(12.8)	(0.0)	(0.0)	(0.0)	(0.0)	(6.2)	(0.0)
Changale	142.4	1.7	37.7	3.2	0.0	0.0	4.9	0.0	0.0
($n=7$)	(147.4)	(5.0)	(33.9)	(9.7)	(0.0)	(0.0)	(8.4)	(0.0)	(0.0)
Dar es Salaam–Kunduchi									
Mbudya 1	0.0	4.6	0.0	0.0	5.7	6.6	0.0	0.0	0.0
($n=11$)	(0.0)	(4.4)	(0.0)	(0.0)	(12.5)	(11.1)	(0.0)	(0.0)	(0.0)
Mbudya 2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
($n=10$)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Bongoyo 1	0.0	0.0	0.9	6.1	0.0	0.0	0.0	0.0	0.0
($n=10$)	(0.0)	(0.0)	(2.8)	(13.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Bongoyo 2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
($n=10$)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Zanzibar–town islands									
Chanuu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0
($n=9$)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(1.6)	(0.0)
Chapwani	0.0	0.0	0.0	12.2	0.0	0.0	0.0	0.0	0.0
($n=9$)	(0.0)	(0.0)	(0.0)	(14.2)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)

(d) Sea urchin by species, their diversity and the predation index on tethered *Echinometra mathaei*. Values are population density (no. per $10m^2$) and the wet weight estimates (kg/ha), without an estimate of error

Sites	*Diadema savignyi*	*Echinothrix diadema*	*Diadema setosum*	*Tripneustes gratilla*	*Echinothrix calamaris*	*Echinometra mathaei*	*Echinostrephus molaris*	*Toxopneustes pileolus*	All urchins	Diversity $D=$	Species richness	Predation index
Individual wet weight (g)	120.3	276.9	141.3	246.5	150	41.7	2.5	100.0				
Protected reef												
Kisite 1	1.1	0.8	0.0	0.0	0.1	1.0	8.8	0.0	11.8	0.42	5	0.82
	(0.7)	(0.3)	(0.0)	(0.0)	(0.0)	(1.0)	(7.7)	(0.0)	(7.6)			
	133.7	230.8	0.0	0.0	2.4	41.7	22.1	0.0	430.6			
Kisite 2	0.4	1.4	0.0	0.0	0.0	0.0	1.1	0.0	2.9	0.60	3	0.86
	(0.7)	(3.4)	(0.0)	(0.0)	(0.0)	(0.0)	(1.8)	(0.0)	(3.3)			
	46.8	400.0	0.0	0.0	0.0	0.0	2.6	0.0	449.4			
Kisite 3	0.1	0.1	0.0	0.0	0.1	0.7	0.6	0.0	2.6	0.88	5	0.88
	(0.5)	(0.4)	(0.0)	(0.0)	(0.0)	(0.0)	(5.6)	(0.0)	(5.6)			
	13.4	30.8	0.0	0.0	4.9	27.8	1.4	0.0	78.2			
Chumbe 1	0.0	0.2	3.2	0.0	0.0	0.0	0.0	0.0	3.4	0.12	2	0.52
	(0.0)	(0.4)	(5.1)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(5.1)			
	0.0	61.5	455.3	0.0	0.0	0.0	0.0	0.0	516.8			
Chumbe 2	0.3	0.1	10.8	0.0	0.0	0.0	0.0	0.1	11.3	0.08	4	0.38
	(0.5)	(0.2)	(12.8)	(0.0)	(0.0)	(0.0)	(0.0)	(0.2)	(12.8)			
	40.1	15.4	1530.8	0.0	0.0	0.0	0.0	5.6	1591.8			

Table 4 (*Continued*)

Sites	*Diadema savignyi*	*Echinothrix diadema*	*Diadema setosum*	*Tripneustes gratilla*	*Echinothrix calamaris*	*Echinometra mathaei*	*Echinostrephus molaris*	*Toxopneustes pileolus*	All urchins	Diversity $D=$	Species richness	Predation index
Unprotected reefs—Tanga-Pangani area												
Funguni	21.9	9.9	0.1	0.0	0.3	0.3	3.8	0.0	36.3	0.55	6	0.05
	(15.8)	(5.8)	(0.3)	(0.0)	(0.5)	(0.5)	(2.5)	(0.0)	(11.5)			
	2633.2	2738.2	15.7	0.0	50.0	13.9	9.4	0.0	5460.5			
Makome	0.1	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.25	2	0.50
	(0.3)	(1.7)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(1.7)			
	13.4	184.6	0.0	0.0	0.0	0.0	0.0	0.0	198.0			
Taa	11.9	3.2	0.3	0.1	0.0	0.4	6.6	0.4	23.0	0.63	7	0.56
	(14.7)	(2.5)	(0.5)	(0.3)	(0.0)	(0.5)	(3.4)	(1.0)	(12.6)			
	1430.2	892.2	47.1	27.3	0.0	18.5	16.4	44.4	2476.3			
Changale	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.00	1	0.37
	(0.0)	(2.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(2.3)			
	0.0	584.6	0.0	0.0	0.0	0.0	0.0	0.0	584.6			
Dar es Salaam–Kunduchi area												
Mbudya 1	1.7	15.2	0.0	3.4	0.5	0.0	0.3	0.0	21.0	0.44	5	0.15
	(1.8)	(13.8)	(0.0)	(5.0)	(0.9)	(0.0)	(0.6)	(0.0)	(14.5)			
	200.5	4199.7	0.0	842.2	75.0	0.0	0.6	0.0	5318.0			
Mbudya 2	8.5	0.9	0.1	0.0	0.0	0.0	0.0	0.0	9.6	0.20	3	0.27
	(11.1)	(1.3)	(0.4)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(11.0)			
	1026.6	258.4	18.8	0.0	0.0	0.0	0.0	0.0	1303.8			
Bongoyo 1	43.4	3.3	2.9	0.0	0.4	0.0	0.2	0.0	50.2	0.25	5	0.42
	(40.5)	(3.5)	(4.3)	(0.0)	(0.7)	(0.0)	(0.8)	(0.0)	(40.5)			
	5221.0	923.0	405.1	0.0	60.0	0.0	0.5	0.0	6609.6			
Bongoyo 2	34.7	2.3	6.5	0.0	0.0	0.0	0.0	0.0	43.5	0.34	3	0.43
	(19.1)	(2.6)	(4.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(20.2)			
	4170.4	646.1	913.7	0.0	0.0	0.0	0.0	0.0	5730.2			
Zanzibar–town islands												
Changuu	1.9	0.3	18.6	0.0	0.0	0.4	0.0	0.0	21.2	0.23	4	0.24
	(2.4)	(1.0)	(16.6)	(0.0)	(0.0)	(1.0)	(0.0)	(0.0)	(16.9)			
	227.2	92.3	2621.9	0.0	0.0	18.5	0.0	0.0	2960.0			
Chapwani	0.1	0.2	32.3	0.0	0.0	0.0	0.0	0.0	32.7	0.02	3	0.26
	(0.3)	(0.4)	(18.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(18.3)			
	13.4	61.5	4568.7	0.0	0.0	0.0	0.0	0.0	4643.6			

Table 4 (*Continued*)

(e) Fish wet weight (kg/ha) by family

Sites	Acanthu-ridae	Balistidae	Chaetodo-ntidae	Labridae	Lutjanidae	Mullidae	Pomacan-thidae	Pomacen-tridae	Scaridae	Siganidae	Others	Total
Protected reefs												
Kisite 1	142.2	23.8	15.1	42.7	176.6	0.9	17.1	48.4	156.7	0.5	59.2	683.3
	(17.0)	(19.3)	(8.8)	(3.1)	(44.0)	(0.3)	(6.8)	(4.3)	(20.7)	(0.4)	(12.1)	(7.4)
Kisite 2	170.6	15.8	21.4	29.6	386.5	11.7	9.2	101.1	100.3	3.2	152.3	1001.6
	(25.6)	(2.6)	(0.0)	(20.0)	(82.5)	(16.4)	(9.0)	(17.2)	(62.1)	(4.5)	(47.2)	(243.7)
Kisite 3	88.5	19.5	11.0	29.8	4.7	1.1	11.5	59.3	109.2	0.3	27.4	362.4
	(31.7)	(4.1)	(5.2)	(2.8)	(4.0)	(0.4)	(10.7)	(28.8)	(38.9)	(0.4)	(5.1)	(121.6)
Chumbe 1	23.8	4.2	45.7	49.7	32.4	32.3	16.2	68.5	554.9	6.38	49.7	890.9
	(18.0)	(6.0)	(3.8)	(41.1)	(23.5)	(5.0)	(5.9)	(16.0)	(104.0)	(9.03)	(19.8)	(175.3)
Chumbe 2	155.2	8.5	75.5	65.6	64.8	0.0	47.7	113.8	317.1	0.00	243.3	1091.7
	(6.5)	(0.0)	(9.2)	(43.0)	(0.0)	(0.0)	(26.9)	(15.6)	(0.4)	(0.00)	(127.2)	(70.6)
Unprotected reefs												
Tanga-Pangani area												
Ufunguni	60.2	0.0	11.6	74.5	19.2	8.5	5.5	47.2	51.3	1.5	28.5	307.9
	(1.4)	(0.0)	(3.8)	(32.7)	(5.4)	(10.6)	(5.5)	(9.2)	(35.1)	(0.8)	(27.3)	(61.8)
Makome	35.2	0.0	6.5	25.7	3.7	0.9	5.0	75.6	16.8	0.1	17.0	186.5
	(4.8)	(0.0)	(0.9)	(0.0)	(3.9)	(0.2)	(6.2)	(3.9)	(5.0)	(0.2)	(1.5)	(3.9)
Taa	74.1	0.9	6.5	37.7	31.0	0.2	4.5	74.1	22.4	4.8	73.8	329.9
	(3.7)	(1.3)	(6.6)	(4.1)	(15.1)	(0.3)	(1.6)	(0.2)	(6.5)	(2.3)	(48.9)	(40.4)
Changale	49.5	0.0	9.8	18.0	24.3	7.1	6.0	76.8	12.5	3.7	9.4	217.1
	(28.8)	(0.0)	(3.8)	(10.7)	(7.7)	(9.9)	(8.5)	(6.8)	(8.2)	(3.7)	(12.1)	(49.6)
Dar es Salaam–Kunduchi area												
Mbudya 1	43.3	0.0	9.2	30.2	7.9	0.0	0.0	59.3	17.3	1.1	25.6	193.9
	(33.4)	(0.0)	(3.0)	(8.1)	(8.3)	(0.0)	(0.0)	(22.0)	(13.3)	(1.0)	(2.3)	(25.5)
Mbudya 2	16.7	0.0	25.9	35.7	0.5	0.0	0.0	133.4	13.8	0.6	7.5	234.1
	(10.6)	(0.0)	(15.9)	(5.0)	(0.7)	(0.1)	(0.0)	(11.4)	(4.8)	(0.8)	(6.5)	(23.1)
Bongoyo 1	27.7	0.0	6.2	31.0	15.5	0.3	2.4	57.4	6.7	0.0	19.7	167.0
	(12.9)	(0.0)	(6.3)	(2.5)	(2.7)	(0.1)	(0.0)	(10.2)	(4.6)	(0.0)	(13.1)	(8.5)
Bongoyo 2	9.2	0.0	7.3	35.6	0.0	0.3	0.0	93.8	16.5	0.0	19.7	182.3
	(10.4)	(0.0)	(5.4)	(17.8)	(0.0)	(0.3)	(0.0)	(24.0)	(6.1)	(0.0)	(10.7)	(32.4)
Zanzibar												
Changuu	7.8	0.0	16.8	38.8	23.7	0.0	7.2	74.9	109.5	3.2	36.5	318.1
	(8.4)	(0.0)	(2.0)	(1.2)	(33.5)	(0.0)	(0.0)	(13.0)	(137.0)	(4.5)	(18.1)	(215.2)
Chapwani	0.0	0.0	5.6	7.4	0.0	0.0	0.0	63.9	26.2	0.0	62.9	166.0
	(0.0)	(0.0)	(1.3)	(2.7)	(0.0)	(0.0)	(0.0)	(32.0)	(16.3)	(0.0)	(4.3)	(21.4)

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