Coral Reefs (2005) 24: 230–246
DOI 10.1007/s00338-004-0471-1

REPORT

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Detriments to post-bleaching recovery of corals

Received: 10 February 2003 / Accepted: 22 November 2004 / Published online: 22 March 2005

Abstract Predicting the response of coral reefs to large-scale mortality induced by climate change will depend greatly on the factors that influence recovery after bleaching events. We experimentally transplanted hard corals from a shallow reef with highly variable seawater temperature (23–36°C) to three unfished marine parks and three fished reefs with variable coral predator abundance and benthic cover. The transplanted corals were fragmented colonies collected from a reef that was relatively undisturbed by the 1997–1998 warm-water temperature anomaly, one of the most extreme thermal events of the past century, and it was assumed that they would represent corals likely to succeed in the future temperature environment. We examined the effects of four taxa, two fragment sizes, an acclimation period, benthic cover components, predators and tourists on the survival of the coral fragments. We found the lowest survival of transplants occurred in the unfished marine parks and this could be attributed to predation and not tourist damage. The density of small coral recruits approximately 6 months after the spawning season was generally moderate (~40–60/m^2), and not different on fished and unfished reefs. Coral recovery between 1998 and 2002 was variable (0–25%), low (mean of 6.5%), and not different between fished and unfished reefs. There was high variability in coral mortality among the three unfished areas despite low variation in estimates of predator biomass, with the highest predation occurring in the Malindi MNP, a site with high coralline algal cover. Stepwise multiple regression analysis with 14 variables of coral predators and substratum showed that coralline algae was positively, and turf algae negatively associated with mortality of the transplants, with all other variables being statistically insignificant. This suggests that alternate food resources and predator choices are more important than predator biomass in determining coral survival. Nonetheless, large predatory fish in areas dominated by coralline algae may considerably retard recovery of eurythermal corals. This will not necessarily retard total hard coral recovery, as other more predator-tolerant taxa can recover. Based on the results, global climate change will not necessarily favor eurythermal over stenothermal coral taxa in remote or unfished reefs, where predation is a major cause of coral mortality.

Communicated by Environmental Editor Bruce Hatcher

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Introduction

The convergence of the El Niño Southern Oscillation and Indian Ocean dipole in 1997–1998 (Saji et al. 1999) created warm seawater temperatures that caused the highest widespread coral mortality in recent history (Goreau et al. 2000). Mortality was particularly severe in the western Indian Ocean where many reefs experienced 40–99% losses of coral cover (Goreau et al. 2000). Many reefs in

the region had coral cover of < 10% of the substratum shortly after this mortality event, and reef-scale losses of a number of genera have been reported (Goreau et al. 2000; McClanahan 2000; McClanahan and Maina 2003). The recovery of these reefs may be slowed by the spatial extent of this disturbance, but also by local-scale ecological forces that may inhibit coral recruitment and delay reef recovery, such as coral predators or competition with fleshy algae (Knowlton 1988; Hughes and Tanner 2000). Given the projected changes in climate and projected mortality of corals (Kleypas et al. 1999; Hoegh-Guldburg 1999; Sheppard 2003), the factors that influence the survival of coral recruits and the recovery process are of concern for the ecological future of coral-dominated tropical reef ecosystems (Done 1992).

There are differences in the susceptibility of corals to warm water; some are locally extirpated (Glynn 2000; McClanahan 2000), while others are largely unaffected (McClanahan 2004). Bleaching and survival of corals vary among taxa (McClanahan 2004), their association with the coral symbiont *Symbiodinium* (Baker 2001), position in the coral colony (Rowan and Knowlton 1995), depth and habitats (Hoegh-Guldberg and Salvat 1995), light quality and quantity (Gleason and Wellington 1993; Brown et al. 2002), thermal and light histories (Jokiel and Coles 1977; Brown et al. 2002; McClanahan and Maina 2003), water flow (Nakamura and van Woesik 2001), fishing management (McClanahan et al. 2001), regions (Marcus and Thorhaug 1981; Coles 1997; McClanahan et al. 2004), and season (Berkelmans and Willis 1999). These studies suggest some acclimation and synergistic interactions among genetics, the environment, and bleaching thresholds (Coles and Brown 2003).

A survey of Kenyan reefs found that one shallow reef (Kanamai) that naturally experienced both high seawater temperature and variation (23–26°C) had low coral mortality across the 1998 temperature anomaly (McClanahan and Maina 2003). It is possible that reefs such as these may form a refuge for coral and their symbiotic *Symbiodinium* taxa or genotypes, which will form source populations for the recolonization of reefs that are catastrophically affected. Increased colonization of species from these refugia could increase the frequency of warm-water tolerant corals and their symbionts in the future. Selective pressure from changing climate could result in changes in taxa and genotypes that could increase the acclimation and recovery rates from warm-water anomalies, producing ecological resilience to climatic changes. The likely alternative is that these eurythermal taxa are not tolerant of conditions outside of their stressful environments, will not be able to colonize stenothermal environments, and will change the resilience or recovery rates of coral communities.

We tested these alternative hypotheses by examining the early recovery process of Kenyan coral reefs after the 1997–1998 bleaching event by experimentally transplanting four common coral taxa from the Kanamai reef to reefs open and closed to fishing. This experiment was done to determine mortality rates of these four taxa in the presence and absence of fishing and to determine if transplantation of eurythermal corals could accelerate the recovery of reefs with poor coral recruitment. We examined the possible effects of tourists, coral transplant fragment size, and an acclimation period to determine if these factors influenced our conclusions. We made direct observations of predation on the corals in and out of fished reefs to identify the important coral predators. Finally, we examined the effect of the abundance of predators and substratum variables on the survival of the transplanted corals.

Materials and methods

Study sites and species

Studies were undertaken in shallow (< 2 m deep at low tide) back-reef environments typical of the Kenyan coast. The substratum is composed of live and dead coral skeletons interspersed with coral rubble, sand, and seagrass. Branching and massive *Porites*, encrusting and massive Faviidae, and branching and encrusting Acroporidae and Pocilloporidae frequently dominate coral communities in these sites (McClanahan and Mutere 1994). Coral transplantation studies were restricted to six sites, of which the three unfished sites were the Malindi, Watamu, and Mombasa Marine National Parks (MNP). Malindi and Watamu sites have been protected from fishing since the mid 1970s and the Mombasa MNP since 1991. All sites have a high abundance and biomass of fish compared to heavily fished reefs (McClanahan and Kaunda-Arara 1996; McClanahan and Arthur 2001). The three unfished reefs chosen for transplant studies were Vipingo, Kanamai, and Ras Iwatine. Study sites were similar in being shallow back reef lagoons protected from strong waves, but differed in fishing, the abundance of fish, and in ranging from 0.3 m to 2.0 m depth at low tide. For a map of the geographic location of the study sites see McClanahan (1994a; Fig. 1).

The corals used in the transplantation experiment were the common massive and branching *Porites* spp., *Pocillopora damicornis*, and *Pavona decussata*. *Pavona frondifera* was used in one study of tourist effects in Watamu MNP. The common massive and branching *Porites* are *Porites lutea* and *Porites palmata*, respectively, but the corallites of each transplant were not examined to determine the species-level taxonomy and we, therefore, refer to them as massive and branching *Porites*.

Benthic cover and fish abundance

In each of the six sites, the benthic cover and biomass of important fish groups were sampled before (February–March 2000) and after (February–March 2001) the coral transplant work. Benthic cover was estimated by the line-intercept method where 12–18 10-m-line transects

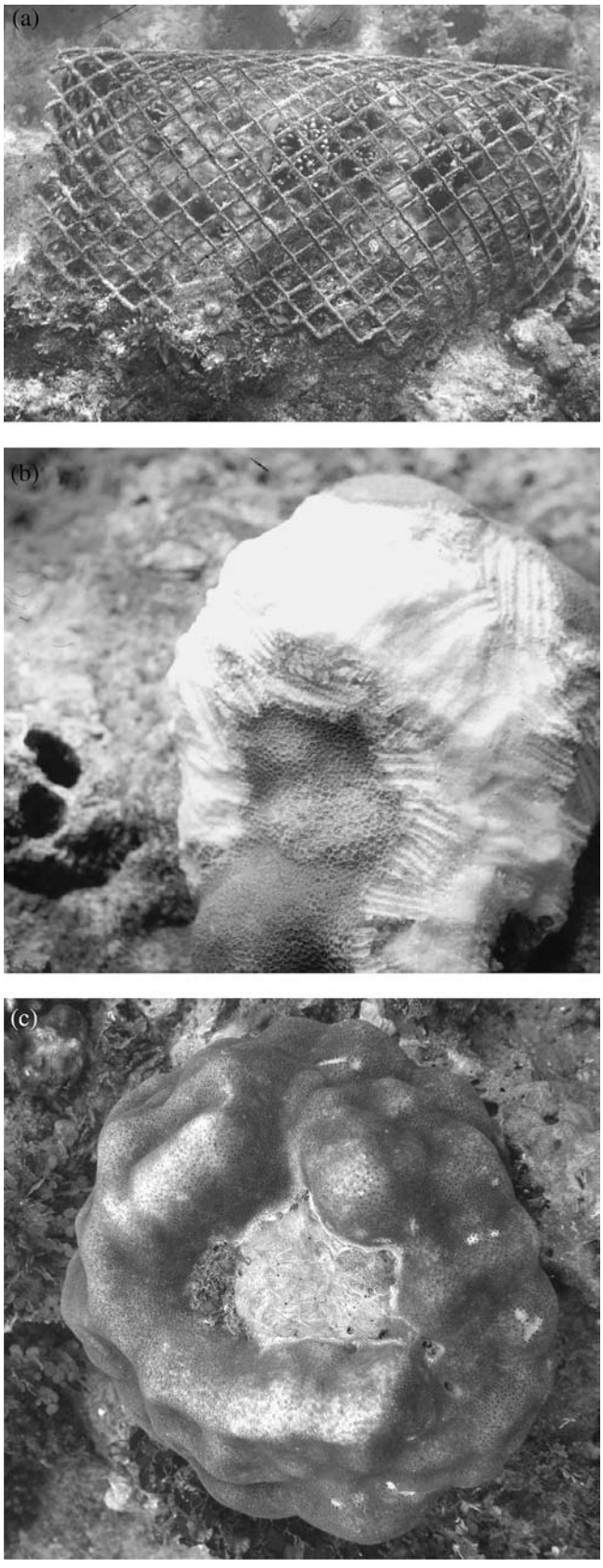

Fig. 1 Photographs of **a** the experimental cages, **b** an example of a massive *Porites* sp. bitten by parrotfish, and **c** a bitten *Porites* sp. 3 years after transplantation to reef substrata in Kenya

were completed per reef site. We classified all organisms >3cm under the line into nine functional groups: hard coral, soft coral, sponge, turf algae, erect fleshy algae, calcareous green algae (i.e. *Halimeda*), encrusting red coralline algae, seagrass, and sand. The cover of each of these categories was calculated and used in single and multiple stepwise regression analysis of the change in transplanted coral length and cover versus the benthic cover groups (Sall and Lehman 1996). We present a time-series of hard coral cover in the six reefs from the period 1995–2002 to estimate rates of coral recovery in these sites after 1998.

The three common coral predator groups (Balistidae, Chaetodontidae, and Scaridae) were sampled by three to four replicates, 100×5 m belt transects per sampling period. Individuals >3 cm in each group were counted in 10 cm size classes. From the mean of these size classes, the weight of each fish and the total wet weight (i.e. biomass) of each group were estimated from length–weight regressions taken from local fish landing sites (McClanahan and Kaunda-Arara 1996). We used predator biomass rather than population density for comparisons and regression analyses as biomass better reflected body size differences, and these were often quite different between the fished and unfished reefs. In particular, parrotfish were numerous and small in fished reefs, but were not observed preying on corals, in contrast to large individuals. Therefore, predator biomass was believed to better reflect predator potential compared to population density. Sea urchin biomass was estimated from 9×10-m^2 quadrats sampled at each site, in which the densities of individual species were counted and multiplied by average wet weight and summed across species to estimate the total wet weight (McClanahan 1998). Population density and biomass estimates were used in single and multiple stepwise regression analysis of changes in coral transplant length and cover. We combined measures of substratum cover and sea urchin and fish abundance (14x variables) for regression factors in a multiple stepwise regression to screen out the significant factors using a minimum acceptable probability of $p < 0.02$.

Coral recruitment

Coral recruits were sampled between 1999 and 2001 within 16 sites: seven located within the three unfished marine parks, and nine fished sites. Data from different years were pooled in the analysis of fished and unfished reefs. Within each site 5×0.25 m^2 quadrats were haphazardly placed such that the distance between individual quadrats always exceeded 5 m and each quadrat had at least 70% of its surface composed of hard substratum. Within each quadrat, corals between 0.5 cm and 5.0 cm in diameter were classified as recruits, identified to the genus (Veron 2000), and counted. We did not try to distinguish corals recruiting from larval settlement versus fragmentation, as we believe this distinction can be

subjective and susceptible to error. The nonparametric data were analyzed using the Kruskal–Wallis rank test to compare quadrats in protected sites to quadrats in unprotected sites for each genus, as well as for total recruitment.

Transplantation and cage design

Coral fragments of the four scleractinian species were removed from the lagoonal reef at Kanamai with a hammer and chisel, and each species' fragments were immersed in seawater in separate buckets that were transported by car and boats to each study site (Table 1). The water was aerated by a 12-V battery-powered air pump (Aquatic Eco-Systems Inc., Part no. DC8). At each study site, coral fragments were immediately placed into a large underwater cage for 1–3 days before being attached to the substratum for the experiments described below. The maximum transportation time from Kanamai to the cage was 2.5 h, and no signs of mortality or stress were observed in the coral fragments, apart from mucus formation. Fragments were broken underwater with a hammer and chisel into "finger-sized" (approx. 5–6-cm-long length) and "fist-sized" (10–15-cm-long length) fragments. For each individual transplant, the reef surface was scrubbed with a plastic or wire brush to remove attached turf algae and sponges. Coral fragments were attached using either epoxy putty or regular masonry cement. After initial trials, it was determined that masonry cement (half quartz sand and half cement mixed with a small amount of fresh water) was most successful and this was used in subsequent experiments.

Many studies involving caging have proven effective in studying predation or herbivory on coral reefs (Sammarco 1980; Connell 1997; Miller and Hay 1998). Our cages were made of 2.5-cm nylon netting (Aquatic Eco-Systems Inc., Part no. N1133) (Fig. 1a). This material does not appear to significantly disrupt water flow, sunlight, particulate matter, and zooplankton, and the purpose of this study was a short-term study focused on predation and not coral growth or survivorship. We, therefore, believe these cages had little artifactual effect on our study. Each cage was a half cylinder shape (length ~60 cm, height ~25 cm). Cages were fixed to the reef substrate with straight nails with plastic washers or

Table 1 Experimental design showing sample sizes for various treatments in transplantation experiments conducted on six back-reefs along the Kenyan coast

Management	Site	Treatment	Size	Control	Experiment	Taxa	Number
Unfished reefs	Malindi MNP	Caged/ previously caged	Finger (< 6 cm)	√	√	Br *Porites*	8
						Mass *Porites*	8
						Pavona	8
						Pocillopora	8
			fist (10 cm to 15 cm)	√	√	4 taxa × 8 fragments	
		Uncaged	Finger		√	4 taxa × 8 fragments	
			Fist		√	Br *Porites*	93
						Mass *Porites*	89
						Pavona	8
						Pocillopora	8
	Mombasa MNP	Uncaged	Fist		√	4 taxa × 16 Fragments	
	Watamu MNP	Uncaged	Finger		√	4 taxa × 8 fragments	
			Fist		√	4 taxa × 24 fragments	
Fished reefs	Kanamai	Uncaged	Fist		√	4 taxa × 16 fragments	
	Raslwatine	Caged/ Previously caged	Finger	√	√	4 taxa × 8 fragments	
			Fist	√	√	4 taxa × 8 fragments	
		uncaged	Finger		√	4 taxa × 8 fragments	
			Fist		√	4 taxa × 8 fragments	
	Vipingo	Uncaged	Finger		√	4 taxa × 8 fragments	
			Fist		√	4 taxa × 8 fragments	

Total finger size = 192
Total fist size = 550
Total caged = 28
Total uncaged = 614
Total number of transplants = 742

U-shaped nails. Most cages were fully closed but in one initial experiment we used cages with open sides to exclude large predators (Table 2).

Measurements

Plastic calipers were used to take measurements of the longest length and the longest perpendicular width of massive *Porites* and *Pocillopora*. The longest length and height were taken for branching *Porites* and *Pavona*. Percent live cover was estimated for each taxon. The last day that measurements were made on the transplants was between 14 and 21 days after the corals were attached to the substratum, day 0. Most commonly, the last measurements were taken between the 18th and the 21st day, except in one Malindi site where day 14 was used. In this site, fragments rapidly disappeared and quickly became unrecognizable from the substratum. Changes in the respective measurements were obtained by subtracting the measurement taken on the last day from that on day 0. The measures of transplant condition are significantly correlated (particularly the measures of dimension, Table 3), and we therefore present results for the change in length and live cover only, which were the two least correlated measures made for all four taxa. Some predators, such as the starfish *Acanthaster planci*, remove the live flesh from a coral but do not reduce the coral size, and this is one reason for the poor correlation between these two measures, and for presenting both measures.

Experimental manipulations

Tourist damage and small predators

The primary focus of our research was natural mortality, but because tourists use some of the study sites, we believed it was important to distinguish natural from tourist-induced mortality, and whether or not tourist effects were confounding our results. In order to minimize tourist effects, all transplant studies were undertaken in the low tourist season between May and August. We chose the most heavily visited tourist site for the tourist-effect experiment, namely the Watamu MNP "coral gardens". In this experiment, we distinguished between small and large-bodied predators by altering the size of the opening of the cages and used only fist-size fragments of two of the more fragile species: branching *Porites* sp. and *Pavona frondifera*.

We established two sites, 150 m apart, one with high and one with low tourist use. The high tourist area had multiple buoys installed by the park service where boats moored, and we transplanted our corals in shallow water directly adjacent to these buoys. One-hundred-and-twenty coral fragments organized into 30 groups of four were attached to each of the two sites with an equal balance of the two species and sites (Table 2). Five of these groups were covered with a fully enclosed cage, five with a cage with open sides, and five were left without a cage. The open-side cage had two lateral openings of ~25 cm that only allowed access to small-bodied predators such as butterflyfish (Chaetodontidae), wrasses (Labridae), tobies (Tetraodontidae), and the Moorish idol (Zanclidae). This design included three treatments: (1) fully caged—no predators or tourist damage, (2) open side cage—no tourist but smaller predator damage, and (3) no cage—damaged by both tourists and all predators. This design does not allow us to distinguish the effects of tourists alone as there was no treatment that had just tourist damage; but by comparing the results between the high and low tourist use and examining the type of damage, it is possible to infer this distinction. The experiment was maintained for 35 days, and the percentage of live cover and size of the fragments were measured (as above) in the beginning and at the end of the experiment. Changes in size and cover of live corals were compared between sites and among caging treatments. Change in coral colony size was calculated from the average of the length and width measurements.

Predation damage

All four species of coral were used in these experiments. Fragments were placed within groups such that each exposed (no cage) and caged group contained eight fragments—one fist and one finger of each of the four species. These groups were replicated in a variety of

Table 2 Experimental design showing sample sizes for various treatments in tourist and small predator effects experiments conducted on six back-reefs along the Kenyan coast

Site	Treatment	Pavona frondifera *Branching Porites*
Control	Caged Half caged Uncaged	4 fragments (two from each taxa) × 5 replicates × 3 treatments × 2 sites
Tourist	Caged Half caged Uncaged	Total coral fragments = 120

Table 3 Coefficients of correlations between the various measures of coral transplant condition at the end (< 22 days) of experiments along the Kenyan coast

Measurement	Length	Height	Width	Live cover%
Length	1			
Height	0.95	1		
Width	0.98	NA	1	
Live cover%	0.77	0.91	0.74	1

NA no analysis (because a single species has either height or width measurements)

locations in each of the three unfished and fished sites, with a minimum of two groups per site. A total of 742 fragments (192 fingers and 550 fists) were sampled: 486 of which were in MPAs and 256 were in fished reefs (Table 1). The condition of each fragment was examined at the end of the experiment to determine the source of mortality. The short time of the experiments (< 22 days) made it unlikely that competition with algae or other invertebrates could cause mortality and, in nearly all observations of coral condition, predation was determined to be the cause of the damage due to presence of bite marks (Fig. 1). Consequently, for the analyses we assumed that predators caused damage to corals outside of the cages. In many cases, as described below, we were able to directly observe predation. These transplants were visited up to 3 years after the study to determine their condition (Fig. 1). Many of the tags were lost or unreadable so no quantitative assessments were made, but the presence and condition, or absence of transplants was recorded.

Acclimation

It is possible that the coral fragments require more than 1–3 days to acclimate to the new environment. The transportation, handling, and cementing might stress the corals and make them susceptible to predation, or the corals might require time to induce chemical or stinging-cell defenses (Gochfeld 2004). To test this possibility we cemented 128 fragments (64 each in MPAs and fished reefs) inside cages in groups of eight as described above for an additional ~14 days prior to removing the cages and exposing them to predators. They were then followed for 18–21 days when the above measurements of size and live cover were taken and compared to the fragments without prior caging.

Observations of predation on corals

Direct observations on corals were made using two methods. The first was a loosely structured method where observations were made on the transplanted corals as the observer was working on the cages and transplanted fragments. The sites were visited every few days to insure that the cages and fragments were in good condition. This time was also used to make observations on predator or tourist damage. Ten, approximately 40-min sampling times were completed by this method, of which four were in MPAs and six in fished reefs. In some cases, we directly observed predation by fish or *Acanthaster planci*, and the number of individuals of a species (using nomenclature of Lieske and Myers 1994) and an estimate of the time spent observing were recorded. This gives largely qualitative information on the species that were feeding on the transplanted corals and, given the interval of a few days between observations, this would allow for observations on slow predators such as starfish, sea urchins, or snails.

The second more structured method was to place a fist-size fragment of each of the four coral species in a group in an open area with a high abundance of fish. The observer positioned at 5–8 m from the area watched these fragments for 15 min and recorded both the number of individuals feeding and number of bites per species on each of the four fragments. A total of 84×15-min observations were made, of which 17 were in fished and 67 in unfished reefs. The unequal distribution of sampling between these management categories was due to the low numbers of observations of predation in the fished compared to unfished reefs. This method gives more quantitative information on bite rates, but is probably biased against sampling of slow moving or shy species of invertebrates and fish.

Statistical analyses

Data were tested for normality with the Shapiro–Wilk and Kolmogorov–Lilliefors tests, and for unequal variances with four tests; the O'Brien, Brown-Forsythe, Levene, and Barlett tests. If three or four tests showed significant differences in variance, then the single-factor Welch's ANOVA was used to test for differences among the means (Sall and Lehman 1996). This test weights the means by the reciprocal of the sample variances of the group means and is equivalent to the *t* test of unequal variances (Sall and Lehman 1996). For multiple comparisons of the four coral taxa, the Tukey–Kramer honest significant difference (HSD) test was used for testing all pairs of means when one-way ANOVAs were significant. When variables were either non-normal or with unequal variances, the nonparametric Kruskal–Wallis test was used. When multiple tests of the same hypothesis were performed, we made Bonferroni corrections to the *p* values as described by Rice (1989).

Results

Coral recruitment and recovery

Coral cover measures between 1995 and 1998 indicate that the MPAs had about twice the hard coral cover as the fished reefs before the 1998 coral bleaching and mortality event (Fig. 2). Coral mortality was greater as a percentage of the total cover in the MPAs. The three MPAs had about 10% hard coral cover after the bleaching event in 1998. Recovery of corals after the bleaching was most rapid in two of the MPAs, Malindi, and Mombasa, where coral cover increased to 20%, or a little less than half its original value, by 2001. No recovery of corals has been recorded for the Watamu MNP after the bleaching event. The bleaching event had very little effect on the Kanamai reef and the small loss recovered by 2001 (Fig. 2). Coral mortality was evident

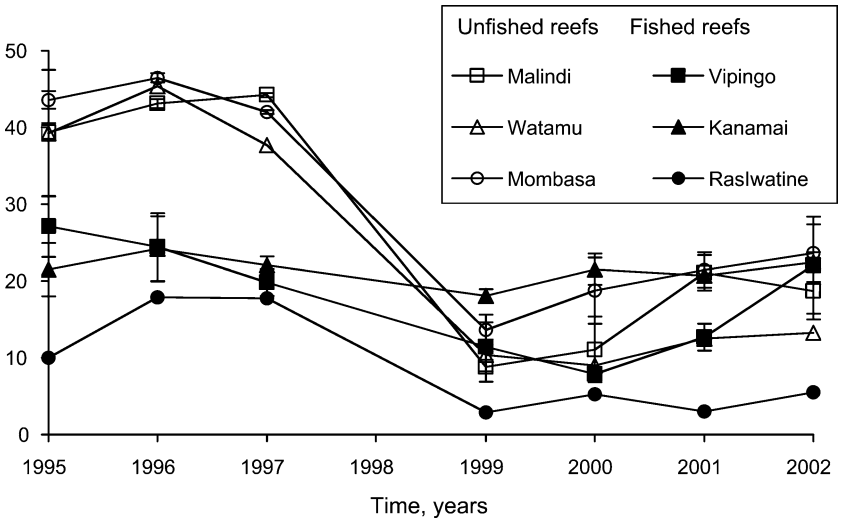

Fig. 2 Changes in hard coral cover in the six study sites along the coast of Kenya from 1995 to 2002. Coral bleaching and mortality was observed and recorded in 1998. Bars represent standard errors of the mean based on sites, but Watamu and Ras Iwatine are based on only one monitoring site and the average of twelve 10-m transects is presented with no measure of within-site variation

and did effect Vipingo and Ras Iwatine reefs, reducing cover from ~20% to 5–10% of the substratum. There was no evidence of recovery of hard corals in either Watamu or Ras Iwatine by 2002. A comparison of recovery in fished and unfished found no significant difference by a t test ($t = 0.49$) with mean recovery of $6.5 \pm 2.4\%$ over the 4-year period.

There were not large differences in total coral recruit abundance between fished and unfished reefs, and there was high variation among reefs (Fig. 3). None of the 23 coral genera showed statistical differences in abundance between fished and unfished reefs (Kruskal–Wallis tests with Bonferroni correction of the p values). Recruit density of branching *Porites* was high but very variable

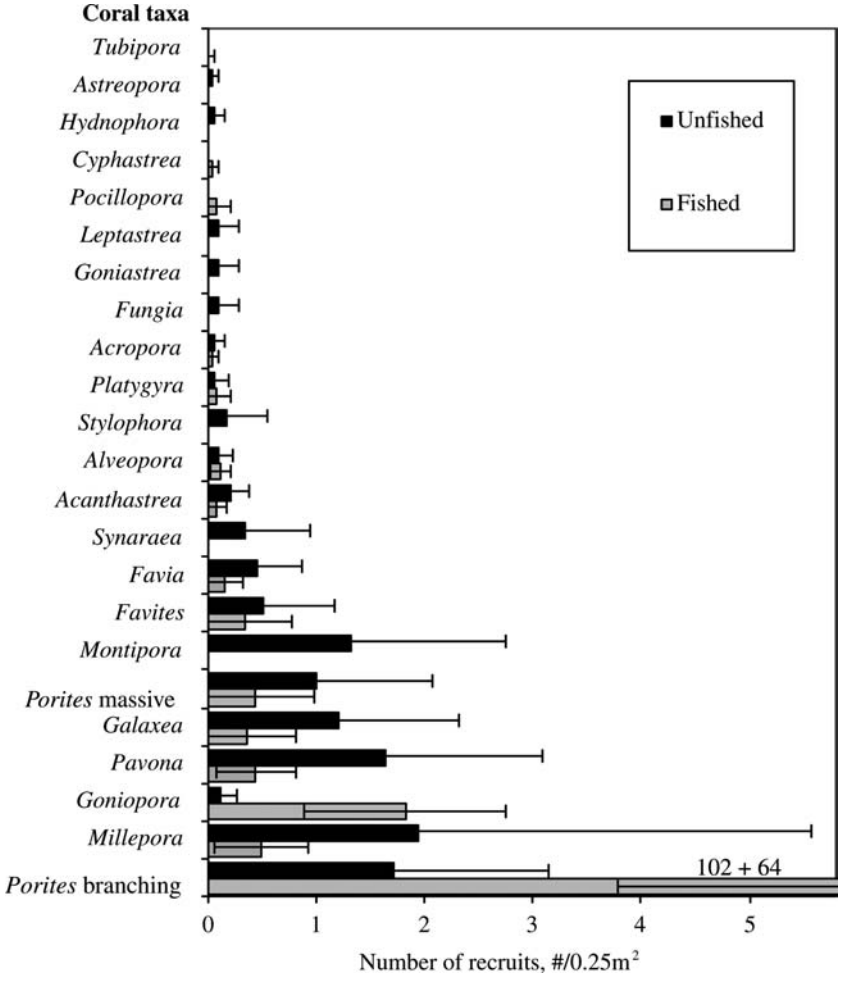

Fig. 3 Population density (#/$0.25m^2$) of the dominant coral recruits to Kenyan reefs open to and protected from fishing. Comparisons of the mean coral density from fished and unfished reefs revealed no significant difference for the whole analysis based on the Bonfferoni multiple comparisons correction and a $p < 0.05$ significance level. *Bars* represent standard deviations

on the fished reefs, and did not result in statistical differences. Overall coral recruitment was moderate at around ~40–60, but was as low as 6–10 individuals per m^2 at some sites such as Watamu and Ras Iwatine.

Tourist and cage design effects

Corals in the fully enclosed and open-side cages in Watamu MNP showed no statistically significant change in size or live cover over the 30-day period in both the high and low-tourist use sites (Table 4). Exposed *Pavona frondifera* were significantly reduced in size in both sites, with greater losses in the control site resulting in significant cage, site, and interaction terms. Branching *Porites* sp. showed less change than *P. frondifera*, with no changes in live cover and a small but statistically insignificant reduction in the size of uncaged transplants at the tourist site. Observations of the transplants of both taxa suggest that fish did most of the damage in both the high and low-tourist sites.

Predation studies

Caging had no effect on the measures of coral condition, as all *t* tests comparing results of the caged fragments at the beginning and end of the caging period showed no statistical differences for any of the four species or size classes (all two-tail *t* values < 0.8). Change in lengths and live cover measures were seldom normally distributed, but variances were nearly always equal. Consequently, when variances were equal we performed normal ANOVA tests, and used Welch's ANOVAs for those cases where variances were unequal (Table 5). Against our prediction, those corals given a >14-day acclimation period experienced statistically significantly greater losses in both length and live cover than the uncaged groups. Many fish, particularly grazing parrot and surgeonfish, were attracted and fed in the area where the cage was previously fastened.

Change in length and live cover of the four taxa differed depending on their location and the measure of their condition. For all sites combined there was a significant difference among taxa for the change in length ($F = 4.9$, $p < 0.002$) but not for the change in live cover. The Tukey–HSD test of the change in length indicates that the only significant difference was due to a greater reduction of size in massive *Porites* sp. compared with *P. damicornis*. Examining just the three reefs with fishing, there were no differences among the four taxa by either measure ($F = 0.6$ and 0.4). Examining the unfished reefs alone, there were differences among taxa in both change in length and live cover ($F = 4.7$, $p < 0.003$, $F = 3.0$, $p < 0.03$). Tukey's test indicates that this was due to greater change in massive *Porites* sp. than branching *Porites* sp. and *P. damicornis*. The living flesh of many massive *Porites* sp. was removed and left a bare white skeleton that was often further reduced over the course of the experiment (Fig. 1).

Reefs sites and management were both identified as significant factors by both measures of coral condition. Malindi experienced the largest changes in length and live cover, and the fished reefs, as a group, also experienced greater losses of length and live cover than the unfished reefs (Table 5). Losses of live coral from unfished reefs were three to four times greater than those from fished reefs, depending on the measure of fragment condition, and this comparison produced the largest *F* values. The Tukey test for all sites suggests that the only truly significant differences between sites were, however, for the comparisons of Malindi with all other sites, regardless of the measure of the transplant condition. Comparing just the unfished reefs indicated that the

Table 4 Differences in the live cover and size of fragments of two species of coral transplants to a high and low tourist use area in the Watamu MNP based on initial and final measurements

	Change in live cover (%)						Change in size (cm)					
	Closed cage		Open side		Uncaged		Closed cage		Open side		Uncaged	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Pavona frondifera												
Tourist site	−2.9	2.6	−11.6	9.9	−29.3	9.2	0.6	0.3	0.3	0.6	−1.6	0.7
Control	−3.6	2.5	−1.5	2.0	−90.0	3.7	1.4	0.5	−0.1	0.5	−6.9	1.0
ANOVA		*df*	*F*	*p*				*df*	F	p		
Tourist site		1	4.6	0.040				1	12.5	0.001		
Cage treatment		2	32.7	0.001				2	10.6	0.000		
Site × treatment		2	9.2	0.001				2	3.2	0.050		
Porites branching												
Tourist site	−9.6	4.9	−9.1	4.5	−21.1	10.2	0.7	0.3	0.7	0.1	−2.3	1.1
Control	−1.7	4.5	−1.2	3.8	−2.5	3.3	1.6	0.2	0.6	0.3	0.3	0.4
ANOVA		*df*	*F*	*p*				*df*	*F*	*p*		
Tourist site		1	0.3	NS				1	0.6	NS		
Cage treatment		2	2.3	NS				2	3.8	0.030		
Site × treatment		2	0.2	NS				2	5.0	0.010		

Results of three-factor ANOVA

Table 5 Change in length in centimetre, and live cover as a percentage of initial condition of coral fragments in five experimental treatments on reefs along the Kenyan coast

Treatment	Category	Number	Mean	SEM	Welch's ANOVA	
					F	*p*
Change in coral transplant length (cm)						
Taxa	Branching *Porites*	229	1.8	0.2	4.9	0.002
	Massive *Porites*	225	2.5	0.2	*df* = 3	
	Pavona decussata	144	2.2	0.4		
	Pocillopora damicornis	144	1.4	0.3		
Reefs	Malindi	294	3.9	0.4	40.4	0.0001
	Watamu	128	0.6	0.4	*df* = 5	
	Mombasa	64	0.9	0.3		
	Vipingo	64	0.2	0.3		
	Kanamai	64	1.0	0.3		
	Ras Iwatine	128	0.8	0.4		
Management	Unfished	486	2.6	0.1	91.0	0.0001
	Fished	256	0.7	0.2	*df* = 1	
Acclimation	Caged > 14 days	128	3.4	0.3	20.8	0.0001
	Uncaged	614	1.7	0.1	*df* = 1	
Size	fingers < 6cm	192	1.3	0.2	17.9	0.0001
	fists 10–15 cm	550	2.2	0.1	*df* = 1	
Change in percentage live coral cover						
Taxa	Branching *Porites*	229	26.9	2.6	1.8	NS
	Massive *Porites*	225	34.3	2.6	*df* = 3	
	Pavona decussata	144	33.4	3.2		
	Pocillopora damicornis	144	31.2	3.2		
Reefs	Malindi	294	58.6	1.9	70.4	0.0001
	Watamu	128	9.1	2.8	*df* = 5	
	Mombasa	64	19.3	4.0		
	Vipingo	64	5.4	4.0		
	Kanamai	64	12.3	4.0		
	Ras Iwatine	128	19.0	2.8		
Management	Unfished	486	40.4	1.7	116.7	0.0001
	Fished	256	13.9	2.3	*df* = 1	
Acclimation	Caged > 14 days	128	53.4	3.3	40.8	0.0001
	Uncaged	614	26.6	1.5	*df* = 1	
Size	Fingers < 6cm	192	38.1	2.8	7.3	0.007
	Fists 10–15 cm	550	28.9	1.7	*df* = 1	

Analyses of treatments other than "Taxa" are for all coral species combined

change in coral condition was greater at Malindi than the two other unfished reefs, with no difference between Mombasa and Watamu reefs. Comparing just the fished reefs for the change in length, Vipingo transplants had less change than either Kanamai or Ras Iwatine. Comparing change in the live cover of transplants in fished reefs, Ras Iwatine experienced a greater loss than either Kanamai or Vipingo. Eighty-six percent of the observed loss at Ras Iwatine was attributable to predation by *A. planci*, which leaves unique feeding scars where the live flesh is gone but the skeleton is undamaged. The death of ten transplants was due to this predator, with an approximately equal loss among the three branching taxa. No predation by *A. planci* was observed in the two other fished reefs, but eight cases of starfish predation were observed in the Mombasa MNP, the reef site nearest Ras Iwatine.

Differences in the size of the coral fragments also depended on the measure of condition and the management of the reefs. For all sites combined the larger fists had a greater change in length than the fingers, but the differences were reversed for the measure of live cover (Table 5). This was also the case for the unfished sites ($F = 5.5$ and 25.5) but fragment size had no effect on changes in condition in the fished reefs ($F = 1.3$ and 2.0, NS).

Predator observations

There were differences in the rates of predation and species composition of predators on corals between the methods used to assess predation and between fished and unfished reefs (Figs. 4, 5, 6). Direct observations of transplanted corals yielded fewer species of predators and observations than those of the four experimental coral fists. Eight species were observed attacking the transplants, of which seven were fish and one the starfish *A. planci*, to which we attributed 20% of the bites (a "bite" for this starfish being a single observation of predation, Fig. 4). Over 50% of the 54 bites observed on fished reefs were from the puffer *Arothron nigropunctatus*, with the remaining 25% of the bites attributable to the combined predation of the black-saddled toby *Canthigaster valentini*, the threadfin butterflyfish *Chae-*

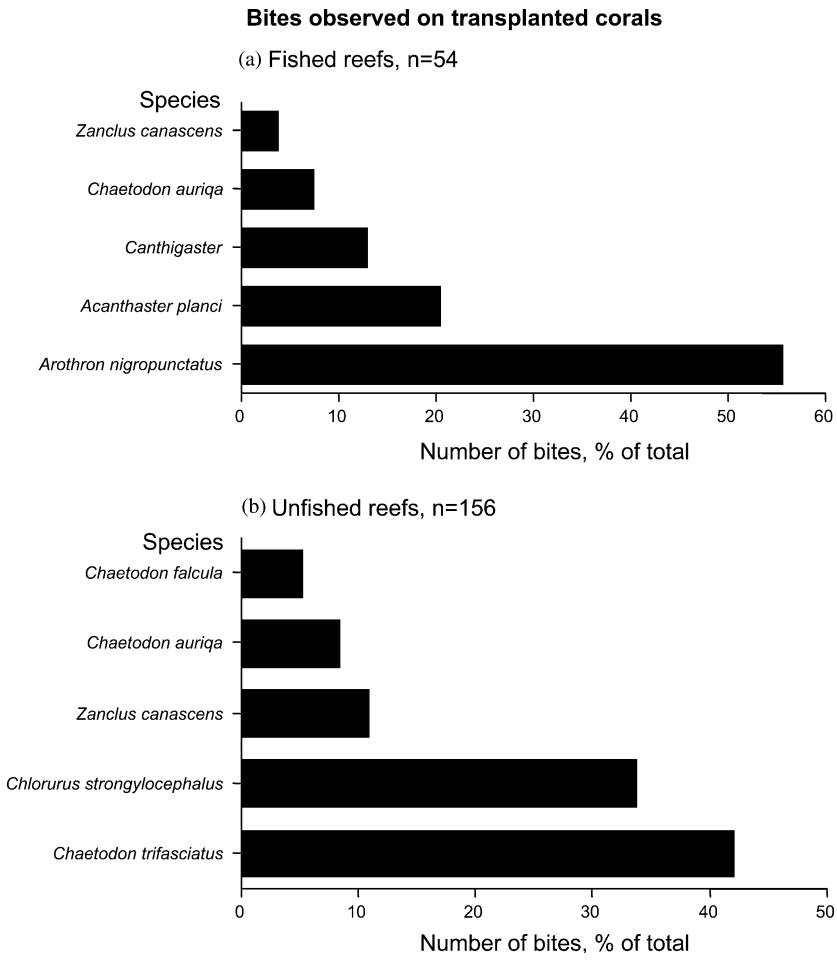

Fig. 4 Relative proportion of coral predators observed biting transplanted scleractinian corals in **a** fished and **b** unfished reefs along the Kenyan coast

todon auriga and the Moorish idol *Zanclus cornutus*. Of the 156 bites observed directly on transplants in the unfished reefs, the redfin butterflyfish *C. trifasciatus* was the most common predator, followed by the steephead parrotfish *Chlorurus strongylocephalus*, two butterflyfish (*C. auriga* and *C. falcula*), and the Moorish idol. *C. strongylocephalus* was observed eating or excavating the skeleton of the bare transplants, not just removing the living flesh (Fig. 1b).

Five species were observed biting the experimental coral fragments placed in fished reefs, and *C. valentini* was the dominant predator, comprising 60% of the individuals and 45% of the observed bites (Fig. 5). The bite rates in these reefs were low, with nine of the 17 sampling intervals producing no observations of predation, although the toby and puffer did take numerous quick bites when feeding such that overall bite rate was approximately 5.7/15-min observation period. These predators in the fished reefs picked at coral tissue, but were not observed breaking coral branches or exposing the bare skeleton, in contrast to *A. planci*. There were significant differences in the numbers of individuals and bite rates among predator species for *Pavona decussata* and massive *Porites* sp. species (the Kruskal–Wallis test, $p < 0.04$), but no differences for the branching *Porites* sp. and *Pocillopora damicornis*. Despite a somewhat higher bite rate on the three branching species, there were no statistically significant differences in the bite rates detected among the four experimental coral taxa.

Fifteen species were observed preying on corals in the unfished reefs, of which the red-lined triggerfish *B. undulatus* and *C. trifasciatus* were the dominant species, whether measured as number of individuals or bites (Fig. 6). Other species were more variable in terms of the number of individuals or frequency of bites, but included three other species of butterflyfish, three parrotfish, three wrasses, two angelfish, the Moorish idol, and the black-saddled toby (Fig. 6). *B. undulatus* and parrotfishes were observed exposing bare skeleton or breaking coral branches, but all other species were only observed picking at the coral heads. Bite rates on the coral heads on the unfished reefs was about three times higher than the fished reefs, at a mean of 16.5 bites per 15 min. There were significant differences in the predation rates among all coral taxa (the Kruskal–Wallis test, $p < 0.03$), except for massive *Porites* sp. that experienced the lowest bite rates in the unfished reefs. *B. undulatus* had a high preference for *P. damicornis*, and there was an overall preference for this species and *P. decussata* by all predators combined.

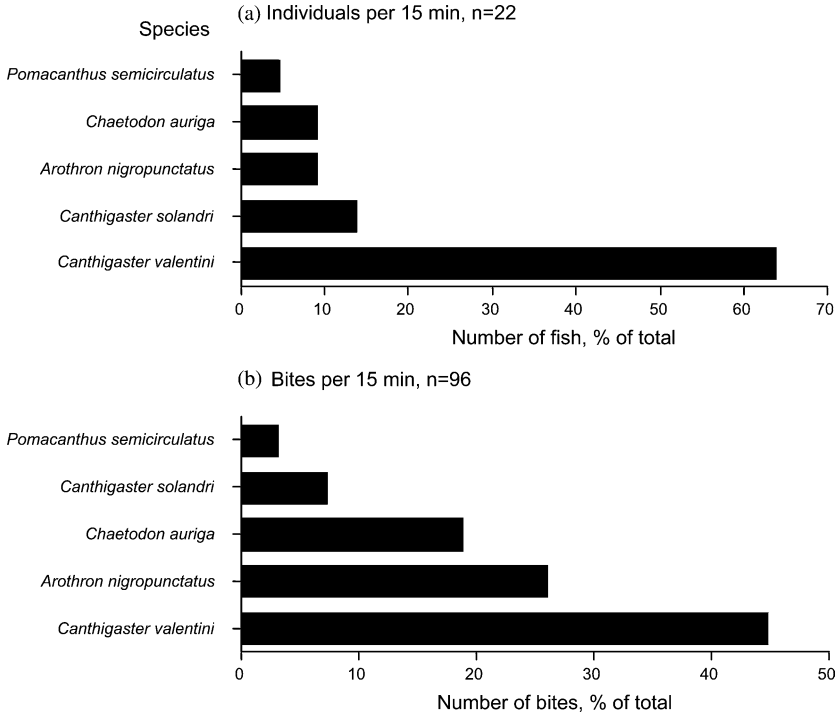

Fig. 5 Coral predators observed eating four scleractinian coral species presented as **a** number of individuals/15 min observation sample and **b** bites/15 min on fished reefs along the Kenyan coast

Ecological inter-relationships and predation

Summary statistics of the coral predators indicate that there was a significantly greater biomass of coral predators in unfished than in fished reef sites, differences in the total biomass being over an order of magnitude for most groups (Table 6). Differences were consistent for all predator group comparisons. Benthic cover estimates of the six reefs were also different for all classes except turf algae and seagrass (Table 7). The multiple stepwise regression analysis showed that the fish predator and sea urchin biomass were not significantly related to the change in the live tissue cover of coral transplants. The only two significant factors were turf and coralline algae, with turf being a negative and coralline algae being a positive predictor of the change in live transplant cover (Table 8). This result is largely attributable to both high predation on coral transplants and high coralline algal cover in Malindi (Tables 5 and 7). Additionally, there were not large differences in the predator biomass among unfished reefs, but there were large differences in transplant survival and benthic cover at these sites.

Discussion

This and other studies (Neudecker 1979; Littler et al. 1989) indicate that predation can occur quickly and influence coral survival, but that it is also complex and variable in space. Our data suggest that a number of factors including site, coral species and colony size, the abundance and species composition of the predator guild at a site, and the availability of alternative food resources may all influence predation. We did not find evidence for a negative influence by tourists, small-bodied predators or the lack of an acclimation period following transplantation on the survival of coral fragments. The study, therefore, indicates that corals that are adapted to temperature variation of a magnitude associated with major bleaching events are also susceptible to predation in some back-reef environments, notably those with large predatory fish and high coralline algal cover.

The results do not appear to be confounded by factors of acclimation to experimental manipulation, tourist activity and size of coral fragments. Our acclimation experiment indicated that predators were more rather than less attracted to corals that had been caged or acclimated for 2 weeks. This may have been an experimental artifact in that grazers and coral predators were attracted to the areas in which cages had been installed, resulting in higher rather than the expected lower mortality in the caged corals. Consequently, for an acclimation period to increase survival, it would need to be tested without the use of cages that promote other noncoral resources, which is difficult for short-term studies. Our study is not unique, however, as Littler et al. (1989) found a 100% loss in 1 day for *Porites porites* fragments that had been caged for 23 months. Taxa may need to colonize and grow in areas with predation in order to acclimate or adapt to it, but this is difficult to experimentally test with short-term experiments.

Tourists, particularly scuba divers, have been shown to damage corals (Hawkins and Roberts 1993), but this and another study in Kisite MNP found small effects in Kenyan parks (Muthiga and McClanahan 1997). There

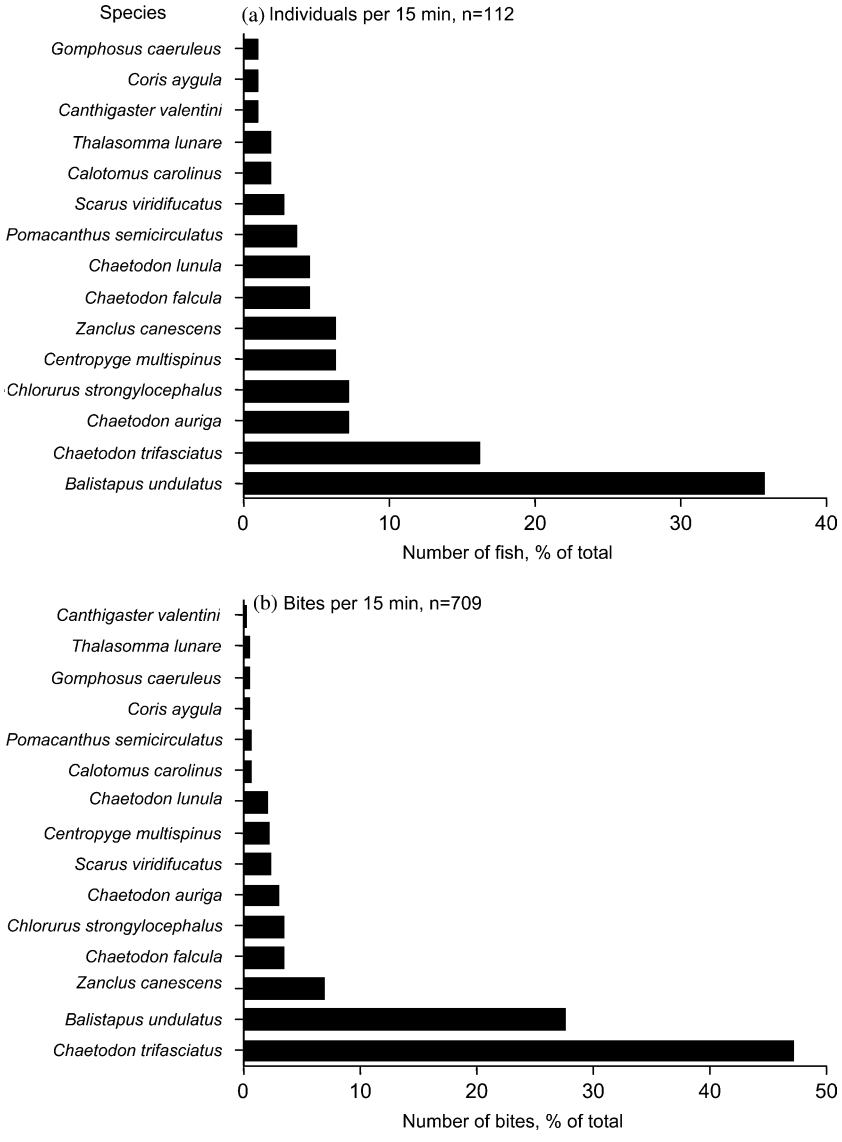

Fig. 6 Coral predators observed eating four scleractinian coral species presented as **a** number of individuals/15 min observation sample and **b** bites/15 min on unfished reefs on the Kenyan coast

were no obvious instances of trampled corals, and observed damage was due to predation. The small overall effect may be due to a combination of low to moderate tourist densities and the tourist education programs maintained by the boat-tourism industry and park service. We might expect larger tourist influences if the experiments were completed during the peak tourist season but the purpose of this study was not to test for tourist effects on corals and recovery, but rather to determine if it was confounding our experiments on predation. We conclude that tourist activity did not influence our experiments or conclusions.

Table 6 Biomass (kg/ha) of the dominant coral predator groups at six study sites along the Kenyan coast

	Unfished						Fished							
	Malindi		Watamu		Mombasa		Ras Iwatine		Vipingo		Kanamai		Kruskal-Wallis test, $df = 5$	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	ChiSquare	Prob > ChiSq
Balistidae	44.5	17.4	42.6	12.6	12.9	3.6	0.0	0.0	0.0	0.0	1.1	1.0	31.4	0.001
Chaetodontidae	6.8	2.0	5.1	0.8	13.6	4.4	1.1	0.7	1.8	0.9	6.8	2.2	18.5	0.001
Scaridae	126.5	7.2	189.6	34.3	157.6	19.9	12.2	3.4	2.3	0.5	6.1	1.5	37.3	0.001
Total	177.8	24.0	237.3	40.0	184.1	20.2	13.3	3.2	4.1	1.2	14.0	1.4	36.9	0.00
Sea urchins	15.0	14.0	8.0	3.0	1932.0	584.0	1638.0	5.0	2265.0	89	3102.0	234.0	16.0	0.01

SEM standard errors of the mean based on $n = 8$ transects at all sites except Watamu where $n = 6$

Table 7 Benthic substratum cover (%) of the dominant functional groups in the six study sites along the Kenyan coast

Sites	Unfished						Fished								
	Malindi		Mombasa		Watamu		Ras Iwatine		Vipingo		Kanamai		Wilcoxon/Kruskal-Wallis Test, $df = 5$		
Substrate category	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Chi Square	Prob > ChiSq	
Hard Coral	16.1	3.5	20.1	1.7	10.8	1.8	4.1	1.1	10.3	1.6	21.1	0.9	13.3	0.02	
Turf algae	31.4	6.7	42.6	5.5	48.2	3.8	35.8	1.8	42.1	4.7	35.9	1.3	5.2	NS	
Calcareous algae	12.9	3.1	1.2	0.2	14.9	2.3	0.4	0.2	0.2	0.1	1.6	0.5	16.2	0.01	
Coralline algae	30.8	2.1	9.4	1.6	11.9	0.3	4.9	2.0	3.6	1.1	1.2	0.9	14.2	0.01	
Fleshy algae	1.3	0.8	19.3	8.4	10.7	2.8	40.8	3.1	16.6	2.9	4.4	2.1	16.5	0.01	
Sand	3.4	0.6	4.8	0.8	1.4	0.1	7.1	0.6	6.6	0.7	8.1	2.2	16.3	0.01	
Seagrass	1.8	0.7	0.4	0.2	1.9	1.9	6.3	2.8	15.7	3.7	24.7	1.5	8.5	NS	
Soft coral	2.1	0.4	1.6	0.3	0.0	0.0	0.2	0.0	2.2	2.0	1.8	0.8	11.7	0.04	
Sponge	0.3	0.1	0.5	0.1	0.2	0.2	0.5	0.1	2.7	0.6	1.2	0.4	12.6	0.03	

Table 8 Results of the multiple stepwise screening regression using the coral predator abundance and substratum cover groups (x variables) against the change in live cover of the transplanted corals (y)

Term	Estimate	SEM	t ratio	Prob > $\lvert t \rvert$	
Intercept	60.9	10.2	5.95	0.0095	
Coralline algae	1.3	0.1	9.86	0.0022	
Turf algae	−1.4	0.2	−5.68	0.011	
Whole–Model Test					
Analysis of variance					
Source	Df	Sum of squares	Mean square	F	Prob > F
Model	2	1852	926	98.3	0.001
Error	3	28	9		
Total	5	1880			

Direct observation and our partial caging experiment suggest that the small-bodied fish predators of corals such as butterflyfish, tobies, the Moorish idol and a few wrasses did not greatly reduce live coral tissue or the size of the transplants. These species were observed picking at the coral tissue and consuming small quantities. In some cases they may have been picking at invertebrates living on the coral rather than the coral tissue itself, but it was difficult to distinguish these two feeding behaviors from the observation distance of 5–8 m. Harmelin-Vivien and Bouchon-Navaro (1983) estimated that butterflyfish remove a minor portion of the coral tissue biomass. Additionally, the relationship between butterflyfish and coral cover is usually positive (Cox 1984; Findley and Findley 2001) and the negative influence of these species on coral cover or biomass is, therefore, minor. Our study indicates that these predators are of relatively minor importance to coral survival compared to the larger triggerfish, parrotfish, and the starfish *A. planci*.

The red-lined triggerfish *Balistapus undulatus* had the greatest influence on branching species, while large parrotfish, such as *C. strongylocephalus*, most influenced massive *Porites* sp. Observations indicate that *B. undulatus* were searching and trying to extract small mobile invertebrates (i.e. crabs, shrimp, and brittle stars) living in the branches and only coincidentally consuming the coral branches. They did, nonetheless, damage and consume corals. Despite the lack of direct observation of *B. undulatus* feeding on the transplants, some of the measured damage may be due to their feeding. Neudecker (1997, 1979) reported high predation of transplanted *P. damicornis* by *B. undulatus* in Guam. The low observed bite rate but high loss of live cover of massive *Porites* sp. in unfished reefs is attributable to the large damage that parrotfish, such as *C. strongylocephalus*, have when biting transplants.

The relationship between parrotfish and living coral is complex and it has not been entirely resolved how important biting is for food versus a social function (Randall 1974; Littler et al. 1989; Bruggemann et al. 1994a; Bruckner et al. 2000). Small parrotfish are only seldom observed feeding or damaging living coral, and our observations here support that finding. Larger parrotfish, particularly initial and terminal phase males, are commonly observed feeding on corals, notably massive species such as *Porites* sp. and *Montastraea* sp. (Littler et al. 1989; Bruggemann et al. 1994a, b; Bruckner et al. 2000) but also branching species (Littler et al. 1989; Bruckner and Bruckner 1998). Littler et al. (1989) found that the parrotfish *Sparisoma viride* preferred branching *P. porites* to massive *P. asteroides* and this resulted in a spatial segregation between these two species.

Massive *Porites* species experienced the greatest losses among the four taxa of transplants, contrary to prediction (Clark and Edwards 1995). Observations on the transplants indicate that this was due to a few species of parrotfish that focused bit the transplants, often two individuals or more, and largely in the Malindi MNP (Fig. 1b; Bruckner et al. 2000). In many cases these parrotfish bit the transplanted corals in areas where the coral tissue was already removed. This does support the possibility that the behavior has a social rather than nutritional function, although they may use the calcium carbonate as grist to aid food processing. Despite the findings of higher loss rates from the massive *Porites* sp., we do not think this resulted in higher mortality for the taxa over the long term. Casual observation in Malindi up to 3 years after this study indicates that the fist-sized massive *Porites* had the highest whole-colony survival. Many transplants were damaged on the top, but, in many cases, the living tissue expanded from the sides (Fig. 1c).

An interesting and unexpected result of the stepwise multiple regression analysis was that two components of the substratum exerted the largest influence on coral predation, while neither fish nor sea urchin biomass was statistically significant. This may have been influenced by the low number of reefs sampled ($n = 6$), but is more likely attributable to the high variation in predation on corals in the unfished reefs, being considerably higher than variation in predator abundance. Consequently, the feeding decisions of predators were more important than their abundance: when turf algae are abundant they avoid hard corals, but feed on it when encrusting red coralline algae are abundant. Parrotfish were responsible for most of the damage to transplants in Malindi and they may have preferentially fed on hard coral when their preferred prey, algal turf (Choat 1991), was not common. This would not, however, explain predation by other taxa unless their alternate prey is more abundant in reefs with higher turf. In Kenya and elsewhere, red coralline alga develops on reefs with a high abundance of herbivorous fish grazing, and is retarded by grazing sea urchins (McClanahan 1997). Coralline algae are reported to induce settlement of hard corals (Heyward and Negri 1999) but our study suggests that they may also promote predation on corals.

The single invertebrate species that influenced the transplants was the crown-of-thorns starfish *Acanthaster planci*. It was observed feeding in two adjacent reefs, the Mombasa MNP and Ras Iwatine. At both reefs, *A. planci* fed on the three branching taxa in approximately equal proportion, but not on massive *Porites* sp. Over a 30-day interval we noted 14 of the 128 transplants were eaten by *A. planci*, suggesting that few of the branching transplant taxa would survive a year. Our observations 1 year later suggest, however, that there was high survival of branching *Porites* sp. and modest survival of *P. damicornis* and *P. decusatta*. Predation by *A. planci* is often partial and coral tissue can grow from the remaining undisturbed tissue. The low coral recovery in Ras Iwatine after the 1998 bleaching is more likely attributable to the interaction between low coral recruitment, high predation by *A. planci* and high fleshy algal cover (40%) on this reef. The Mombasa MNP, the other site where *A. planci* were observed killing corals, lost 8 of the 132 transplants to *A. planci* in 19 days. The rate of mortality by *A. planci* and fish in both areas is, therefore, similar. The Mombasa reef also had moderate to high fleshy algal cover, although half the level of Ras Iwatine. Consequently, higher coral growth and recruitment or reduced competition with macroalgae in Mombasa may influence the different coral recovery rates in the two reefs. Although most taxa have increased in Mombasa since the bleaching (McClanahan and Maina 2003), 72% of the coral cover recovery over the 3 years since the mortality is attributable to massive *Porites* sp., which is not commonly fed on by *A. planci* (T.R. McClanahan, unpublished data). Massive *Porites* sp. was not abundant in Ras Iwatine, and differences in its abundance prior to the bleaching can explain the large differences in the rates of recovery between these two sites.

There was little evidence that other invertebrates such as the coral-eating snails *Coralliophila* and *Drupella* (McClanahan 1994b; Cumming 1999), crabs, or sea urchins fed on the transplanted corals. Sea urchins are abundant in the fished reefs and may influence coral abundance and recovery (Sammarco 1980; McClanahan and Mutere 1994), but we found no evidence of sea urchin feeding scars on the transplants. This was against the expectation as the lower coral cover and the low recovery rate of corals on bleaching-disturbed reefs might be attributable to high sea urchin abundance, particularly on fished reefs. The loss of hard coral over the bleaching period resulted in an increase in turf and fleshy algae, the preferred food of sea urchins (Carpenter 1981). This is likely to have produced more feeding on algae and less feeding on hard corals (Carpenter 1981).

The rapid recovery of hard corals in Malindi is unexpected from our experiments with the transplants. Two factors probably influenced the discrepancy: one is the low fleshy algal cover on this reef, and the second is that the recovering taxa were not the taxa that we transplanted. This reef was originally dominated by *Acropora* spp. and branching *Porites* spp. before the bleaching, but *Echinopora* spp. and *Galaxea* spp. were the dominant taxa after 1998 (T.R. McClanahan et al. 2001, unpublished data). Massive *Porites* sp. was and is moderately abundant in this reef, which indicates a discrepancy between our measure of predation and survival of the indigenous massive *Porites* sp. in this reef. One observation was that the massive *Porites* sp. in the reef had far fewer bite scars compared with the transplanted corals. Consequently, a difference between the transplants and the indigenous corals in their predator defenses is the likely cause. It would be useful to know if these are genetic or acquired differences, but it is possible to induce defenses such as stinging-cell densities with

only brief exposures to predation (Gochfeld 2004). Regardless, eurythermal corals from Kanamai will not transplant and survive well in coral reef parks with high coralline algal cover such as Malindi. Where turf and fleshy algae are more abundant, such as in the Watamu and Mombasa MNP, transplantation is a feasible means of introducing eurythermal corals. It is likely that fleshy algae are inhibiting coral recruitment in some reefs, such as Ras Iwatine and Watamu, and without transplantation rapid coral population recovery is unlikely.

Cyclical models of coral mortality by bleaching and *A. planci* infestation, developed to predict the future of coral reefs, indicate that the present and future rates of disturbance to corals are at frequencies higher than will allow for full coral recovery (Bradbury et al. 1985; Done 1987, 1988; Bradbury and Seymour 1997; Ware 1997; Huppert and Stone 1998; Fong and Glynn 1998, 2000; Hoegh-Guldberg 1999; Sheppard 2003). The results reported here and our other studies (McClanahan et al. 2002; McClanahan and Maina 2003; McClanahan et al. 2004) show that there is high spatial variability and functional complexity in the response of corals, their recovery, and susceptibility to predation by fish and *A. planci*, bleaching, and competition with fleshy algae. The high diversity of coral reefs and their ecological complexity is, therefore, likely to result in surprising changes in the future that will be hard to predict from existing models. Existing models have a few dominant variables such as single or composite coral taxa, one predator and a cycle of warm water. These models are good for preliminary evaluations of simplistic ecosystems, but lack the complexity and potential for surprise imposed by the diversity of real ecosystems.

Global climate change and the increased frequency and intensity of warm-water anomalies are expected to influence coral reef ecology in as yet unexpected ways. Warm water anomalies are often associated with the ENSO, which presently has a 3–4-year periodicity (Charles et al. 1997; Huppert and Stone 1998; Urban et al. 2000). Until recently, mass coral-mortality events have occurred every 10–20 years (Hoegh-Guldberg 1999; Glynn 2000; Goreau et al. 2000). The frequency of these strong coral mortality events is likely to increase in the coming decades, perhaps to the frequency of every warm ENSO period (Ware 1997; Hoegh-Guldberg 1999; Sheppard 2003). Our study of coral recovery over a 4-year period approximates the typical recovery interval predicted for the near future. Coral recovery rates across our six reefs over 4 years were highly variable, from 0% to 25% with a mean of 6.5%. For shallow sites, this is considerably lower than the usual annual increase range of 2% and 12%, increasing from deep to shallow reefs (Pearson 1981; Connell 1997), and may be due to the large spatial scale of the disturbance. In some past studies, however, no recovery was recorded after many years (Connell 1997) and many of the slow-growing coral species such as *Gardineroseris planulata* and massive *Porites* spp. require periods of 50–100 years to recover to predisturbance levels (Done 1987; Fong and Glynn 2000). Site and taxa-specific recovery rates will result in considerable ecological reorganization of coral reefs and, as suggested by our study, a variety of other factors such as fishing, benthic cover, coral predators and herbivores will further influence the local outcomes of this change in coral reef ecology. The ability of eurythermal corals to colonize and increase recovery rates of reefs disturbed by warm water is limited to some reef environments, depending on the interaction of predators and their alternative prey.

Acknowledgments This study received support from The Wildlife Conservation Society with partial financial support from the Dutch Wetland's Program. The assistance of Kenya Wildlife Service in the three marine parks is greatly appreciated. Kenya's Office of the President provided permission to undertake research. C. Starger received support from the Center for Environmental Research and Conservation at Columbia University, P. Herron-Perez from the Department of Marine Sciences and Coastal Management at the University of New-castle upon Tyne and E. Dusek from the Department of Biological Sciences at Stanford University.

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