

## ***Changes in northern Tanzania coral reefs during a period of increased fisheries management and climatic disturbance***

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### ABSTRACT

1. Surveys of coral reefs in northern Tanzania were conducted in 2004/5 with the aim of comparing them over an ~8-year period during a time of increased efforts at fisheries management and the 1998 El Niño Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) coral mortality event that caused 45% mortality in northern Tanzania and much of the Indian Ocean.

2. Changes associated with both management, its absence, and the ENSO were found but changes were generally small and ecological measures indicated stability or improvements over this period, particularly when compared with reports from much of the northern Indian Ocean.

3. Fisheries management in two areas increased the biomass of fish and benthic communities. A small fisheries closure (0.3 km<sup>2</sup>) displayed little change in the coral community but ecological conditions declined as measured by sea urchins and fish abundances. This change may be associated with its small size because similar changes were not measured in the large closure (28 km<sup>2</sup>).

4. The few sites without any increased management were still degraded and one site had experienced a population explosion of a pest sea urchin, *Echinometra mathaei*.

5. The lack of significant changes across this disturbance indicates that these reefs are moderately resilient to climate change and, therefore, a high priority for future conservation actions.

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### INTRODUCTION

Climatic change and associated disturbances to coral reefs are creating challenges for their management (Hoegh-Guldberg, 1999; McClanahan, 2002; Hughes *et al.*, 2003; Sheppard, 2003; Wooldridge *et al.*, 2005). A scientific debate with important implications for management revolves around the extent to which management of resources can influence the outcomes of climatic disturbances (Bellwood *et al.*, 2004; Pandolfi *et al.*, 2005; Aronson and Precht, 2006). Opinions and evidence vary but generally fall into four arguments and associated management actions. These are (1) climate overrides and undermines local resource use and management (Jones *et al.*,

2004) and this position emphasizes the need for management of the atmosphere at the global scale (Aronson and Precht, 2006); (2) reduced fisheries extraction, particularly of herbivores, will interact to reduce reef degradation and this view promotes the use of fisheries closures and bans on the fishing of herbivores (Mumby *et al.*, 2006; Hughes *et al.*, 2007); (3) fisheries closures are not a refuge from climate change because they encourage disturbance-susceptible taxa, which emphasizes the need for closures and fisheries management for reasons other than resilience to climate change (McClanahan *et al.*, 2006); and (4) responses to climate change are site-specific and influenced by local and regional environmental factors, and this view encourages prioritizing closure

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placement and management based on this knowledge (West and Salm, 2003; Wooldridge and Done, 2004; McClanahan *et al.*, 2007a; Maina *et al.*, 2008). Improving understanding and resolving these issues will require examination of the findings of a number of field cases where climatic disturbances and management have interacted (McClanahan *et al.*, 2001, 2005a, 2006).

Tanzania offers a useful case study of this interaction as it has experienced both increased efforts to improve management of its fisheries (Horrill *et al.*, 2000; Muthiga *et al.*, 2000; Verheij *et al.*, 2004; Wells *et al.*, 2007) and was also influenced by the 1998 bleaching event (Figure 1; Muhando and Mohammed, 2002; McClanahan *et al.*, 2007b). For example, Muhando and Mohammed (2002) report a decline but patchy response in coral cover from 1997 to 1999, with a decline from 67% to 12% in Tanga, and from 51% to 28% in Chumbe Island Coral Park and a minor increase from 49% to 55% in the Dar es Salaam Marine Reserves System. This study presents a comparison of Tanzanian reefs across this time period where the baseline ecological data were collected in 1996–1997 (McClanahan *et al.*, 1999) and again in 2004–2005. Studies were conducted for a number of taxa including coral, algae, sea urchins and fish, and also included two ecological process assays, herbivory on a seagrass and predation on a sea urchin. These ecological parameters were studied in order to evaluate the ecosystem change associated with this large-scale disturbance and its interactions with fisheries management.

## METHODS

### Study sites

Field studies were conducted in three regions of Tanzania, namely Tanga, Dar es Salaam, and the leeward side of Unguja Island (Figure 1). A further three sites in the Kisite Marine National Park (MNP) in Kenya (established in 1973, 28 km<sup>2</sup>) were also studied but are considered to be geographically associated with Tanga in terms of the close distance, reef morphology, and coral taxonomic composition (McClanahan *et al.*, 2007b). All of the reefs are isolated platform or rock

island reefs that are located 1–10 km offshore from the mainland (see locations in McClanahan *et al.*, 1999). The islands are situated on the shallow continental shelf where the depth at the base of the reefs is less than 20 m. Studies were carried out on the shallow water (< 3 m) leeward sides of these rock island reefs. Process assays were haphazardly located in ~30 m × 30 m areas on these reefs. Fish transects of 5 m × 100 m passed through these study areas.

Within Tanga four sites were studied, namely Taa, Makome, Chanjale, and Funguni reefs, located ~25 km south of Tanga municipal (population 200 000). Sites in Dar es Salaam Marine Reserves System lie close to this capital city (population 3.5 million) and included two of the three islands in the reserve with restricted gear use, namely two sites in Mbudya and two in Bongoyo. In Zanzibar, sites studied were located on rock island reefs offshore from the main island of Unguja. Two sites, Changuu and Chapwani islands, with no formal management, located off Zanzibar Town (population ~300 000), and two sites in the Chumbe Island Coral Park (CHICOP established in 1991, 0.3 km<sup>2</sup>).

### Management systems

The Kisite MNP and Reserve was legally gazetted in 1978 and is managed by Kenyan Wildlife Service. Watson *et al.* (1997) described a period of increased management efforts in the early 1990s that resulted in improved fisheries catch in this region and McClanahan *et al.* (2006) report that fisheries management in nearby Tanga increased the biomass of fish in the managed area. Management efforts in Tanga began with the creation of the Tanga Coral Gardens and Maziwi Island Marine Reserves in June 1975 under the Fisheries Act No. 6 of 1970 from recommendations put forward by Ray (1968), but the declared closure was not implemented and dynamite fishing in this area damaged the reefs in the proposed reserve areas (Sheppard and Wells, 1988; Horrill *et al.*, 2000; Muthiga *et al.*, 2000). This recognition led to the formulation of the Tanga Coastal Zone Conservation and Development Programme (TCZCDP) in 1994 (Makoloweka and Shurcliff, 1997; Wells *et al.*, 2007). The objective of the TCZCDP was to enhance the wellbeing of the coastal communities by improving fisheries management and alternative uses through a collaborative approach (Makoloweka and Shurcliff, 1997; Wells *et al.*, 2007). The project created collaborative management areas and the study sites are within the oldest of these, Mtang'ata, ~25 km south of Tanga town. Since 1995, there has been increased enforcement of laws on illegal and destructive fishing practices, including the use of dynamite, drag nets and poisons, and the establishment of small (<0.5 km<sup>2</sup>) and temporary closures (Horrill *et al.*, 2000; Wells *et al.*, 2007).

The Dar es Salaam Marine Reserves System (DMRS) was first gazetted as a Marine Protected Area (MPA) in June 1975 under the Fisheries Act No. 6 of 1970 from recommendations put forward by Ray (1968). Early study in DMRS indicated that some parts had a significant live coral cover for tourist attraction with some parts damaged as a result of dynamite fishing (Hamilton, 1975). It was characterized by unregulated fishing; including widespread use of beach seines and spear fishing (Benno, 1992). Two reports suggested that natural systems in DMRS have been degraded due to widespread use of dynamite and destructive fishing techniques and that it was

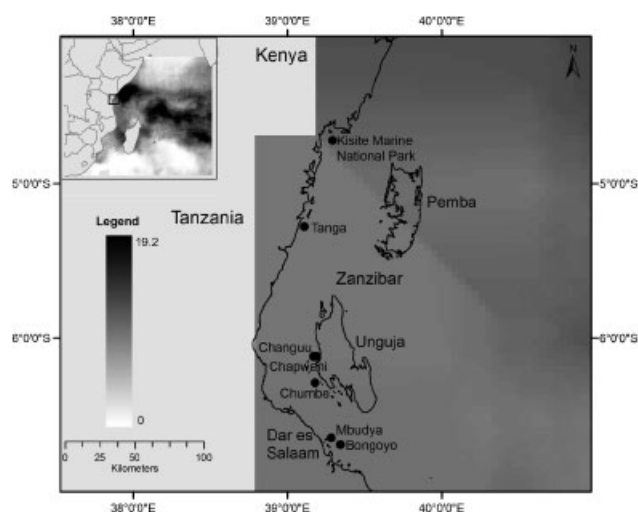


Figure 1. Map of the study sites and the intensity of the temperature anomaly in 1998 expressed as degree heating weeks.

no longer worthy of protection (UNEP, 1989; Gaudian *et al.*, 1995), but a subsequent study found that, although resources were heavily depleted, the area was still viable and should retain MPA status (McClanahan *et al.*, 1999). A new government gazette and management framework was made by the Ministry of Natural Resources and Tourism that led to the establishment of the Marine Parks and Reserves Act No. 29 of 1994. The 1994 Act gave the Marine Parks and Reserves Unit (MPRU) the responsibility of management of all Tanzania's MPAs with effective management of DMRS and this came into place in 2002.

The Zanzibar reefs of Changuu and Chapwani did not receive any increased management efforts during this time period. The adjacent privately owned marine park, CHICOP has been actively managed since its inception in 1991, with extractive activities prohibited on its main reefs.

### Field methods

Field methods replicated the original methodology (McClanahan *et al.*, 1999) with the addition of a herbivory assay using tethered seagrass during the second sampling period. The field methods are briefly described below.

Benthic cover on each reef was assessed by nine haphazardly placed 10 m transects (line intercept method) where all benthic organisms 3 cm or larger directly under the draped line were measured and recorded. Coral and frondose algae were identified to genus and other groups were pooled into larger functional groups, such as turf algae, sponge, and soft coral. Herbivory was studied using assays of the seagrass *Thalassia hemprichii* that were clipped to a weighted clothespin and attached to a thin nylon line at approximately 2 m intervals (Hay, 1981; McClanahan *et al.*, 1994). Thirty clippings were deployed per site and left for 24 h before retrieving for examination. Observers recorded whether or not the samples had been bitten, the amount bitten (to the closest 0.5 cm) and, based on bite scar characteristics, which herbivores were responsible for the bites, i.e. fish or sea urchin (McClanahan *et al.*, 1994).

Sea urchins were sampled in nine haphazardly placed 10 m<sup>2</sup> circular quadrats per site and all individuals were counted and recorded to the species level. Haphazard collections of ~20 individuals of each species were taken and their wet weights measured for converting population densities to wet weight biomass. Predation on sea urchins was estimated by piercing 30 individual *E. mathaei* with a hypodermic needle and threading with monofilament line. At each site three lines with ten loops at 2 m intervals each were tied to the reef at 5–10 m intervals and a threaded individual tied to each of the loops. Sea urchins were visited after 24 h to determine the number of individuals that died and to classify the condition of the carcass (McClanahan and Muthiga, 1989). A predation index was calculated where predation index =  $1 - S/1$ , where  $S$  is the survival, given either a 0 or a 1 for alive or dead. Those few individuals (<3%) that died from means other than predation were eliminated from this calculation.

Fish were sampled by visual counts in 5 m × 100 m belt transects using two methods. One was the discrete group sampling (DGS) method where a limited number of species and families were sampled, each during a single pass of the transect (McClanahan, 1994). The transect was passed four times and during each pass the groups were counted in the

order; 1—Scaridae, Acanthuridae, 2—Balistidae, Chaetodontidae, Diodontidae, Pomacanthidae, 3—Labridae, and 4—Pomacentridae. The second method is a single pass of the belt where encountered individuals were categorized into family groups and 10 cm size class intervals with no individuals less than 3 cm counted. The wet weight of the fish in each family group was estimated from length-weight relationships for these families (McClanahan and Kaunda-Arara, 1996).

### Data analysis

Studied components (fish family, sea urchin, and substratum) were tested for variation in time, location, and their interaction using a repeated measure ANOVA model. Herbivory experiments were performed only once and therefore a single-factor ANOVA testing for differences in sea urchin, herbivorous fish, and total herbivory between sites was performed. The large number of fish species and coral genera did not have enough degrees of freedom to allow the use of the MANOVA and, therefore, fish species abundance was tested for difference in abundance between the two sampling periods with *t*-tests for each individual taxon. Repeated measures ANOVA was also used to determine the effect of reef, area, time, and their interactions on fish species richness. Data for all comparisons were tested for homogeneity of variance across the reefs by each species, and if found to be non-homogenous a statistical test assuming unequal variance was performed. If fish or substratum variables differed significantly over time and between locations, detrended correspondence analysis (DCA) was performed to present the relationships of time, sites, and taxa in a graphic form. Additionally, a hierarchical cluster analysis using Ward similarity was performed on the coral genera data to investigate similarities in coral community distribution patterns. Cumulative numbers of coral genera and fish species were plotted against the sampling effort and a summary table of coral species richness in each reef for the maximum observation time is presented. All statistical tests were undertaken using the JMP statistical program (Sall *et al.*, 2001).

## RESULTS

### The benthic community

An analysis of the benthic substratum cover at all the reefs indicates that hard coral and turf algae were the largest component of the substratum ranging from 22–73% and 12–48% cover (respectively) followed by soft coral, coralline algae, sponge and calcareous algae (Table 1). The MANOVA and DCA analysis of the substratum cover indicates that in general the reefs of Kisite, Zanzibar, and Dar es Salaam tend to group together and are separate from the Tanga reefs (Table 1; Figure 2). This is attributable to the higher cover of frondose and calcareous algae and sponge at Tanga sites and higher soft and hard coral at the Kisite, Zanzibar, and Dar es Salaam sites. Change in substratum cover was variable depending on the location and substratum type but only turf algae, coralline algae and soft coral showed significant changes over time (Table 1). Turf algae declined and coralline algae increased with only a few exceptions. Soft coral displayed a strong reef × time interaction due to variable responses in the different reefs.

Table 1. Mean substratum cover before and after bleaching and statistical results for comparison of reefs across time and the interaction of reef with time

Reefs	Dar es Salaam		Kenya		Tanga		Zanzibar				Repeated measures													
	Bongoyo		Mbudya		Kisite		Tanga		Changuu		Chapwani		Chumbe		ANOVA									
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Reef		Time		Time*Reef					
															F	p	F	p	F	p				
Turf algae	47.7	13.8	27.9	15.8	48.0	38.8	33.2	32.4	40.6	22.7	31.2	13.1	12.8	24.6	1.8	0.23	9.9	<b>0.02</b>	2.8	0.10				
Calcareous algae	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.3	0.0	0.0	0.0	0.0	0.6	0.0	1.0	0.51	0.4	0.54	0.8	0.60				
Coralline algae	9.7	14.8	16.3	7.8	0.0	9.7	3.3	13.0	5.1	18.6	7.9	18.1	7.3	6.7	2.6	0.12	7.5	<b>0.03</b>	2.2	0.16				
Hard coral	32.4	67.0	52.8	73.1	21.9	43.0	33.8	27.8	44.7	45.0	52.3	51.6	62.7	61.5	4.4	<b>0.04</b>	2.2	0.18	1.0	0.47				
Fronlose algae	0.3	1.0	0.4	0.3	0.8	3.2	19.6	18.8	0.0	0.0	1.0	0.0	6.6	0.2	18.0	<b>0.001</b>	0.1	0.79	0.2	0.97				
Sand	4.1	0.1	0.1	0.2	17.0	1.8	3.7	2.1	5.2	1.6	2.3	0.4	8.9	6.8	1.9	0.21	2.9	0.13	0.8	0.59				
Seagrass	0.4	0.0	1.7	1.4	4.7	0.0	2.4	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.62	0.7	<b>0.44</b>	0.4	0.86				
Soft coral	5.1	3.3	0.6	1.4	7.7	2.7	3.7	3.7	4.3	12.1	4.7	16.8	0.8	0.0	6.5	<b>0.01</b>	9.8	<b>0.02</b>	10.3	<b>0.001</b>				
Sponge	0.4	0.0	0.1	0.1	0.0	0.8	0.2	0.5	0.0	0.0	0.6	0.0	0.3	0.0	5.3	<b>0.02</b>	0.2	0.67	3.7	0.06				

Boldface text =  $P < 0.05$ .

The number of coral genera recorded using the search sampling method was highest at the protected reefs of Chumbe (44 genera), then Kisite (39 genera) and Tanga (39 genera) (Figure 3). The lowest number of coral genera was recorded at the unmanaged Zanzibar reefs, with 23 and 25 for Changuu and Chapwani, respectively, and intermediate values were found at the Dar es Salaam marine reserves reef. The DCA ordination analysis of coral genera indicated that the fisheries closures at Kisite and Chumbe reefs were most similar, characterized by a coral assemblage that consisted of *Acropora*, several genera in the family Faviidae such as *Cyphastrea* and *Leptoria*, and members of the Pocilloporidae including *Pocillopora* and *Astreopora* (Figure 4). Kisite was differentiated from Chumbe in having more *Seriatopora* (Figure 5). The Tanga sites were closest in coral community composition to the closures. The Mbudya sites in the Dar es Salaam marine reserves reef were dominated by the genus *Montipora*, which maintained its dominance across the 1998 disturbance. Bongoyo reef sites were intermediate between Zanzibar's unmanaged reefs, which were differentiated by *Synarea*, *Lobophyllia*, *Stylophora*, *Halomitra* and *Galaxea*, and the Tanga sites. Pooling all fisheries closures and fished sites and comparing sites over time revealed no statistical differences in the abundance over time for specific coral genera (all *t*-tests not significant).

### Sea urchins and predation

The estimated total wet weight of sea urchins was highly variable ranging from  $512 \text{ kg ha}^{-1}$  to  $6468 \text{ kg ha}^{-1}$  with the larger bodied sea urchins *Diadema savignyi*, *D. setosum* and *Echinothrix diadema* contributing the largest component of the biomass of sea urchins. Statistically significant differences were found between reefs for the two *Diadema* species (Table 2). The full closures of Kisite and Chumbe had the lowest biomass of sea urchins compared with the fished reefs. In general, the change in biomass of the different species was also variable over time but only *D. savignyi* showed a statistically significant decline in wet weight between the reefs, with decreases ranging from 17–100% at all reefs except Chumbe where the biomass increased from 20 to  $40 \text{ kg ha}^{-1}$  (100%) during the 9-year period. Chumbe had an overall increase in sea urchin wet weight from 1000 to  $2300 \text{ kg ha}^{-1}$  over time. *Toxopneustes*

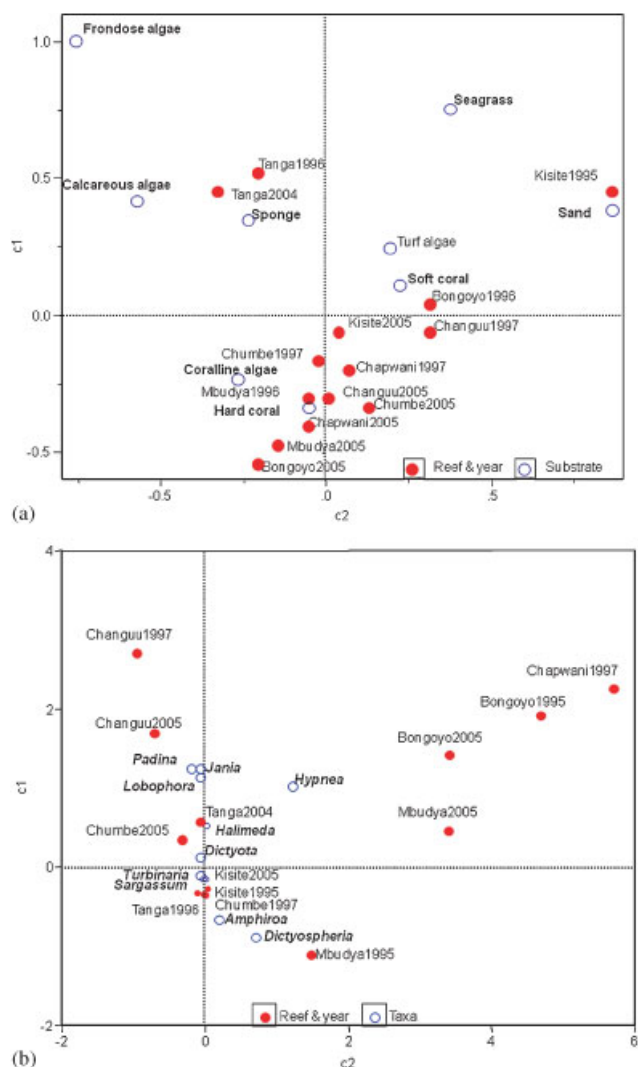


Figure 2. Ordination (detrended correspondence analysis) of reefs for before and after 1998 ENSO disturbance on the basis of (a) substratum functional group cover and (b) genera of erect algae.

*pileolus* occurred in the lowest abundance and was only recorded in Tanga and Chumbe reefs while *Tripneustes gratilla*

CHANGES IN TANZANIAN CORAL REEFS

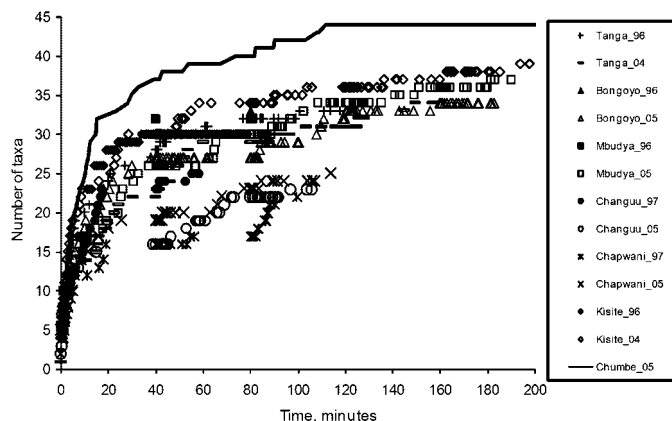


Figure 3. Plot of number of coral genera observed against searching time for all studied reefs before and after the 1998 ENSO disturbance.

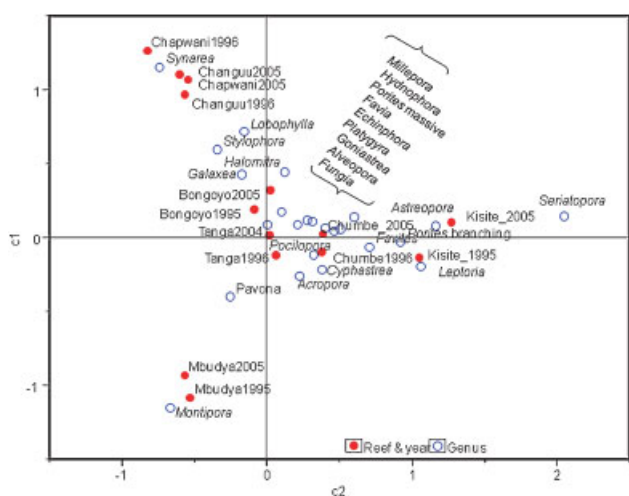


Figure 4. Ordination of hard coral cover genera on studied reefs before and after 1998 the ENSO disturbance.

was only recorded in Mbudya and Tanga and decreased from 420 to 0 kg ha<sup>-1</sup> at Mbudya in the 9-year period. The small bodied sea urchins *Echinometra mathaei* and *Echinostrephus molaris* occurred at very low abundances at most of the reefs, although *E. mathaei* showed a large increase from 20 to 2900 kg ha<sup>-1</sup> at Changuu reef over the 9-year period (Table 2, Figure 6). In general, the Zanzibar reefs including Chumbe were similar in their dominance of *D. setosum* over time (Figure 6).

Estimates of the rates of predation, using tethered *E. mathaei* at each reef were variable across the reefs (Table 2) but were highest at the protected sites at Kisite (predation index = 0.66–0.99) and Chumbe (0.31–0.45). Although there were some changes in predation rates in the 9-year period with increases mainly at the protected sites (~40%), this was not significant when reefs were compared across time and when these two factors were combined (Table 2).

**Finfish**

The estimated biomass of finfish ranged from wet weights of 130 to 1350 kg ha<sup>-1</sup> at the different reefs (Table 3). A

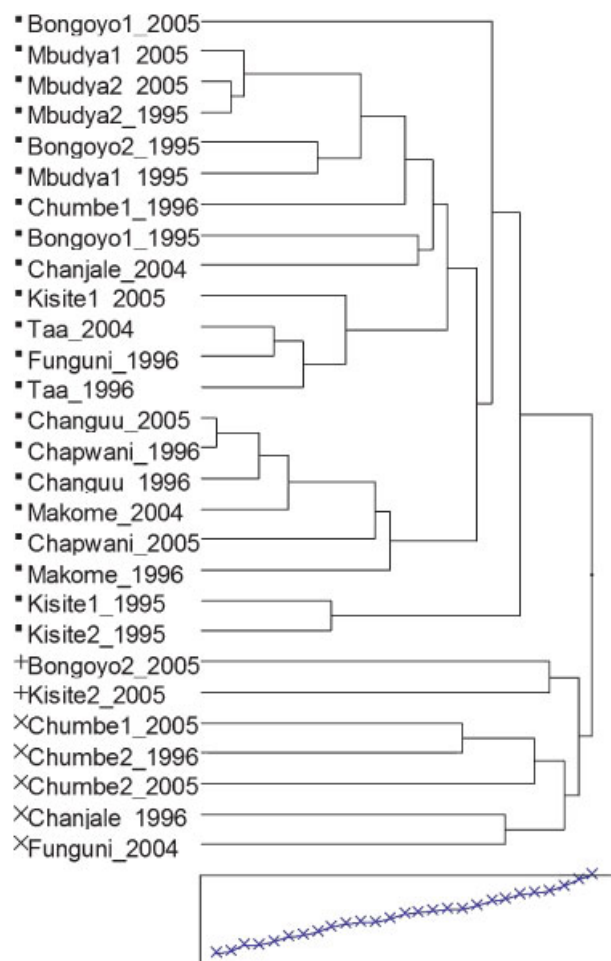


Figure 5. Hierarchical cluster analysis of sites grouped on the basis of their similarity (Ward method) in hard coral genera abundance.

comparison of different finfish family groups showed a statistically significant difference in biomass between reefs for all the families except for the Diodontidae, Pomacentridae, and Siganidae. In general, the Scaridae, Lutjanidae, and Acanthuridae had the highest biomass but varied considerably between reefs, but were notably most abundant in the fisheries closures (Table 3).

Table 2. Sea urchin biomass by species (kg ha<sup>-1</sup>), standard error of the mean (sem), predation index (0–1), and the statistical results for comparisons between reefs, across time, and the interaction of reef with time

Species	Dar es Salaam						Kenya						Tanga						Zanzibar						Repeated measures					
	Bongoyo		Mbudya		Kisite		Tanga		Changuu		Chapwani		Chumbe		Reef		MANOVA		Time		Time*Reef									
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	F	p	F	p	F	p	F	p								
<i>Diadema savignyi</i>	4696	1924	614	507	94	7	1019	358	227.2	125.1	13.4	0.0	20	40	9.1	<b>0.003</b>	6.6	<b>0.03</b>	3.7	<b>0.04</b>										
sem	525	410	413	174	45	7	634	274					20	13																
<i>Diadema setosum</i>	659	608	9	267	0	8	16	46	2622	3442	4569	2991	993	2122	26.4	<b>&lt;0.0001</b>	0.0	0.95	0.4	0.87										
sem	254	275	9	250	0	8	11	46					538	483																
<i>Echinothrix calamaris</i>	30	270	38	0	10	39	13	39	0	0	0	0	0	0	2.7	0.09	1.8	0.22	1.7	0.24										
sem	30	154	38	0	10	0	13	39					0	0																
<i>Echinothrix diadema</i>	785	1986	2229	1716	395	1157	1100	1243	92	0	62	0	38	171	1.0	0.50	2.5	0.15	2.3	0.14										
sem	138	135	1971	1330	106	810	565	493					23	171																
<i>Echinometra mathaei</i>	0	2	0	0	2	2	8	17	19	2901	0	11	0	3	1.2	0.41	1.1	0.33	1.1	0.43										
sem	0	2	0	0	2	2	5	14					0	3																
<i>Echinostrephus molaris</i>	0	0	0	0	12	3	6	8	0	0	0	0	0	0	0.9	0.56	1.4	0.27	2.2	0.15										
sem	0	0	0	0	10	3	4	5					0	0																
<i>Triploneustes gratilla</i>	0	0	421	0	0	0	7	85	0	0	0	0	0	0	0.9	0.51	0.6	0.46	1.2	0.41										
sem	0	0	421	0	0	0	7	69					0	0																
<i>Toxopneustes pileolus</i>	0	0	0	0	0	0	11	3	0	0	0	0	3	0	8.4	0.01	1.6	0.25	2.9	0.09										
sem	0	0	0	0	0	0	11	3					3	0																
Total biomass	6170	4789	3311	2489	512	1215	2180	1799	2960	6468	4644	3002	1054	2336	0.3	0.92	0.3	0.59	0.3	0.92										
sem	440	114	2007	907	40	790	1202	702					537	670																
Predation index	0.24	0.15	0.07	0.08	0.66	0.93	0.29	0.21	0.15	0.23	0.10	0.33	0.31	0.45	2.1	0.17	0.0	0.92	0.4	0.81										
sem	0.13	0.05	0.07	0.02	0.01	0.03	0.10	0.07					0.09	0.08																

Boldface text =  $P < 0.005$ .

The biomass of the different finfish families showed that the reefs closed to fishing clustered together (Figure 7). The Labridae, Pomacentridae and Chaetodontidae dominated the reefs open to fishing, while Acanthuridae, Balistidae, Lutjanidae, and Siganidae were more common in closures. Permanent full closures at Chumbe and Kisite had the highest estimated wet weight of fish (990 and 1350 kg ha<sup>-1</sup>, respectively) and the fished sites at Bongoyo, Changuu and Chapwani had the lowest biomass (130–280 kg ha<sup>-1</sup>) (Table 3). The unmanaged Zanzibar reefs were most similar to each other and separated out from the other reefs. Tanga sites showed an increase in wet weight over time and became more similar to the permanent fishery closure in Kisite.

In general, there was an increase in fish biomass in many reefs (ranging from 23% at Bongoyo to 97% at Kisite) except

at the unmanaged reefs in Zanzibar at Changuu and the closure at Chumbe (~8% and 10% decrease, respectively) over the 9-year period. Although there was a general increase in fish biomass at most of the reefs, this increase in biomass between sampling dates failed to show any significant differences when combining all of the categories of fish families. However, the interaction between reef and time found that Chaetodontidae and Scaridae responded differently in different reefs. Chaetodontidae increased in many reefs but declined in Changuu and Chumbe while Scaridae declined in fished reefs except Mbudya, increased in Kisite but declined in Chumbe.

In total, 142 species in eight families of finfish were recorded in the belt transects, 130 species in the closures and 121 in fished reefs (Table 4). The cumulative number of species was highest at the fully protected reefs at Kisite while the Zanzibar reefs Changuu and Chapwani, showed the lowest number of species (Figure 8(a)). There was no indication of a change in numbers of species over time for all reefs pooled by

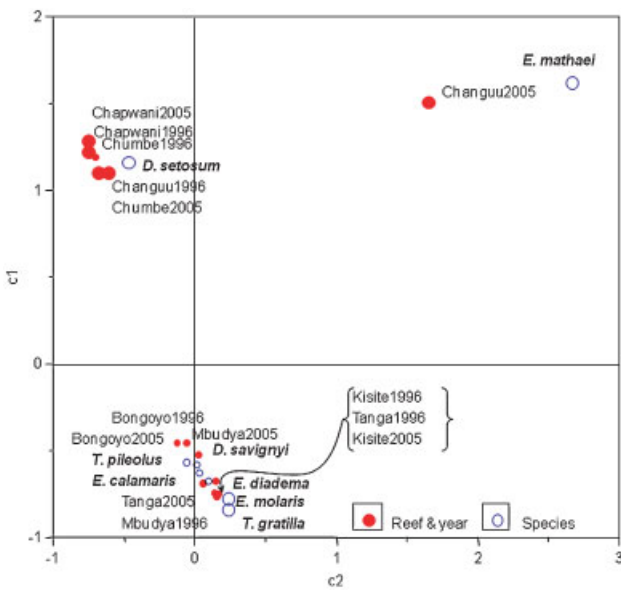


Figure 6. Ordination of sea urchin abundance on studied reefs before and after the 1998 ENSO disturbance.

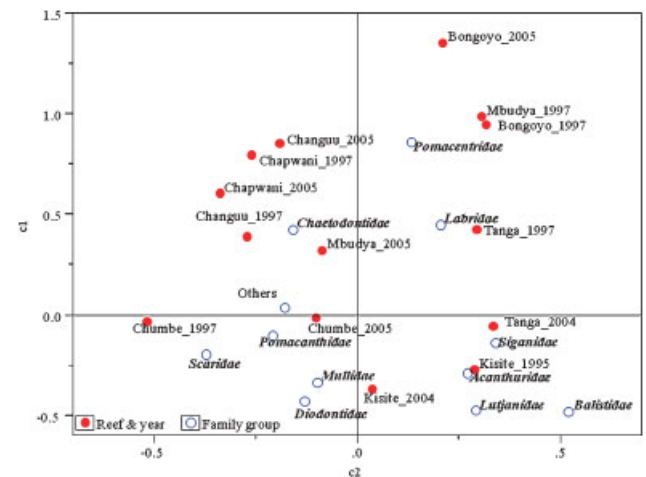


Figure 7. Ordination of the biomass of studied fish families on studied reefs before and after the 1998 ENSO disturbance.

Table 3. Biomass of fish by families (kg ha<sup>-1</sup>) for the two time periods and the results of the repeated measures ANOVA for reef, time, and their interaction

Fish family	Dar es Salaam		Kenya		Tanga		Zanzibar				Repeated measures											
	Bongoyo		Mbudya		Kisite		Tanga		Changuu		Chapwani		Chumbe		ANOVA							
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Reef	Time	Time*Reef					
																	F	p	F	p	F	p
Acanthuridae	18.4	5.8	30.0	21.2	133.8	260.1	54.7	82.5	7.8	0.9	0.0	0.0	89.5	104.2	15.8	<b>0.001</b>	0.7	0.43	0.9	0.52		
Balistidae	0.0	0.0	0.0	0.0	19.7	31.9	0.2	41.3	0.0	0.0	0.0	0.0	6.4	13.4	2.6	<b>0.05</b>	1.9	0.47	1.0	0.47		
Chaetodontidae	6.8	26.8	17.6	23.3	15.8	39.1	8.6	11.1	16.8	1.9	5.6	15.7	60.6	14.8	6.7	<b>0.00</b>	0.0	0.97	8.0	<b>0.001</b>		
Diodontidae	0.0	0.0	0.0	0.0	0.0	3.5	0.0	3.6	0.0	0.0	0.0	0.0	3.6	0.0	0.5	0.84	0.2	0.67	0.9	0.53		
Labridae	33.3	19.4	33.0	20.4	34.1	50.0	39.0	59.8	38.8	32.9	7.4	14.0	57.7	42.8	5.8	<b>0.001</b>	0.0	0.93	1.0	0.45		
Lutjanidae	7.8	0.0	4.2	36.6	189.3	300.1	19.6	57.5	23.7	0.0	0.0	0.0	48.6	134.6	3.7	<b>0.01</b>	0.6	0.44	0.2	0.96		
Mullidae	0.3	0.0	0.0	5.5	4.6	21.2	4.2	7.7	0.0	0.0	0.0	0.0	16.2	3.6	2.4	0.07	0.5	0.47	2.6	0.06		
Pomacanthidae	1.2	0.0	0.0	4.3	12.6	7.1	5.2	19.9	7.2	0.0	0.0	0.0	32.0	47.0	14.3	<b>0.00</b>	0.4	0.56	0.6	0.72		
Pomacentridae	75.6	87.6	96.4	64.8	69.6	51.1	68.4	54.6	74.9	125.4	63.9	66.5	91.1	131.3	2.4	0.07	0.3	0.58	1.3	0.32		
Scaridae	11.6	2.4	15.5	48.5	122.0	339.5	25.8	68.3	109.5	81.9	26.2	10.7	436.0	222.1	4.8	<b>0.001</b>	0.0	0.87	6.3	<b>0.001</b>		
Siganidae	0.0	0.0	0.8	0.0	2.4	5.9	2.5	3.8	3.2	0.0	0.0	0.2	3.2	0.0	0.8	0.59	0.0	0.86	0.4	0.90		
Others	19.7	17.1	16.6	73.9	79.6	244.6	32.2	45.7	36.5	47.6	62.9	175.8	146.5	171.8	3.2	<b>0.02</b>	2.9	0.11	0.8	0.61		
Total	129.1	159.1	214.0	298.6	683.5	1354.2	260.4	457.4	318.1	290.6	166.0	283.0	991.3	885.6	27.9	<b>0.001</b>	2.2	0.15	1.7	0.18		

Boldface text =  $P < 0.05$ .



Table 4. Fish species abundance sorted from most to least abundance before and after the 1998 ENSO disturbance and tests of significance for the difference in abundance between the two periods

Family	Species	Total						Unfished			Fished			
		Pre		Post		Difference	t-test	Prob >  t	d	t-test	Prob >  t	d	t-test	Prob >  t
		Mean	Stdev	Mean	Stdev									
Acanthuridae	<i>Ctenochaetus striatus</i>	9.8	10.3	10.1	12.0	0.3	0.1	0.95	-2.7	-0.3	0.76	1.8	0.4	0.71
	<i>Naso annulatus</i>	5.9	11.4	2.9	5.1	-3.1	-0.9	0.35	-10.6	-1.5	0.18	0.7	1.1	0.30
	<i>Acanthurus nigrofasciatus</i>	5.6	9.3	1.9	3.2	-3.8	-1.5	0.16	-9.4	-1.9	0.13	-1.0	-0.4	0.73
	<i>Zebrossoma scopas</i>	4.3	4.7	2.0	3.4	-2.3	-1.5	0.14	-4.6	-1.8	<b>0.10</b>	-1.2	-0.7	0.52
	<i>Ctenochaetus strigosus</i>	2.3	3.1	3.0	5.0	0.8	0.5	0.62	2.7	0.7	0.48	-0.2	-0.3	0.80
	<i>Acanthurus leucosternon</i>	1.1	1.6	0.6	1.1	-0.5	-0.9	0.35	-0.8	-0.7	0.52	-0.3	-1.1	0.30
	<i>Acanthurus tenneinti</i>	1.1	2.9	0.1	0.3	-1.1	-1.4	0.18	-3.4	-1.7	0.16	-0.2	-0.9	0.39
	<i>Zebrossoma veliferum</i>	0.5	0.5	0.5	0.7	0.0	0.0	1.00	0.3	0.5	0.62	-0.2	-0.9	0.39
	<i>Acanthurus nigricauda</i>	0.2	0.4	0.5	1.4	0.3	0.9	0.40	-0.2	-1.6	0.18	0.6	1.1	0.30
	<i>Naso lituratus</i>	0.1	0.3	0.5	0.9	0.3	1.4	0.17	0.6	1.0	0.33	0.2	1.3	0.22
	<i>Paracanthurus hepatus</i>	0.5	1.9	0.1	0.3	-0.4	-0.9	0.40	-1.3	-0.9	0.44	-0.1	-1.0	0.34
	<i>Acanthurus dussumieri</i>	0.3	0.8	0.0	0.0	-0.3	-1.3	0.20	-0.7	-1.2	0.30	0.2	1.0	0.34
	<i>Acanthurus triostegus</i>	0.1	0.4	0.1	0.4	0.0	-0.2	0.81	-0.4	-1.6	0.18	0.2	1.0	0.34
	<i>Acanthurus xantheropus</i>	0.1	0.3	0.0	0.0	-0.1	-1.7	<b>0.10</b>	-1.0	-1.0	0.37	-0.2	-1.4	0.19
	<i>Acanthurus blochii</i>	0.1	0.4	0.0	0.0	-0.1	-1.0	0.33	-0.7	-1.8	0.12	-0.2	-1.0	0.34
	<i>Naso tuberosus</i>	0.0	0.0	0.1	0.4	0.1	1.0	0.33	0.3	1.0	0.37	0.1	1.0	0.34
	<i>Acanthurus lineatus</i>	0.0	0.0	0.1	0.3	0.1	1.0	0.33	-0.1	-1.0	0.37	0.1	1.0	0.34
<i>Naso unicornis</i>	0.0	0.1	0.0	0.0	0.0	0.0	1.00	-0.1	-1.0	0.37	0.1	1.0	0.34	
<i>Sufflamen chrysoptera</i>	0.6	1.3	0.5	1.0	0.0	-0.2	0.88	-0.8	-0.8	0.44	0.3	1.0	0.34	
<i>Sufflamen fraenatus</i>	0.0	0.0	0.9	2.0	0.9	1.8	<b>0.10</b>	-0.7	-1.8	0.12	1.4	1.9	<b>0.10</b>	
<i>Balistapus undulatus</i>	0.5	0.7	0.2	0.4	-0.3	0.1	0.57	-0.7	-1.8	0.12	-0.2	-2.0	<b>0.08</b>	
<i>Balistes viridescens</i>	0.0	0.1	0.5	1.8	0.4	0.9	0.36	1.3	0.9	0.41	0.1	1.0	0.34	
<i>Balistes conspicillum</i>	0.0	0.0	0.1	0.2	0.1	1.5	0.16	0.2	1.6	0.18	0.1	1.0	0.34	
<i>Pseudobalistes fuscus</i>	0.0	0.0	0.1	0.3	0.1	1.0	0.33	0.2	1.0	0.37	0.3	1.0	0.34	
<i>Chaetodon trifasciatus</i>	4.2	5.8	6.9	8.9	2.7	1.0	0.33	-4.4	-1.9	0.27	6.3	1.8	<b>0.09</b>	
<i>Chaetodon trifasciatis</i>	2.1	3.5	0.9	0.9	-1.6	-1.7	<b>0.10</b>	-0.4	-1.6	0.18	-0.4	-0.7	0.48	
<i>Chaetodon auriga</i>	1.2	1.6	0.9	1.2	-0.3	-0.6	0.56	-0.8	-1.0	0.34	-0.1	-0.1	0.94	
<i>Chaetodon guttatissimus</i>	0.4	0.8	0.9	1.8	0.5	0.9	0.37	0.7	0.5	0.62	0.4	1.7	0.13	
<i>Chaetodon vagabundus</i>	0.0	0.1	1.0	2.9	1.0	1.3	0.19	3.0	1.4	0.22	-0.1	-0.1	0.93	
<i>Chaetodon kleinii</i>	0.5	1.0	0.5	1.0	0.0	0.1	0.93	0.2	0.6	0.54	0.5	1.5	0.15	
<i>Chaetodon lunula</i>	0.2	0.4	0.6	0.7	0.3	1.6	0.13	0.1	0.6	0.54	0.4	1.1	0.29	
<i>Chaetodon melanotus</i>	0.1	0.3	0.4	0.9	0.3	1.2	0.25	0.1	0.4	0.67	0.4	1.1	0.29	
<i>Chaetodon zanzibarensis</i>	0.3	0.6	0.2	0.5	-0.1	-0.5	0.61	0.0	0.0	1.00	-0.2	-0.6	0.56	
<i>Chaetodon faacula</i>	0.2	0.3	0.1	0.3	0.0	-0.3	0.77	-0.5	-3.2	<b>0.01</b>	0.2	1.8	<b>0.10</b>	
<i>Chaetodon xanthocephalus</i>	0.1	0.3	0.1	0.2	0.0	-0.4	0.70	-0.1	-0.4	0.67	0.0	0.0	1.00	
<i>Chaetodon lineolatus</i>	0.0	0.0	0.2	0.3	0.2	2.1	<b>0.06</b>	0.3	1.5	0.21	0.3	2.2	<b>0.05</b>	
<i>Chaetodon meyeri</i>	0.0	0.0	0.1	0.3	0.0	1.7	<b>0.10</b>	0.0	0.0	1.00	0.1	1.0	0.34	
<i>Chaetodon bennetti</i>	0.0	0.0	0.0	0.1	0.0	1.0	0.33	0.0	0.0	1.00	0.1	1.0	0.34	
<i>Diodon liturosus</i>	0.1	0.2	0.1	0.2	0.0	0.5	0.64	0.0	0.0	1.00	0.1	0.6	0.56	
<i>Thalassoma hebraicum</i>	19.9	10.8	14.1	12.7	-5.9	-1.4	0.18	-0.2	0.0	0.98	-8.7	-1.7	<b>0.10</b>	
<i>Thalassoma amblycephalum</i>	24.9	27.1	6.2	11.8	-18.7	-2.4	<b>0.02</b>	-16.2	-0.9	0.40	-19.9	-2.6	<b>0.03</b>	
<i>Gomphosus coeruleus</i>	9.8	5.8	6.7	5.3	-3.1	-1.5	0.14	-5.5	-3.0	<b>0.02</b>	-1.9	-0.7	<b>0.48</b>	
<i>Labroides dimidiatus</i>	9.4	6.9	5.9	3.8	-3.5	-1.7	<b>0.10</b>	-1.0	-0.3	0.77	-4.8	-2.1	<b>0.05</b>	
<i>Thalassoma hardwicke</i>	6.4	7.1	2.7	2.3	-3.7	-1.9	<b>0.07</b>	-4.8	-2.1	<b>0.07</b>	-3.2	-1.2	0.26	
<i>Stethojulis albivittata</i>	5.8	5.2	2.5	2.7	-3.4	-2.2	<b>0.03</b>	-5.9	-1.7	0.13	-2.1	-1.6	0.14	
<i>Pseudoheilinus hexataenia</i>	3.7	3.5	2.8	3.4	-1.0	-0.8	0.45	-2.1	-0.7	0.51	-0.4	-0.4	0.67	
<i>Labrichthys unilineatus</i>	3.5	4.7	2.3	3.4	-1.2	-0.8	0.44	-3.9	-1.5	0.21	-1.4	-0.7	0.50	
<i>Halichoeres hortulanus</i>	3.6	4.1	2.2	3.9	-1.4	-1.0	0.35	-1.4	-0.7	0.52	-1.4	-0.7	0.50	



CHANGES IN TANZANIAN CORAL REEFS

<i>Thalassoma lunare</i>	1.4	3.5	2.1	3.0	0.7	0.6	0.54	2.9	2.7	0.05	-0.4	-0.2	0.84
<i>Cheilinus trilobatus</i>	0.7	1.1	1.4	3.4	0.7	0.8	0.45	0.2	0.6		1.0	0.7	0.49
<i>Halichoeres cosmetus</i>	0.0	0.0	2.1	3.6	2.1	2.3	0.04	5.8	3.0	0.04	0.3	1.0	0.34
<i>Labroides bicolor</i>	1.3	2.2	0.7	1.3	-0.5	-0.8	0.42	-0.2	-1.4	0.21	0.2	0.4	0.68
<i>Coris caudimaculata</i>	0.7	1.3	1.2	2.0	0.6	0.9	0.37	0.9	1.4	0.22	0.4	0.5	0.66
<i>Anampses caeruleopunctatus</i>	0.8	1.3	1.1	2.1	0.3	0.4	0.68	-0.3	-0.2	0.83	0.6	0.8	0.45
<i>Hemigymnus fasciatus</i>	0.7	0.8	1.1	1.7	0.3	0.7	0.50	0.6	0.4	0.67	0.3	0.8	0.44
<i>Hemigymnus melapterus</i>	1.3	2.0	0.4	0.5	-0.9	-1.7	0.12	0.0	0.0	1.00	0.2	0.6	0.57
<i>Pteragogus pelycus</i>	0.0	0.0	1.5	2.1	1.5	2.7	0.01	0.4	1.6	0.18	2.1	2.6	0.03
<i>Anampses meleagrides</i>	1.1	1.2	0.4	0.5	-0.7	-2.1	0.04	-1.9	-2.9	0.02	-0.2	0.4	0.66
<i>Coris formosa</i>	0.4	0.6	0.8	1.5	0.4	0.9	0.39	0.7	0.8	0.47	0.2	0.4	0.67
<i>Cheilinus oxycephalus</i>	1.0	1.8	0.2	0.3	-0.8	-1.7	0.10	0.4	2.1	0.10	-1.4	-2.2	0.06
<i>Cheilio inermis</i>	0.7	1.4	0.4	0.6	-0.4	-0.9	0.36	-0.3	-1.0	0.36	-0.4	-0.7	0.50
<i>Cirrhitilabrus exquisitus</i>	0.1	0.4	1.0	1.9	0.9	1.7	0.11	1.3	1.0	0.37	0.7	1.4	0.19
<i>Bodianus axillaris</i>	0.4	0.5	0.6	0.9	0.2	0.6	0.55	-0.2	-0.6	0.57	0.4	0.9	0.37
<i>Anampses twistii</i>	0.8	1.0	0.2	0.4	-0.6	-2.2	0.04	-0.1	-0.6	0.58	-0.9	-2.2	0.04
<i>Macropharyngodon bipartitus</i>	0.0	0.0	0.8	1.9	0.8	1.6	0.13	2.2	1.6	0.18	0.1	1.0	0.34
<i>Epibulus insidiator</i>	0.2	0.7	0.5	0.7	0.2	0.9	0.36	0.1	0.6	0.54	0.3	0.8	0.42
<i>Halichoeres marginatus</i>	0.4	1.2	0.3	1.0	0.0	-0.1	0.93	0.9	1.2	0.31	-0.5	-1.1	0.30
<i>Novachulichthys taenourus</i>	0.3	0.4	0.2	0.5	0.0	0.0	0.85	0.2	0.6	0.54	-0.2	-0.7	0.49
<i>Stethojulis strigiventer</i>	0.3	0.8	0.2	0.4	-0.1	-0.4	0.66	0.4	1.6	0.18	-0.4	-1.1	0.28
<i>Coris gaimardus = africana</i>	0.2	0.3	0.2	0.5	0.0	0.2	0.82	-0.1	-0.3	0.78	0.1	0.8	0.41
<i>Hologymnosus annulatus</i>	0.0	0.1	0.3	0.8	0.3	1.2	0.24	0.9	1.5	0.21	-0.1	-1.0	0.34
<i>Halichoeres scapularis</i>	0.2	0.5	0.0	0.1	-0.2	-1.4	0.17	-0.3	-1.0	0.37	-0.2	-0.9	0.36
<i>Cheilinus mentalis</i>	0.1	0.3	0.1	0.3	0.0	-0.3	0.75	0.1	0.4	0.68	0.1	-1.0	0.34
<i>Halichoeres nebulosus</i>	0.1	0.3	0.2	0.6	0.1	0.6	0.58	-0.2	-1.0	0.37	0.2	0.6	0.58
<i>Coris aygula</i>	0.1	0.3	0.1	0.3	0.1	0.7	0.52	0.5	1.3	0.27	0.2	1.8	0.10
<i>Thalassoma genivittatum</i>	0.0	0.0	0.2	0.5	0.2	1.2	0.24	0.0	0.0				
<i>Cheilinus diagamnus</i>	0.0	0.0	0.1	0.2	0.1	1.5	0.16	0.0	0.0		0.1	1.5	0.17
<i>Cheilinus fasciatus</i>	0.0	0.1	0.0	0.1	0.0	0.0	1.00	-0.1	-1.0	0.37	0.0	0.0	1.00
<i>Hologymnosus doliaatus</i>	0.0	0.1	0.0	0.0	0.0	-1.0	0.33	-0.1	-1.0	0.37	0.2	0.1	0.91
<i>Centropyge multispinis</i>	3.1	3.8	2.0	2.6	-1.0	-0.9	0.39	-2.3	-1.2	0.25	-0.4	-0.3	0.79
<i>Pomacanthus chrysurus</i>	0.0	0.1	0.6	1.3	0.5	1.5	0.15	1.5	1.6	0.18	0.1	1.0	0.34
<i>Pomacanthus semicirculatus</i>	0.4	0.8	0.2	0.4	-0.1	-0.6	0.57	0.0	0.0	1.00	-0.2	-0.7	0.55
<i>Pygoplites diacanthus</i>	0.1	0.3	0.1	0.4	0.0	0.0	1.00	0.3	1.0	0.36	-0.2	-1.4	0.19
<i>Pomacanthus imperator</i>	0.1	0.2	0.1	0.3	0.0	0.0	1.00	0.0	0.0	1.00			
<i>Centropyge acanthops</i>	0.0	0.0	0.1	0.3	0.1	1.0	0.33				0.1	1.0	0.34
<i>Neopomacentrus azyron</i>	58.6	138.8	67.7	91.6	9.2	0.2	0.83	-22.7	-1.4	0.23	25.1	0.4	0.69
<i>Plectroglyphidodon laeeyron</i>	61.6	67.7	59.9	78.7	-1.7	-0.1	0.95	3.6	0.3	0.75	-4.3	-0.1	0.91
<i>Chromis viridis</i>	85.4	103.4	22.4	40.2	-63.0	-2.2	0.00	7.9	1.1	0.30	-50.0	-1.7	0.12
<i>Chromis dimidiata</i>	51.5	78.4	42.0	58.4	-9.5	-0.4	0.71	-24.3	-0.4	0.69	-2.1	-0.1	0.92
<i>Chromis weberi</i>	7.5	15.2	69.9	137.5	62.3	1.7	0.10	167.7	1.8	0.15	9.7	0.7	0.51
<i>Pomacentrus sulfureus</i>	39.6	80.9	19.3	26.0	-20.3	-0.9	0.36	-76.5	-1.3	0.27	7.8	0.7	0.47
<i>Chromis nigra</i>	19.0	31.7	22.3	50.7	3.3	0.2	0.83	19.1	0.5	0.65	-4.7	-0.9	0.40
<i>Chrysiptera unimaculata</i>	27.4	28.5	12.2	24.3	-15.3	-1.6	0.13	1.3	0.3	0.09	-16.8	-1.2	0.23
<i>Dascyllus aruanus</i>	32.5	83.0	4.6	7.9	-27.9	-1.3	0.22	7.3	1.2	0.27	-45.6	-1.4	0.17
<i>Neopomacentrus cyanomos</i>	0.0	0.0	33.2	89.1	33.2	1.4	0.17	99.5	1.6	0.19			
<i>Stegastes nigricans</i>	27.5	60.2	3.6	13.7	-23.9	-1.5	0.15	-13.5	-1.0	0.37	-29.1	-1.3	0.24
<i>Chromis ternatensis</i>	16.6	35.3	7.8	18.1	-8.8	-0.9	0.40	-29.2	-1.2	0.26	1.4	0.1	0.88
<i>Plectroglyphidodon diekii</i>	12.0	12.7	9.5	16.4	-2.5	-0.5	0.64	-18.6	-3.2	0.01	5.6	0.8	0.44
<i>Dascyllus trimaculatus</i>	13.9	30.5	30.5	11.7	-7.6	-0.9	0.38	1.2	0.4	0.73	-12.0	-1.0	0.35
<i>Abudefduf sexfasciatus</i>	11.9	21.7	3.2	4.9	-8.7	-1.6	0.14	-17.9	-1.1	0.35	-4.1	-1.4	0.17
<i>Amphiprion akallopisos</i>	6.4	8.2	8.4	14.8	2.0	0.5	0.64	14.8	1.4	0.20	-4.4	-1.4	0.91
<i>Chromis vanderbilti</i>	0.0	0.0	14.5	54.8	14.5	1.0	0.32	43.4	1.0	0.36			
<i>Abudefduf vaigiensis</i>	7.2	14.0	1.4	3.0	-5.8	-1.6	0.13	-7.3	-0.9	0.43	-5.1	-1.3	0.23
<i>Pomacentrus pavo</i>	3.7	8.2	3.8	10.8	0.1	0.0	0.99	-1.2	-0.6	0.59	0.7	0.1	0.89

Pomacanthidae

Pomacentridae

Table 4. Continued

Family	Species	Total				Difference				Unfished				Fished					
		Pre		Post		Mean		Stdev		r-test		Prob >  t		d		r-test		Prob >  t	
		Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev	r-test	Prob >  t	r-test	Prob >  t	d	r-test	Prob >  t	d	r-test	Prob >  t
	<i>Amphiprion allardi</i>	3.5	7.1	2.8	5.4	-0.7	0.76	-0.3	0.76	0.5	0.7	0.53	-1.3	-0.4	0.71				
	<i>Amblyglyphidodon leucogaster</i>	1.2	2.1	4.7	6.5	3.5	<b>0.07</b>	2.0	<b>0.07</b>	-0.8	-1.0	0.36	5.6	2.3	<b>0.04</b>				
	<i>Abudefduf sparoides</i>	4.2	7.0	1.3	2.5	-2.9	0.14	-1.5	0.14	-2.5	-0.6	0.56	-3.2	-0.1	0.17				
	<i>Neoglyphidodon melas</i>	2.2	2.8	1.5	2.2	-0.7	0.45	-0.8	0.45	-1.2	-1.0	0.35	-0.5	-0.4	0.72				
	<i>Pomacentrus caeruleus</i>	1.6	2.2	1.5	2.3	-0.1	0.92	-0.1	0.92	0.9	0.6	0.59	-0.1	-0.1	0.92				
	<i>Stegastes lividus</i>	3.0	8.0	0.0	0.0	-3.0	0.17	-1.5	0.17	7.0	1.3	0.26	-4.5	-1.5	0.17				
	<i>Plectroglyphidodon nitidus</i>	0.0	0.0	2.3	7.2	2.3	0.23	1.3	0.23	0.6	0.3	0.74	0.1	0.1	0.91				
	<i>Pomacentrus baenschi</i>	1.0	1.5	1.2	2.1	0.2	0.72	0.4	0.72	2.2	1.0	0.39	0.4	1.2	0.24				
	<i>Plectroglyphidodon johnstonian</i>	0.6	1.1	1.5	3.1	1.0	0.28	1.2	0.28	-0.4	-1.0	0.37	-2.8	-1.1	0.32				
	<i>Dascyllus carneus</i>	2.0	6.7	0.0	0.0	-2.0	0.27	-1.1	0.27	2.2	1.3	0.25							
	<i>Pomacentrus fasciatus</i>	0.0	0.0	0.7	2.2	0.7	0.33	1.3	0.33	1.2	2.1	1.09	-0.2	-7.8	0.44				
	<i>Stegastes fasciatus</i>	0.2	0.6	0.4	0.9	0.3	0.77	0.9	0.77	0.9	1.6	0.18							
	<i>Abudefduf septemfasciatus</i>	0.0	0.0	0.3	0.8	0.3	0.17	1.5	0.17	1.2	1.0	0.37							
	<i>Chrysiptera leucopoma</i>	0.1	0.4	0.0	0.0	-0.1	0.33	-1.0	0.33	-0.3	-1.0	0.37							
	<i>Chrysiptera annulata</i>	0.0	0.0	0.1	0.3	0.7	0.33	1.0	0.33	0.2	1.0	0.37							
	<i>Pomacentrus pikei</i>	0.0	0.0	0.1	0.2	0.1	0.16	1.5	0.16	0.2	0.6	0.18							
	<i>Chromis pombae</i>	0.0	0.0	0.0	0.1	0.0	0.33	1.0	0.33	0.1	1.0	0.37							
	<i>Chrysiptera glauca</i>	0.0	0.1	0.0	0.0	-0.3	0.33	-1.0	0.33	0.1	1.0	0.37							
	<i>Stegastes limbatus</i>	0.0	0.0	0.0	0.1	0.0	0.36	1.0	0.36	0.1	1.0	0.37							
Scaridae	<i>Scarus sordidus</i>	7.1	7.2	8.6	9.8	1.6	0.62	0.5	0.62	-2.0	-0.3	0.76	3.4	1.5	0.17				
	<i>Scarus frenatus</i>	2.8	2.7	1.6	3.6	-1.2	0.33	-1.0	0.33	-2.1	-0.7	0.50	-0.7	-1.3	0.21				
	<i>Scarus niger</i>	1.9	2.8	0.7	0.8	-1.2	0.13	-1.6	0.13	-0.3	-1.7	0.16	-0.3	-0.5	0.62				
	<i>Scarus ghobban</i>	1.0	2.3	1.0	1.2	-0.1	0.92	-0.1	0.92	0.3	0.3	0.80	-0.3	-0.3	0.78				
	<i>Scarus rubroviolaceus</i>	0.3	0.6	1.6	3.9	1.2	0.24	1.2	0.24	2.5	0.8	0.45	0.6	1.3	0.22				
	<i>Calotomus carolinus</i>	1.0	1.5	0.9	1.6	-0.1	0.86	-0.2	0.86	-0.3	-4.8	<b>0.10</b>	0.0	0.0	1.00				
	<i>Scarus tricolor</i>	0.2	0.6	1.6	3.2	1.4	0.12	1.7	0.12	4.1	2.1	<b>0.10</b>	0.0	0.0	1.00				
	<i>Scarus psittacus</i>	0.4	1.4	1.2	2.4	0.7	0.32	1.0	0.32	1.7	0.8	0.43	0.3	1.4	0.19				
	<i>Chlorurus strongylocephalus</i>	0.6	0.9	0.7	1.0	0.1	0.78	0.3	0.78	-0.6	-0.9	0.39	0.5	1.1	0.29				
	<i>Scarus scaber</i>	0.8	2.2	0.3	0.8	-0.6	0.36	0.9	0.36	-0.8	-1.7	0.27	-0.5	-0.5	0.60				
	<i>Hipposcarus harid</i>	0.6	1.6	0.1	0.3	-0.5	0.26	-1.2	0.26	-1.4	-1.2	0.29	-1.3	-1.8	0.11				
	<i>Scarus falcipectus</i>	0.4	0.6	0.2	0.5	-0.2	0.44	-0.8	0.44	-0.8	-2.1	<b>0.09</b>	0.2	0.7	0.52				
	<i>Cetoscarus bicolor</i>	0.4	0.8	0.2	0.5	-0.1	0.58	-0.6	0.58	-0.4	-0.7	0.52	0.0	0.0	1.00				
	<i>Scarus russelli</i>	0.3	0.6	0.0	0.0	-0.3	<b>0.10</b>	-1.8	<b>0.10</b>	-0.9	-2.3	<b>0.09</b>	0.0	0.0	1.00				
	<i>Scarus viridifucatus</i>	0.1	0.4	0.2	0.4	0.0	0.82	0.2	0.82	0.0	0.0	1.00	0.1	1.0	0.34				
	<i>Scarus caudofasciatus</i>	0.0	0.0	0.3	1.0	0.3	0.33	1.0	0.33	0.8	1.0	0.37							
	<i>Scarus atrilunula</i>	0.0	0.1	0.1	0.3	0.0	0.66	0.4	0.66	-0.1	-1.0	0.37	0.1	1.0	0.34				
	<i>Scarus festivus</i>	0.0	0.0	0.1	0.4	0.1	0.33	1.0	0.33	0.2	1.0	0.37	0.2	1.0	0.34				
	<i>Leptoscarus vaigiensis</i>	0.0	0.1	0.0	0.0	0.0	0.33	-1.0	0.33	-0.1	-1.0	0.37	-0.1	-1.0	0.34				

Boldface text =  $P < 0.10$ .

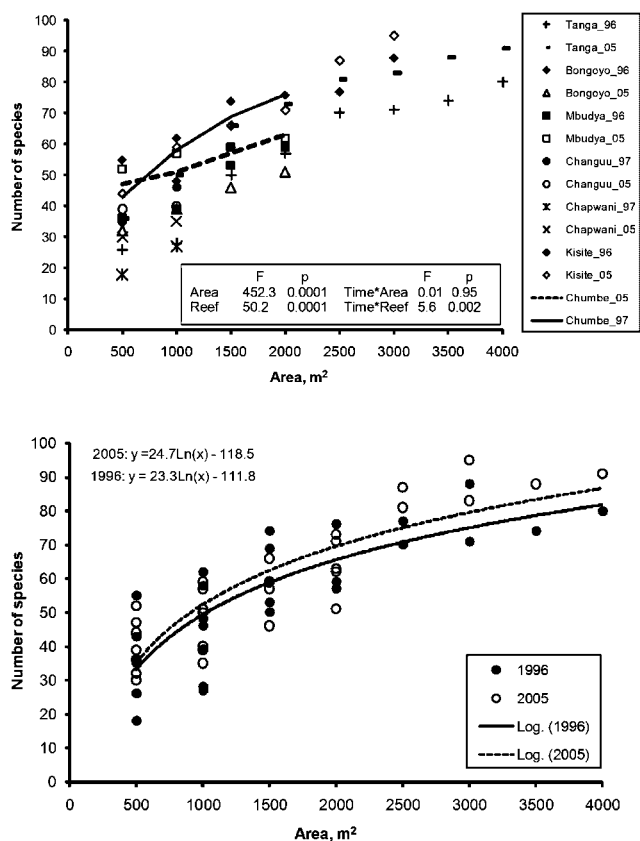


Figure 8. (a) Plot of the number of fish species against sampling area and results of statistical tests for reef, area, time and their interactions and (b) pooling data into before and after ENSO periods. Logarithmic curves are fitted for the two time periods.

time periods but there was an increase in the number of species per transect between 1997 and 2005 at Kisite (8–13%) and Tanga (16–24%), while the full closure at Chumbe showed a decrease of between 13 and 17% (Figure 8(b)).

The average abundance of individual species was highly variable ranging from less than 0.1 to 85 individuals per 500 m², with more than 90% of the species occurring in the 0.1 to 10 individuals per 500 m² range (Table 4). The most abundant species included the pomacentrids *Chromis viridis* (85 ± 103 individuals per 500 m²), *C. weberi* (70 ± 138), *C. dimidiata* (52 ± 78 individuals per 500 m²), *Plectroglyphidodon lacrymatus* (62 ± 68 individuals per 500 m²) and *Neopomacentrus azyron* (68 ± 92 individuals per 500 m²). There was little change in the abundance of individual finfish species between sampling dates with only seven species showing a significant change in abundance over this time period (Table 4). The labrids *Pteragogus pelycus* and *Halichoeres cosmetus* showed a statistically significant increase in abundance while the pomacentrid *C. viridis*, and the labrids *Thalassoma amblycephalum*, *Stethojulis albobittata*, *Anampses twistii* and *A. meleagrides* decreased significantly in abundance over this period.

Most species generally did display differences in abundance in relation to management over the study period (Table 4). A few pomacentrid and labrid species displayed differences with management but the directions of the responses were not consistent. For example, at the full closures, *Thalassoma lunare*

Table 5. Comparison of fish and sea urchin herbivory on a seagrass assay (*Thalassia hemprichii*) between studied reefs

Reef	n	Total herbivory, %		Urchins, %		Fish, %	
		Mean	sem	Mean	sem	Mean	Sem
Bongoyo	6	33.3	8.8	28.3	8.3	5.0	2.2
Mbudya	6	45.6	11.6	33.1	8.0	12.4	5.2
Kisite	6	84.4	8.9	9.8	7.3	74.6	6.2
Tanga	8	51.0	10.1	45.7	9.6	5.3	3.5
Changuu	3	66.7	12.0	63.3	8.8	3.3	3.3
Chapwani	3	76.3	8.5	62.2	2.2	14.1	7.1
Chumbe	6	70.0	9.3	63.3	8.0	6.7	4.2
		F ratio	Prob>F	F ratio	Prob>F	F ratio	Prob>F
		3.2	0.02	5.2	0.001	32.5	<.0001
Post hoc -		Kisite > Tanga,		Changuu,		Kisite > All	
Tukey test		Mbudya, Bongoyo		Chumbe >			
		Chapwani > Tanga,		Mbudya,			
		Bongoyo		Bongoyo,			
				Kisite;			
				Tanga > Kisite			

and *Halichoeres cosmetus* showed increased abundance while *A. meleagrides*, *Chaetodon falcula*, *Gomphosus caeruleus* and *P. dickii* showed decreased abundance and no statistically significant changes at the fished sites. In the fished reefs, *Amblyglyphidodon leucogaster*, *Chaetodon lineolatus* and *P. pelycus* increased in abundance while *Labroides dimidiatus* and *T. amblycephalum* showed a decrease in abundance but no change in the full closures.

### Herbivory

The highest rates of herbivory of the tethered *Thalassia hemprichii* blades occurred at the protected reefs at Kisite (84%) and the lowest at the Dar es Salaam marine reserves reefs of Bongoyo (33%) and Mbudya (45%) (Table 5). The herbivory assays indicated that grazing by fish was generally less than by sea urchins at most of the reefs, with the exception of Kisite where 74% of the herbivory was due to fish and only 7% due to sea urchins.

## DISCUSSION

### Climate change disturbances

The repeated surveys indicate general stability of these reefs over time, with a mix of further degradation and modest improvements that may have resulted from increased management, continued degradation due to fishing or small closure size, and the coral bleaching and mortality disturbance of 1998. In the context of the high bleaching and mortality of western Indian Ocean reefs after 1998 (Goreau *et al.*, 2000; McClanahan *et al.*, 2007b), the general stability and improvement of these reefs 6–7 years after the largest ENSO in recent history (McPhaden, 1999) indicates reefs with considerable resilience to climate change, and therefore a regional or global conservation priority (West and Salm, 2003). The findings here contrast with other post-1998 studies of reefs in the northern Indian Ocean, including Kenya, Seychelles, and Maldives (McClanahan *et al.*, 2001; 2007b; Obura, 2005; Graham *et al.*, 2006), but are more

similar to the lack of, or minor changes reported for fish and corals in some southern low latitude Indian Ocean sites including Mauritius (McClanahan *et al.*, 2005b; Graham *et al.*, 2007) and South Africa, where low bleaching and coral mortality were reported (Moothien-Pillay *et al.*, 2002; Schleyer and Celliers, 2002). Northern Tanzania is, however, near the equator and has higher water temperatures and bleaching threshold than mid-latitude reefs. It also bleached and experienced considerable coral mortality, averaging 45% for all northern Tanzania sites combined (Muhando and Mohammed, 2002).

Resilience to climate change will have two important components; one is the resistance to warm water anomalies while the second will be recovery after the disturbance (Holling, 2001). Resistance and recovery are each influenced by important biological and ecological factors that moderate responses, but given the high mortality and the general return to the original coral community, northern Tanzania reefs may exhibit the second component of resilience—high recovery rates. Some reefs in the northern Indian Ocean have shown recovery in hard coral cover but this is also associated with large changes in dominance and losses in the taxonomic composition (McClanahan and Maina, 2003; McClanahan *et al.*, 2007b). Northern Tanzania reefs have largely maintained the original diversity and community structure and the recovery is, therefore, not restricted to functional aspects such as hard coral cover and calcium carbonate deposition but also the diversity and community composition of corals and associated fish.

The causes of the rapid recovery remain obscure and unstudied but there are some notable differences in Tanzanian reef ecology compared with reefs with poor recovery that deserve speculation for future studies. First, the geological structure of the Tanzanian reefs is complex in terms of Pleistocene islands, reefs spread over large distances from shore, and their complex morphology (McClanahan and Arthur, 2001). The retention of larvae, the existence of reefs that survive disturbances, and meta-population nature of the reef complex is likely to create more stability across disturbance events (James *et al.*, 2002). This is possibly expressed in the high variability in the measured mortality in these reefs across 1998 (Muhando and Mohammed, 2002). Secondly and related, is that the environmental conditions in Tanzania are influenced by the island nature including being in the current shadow of Madagascar, as shown by the low ocean surface topography and reduced wind speeds for Tanzania (McClanahan *et al.*, 2007a; Maina *et al.*, 2008). This produces slower and more variable currents and water temperature variations that produce more stressful conditions that may create some acclimatization or adaptation to environmental extremes, such as strong ENSO events (McClanahan *et al.*, 2007a). Thirdly, measured coral larval recruitment rates in Tanzania are high and generally considerably higher than in neighbouring Kenya (Muhando, 2002; Tamelander, 2002; McClanahan *et al.*, 2005a) or Maldives where recovery has been slower (McClanahan, 2000; Loch *et al.*, 2004). This may be associated with the higher coral cover but also related to higher retention of larvae due to the slower and more zonal than meridional currents in Tanzania than Kenya (McClanahan *et al.*, 2007a; Maina *et al.*, 2008). It is possible these and other unstudied factors have influenced the rapid recovery and deserve further investigation.

## Fisheries and closure management

Tanzanian reefs generally reflect many of the ecological states and changes that are associated with moderate to heavy fishing and closures from fishing in this region (McClanahan *et al.*, 1999). In terms of the fish, these are the dominance of small-bodied Chaetodontidae, Labridae, and Pomacentridae in fished reefs, and Acanthuridae, Balistidae, Lutjanidae, and Scaridae in fisheries closures. Sea urchins, and specifically *Diadema* in these reefs, dominate grazing in fished reefs and this has largely been attributed to a decline of sea urchin predators in such reefs (McClanahan, 2000). Coral cover was high in most reefs but closures had the highest number of coral taxa and generally lacked high frondose algae cover. These differences, associated with fishing, have been reported in a number of other studies (McClanahan and Arthur, 2001). Some of the changes reported in this study period confirm these findings while others do not.

The changes in Tanga largely appear to confirm the overfishing model in that as increased fisheries management occurred across the study period (Wells *et al.*, 2007) the response was an increase in fish reported to be more abundant in both fished areas and the large closure. Similarly, one of the unmanaged reefs, Changuu, saw an eruption of the sea urchin *Echinometra mathaei* over time and this is likely to be due to increased fishing, low predation, and possibly a successful settlement or recruitment pulse (McClanahan, 1998). In contrast, in the small fishery closure of Chumbe, an increase in *Diadema* and a considerable decline in the Scaridae over time were measured. An increase in sea urchins and decline in herbivorous fish is expected due to competition for grazing space and food, but a closure is expected to increase the abundance of sea urchin predators and open space for the grazers, such as parrotfish (Hay, 1981; McClanahan, 1992; Tuya *et al.*, 2004). The abundance of key predators, such as the red-lined triggerfish (*Balistapus undulatus*), are quite low in Chumbe (McClanahan, T. unpublished data), despite the closure. These fish are known to be slow to colonize after closure (McClanahan *et al.*, 2007c). This remains the most likely cause but other likely factors include good larval survival and recruitment of *Diadema*. Additionally, it should be appreciated that Chumbe is a small closure and in the midst of heavily utilized reefs that have a low abundance of sea urchin predators and a high abundance of sea urchins. Consequently, another factor is that the small size of the closure and the dominance of fishing around it slows the recruitment and recovery of sea urchin predators and increases sea urchin recruitment. McClanahan *et al.* (2006) suggested that improved management around the Kisite closure resulted in increased recovery of fish abundance and diversity inside the closure, and the opposite situation described here could explain the observed change.

## CONCLUSIONS

Northern Tanzania reefs have exhibited considerable resilience and in some cases improvements in reef conditions in the face of dire global predictions for overfishing, climate change, and their interaction (Sheppard, 2003; Bellwood *et al.*, 2004; Pandolfi *et al.*, 2005). Closures in this region generally support greater abundances of fish and coral, but all areas

are influenced by fishing and climate, either through the small size of closures or supporting temperature-sensitive coral taxa. No reefs would appear to be immune to these effects but all reefs exhibited some resilience and ecological stability and even improvements during this time of climate and management change. This creates considerably more optimism for poor countries, such as Tanzania, to effectively manage their reefs in an environment of climate change. Consequently, it is suggested that Tanzanian and possibly many other reefs that exhibit similar environmental conditions have the ability to recover from large-scale climatic and human disturbances and this may render them a priority for conservation under predicted climate change scenarios where many reefs are expected to suffer further degradation (Sheppard, 2003; West and Salm, 2003).

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