Comparing the management effectiveness of a marine park and a multiple-use collaborative fisheries management area in East Africa

T.R. McCLANAHAN[a],*, E. VERHEIJ[b] and J. MAINA[c]

[a] *Marine Programs, Wildlife Conservation Society, Bronx, NY 10460, USA*
[b] *IUCN, TCZCDP, PO Box 5036, Tanga, Tanzania*
[c] *Coral Reef Conservation Project, PO Box 99470, Mombasa, Kenya*

ABSTRACT

1. The coral reefs across the international border between Kenya and Tanzania, where historical differences in government policy and socio-economic conditions created two different management systems, were examined: a large permanent closed area and a collaborative fisheries management project that used gear management and small voluntarily and temporary closed areas, respectively. The diversity and ecology of the reefs in these two management systems were compared spanning a seven-year period to evaluate the effectiveness of the management and to assess the ecological response to a large-scale water-temperature anomaly in 1998.

2. Comparisons of rates of predation on sea urchins and of herbivory, using a seagrass assay, were made along with measures of benthic cover and fish abundance and diversity.

3. The collaborative fisheries management system was successful in increasing fish stocks, reducing erect algae, and maintaining ecological diversity and stability across the thermal anomaly. This management system, however, was not successful in protecting the expected full biodiversity of fish, predation rates on sea urchins, or the sensitive, branching coral species. Management of the fishery also increased fish stocks in the adjacent, large, permanently closed area, compared to Kenyan parks without this management.

4. The large, permanently closed area in the other system maintained high diversity, high predation rates on sea urchins and high herbivory rates, which maintained erect algae abundance and diversity at low levels. The temperature anomaly was destructive to a number of the dominant delicate branching coral species, but overall coral cover and diversity were maintained, although dominance switched from branching *Porites* spp. to *Seriatopora* spp. over this period. The large closed area system protected the undisturbed ecology of these reefs and associated ecological processes, and the full diversity of fish and coral, including sensitive species such as branching corals and slow-growing fish.

5. Collaborative fisheries and large permanent closed area management have different attributes that, when combined, should achieve the multiple purposes of sustainable fisheries, ecosystem functions and protection of fishing-sensitive species.
Copyright © 2005 John Wiley & Sons, Ltd.

*Correspondence to: T.R. McClanahan, CRCP, Kibaki Flats #12, Bamburi, Kenyatta Beach, PO Box 99470, Mombasa, Kenya 80107.
E-mail: tmcclanahan@wcs.org

INTRODUCTION

The management of tropical fisheries is complicated by the high diversity of fish, their habitats, diverse gear use, and the poverty of fishers and management organizations (Polunin et al., 1996). This creates considerable challenges for management that requires a consideration of socio-economic and ecological conditions of the fishery in order to achieve a management regime that sustains harvested populations, biological diversity and ecological processes. The mechanism needed to encourage and achieve sustainable management is an area of applied science needing active investigation and evaluation. Means to manage ecosystems and associated resource users vary considerably from full closure to various forms of restricted use. Variants of natural resource management are often influenced by moral and political philosophies that differ in their values towards the protection of nature and means to control people, achievement of sustainability and alleviation of poverty (Adams et al., 2004). Success of the various management systems can be measured by many social and ecological criteria but will ultimately rely on an evaluation of the populations and diversity of the species inhabiting the ecosystems.

This study presents an evaluation of coral reefs that lie within the same ecological region but on opposite sides of an international border and that have, because of different political histories, experienced different management systems. These are: a permanently closed area, the Kisite Marine National Park (MNP) in southern Kenya, and a collaborative fisheries management programme in the Tanga region of northern Tanzania (Figure 1). We evaluate the ecological and biodiversity status of these reefs over a seven-year period during which active management has increased protection, and a large-scale climatic disturbance, the 1998 El Nino Southern Oscillation (ENSO), affected many reefs in the region (Goreau et al., 2000). We also contrast the ecological effects of the large permanently closed-area versus the more complex collaborative fisheries management programme with control sites, namely the fished and unfished sites in Kenya, and assess the response of their ecology and diversity to climatic disturbance.

The management environment

Coastal marine management in Kenya and Tanzania has followed two different paths resulting from different philosophies of governance, socio-economic conditions, and associated policies. Both countries began the process of declaring national parks in the 1970s, including the Kisite MNP in 1978 and the Tanga Coral Gardens Marine Reserve in 1981 (Ray, 1968; Sheppard and Wells, 1988). The proposed and declared closed area in Tanga was, however, not implemented and it was believed that dynamite fishing in this area had largely destroyed the proposed park area (Horrill et al., 2000; Muthiga et al., 2000). In contrast, the Kisite MNP closed area eliminated fishing inside the park (Watson and Ormond, 1994), and restricted the use of destructive fishing gear in the adjacent reserve area (Watson et al., 1997).

McClanahan (1999) argued that the greater economic success of nature and beach tourism in Kenya during the 1970s and 1980s created the conditions needed to support a large and permanently closed-area management regime. In contrast, Tanzania had lower levels of tourism and, therefore, focused on community development and poverty alleviation that was less reliant on international tourism. These histories resulted from the different political–economic philosophies, socialism in Tanzania and capitalism in Kenya. In Tanzania, this led to a change in the purpose of natural resource management away from the creation of large closed areas for preservation and tourism towards sustainable use as a means to support small-scale natural resource users in order to alleviate their poverty. The different histories of these two management programmes, both within a short distance across the Kenya–Tanzania border, offers a unique opportunity for contrasting and evaluating the outcomes of these two management approaches. All study
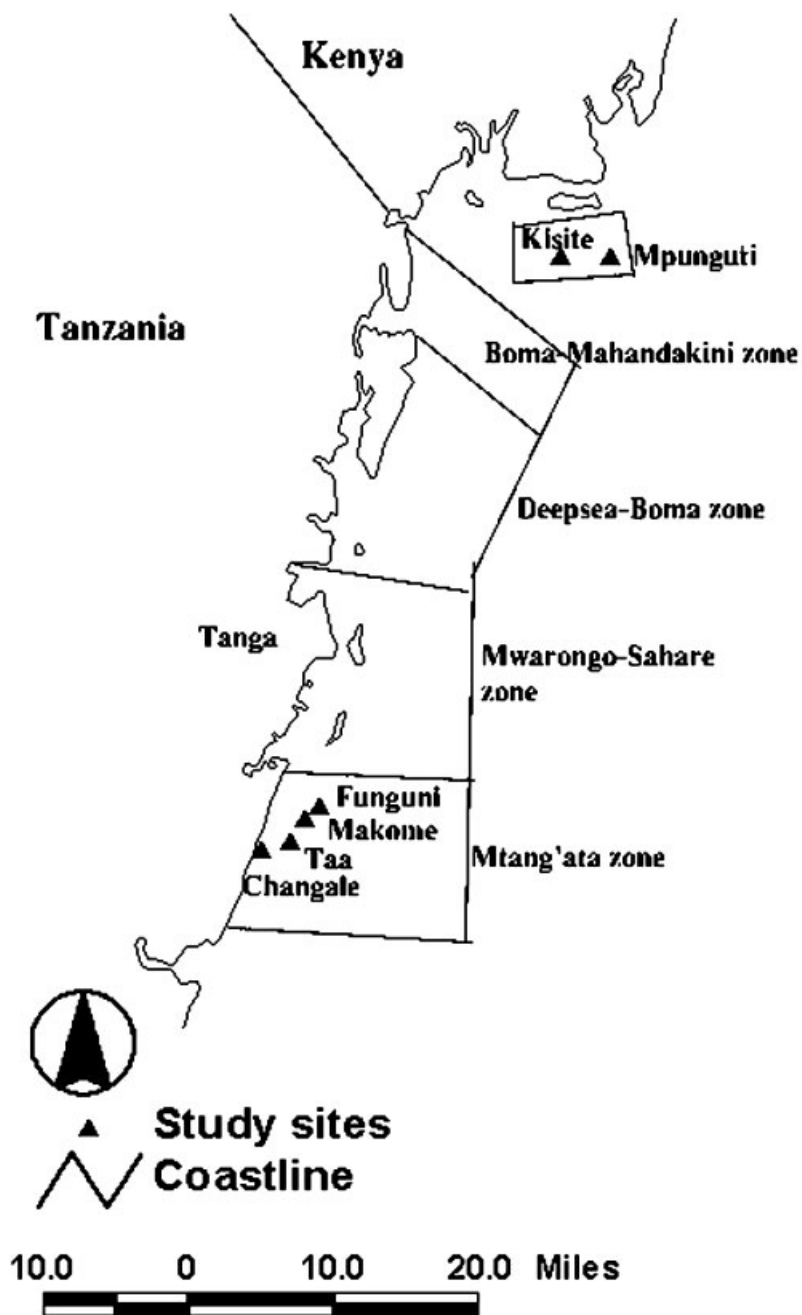
Figure 1. Map of the study areas, showing the collaborative fisheries management zones studied in Tanzania and the fully closed and adjacent gear-restricted zones in Kisite, Kenya.

sites experienced large-scale disturbances over the study period, with a coral bleaching and mortality event in 1998 (McClanahan et al., 2001) and an unidentified factor that killed coral in 2002 (McClanahan et al., 2004).

History of the Tanga Coastal Zone Conservation and Development Programme

Recognition of the degradation of coastal and marine resources led to the formulation of the Tanga Coastal Zone Conservation and Development Programme (TCZCDP) in 1994 (Makoloweka and Shurcliff, 1997; Muthiga et al., 2000; Horrill et al., 2001). The general goal of the programme was to enhance the well-being of the coastal communities by improving fisheries management and alternative uses. A collaborative approach was used to facilitate management by fishing villages and by local government authorities that relied on coral reefs, mangroves, and other coastal resources (Makoloweka and Shurcliff, 1997; Verheij et al., 2004).

The priority environmental issues identified were the declining fish catches, destructive fishing methods, in particular dynamite fishing, and the illegal mangrove cutting. Villages that shared the same resources delineated a Collaborative Management Area (CMA). The operating CMAs, from north to south, are Boma–Mahandakini (established in 2000), Deepsea–Boma (1998), Mwarongo–Sahare (1998) and Mtang'ata (1996), and together they cover a total of area 1600 km^2. The reefs evaluated in the present study are situated in the oldest CMA, Mtang'ata 25 km south of the regional capital Tanga (Figure 1).

The management of each CMA identified one or more small 0.25 to 3.0 km^2 reefs to be closed from extractive use. In Mtang'ata CMA they selected Kitanga and Upangu reefs for closure in 1996 (not shown on map). However, owing to political pressure they were forced to open these reefs in October 2000. Subsequently, during the 2001 review of the Mtang'ata CMA Plan, Makome reef and Shenguwe reef were closed as replacement for the two reopened reefs.

Since 1995, existing laws on illegal and destructive fishing practices have been enforced. Illegal and destructive fishing practices include dynamite and poison fishing, beach seining and dragging of nets. In addition, the enforcement units implement local and village by-laws related to fisheries. Part of their efforts is focused on monitoring the compliance with the government Fisheries Act, including boat and fishing licences. The enforcement agency has changed over time from the Marine Police to a Village Militia, and finally to the Navy in 1998. This was part of the changing role of the Navy in Tanzania, from a purely defence role towards a defence and civil role.

The enforcement activities have resulted in a reduction of dynamite fishing from about 180 blasts per month in 1995 to less than five blasts per month in 2003. In addition, large numbers of beach seines have been confiscated and destroyed, resulting in no further use of beach seines by 2001 (DoFi, 2001). Continuous enforcement of the ban on beach seines is necessary, however, because they are still sporadically used. Meanwhile, there has also been greater peer pressure to reduce illegal activities, encourage non-destructive gear and support closed areas within the CMAs. For example, the management committee of the Mtang'ata CMA has requested to change the limited 5–7-year closure to a permanent closure.

History of Kisite Marine National Park

The Kisite–Mpunguti MNP was first legally gazetted in 1973, regazetted in 1978 to open a previously closed reef in Mpunguti, and managed by the government park service, Kenya Wildlife Service. The park includes a fully closed area (~ 10 km^2) in which no resource extraction is allowed and an adjacent reserve around the small island of Mpunguti, in which enforcement of gear restrictions was the major management action (Figure 1). Watson et al. (1997) describe a period of increased management efforts in the early 1990s that resulted in improved fisheries catch in this region and differences in the populations of sea urchins between the closed and gear-managed areas (Watson and Ormond, 1994). Evaluation of the attitudes and economics

of those living adjacent to this management region found that people living closest to the park had the highest food security (Malleret-King, 2000). Dynamite fishing was reported in the mid-1980s on one remote reef (Mako Kokwe) not visited by tourists (Samoilys, 1988), but has not been reported since. Owing to high coral cover and diversity measurements, it is expected that enforcement has improved with the increasing levels of tourism and income at this site (Muthiga and McClanahan, 1997). In order to reduce the chance that the observed changes in these management systems were due to large-scale changes in East Africa, we compared the results of the Tanga–Kisite study with four fished reefs and three unfished marine parks in Kenya over the same time period.

METHODS

Study sites and experimental design

Four small reefs Chanjale (1.5 km^2), Taa (1.0 km^2), Makome (0.25 km^2), and Funguni (3.0 km^2) in the Mtang'ata CMA and three separate and comparable sites in the Kisite MNP were evaluated. The control or reference sites were located between $\sim$20 to $\sim$200 km north of the experimental sites and included five sites in Malindi, Watamu and Mombasa MNPs and seven sites at the heavily fished reefs of Vipingo, Kanamai, RasIwatine and Diani (for locations see map in McClanahan and Arthur, 2001). The sites were hard-bottom areas located in shallow ($<$3 m deep at low tide) lagoons protected from direct wave action and dominated by living and dead coral. Despite these similarities, the sites were selected to reflect the full reef diversity, differing in reef morphology and aspect.

At each site, measurements included two assays, one for herbivory and one for predation on sea urchins, together with quantitative studies of the cover of benthic macrobiota, sea urchin populations and fish communities. All studies, except herbivory measurements, were undertaken twice, once around the time of the initiation of the Tanga collaborative fisheries management programme in 1996 and once in late 2003 to early 2004. Herbivory assays were only performed in the latter period. In the Kenyan control sites, the same measurements were made except for the assay of herbivory and estimates of fish diversity.

Field measurements

Benthic substratum

Attached benthic communities were described by the line–intercept method using nine 10-m line transects at each site. Cover of benthic biota >3 cm in length under the line were classified into nine gross substrate 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 genus; branching and massive *Porites* spp. were also distinguished because they are functionally different. From these measurements the percentage cover of the various categories was calculated for each reef. Cover of the biotic groups was calculated as the mean numbers of centimetre per metre of line transect. Diversity of hard corals and fleshy algae was calculated as the number of taxa in each of these groups found in the 90 m of line transect.

In order to determine the number of coral genera, on a scale larger than permitted by line transects, a search-sampling technique was completed at the studied reefs (McClanahan and Muthiga, 1992). The observer swam haphazardly along the shallow reef sites for 40 min and recorded the time taken to observe the first individual of a coral genus. This was repeated at the different reef sites. The cumulative number of taxa was plotted as a function of the search interval for each of the times and management systems.

Sea urchins

Sea urchins > 1 cm maximum body length 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 nearby reefs. Total sea urchin wet weight was estimated by summing the wet weights of each species. Total number of species per site was determined as the total number of species counted in the 90 m^2 of sampling.

Fish

Fish communities were quantified in two ways in two 5 × 100 m belt transects per site (McClanahan, 1994; McClanahan and Kaunda-Arara, 1996). One method estimated the wet weight while a second determined the numbers of species. Wet-weight estimates were made by classifying each individual encountered in transects to the family, estimating its length, and placing it into 10-cm size-class intervals. Three families with similar morphologies, the Haemulidae, Lethrinidae and Lutjanidae, were pooled into a single group named small-invertebrate predators and 10 other common families were identified, while individuals not in these families were placed in an 'others' group. Wet weights per family were estimated from length–weight correlations established from measurements of the common species in each family taken at local fish landing sites in Kenya (McClanahan and Kaunda-Arara, 1996). No individuals < 3 cm in length were recorded. This method is 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 the largest fraction of the total fish weight.

  The second method used a Discrete-Group Sampling (DGS) method where one to three families were sampled with each pass through the belt transect (Greene and Alevizon, 1989). The belt 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). The number of species per family and transect was calculated as a measure of fish diversity.

Predation

Herbivory

During the sampling interval, 30 9 cm long blades of *Thalassia hemprichii* were attached to weighted clothespins and left at each reef site for 24 hours. Blades were collected and measured to the nearest half-centimetre and the scars were identified as either sea urchin or fish scars (McClanahan *et al.*, 1994). The average amount eaten and the percentage bitten were calculated and used as estimates of herbivory rates by each grazer group.

Sea urchins

Predation rates were estimated by a tethering experiment where 30 rock-boring sea urchins, *Echinometra mathaei*, at each site were pierced with a hypodermic needle, a monofilament line was threaded through their body and tied to three nylon lines separated by ∼ 10 m and fastened to the bottom (McClanahan and Muthiga, 1989). After 24 hours the urchins were visited, their body condition recorded, and the experiment terminated. Broken tests or body walls indicated death by a predator (McClanahan, 2000). Experiments with tethering have found that less than 5% of the tethered urchins die from the procedure and that these urchins are easily recognized and removed from the sample (McClanahan and Muthiga, 1989). Predation was calculated for each site and normalized to a 0 to 1 scale – 0 corresponding to no predation and 1 to all

urchins being preyed upon. Animals dying from causes other than predation ($<3\%$) were eliminated from the analyses.

Statistical analyses

The design of sites and measurements allowed for an orthogonal fixed two-factor ANOVA comparison whereby differences in time and management treatments, together with their interaction, were determined (Sall *et al.*, 2001). This was done separately for the Kisite–Tanga and the Kenyan fished and unfished management systems and compared to determine if the statistically significant patterns found in Kisite–Tanga were different from the larger Kenyan management system. The repeated-measures ANOVA was not used because sites were not permanently marked; but sites were selected as representative of each reef in the first sampling period and it was attempted to return close to these sites in the second sampling interval. For statistical tests, the $500 \, \text{m}^2$ belt transect was the unit of replication for fish measurements, but replicate line transects and quadrats at each site were pooled and the site was used as the unit of replication for all other statistical tests to avoid a pseudo-replicated design (Oaten *et al.*, 1986). Because of the high variability in site selection and the conservative statistical design we present *p*-values of less than 0.1 and refer to them as marginal differences, but restrict statistical significance to $p < 0.05$.

RESULTS

Substratum

Estimates of the major functional groups indicated that the only difference between Kisite and Tanga was that Tanga had more erect algae than Kisite, while the cover of sand is about four times greater in Kisite (Table 1). The cover of erect algae pooled for all sites and locations declined by around 100% over time, but the difference was marginal ($p < 0.09$) owing to high between-site variation. Similarly, coralline algae pooled for all sites and locations declined over time ($p < 0.02$), while sponge experienced a marginal ($p < 0.08$) increase over time. In the Kenyan control sites there was higher coral and coralline algae and lower turf cover in the unfished than fished reefs. These three substratum groups also changed over time, with decreased hard coral and increased turf and coralline algae in the parks over time. Hard coral and turf declined marginally in the fished reefs.

The number of erect algal taxa per 90 m of line at each management experimental site was small, at two to six taxa per site, but higher in Tanga than Kisite and did not change over time (Table 2). In the Kenyan control sites, the number of erect algal taxa was not different between management categories and did not change over time. The average number of hard coral taxa per 90 m of line transect at each experimental site was very similar at between 12 and 13 taxa and did not change over time (Table 2). There were more hard coral taxa in the unfished than fished Kenyan control sites and no changes over time. Numbers of taxa, as assessed by the search-sampling method, was considerably higher than by the transect method and produced a maximum of 35 and 40 genera for Tanga and Kisite respectively (Figure 2(a)). Comparing the cumulative number of taxa after a total search interval of 80 minutes (two 40-minute search intervals), found a small decline in the number of recorded taxa from 33 to 30 at Tanga and an increase from 30 to 35 at Kisite over the study period. The dominant coral taxa at Tanga were *Galaxea*, *Montipora* and massive and branching *Porites*, with no indication of a change over time (Figure 3(b)). In contrast, there was a large loss in the cover of branching *Porites* at Kisite, and a large increase in *Seriatopora* and *Galaxea* (Figure 3(a)). The two subdominant genera, *Acropora* and *Montipora*, were also reduced at Kisite.

Table 1. Summary statistics (mean ± standard error of the mean (SEM), cm/m of line) for gross substratum macrobiota in (a) control Kenya fished and unfished reefs, and (b) Kisite and Tanga during 1996 and 2004 sampling periods, and results from the two-factor interactive ANOVA

(a) Control sites

Substratum	Unfished 1996		Unfished 2004		Fished 1996		Fished 2004		Management		Time		Time * Management	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	F	p	F	p	F	p
Hard coral	44.9	0.6	22.2	3.5	21.4	2.0	19.7	2.5	13.3	0.01	25.4	0.001	16.6	0.01
Turf algae	24.0	1.9	32.2	4.8	42.1	2.4	35.6	3.6	7.1	0.04	0.6	ns	5.8	0.06
Calcareous algae	7.5	2.2	9.7	3.9	0.8	0.3	1.4	0.3	5.2	0.07	8.4	0.03	3.4	ns
Erect algae	5.1	1.4	2.5	0.8	5.1	1.7	6.1	2.1	0.5	ns	1.1	ns	4.2	ns
Coralline algae	7.6	1.0	22.0	2.7	1.1	0.5	5.2	1.9	21.3	0.01	59.2	0.001	15.1	0.01
Seagrass	3.1	1.0	1.4	0.7	11.8	2.2	14.3	2.8	6.8	0.05	0.2	ns	3.9	ns
Soft coral	3.1	0.8	3.9	0.9	2.1	0.4	4.2	0.6	0.0	ns	4.0	0.10	1.3	ns
Sand	4.4	1.0	5.5	1.4	15.3	1.8	12.4	2.6	32.1	0.001	1.3	ns	3.6	ns
Sponge	0.3	0.1	0.5	0.3	0.5	0.2	1.2	0.4	1.8	0.23	1.6	ns	0.5	ns

(b) Experimental sites

Substratum	Kisite 1996		Kisite 2004		Tanga 1996		Tanga 2004		Management		Time		Time * Management	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	F	p	F	p	F	p
Hard coral	22.1	4.9	32.7	5.8	24.4	4.7	27.8	4.3	0.0	ns	0.8	ns	0.2	ns
Turf algae	44.6	4.5	36.5	6.9	34.9	4.3	32.4	5.1	3.4	ns	0.1	ns	0.5	ns
Calcareous algae	0.0	0.0	0.1	3.6	0.0	0.0	0.3	0.1	0.6	ns	1.2	ns	0.2	ns
Erect algae	14.0	3.0	4.0	2.5	27.0	4.1	18.8	4.7	9.0	0.02	3.9	0.09	0.0	ns
Coralline algae	5.7	0.0	0.0	2.3	4.9	0.9	1.6	2.5	0.1	ns	8.1	0.02	0.5	ns
Seagrass	0.0	1.4	10.5	1.3	2.1	1.1	13.0	0.8	1.2	ns	0.0	ns	0.0	ns
Soft coral	3.4	1.3	4.3	2.6	3.6	1.4	3.7	1.3	0.0	ns	0.1	ns	0.1	ns
Sand	10.0	3.0	11.4	4.9	2.8	1.0	2.1	0.9	15.1	0.001	0.3	ns	0.2	ns
Sponge	0.1	0.1	0.5	1.9	0.3	0.2	0.5	0.3	0.1	ns	4.0	0.08	0.3	ns

Table 2. Numbers of coral and erect algal genera (mean ± standard errors of the mean) per site in (a) Kenyan fished and unfished reefs, and (b) Kisite and Tanga during the two sampling periods and the two-factor ANOVA statistics. Each site taxa count is based on 90 m of line transects

(a) Control sites

Substratum	Unfished 1996		Unfished 2004		Fished 1996		Fished 2004		Management		Time		Time * Management	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	F	p	F	p	F	p
Hard coral	14.0	1.3	15.0	0.9	10.4	1.3	11.3	1.2	6.2	0.03	0.8	ns	0.0	ns
Erect algae	6.3	1.9	5.3	1.2	7.5	0.9	7.5	1.4	1.0	ns	0.31	ns	0.31	ns

(b) Experimental sites

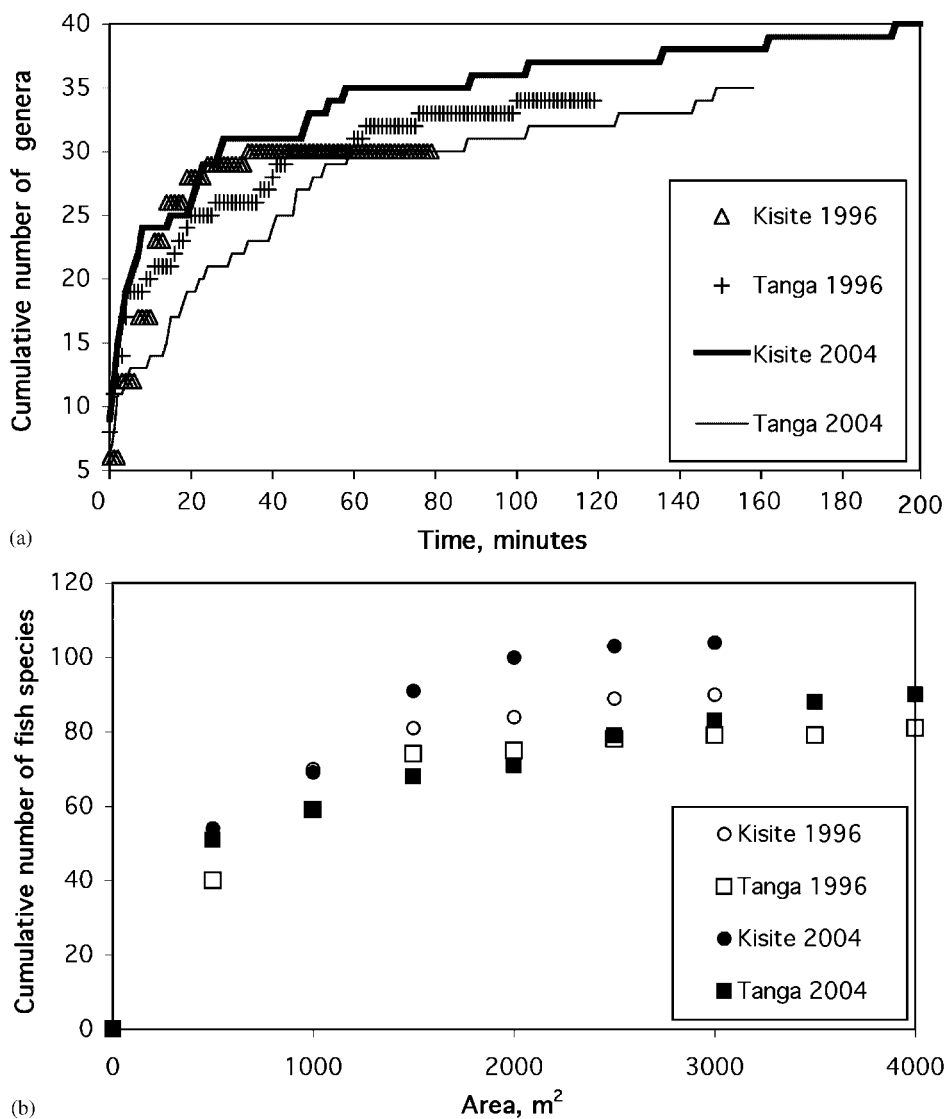| Substratum	Kisite 1996		Kisite 2004		Tanga 1996		Tanga 2004		Management		Time		Interaction	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	F	p	F	p	F	p
Hard coral	12.0	0.6	12.7	0.7	11.5	2.1	13.3	2.6	0	ns	0.4	ns	0.1	ns
Erect algae	2.0	0.0	2.3	0.3	4.8	0.5	5.5	0.5	46.8	<0.0001	1.6	ns	0.2	ns

Figure 2. Cumulative numbers of (a) hard coral and (b) fish taxa for both Tanga and Kisite in 1996 and 2003–2004.

Sea urchins

In the experimental sites, there was high between-site variation in sea urchin numbers and wet weight that produced no statistical differences between management locations and time, despite considerably larger numbers and wet weights at the Tanga study sites (Table 3). Predation on sea urchins was, however, four times higher at the Kisite than Tanga reefs, with no change in estimates over time. Sea urchin abundance was lower and predation higher in unfished than fished Kenyan control sites and did not change over time.

Fish

The total wet weight estimate of fish was about 2.8 times higher in the Kisite MNP than at Tanga (Table 4). Surgeonfish, parrotfish, butterflyfish, the small-invertebrate predator group and the 'others' group were
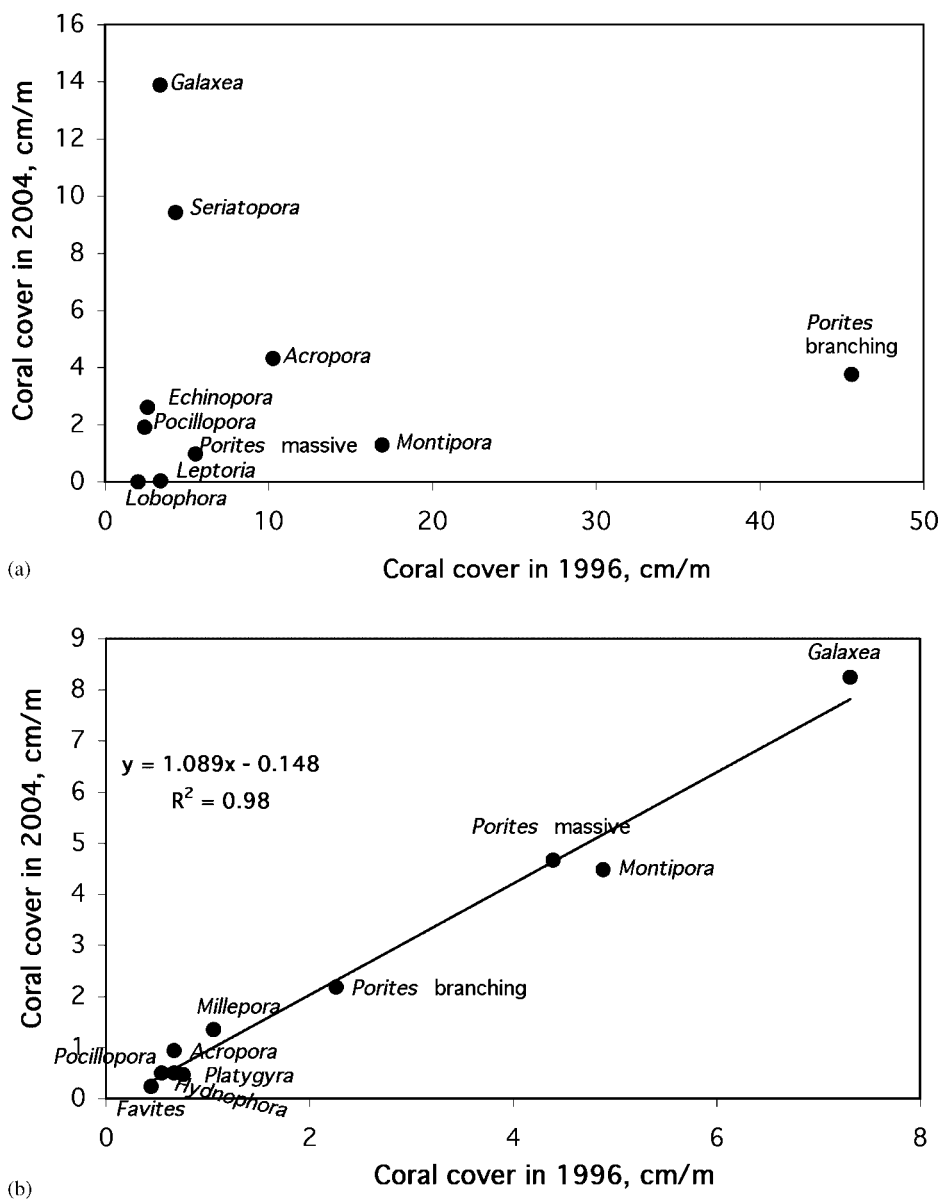
Figure 3. Scatterplots of the abundance of the dominant coral taxa at the beginning and end of the study in (a) Kisite and (b) Tanga.

more abundant at Kisite than Tanga, but the opposite was true for the wrasses, goatfish and rabbitfish. Damselfish were marginally ($p < 0.07$) more abundant at Tanga than Kisite. In the Kenyan control sites all fish groups, except for pufferfish, were more abundant in the unfished than fished sites.

Combining all experimental sites, total wet weight nearly doubled over time at Tanga and Kisite from 470 to 900 kg ha^{-1} and there was a positive interaction attributable to the stronger effect of time at Kisite than at Tanga (Table 4). There were significant increases in parrotfish, rabbitfish and the 'others' group and a decline over time in the damselfish (Table 4). The interaction with time and management locations was

Table 3. Density (per 10 m^2), wet weight (kg/ha), and relative predation rates (0 to 1) in (a) Kenyan fished and unfished reefs, and (b) Kisite and Tanga sites during 1996 and 2004 and the two-factor interactive ANOVA statistics

(a) Control sites

	Unfished 1996		Unfished 2004		Fished 1996		Fished 2004		Management		Time		Time * Management	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	F	p	F	p	F	p
Density, 10 m^{-2}	7.4	4.2	6.9	3.8	77.2	27.8	78.7	26.6	4.9	0.05	0.0	ns	0.0	ns
Wet weight, kg/ha	701.0	485.3	384.5	212.2	3654.7	773.9	3687.4	671.0	12.9	0.01	0.2	ns	0.3	ns
Predation rate	0.8	0.1	0.9	0.0	0.2	0.1	0.2	0.1	83.4	0.0001	0.5	ns	0.2	ns

(b) Experimental sites

	Kisite 1996		Kisite 2004		Tanga 1996		Tanga 2004		Management		Time		Time * Management	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	F	p	F	p	F	p
Density, 10 m^{-2}	5.8	3	9.6	4	15.5	8.6	11.5	5.4	0.8	ns	0.0	ns	0.4	ns
Wet weight, kg/ha	320	120	960	320	2180	1200	1800	700	2.6	ns	0.0	ns	0.4	ns
Predation rate	0.9	0.03	0.7	0.02	0.23	0.1	0.21	0.07	48.6	0.0001	1.0	ns	0.7	ns

Table 4. Fish wet weight (kg/ha) estimates for (a) Kenyan fished and unfished reefs, and (b) Kisite and Tanga in 1996 and 2004 and two-factor interactive ANOVA statistics

(a) Control sites

Family	Unfished 1996		Unfished 2004		Fished 1996		Fished 2004		Management		Time		Time * Management	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	F	p	F	p	F	p
Acanthuridae	150.3	12.3	211.1	14.5	12.3	3.5	4.9	2.2	10.6	0.02	5.4	0.07	9.2	0.03
Balistidae	22.1	4.7	36.8	6.1	1.0	1.0	0.0	0.0	6.5	0.05	2.6	ns	3.6	ns
Chaetodontidae	17.8	4.2	8.9	3.0	2.0	1.4	2.5	1.6	5.1	0.07	0.3	ns	0.4	ns
Diodontidae	0.0		3.8	1.9	0.0		2.2	1.5	0.2	ns	3.6	ns	0.2	ns
Labridae	56.2	7.5	55.0	7.4	23.3	4.8	19.1	4.4	13.8	0.01	0.1	ns	0.0	ns
Lutjanidae	62.2	7.9	197.2	14.0	3.4	1.8	0.7	0.8	13.8	0.01	59.2	0.001	64.7	0.001
Mullidae	6.4	2.5	7.7	2.8	0.2	0.4	2.2	1.5	7.7	0.04	0.6	ns	0.0	ns
Others	140.4	11.8	340.0	18.4	8.3	2.9	14.3	3.8	10.8	0.02	4.8	0.08	4.2	0.09
Pomacanthidae	14.0	3.7	21.5	4.6	0.6	0.8	5.6	2.4	5.5	0.07	1.4	ns	0.0	ns
Pomacentridae	90.9	9.5	72.2	8.5	39.2	6.3	26.4	5.1	5.7	0.06	2.7	ns	0.1	ns
Scaridae	187.5	13.7	233.5	15.3	10.3	3.2	3.6	1.9	111.7	0.001	0.1	ns	0.2	ns
Siganidae	25.7	5.1	17.1	4.1	0.1	0.3	0.6	0.8	14.9	0.01	4.5	0.09	5.8	0.06
Total	772.7	27.8	1204.7	34.7	100.6	10.0	81.9	9.0	716.0	0.001	2.7	ns	3.3	ns

(b) Experimental sites

Family	Kisite 1996		Kisite 2004		Tanga 1996		Tanga 2004		Management		Time		Time * Management	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	F	p	F	p	F	p
Acanthuridae	133.8	19.6	260.1	27.8	54.7	6.7	82.5	6.9	7.6	0.02	1.6	ns	1.5	ns
Balistidae	19.7	3.0	31.9	4.8	0.2	0.5	41.3	1.0	5.0	0.05	0.9	ns	0.07	ns
Chaetodontidae	15.8	3.1	39.1	6.8	8.6	2.1	11.1	1.4	29.3	0.001	3.2	0.1	13.7	0.004
Diodontidae	0.0	0.0	3.5	0.7	0.0	2.0	3.6	0.3	0.22	ns	2.1	ns	0.22	ns
Labridae	34.1	3.2	50.0	3.8	39.0	8.4	59.8	1.9	23.9	0.001	3.4	0.09	0.09	ns
Lutjanidae	189.3	22.9	300.1	41.0	19.6	4.1	7.7	2.4	4.8	0.05	0.3	ns	0.3	ns
Mullidae	4.6	0.9	21.2	3.5	4.2	3.2	57.5	0.4	7.3	0.02	3.8	0.08	6.7	0.02
Pomacanthidae	12.6	1.9	7.1	1.4	5.2	3.5	19.9	1.8	0.5	ns	1.1	ns	0.07	ns
Pomacentridae	69.6	13.5	51.1	10.0	68.4	5.7	54.6	3.0	4.1	0.07	12.8	0.01	3.6	0.08
Scaridae	122.0	12.8	339.5	33.3	25.8	6.9	68.3	2.4	32.6	0.001	8.3	0.02	9.4	0.01
Siganidae	1.3	0.7	5.9	6.0	2.5	2.2	5.6	0.2	29.4	0.001	7	0.02	3.1	0.10
Others	79.6	8.4	244.6	23.7	32.2	18.1	45.7	2.0	25.9	0.001	6.4	0.03	11.5	0.01
Total	682.4	48.9	1354.2	89.1	260.4	24.4	457.4	7.9	25.6	0.001	4.4	0.06	4.9	0.05

Table 5. Number of fish species per 500 m^2 in Kisite and Tanga for 1996 and 2004 and two-factor interactive ANOVA statistics

Family	Kisite 1996		Kisite 2004		Tanga 1996		Tanga 2004		Treatment		Time		Interaction	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	F	$p <$	F	$p <$	F	$p <$
Acanthuridae	8.8	0.8	7.0	1.3	3.4	0.4	4.6	0.6	10.3	0.009	0.06	ns	1.60	ns
Balistidae	2.0	0.3	2.0	0.6	0.3	0.0	1.0	0.2	19.9	0.001	1.50	ns	1.50	ns
Chaetodontidae	4.0	0.6	4.2	0.8	1.6	0.3	2.9	0.4	14.3	0.004	2.10	ns	1.30	ns
Diodontidae	0.7	0.3	0.3	0.0	0.1	0.0	0.1	0.0	6.80	0.03	1.30	ns	1.30	ns
Labridae	14.2	0.7	14.5	0.8	14.6	1.1	16.1	1.0	1.00	ns	0.80	ns	0.30	ns
Pomacanthidae	1.0	0.0	1.5	0.3	1.3	0.3	1.6	0.3	0.40	ns	2.20	ns	0.04	ns
Pomacentridae	13.2	1.0	12.2	1.0	12.5	1.4	9.1	1.0	1.30	ns	1.80	ns	0.50	ns
Scaridae	7.5	0.4	5.7	1.3	4.1	0.6	5.6	0.9	1.60	ns	0.01	ns	1.50	ns
Total	51.3	0.4	47.4	3.3	37.9	5.8	41.1	2.7	5.90	0.040	0.03	ns	0.70	ns

Table 6. Herbivory rates on the experimental seagrass assay, *Thallasia hemprichii*, in Kisite and Tanga in 2004. The percentage bitten and the amount eaten as a percentage of the total length of the seagrass are presented, as well and the as the amount attributed to fish or sea urchins. Single-factor ANOVA results presented

Herbivory type	Kisite 2004		Tanga 2004		Management	
	Mean	SEM	Mean	SEM	F	$p <$
Percentage bitten by fish and sea urchins, %	98.8	1.2	51.0	15.2	7.0	0.05
Amount eaten by fish and sea urchins, %	79.5	3.2	31.6	16.2	6.2	0.06
Amount bitten by fish, %	68.0	12.3	5.2	3.1	33.2	0.002
Amount bitten by sea urchins, %	34.5	16.3	45.7	13.2	0.3	ns

significant for the butterflyfish, goatfish, parrotfish and 'others' group. In the Kenyan control sites, there were few changes apart from the surgeonfish and small-invertebrate predator groups, which increased in the unfished and decreased in the fished reefs over time, but with no change in total wet weight with time.

Total numbers of sampled fish species per 500 m^2 was higher at Kisite than Tanga by ∼10 species, with higher numbers in the butterflyfish, surgeonfish, triggerfish and pufferfish families (Table 5). There were no changes in the numbers of species over time at this scale of sampling. Cumulative species plots also indicated more species at Kisite than Tanga but, in contrast to the comparison at 500 m^2, these data suggest an increase in numbers of fish taxa at both locations over time (Figure 2(b)). At Kisite, over a 3000 m^2 area of search, 90 species were encountered in 1996 compared to 104 in 2004. Similarly at Tanga, for the same-sized area of search, 79 species were encountered in 1996 and 83 in 2004.

Herbivory levels in 2003–2004 were higher ($p < 0.06$) at Kisite than at Tanga, by around 100%, whether measured as the mean percentage of blades bitten, or amount eaten (Table 6). Virtually all of the seagrass blades at Kisite were bitten, compared to half at Tanga. There was no difference in the estimated bite rate by sea urchins between the two locations, with around 40% being bitten by sea urchins; but fish bites were nearly twelve times higher at Kisite than Tanga.

DISCUSSION

Comparison of the ecology and species diversity in the different management areas over time indicates some important differences in the effects of management on coral reefs in this region. One of the more notable

differences was the level of predation. For example, the large closed-area parks in Kenya had a higher abundance of herbivorous parrotfish and surgeonfish. The high numbers of parrotfish are responsible for the high levels of herbivory on experimental seagrass assays (McClanahan et al., 1994). Common to other coral reef studies (Williams and Polunin, 2001; Hawkins and Roberts, 2004), this difference in herbivory is the expected cause of the lower cover and number of taxa of erect algae. Lower cover of erect algae is expected to improve conditions for coral that can, at times, be competitively excluded by erect algae (McCook et al., 2001). Collaborative fisheries management of the Tanga fishery resulted in an increase in herbivorous parrotfish and rabbitfish, an increase which may be partly responsible for the decline in erect algae on the Tanga reefs over time. Given that there was no evidence for a decline in erect algae in the fished Kenyan control sites, the change is mostly likely due to the new management at Tanga. Consequently, this study indicates that large closed areas and collaborative fisheries management can increase herbivorous fish and reduce erect algae.

Predation on sea urchins was considerably higher in the large closed area compared to the collaborative fishery-managed areas, but the effect on sea urchin populations was more equivocal than the effect of herbivores on algae. Despite large differences in the mean sea urchin biomass between sites in the two management systems, the high spatial variability of sea urchin abundance resulted in statistically insignificant differences. Herbivory rates attributed to sea urchins were similar between the management areas. Other studies in Kenya and Tanzania have found higher sea urchin abundance and associated herbivory on unfished than fished reefs (Watson and Ormond, 1994; McClanahan et al., 1999). Consequently, the pattern seen here may result from low site replication and high variability and because the relationship is not always strong. Furthermore, sea urchin abundance is not controlled entirely by predation; there are also other factors at work, including the body size of the sea urchins and the complexity of the reef structure (McClanahan, 1998).

Predation rates on sea urchins were constant over time and this suggests that the implemented collaborative fisheries management was either slow to or did not greatly influence those species responsible for sea urchin predation. The dominant predator in these reefs is the red-lined triggerfish (Balistapus undulatus), which is both sensitive to fishing and slow to recover from the cessation of fishing (McClanahan, 2000), and not seen in the Tanga study sites. Its aggressive behaviour makes it susceptible to bait (Watson, 1996; Kaunda-Arara and Rose, 2004) associated with trap and line fishing, and its populations can, therefore, be reduced or eliminated at very low levels of fishing. The lack of statistical differences in the abundance of balistids between Tanga and Kisite was due to a large increase in Sufflamen fraenatus at Tanga over the study period. S. fraenatus is, however, not an important predator of adult sea urchins (McClanahan, 2000) and therefore the increase in abundance is unlikely to have affected sea urchin abundance at Tanga. The degree to which the ecological functions of the red-lined triggerfish can be compensated for by other sea urchin predators is still unresolved. A variety of wrasses are the subdominant sea urchin predators (McClanahan, 2000), and wrasses were more abundant in the fishery than the large closed area. Consequently, our data suggest that there is poor compensation for the loss of the red-lined triggerfish and that this species and its ecological functions are best managed through closed areas.

Closed areas are also expected to protect biological diversity more than areas with heavy fishing (Halpern, 2003). We found support for this diversity effect for fish, but not for erect algae, while detection of this effect on hard corals was only evident at large spatial scales of sampling. Since fish are the target for resource users, this finding is not surprising. The effect on corals appears to be restricted to rare members of the community, since the total number of taxa was higher in the large closed than the collaborative fisheries management areas, only beyond the 90 m of line-transect sampling. Studies in the region have found indirect negative effects of fishing on the diversity of unharvested resources such as corals (McClanahan and Obura, 1996). In some cases, however, small increases in the numbers of unharvested species have been found for sea urchins and snails (McClanahan and Obura, 1996), and now for erect algae. These increases were probably due to reduced predation by fish and the persistence of the predator-susceptible species, as

found for sea urchins (McClanahan, 1998). Direct experimental control of herbivory has produced higher levels of algal diversity with low grazing (McClanahan *et al.*, 2003).

Collaborative fisheries management at Tanga did not produce increases in numbers of fish species at the scale of 500 m^2, but a minor increase at the scale of 3000 m^2. The site did, however, have a moderately high diversity of fish, and with values of 38–41 species per 500 m^2 it was considerably higher than many heavily fished reefs of southern Kenya, where the same method produced around 20–35 species (McClanahan, 1994; McClanahan and Arthur, 2001). The initial high diversity at Tanga may have left less possibility for further increases. Nonetheless, this and another study in the region (McClanahan and Arthur, 2001) suggest that permanently closed areas maintain higher numbers of fish species than areas subjected to collaborative fisheries management.

The number of coral genera found in 90 m of line transect was high at both Tanga and Kisite and unchanged with time. When using the search-sampling method, which samples numbers of taxa at a scale larger than the line transects, a small decline in numbers of taxa was recorded, owing to the disappearance of a few rare taxa at Tanga. Despite this possible loss of rare taxa, the coral community composed of the dominant taxa was very stable at Tanga compared to the Kisite. Kisite experienced considerable reorganization of the dominant coral taxa over the study period. The cause of this change was the 1998 warm ENSO event that killed corals in much of southern Kenya (McClanahan *et al.*, 2001), but was less destructive in northern Tanzania. It is not clear to what extent this is due to differences in physicochemical environmental factors or management, but previous findings in southern Kenya found higher levels of coral mortality in unfished marine parks than neighbouring fished reefs (McClanahan *et al.*, 2001). This was due to higher numbers of branching species, such as *Acropora*, *Stylophora* and branching *Porites* in the parks that were susceptible to temperature stresses (McClanahan, 2004). The dominant corals at Tanga were largely sub-massive *Galaxea*, massive *Porites* and the encrusting taxa *Montipora* that may survive bleaching and destructive fishing better than branching taxa (McClanahan *et al.*, 2001). Branching *Porites*, which was the dominant taxa at Kisite, was the taxa most susceptible to this warm ENSO (McClanahan *et al.*, 2001) and has largely failed to recover at Kisite after seven years, being replaced by *Seriatopora hystrix*, another delicate and easily stressed branching species.

Branching taxa, such as *Acropora*, are fast-growing and can overgrow and shade other coral species (Baird and Hughes, 2000). It is possible that disturbances due to fishing discourages branching taxa, while the lack of fishing and bleaching disturbances could lead to localized competitive exclusion of competitively subordinate coral taxa. Therefore, there could be a shift in the dominance of the coral communities in each disturbance regime without a loss of coral diversity at the local scale. These findings suggest that fishing may reduce the abundance of branching taxa, and this may predispose these reefs to greater resilience to bleaching. In contrast, large closed areas are a refuge for delicate branching taxa, but this also makes these reefs more susceptible to warm-water anomalies. Collaborative fisheries management at Tanga did not result in a change in the dominant coral taxa towards those more similar to Kisite, which, similar to predation on sea urchins, suggests either a slow or no tendency for the implemented collaborative fisheries management to influence coral communities towards large closed areas and their dominance by branching taxa.

The implementation of the collaborative fisheries management system appeared to increase the fish wet-weight estimates in the large closed area more than in the collaboratively managed area. This is despite the closed area being unfished for nearly 20 years before the initial measurements. This finding is supported by the lack of an increase in the total fish weight in the unfished control sites over time and recent findings that coral reef fish reach their maximum biomass at around 20–25 years after closure from fishing (Russ and Alcala, 2004; McClanahan and Graham, 2005). This suggests connectivity between the closed areas and the adjacent managed fishery, where improved management of the fishery produced a response in the adjacent closed area. Studies suggest that closed areas act as fish stock refugia where increased fish abundance leads to 'spillover' into the adjacent fishery (Russ and Alcala, 1996; McClanahan and Mangi, 2000; Kaunda-Arara and Rose, 2004). It is expected, however, that fish will move both ways across this boundary,

influenced by the quality of the habitat, and that management will, therefore, affect both areas (Rodwell *et al.*, 2003). Our study suggests that fish in large closed areas may benefit considerably from management of fisheries outside of the boundaries.

CONCLUSIONS

The collaborative fisheries management programme at Tanga was notably successful in increasing fish stocks in the managed area, in patchily reducing erect algal cover, and may have played some part in maintaining stability in the diversity and community structure of the reef community during a period which experienced large-scale environmental disturbance. Increased restrictions on the fishery appeared to have a positive influence on fish stocks inside the adjacent closed area. Collaborative fisheries management did not, however, appear to result in recovery of predation rates on sea urchins or in the abundance of sensitive branching or rare coral taxa. It would, therefore, seem that there are limits to the conservation benefits of collaborative fisheries management, at least on the timescale of our study of this management system. The large closed area provided better protection for rare, delicate and fishing-sensitive species, and was better for the full protection of biodiversity.

Weaknesses of collaborative fisheries management, from a biodiversity conservation perspective, are that the areas of closure are often small and can be periodically opened depending on the consensus of the resource users. The opening and closing of study sites at Tanga was likely to affect the degree of recovery that we recorded, given that ~ 20 years may be necessary for coral reef fish to recover fully (McClanahan and Graham, 2005). Periodic harvesting could result in a slow decline in biodiversity and ecosystem functions, while maintaining resource and harvest levels. The political and economic conditions in Tanzania have not created conditions favourable for large closed areas, as previous legal gazettements of large closed areas have not been successful. The collaborative fisheries management alternative has provided a successful way of increasing resources, reducing destructive fishing practices and alleviating poverty of resource users. Consequently, it is possible that the collaborative fisheries management system may act as a transitional system that will ultimately include larger and permanently closed areas as the economic conditions improve and the recognition of the significance of large and permanent closed areas increases. In fact, there is a growing consensus among resource users at Tanga focused on developing permanent closures, although the currently identified areas are small. These efforts, if they continue to develop, may provide a basis on which to build a fully sustainable resource use system that conserves total regional biodiversity and maintains sustainable harvests.

This project provides a case study in which the ecological benefits and detriments of these two management systems can be compared. It suggests the need for both types of management when attempting to achieve and reconcile the potentially conflicting goals of sustainable fisheries and poverty alleviation, the protection of sensitive species, and biological diversity. It also suggests the importance of international boundaries in influencing national management systems. It would appear to be in the greater interest of countries with richer natural resources and effective management to influence resource use in neighbouring countries in order to protect their own resources. It must be appreciated, however, that management will change and be influenced according to local socio-economic and political philosophies, associated policies, and actions, which may be more influenced by local histories than by neighbours.

ACKNOWLEDGEMENTS

REFERENCES

Adams WM, Aveling R, Brockington D, Dickson B, Elliott J, Hutton J, Roe D, Vira B, Wolmer W. 2004. Biodiversity conservation and the eradication of poverty. *Science* **306**: 1146–1149.

Baird AH, Hughes TP. 2000. Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages. *Journal Experimental Marine Biology and Ecology* **251**: 117–132.

DoFi. 2001. National Frame Survey. Department of Fisheries, Dar es Salaam, Tanzania 25 pp.

Goreau T, McClanahan T, Hayes R, Strong A. 2000. Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology* **14**: 5–15.

Greene LE, Alevizon WS. 1989. Comparative accuracies of visual assessment methods for coral reef fishes. *Bulletin of Marine Science* **44**: 899–912.

Halpern B. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* **13**: S117–137.

Hawkins JP, Roberts CM. 2004. Effects of artisanal fishing on Caribbean coral reefs. *Conservation Biology* **18**: 215–226.

Horrill C, Kamukuru AT, Mgaya YD, Risk M. 2000. Northern Tanzania, Zanzibar and Pemba. In *Coral Reefs of the Indian Ocean: Their Ecology and Conservation*, McClanahan TR, Sheppard CRC, Obura DO (eds). Oxford University Press: New York; 167–198.

Horrill C, Kalombo H, Makoloweka S. 2001. Collaborative reef and reef fisheries management in Tanga, Tanzania. IUCN/SEACAM, New York 32 pp.

Kaunda-Arara B, Rose GA. 2004. Effects of marine reef National Parks on fishery CPUE in coastal Kenya. *Biological Conservation* **118**: 1–13.

Malleret-King D. 2000. A food security approach to marine protected area impacts on surrounding fishing communities: the case of Kisite Marine National Park in Kenya. PhD thesis, University of Warwick.

Makoloweka S, Shurcliff K. 1997. Coastal management in Tanga, Tanzania: a decentralized community-based approach. *Ocean and Coastal Management* **37**(3): 349–357.

McClanahan TR. 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* **13**: 231–241.

McClanahan TR. 1998. Predation and the distribution and abundance of tropical sea urchin populations. *Journal of Experimental Marine Biology and Ecology* **221**: 231–255.

McClanahan TR. 1999. Is there a future for coral reef parks in poor tropical countries? *Coral Reefs* **18**: 321–325.

McClanahan TR. 2000. Recovery of the coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biological Conservation* **94**: 191–198.

McClanahan TR. 2004. The relationship between bleaching and mortality of common corals. *Marine Biology* **144**: 1239–1245.

McClanahan TR, Arthur R. 2001. The effect of marine reserves and habitat on populations of East African coral reef fishes. *Ecological Applications* **11**: 559–569.

McClanahan TR, Graham NAJ. 2005. Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. *Marine Ecology Progress Series*, in press.

McClanahan TR, Kaunda-Arara B. 1996. Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology* **10**: 1187–1199.

McClanahan TR, Mangi S. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications* **10**: 1792–1805.

McClanahan TR, Muthiga NA. 1989. Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. *Journal of Experimental Marine Biology and Ecology* **126**: 77–94.

McClanahan TR, Muthiga NA. 1992. Comparative sampling of epibenthic subtidal gastropods. *Journal of Experimental Marine Biology and Ecology* **164**: 87–101.

McClanahan TR, Obura DO. 1996. Coral reefs and nearshore fisheries. In *Coral Reefs of the Indian Ocean: Their Ecology and Conservation*, McClanahan TR, Young TP (eds). Oxford University Press: New York; 67–99.

McClanahan TR, Shafir SH. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* **83**: 362–370.

McClanahan TR, Nugues M, Mwachireya S. 1994. Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. *Journal of Experimental Marine Biology and Ecology* **184**: 237–254.

McClanahan TR, Muthiga NA, Kamukuru AT, Machano H, Kiambo R. 1999. The effects of marine parks and fishing on the coral reefs of northern Tanzania. *Biological Conservation* **89**: 161–182.

McClanahan TR, Muthiga NA, Mangi S. 2001. Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* **19**: 380–391.

McClanahan TR, Sala E, Stickels P, Cokos BA, Baker A, Starger CJ, Jones S. 2003. Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. *Marine Ecology Progress Series* **261**: 135–147.

McClanahan TR, McLaughlin SM, Davey JE, Wilson WH, Peters EC, Price KL, Maina J. 2004. Pathology of a new source of coral mortality along the Kenyan coast. *Hydrobiologia* **530/531**: 469–479.

McCook LJ, Jompa J, Diaz-Pulido G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* **19**: 400–417.

Muthiga NA, McClanahan TR. 1997. The effect of visitor use on the hard coral communities of the Kisite Marine Park, Kenya. In *Proceedings of the Eighth International Coral Reef Symposium*, Panama 1879–1882.

Muthiga NA, Riedmiller S, Carter E, van der Elst R, Mann-Lang J, Horrill C, McClanahan TR. 2000. Management status and case studies. In *Coral Reefs of the Indian Ocean: Their Ecology and Conservation*, McClanahan TR, Sheppard CRC, Obura D (eds). Oxford University Press: New York; 473–505.

Oaten AS, Murdoch WW, Parker KR. 1986. Environmental impact assessment: 'Pseudoreplication' in time? *Ecology* **67**: 929–940.

Polunin NVC, Roberts CM, Pauly D. 1996. Developments in tropical reef fisheries science and management. In *Reef Fisheries*, Vol. 20, Polunin NVC, Roberts CM (eds). Chapman & Hall: London; 361–377.

Ray C. 1968. Marine parks for Tanzania. Department of Fisheries Dar es Salaam Report. 47 pp.

Rodwell LD, Barbier EB, Roberts CM, McClanahan TR. 2003. The importance of habitat quality for marine reserve — fishery linkages. *Canadian Journal of Fisheries and Aquatic Science* **60**: 171–181.

Russ GR, Alcala AC. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, Central Philippines. *Marine Ecology Progress Series* **132**: 1–9.

Russ GR, Alcala AC. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* **138**: 622–627.

Sall J, Lehmaan A, Creighton L. 2001. *JMP Start Statistics*, 2nd edn. Thomson Learning: Duxbury.

Samoilys MA. 1988. Abundance and species richness of coral reef fish on the Kenyan Coast: The effects of protective management and fishing. In *Proceedings of the Sixth International Coral Reef Symposium*, Tahiti 261–266.

Sheppard C, Wells S (eds). 1988. In *Coral Reefs of the World*, Vol. 2. UNEP/IUCN: Gland, Switzerland; 389.

Verheij E, Makoloweka S, Kalombo H. 2004. Collaborative coastal management improves coral reefs and fisheries in Tanga, Tanzania. *Ocean and Coastal Management* **47**: 309–320.

Watson M. 1996. The role of protected areas in the management of Kenyan reef fish stocks. DPhil, University of York.

Watson M, Ormond RFG. 1994. Effect of an artisanal fishery on the fish and urchin populations of a Kenyan coral reef. *Marine Ecology Progress Series* **109**: 115–129.

Watson M, Ormond RFG, Holliday L. 1997. The role of Kenya's marine protected areas in artisanal fisheries management. In *Proceedings of the Eighth International Coral Reef Symposium*, Panama 1955–1960.

Williams ID, Polunin NVC. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* **19**: 358–366.