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Are corallivores limiting the recovery of corals on Kenyan reefs?

Angelica Klaussén

Arbetsgruppen för Tropisk Ekologi
Committee of Tropical Ecology
Uppsala University, Sweden

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Angelica Klaussén

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Biology Education Centre and Department of Ecology and Evolution, Limnology, Uppsala University
Supervisors: Peter Eklöv, Department of Ecology and Evolution, Limnology, Uppsala University and
Emily Darling, Department of Biological Sciences, Simon Fraser University

Abstract

As one of the most diverse and productive ecosystems in the world, coral reefs are faced with several environmental stresses such as pollution, overexploitation and climate change, which can result in coral bleaching. Several reefs and coral species have not yet recovered since the most severe global bleaching event in 1998. *Acropora* and *Montipora* species in particular show extremely low rates of recovery on Kenyan reefs and long term data indicates that recovery is lower on protected (un-fished) reefs compared to un-protected (fished) reefs. Coral-eating fishes (corallivores) can negatively affect coral growth rates and reproduction. In this study I evaluate the impacts of corallivores on the recovery of corals, by identifying the coral species that are preferentially consumed by coral-eating fishes in order to clarify the impacts of corallivores on the dynamics and resilience of coral communities. I found a significant loss in coral surface area (cm^2) of 3.9 % for transplants exposed to fishes, compared to caged coral transplants (positive change 0.15 %). Electivity index values, resulting from observations of coral grazing scars, showed that *Montipora* and branching *Porites* were preferentially selected. The combination of low abundance, high incidence of grazed colonies, high electivity values and the high abundance of coral predators suggests that corallivores may be limiting the recovery of *Montipora* in Malindi Marine National Park, Kenya. Since severe coral bleaching events are predicted to be more common in the future, understanding of recovery and growth after disturbances is becoming increasingly important.

Keywords: coral reefs, grazing, coral recovery, fish predation, corallivores.

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Introduction

Coral reefs are among the most productive and diverse ecosystems on earth, with the Scleractinian corals being the main reef-builders (Muscatine & Porter, 1977). Reefs around the world are threatened by a combination of climate change resulting in coral bleaching, ocean acidification, pollution, coastal development, overexploitation, diseases and crown-of-thorns starfish outbreaks (Hughes 1994, Bellwood *et al.* 2004, Hoegh-Guldberg *et al.* 2007). This increasing variability in the environment can reduce species richness (McClanahan, 2002) and alter ecological functions, including reef calcification and growth (Cortes, 1993). In 1998, elevated seawater temperatures promoted severe coral bleaching worldwide (Hoegh-Guldberg 1999, Hoegh-Guldberg *et al.* 2007). Since then some coral reefs have not yet recovered (Lambo & Ormund, 2006) and the mechanism behind this remains unclear (McClanahan *et al.,* 2005). *Acropora* and *Montipora* species abundances on the Kenyan coast are still very low and long term data indicate that coral species recover faster on fished reefs (un-protected) compared to un-fished reefs (protected) (Coral Reef Conservation Project (CRCP), unpublished data). This suggests that predators can potentially play a role in the recovery rate of coral species when subjected to environmental disturbances.

Predators can change the distribution and abundance of organisms and hence influence the diversity and structure of communities (Almany 2003, Addicott 1974, Kelley *et al.* 2003). The hypothesis that marine ecosystems can be organized by predators is well supported (Paine 1969, 1974), but if predators have negative or positive impacts on community diversity and how this varies between communities is less clear. Predators can increase species diversity through trophic cascades by reducing the most abundant prey (keystone predator). For example, in the Pacific Northwest, the keystone predator sea otter (*Enhydra lutris*) feeds on sea urchins (herbivores), which in turn graze on kelp (macroalgae) (Lowry & Pearse, 1973). Where sea otters occur, sea urchins are rare and kelp is abundant and where sea otters are absent sea urchins are common and kelp forests rare (Estes & Duggings, 1995). Predation can also be selective. For example predators can affect the size distribution of prey when a certain size of the prey is preferred (Mullin, 1963) and reduce the abundance of an already rare species (Saage *et al.*, 2009).

Coral reefs are characterized by a high diversity of predator-prey relationships, many of which include coral reef fishes (McClanahan *et al.*, 1999). Herbivorous fishes that feed selectively on different types of algae play an important role in the resilience of coral reefs by limiting overgrowth of competitive macroalgae that can outcompete reef-building corals (Bellwood *et al.,* 2004). In addition, some species of parrotfish (Scaridae) can feed directly on living corals (Rotjan & Lewis, 2005). A recent study in Malindi Marine National Park (MNP) suggests that the levels of recovery are poor and that there is a continued decline of live coral cover (Lambo & Ormund, 2006), especially *Acropora* and *Montipora* species (CRCP, unpublished data). Before the bleaching event in 1998, *Acropora* was the dominant reef-builder on the Kenyan reefs covering as much as 20 % of the benthic cover. Following the 1998 bleaching event, *Acropora* abundance declined to < 1 % and has still in 2009, 11 years after the bleaching event, remained on this low level. *Montipora* covered about 4 % of the benthic cover the year before the bleaching event and covers now < 0.1 % (CRCP, unpublished data). On other reefs in the Indo-Pacific, *Acropora* has shown extremely rapid recovery after bleaching and has reached its pre-bleaching levels within a year (Diaz-Pulido *et al.*, 2009). Studies of *Montipora* in Northwest Pacific have shown that it recovered to pre-bleaching coverage in two years (Kayanne *et al.,* 2002). Research of the Kenyan reefs is in need and studies contributing to a better understanding of these differences in recovery are of highly interest.

Reefs protected from fishing have higher fish abundance and diversity, including coral eating fishes (corallivores) (McClanahan & Arthur, 2001). Parrotfishes are known herbivorous on Kenyan reefs, characterized by their beak-like jaws that enable them to remove

both algae and underlying substrate (Bellwood & Choat, 1990). Previous research has suggested that predation by coral-eating fishes can affect the dynamics of coral communities in Kenyan marine parks (McClanahan *et al.,* 2005). The relationship between corallivores and living coral has not been entirely resolved (McClanahan *et al.* 2005, Mumby 2009), but there is a growing evidence that coral predation is more selective than previously thought and can be an important source of coral mortality (Rotjan & Lewis, 2005). Live coral is also included in the diet of the red-lined triggerfish (*Balistapus undulatus*) (McClanahan, 2000). Corallivores can reduce coral reproduction (Rotjan & Lewis, 2008), growth rate (McClanahan *et al.,* 2005) and fitness (Cole *et al.* 2008, Rotjan & Lewis 2008), by removing coral tissue and parts of the underlying calcium carbonate skeleton.

This study investigates if direct consumption of live corals by corallivores can negatively affect the recovery of corals. I evaluate the impacts of corallivores on corals and whether corallivory is selective, by identifying the corals that are preferentially consumed by coral-eating fishes in order to fully elucidate the impacts of corallivores on the dynamics and resilience of coral communities. If corallivores prefer only a few species of corals, such as the important reef-building *Acropora* (Cole *et al.*, 2008) and *Montipora*, predation can be an explanation of why these dominant reef-builders have not recovered following the mass bleaching event in 1998. Many coral reefs are characterized by a high diversity of predator-prey relationships and the insights gained from this research are applicable to other marine parks in Kenya and can also contribute to coral restoration and recovery efforts throughout the Western Indian Ocean and the wider Indo-Pacific.

Methods

Study site

Studies were undertaken in November and December 2009 on a fully protected reef in Malindi MNP (3°18'35S; 40°06'57E) on the Kenyan coast. Malindi MNP is a shallow (1-4 m) platform reef with a lagoon dominated by coral and seagrass habitats. It has been protected from fishing since 1968 (McClanahan, 2000). Within this site, I assessed corallivore impacts using a manipulative predator exclusion experiment, fish transects, fish feeding observations, measurements of coral abundance and incidences of grazing scars on coral colonies.

Predator exclusion experiment

Collecting transplants

Transplants for the experiment were collected within a fringing reef lagoon in Kanamai, 20 km north of Mombasa. Kanamai reef (3°55'S, 39°50'E) is an un-protected reef and is also extremely shallow in low tide (< 1 m) and was chosen to facilitate the collection of transplants. In this and the other parts of the study, corals were identified to genus except the genus *Porites* that was separated by the different growth forms, massive and branching. Fist-sized coral fragments of 15 genera (210 transplants) were removed from the reef in Kanamai using chisel and hammer. The corals were *Acropora, Heliopora, Millepora, Pavona, Pocillopora, Psammocora, Stylophora*, *Favites, Hydnophora, Platygyra,* massive *and* branching *Porites, Echinopora*, *Galaxea* and *Fungia*. *Montipora* was unable to be included in the experiment as it was not found on the Kanamai reef. The transplants were immediately put in buckets with fresh seawater to ensure minimal transplant and transportation damage. For the massive corals, a nail was attached to them with waterproof glue (Z-Spar SplashZone A-788 underwater epoxy). Corals were collected during two days and the transplants were kept under water in a holding cage (2.5 cm

mesh cage) for three nights before being transported by car and boat on the third day to the experimental site in Malindi MNP. The transportation time was two hours and the transplants showed, except from minor mucus formation, no signs of stress or mortality.

Preparing experimental site and cages

The experimental site consisted of 7 pairs of natural hard bottom platforms (~1 m^2 each), that were cleared of algal substrate. Each pair had one open (exposed to fish) and one caged (control, not exposed to fish) plot. The distance between the pairs were approximately 4 m and the distance within a pair, between paired plots, was 1-2 m. The cages were made of 2.5 cm nylon netting (Aquatic Eco-Systems Inc., Part no N1133), which has been proven effective in studying short-term predation with insignificant effect on the coral (McClanahan *et al.,* 2005). Each cage was a half cylinder shape to cope with the currents better (maximum height 25 cm) and the base was a square (0.7 * 0.7 m) (Fig. 1A).

Experimental set-up

The surface area of the transplants was photographed in air together with a scale bar (cm) with a Canon PowerShot D10 just before putting them out on the plots. To keep track of the different transplants they were placed in a tagged mesh bags, which were then transported to the different plots and the transplants were attached to the substrate with galvanized steel nails and cable ties (Fig. 1B). All nails used in this experiment were galvanized and non-corrosive. Halfway through the experiment (9 days), algal growth was removed from the plots with a steel brush, which may otherwise reduce coral growth (McCook *et al.,* 2001). At the end of the experiment (18 days) the transplants were again photographed and any size or change in condition was measured. The photos were analyzed in the image-analysis computer program IMAGE J.

A) B)

Fig. 1. A) Photograph of an experimental cage and B) coral transplant of *Acropora* striped on to the bottom substrate.

Fish transects

Corallivore fish density was recorded along a 50 m x 5 m belt. Corallivores in an area of 2.5 m on each side of the transect line were estimated by visual counts and pooled by transect (number of individuals/ 250 m^2). Individuals from common coral predator families i.e. Scaridae, Chaetodontidae, Zanclidae, Balistidae and Tetraodontidae (Rotjan & Lewis 2008, Cole *et al.* 2008) were recorded to species and total length (estimated by cm) with 6 replicates

(transect lines parallel to each other). In the fish transects and in the feeding observational study (see below) all fishes > 7 cm were studied, except species within family Scaridae and Balistidae that were only studied and counted if > 15 cm. Smaller fishes from Scaridae are seldom observed feeding or damaging corals (McClanahan *et al.*, 2005).

Feeding observations

Snorkeling observations were conducted for 5 days (11 am – 3 pm) in mid neaps (depth ~3 m). Individuals from the corallivore families Chaetodontidae, Balistidae and Scaridae were followed at a discrete distance (3-5 m) and observed for ideally 3 min, using a stopwatch. If the fish stayed at the site for 1-3 min, the exact time was recorded whereas those that stayed < 1 min were discarded from the analysis. Species and size (total length, cm) of the fish, as well as all feeding bites considering type of food source and number of bites on each were recorded. Feeding categories were algal turf, soft coral, hard coral (identified to genus) and coralline. In total 9 species and 78 individuals were observed (4 to 23 observations/species). I expected the individuals to move between the experimental sites and other surrounding areas between the days and the probability of double following individuals were considered small within each observation period. The size of each individual fish was also recorded to minimize pseudo-replication. A three minutes observation period of corallivores has been successfully used in earlier studies of feeding observations (Pratchett, 2005) and daytime observations constitute a good estimate since feeding activities has shown to be highest and relatively consistent during mid day (Bellwood 1995, Choat & Clements 1993, Righton *et al.* 1998). Individuals of *B. undulatus* (family Balistidae), also a common corallivore on the Kenyan reefs (McClanahan *et al.,* 2005), were recorded at the reef in Malindi MNP but not included in the feeding observation data as they were unable to be followed.

Grazing incidence and coral abundance

A grazing survey was conducted to assess whether there was any selectivity by corallivores across coral genera. Coral colonies (> 3 cm) within quadrates of 2 m^2 were counted and identified to genus. In all quadrates the benthic cover was estimated to the nearest 5 % for the categories turf algae, soft coral, hard coral, erect macroalgae and coralline algae. All live coral colonies were counted and carefully examined for recent damage (following Rotjan & Lewis, 2005) based on presence or absence of recent parrotfish scars. I conducted 5 grazing surveys, with 12-21 replicate quadrates per survey. The hard coral genera with the highest number of colonies (15 genera, 298 to 9 colonies) that were found in at least 3 of 5 replicates were used in the analysis. Relative abundance was calculated as the number of colonies of each species divided by the total numbers of coral colonies counted per transect. To determine grazing selectivity on coral genera, I calculated Ivlev´s electivity index (E_i) (Ivlev, 1961):

$$E_i = (r_i - n_i) / (r_i + n_i)$$

Where r_i is the proportion grazed of the total abundance of a particular genus (number of grazed colonies/total number of colonies of that genus) and n_i the proportion abundance of that particular genus (number of colonies of that genus/total number of colonies for all genera found in the replicate). Electivity index varies from -1 to +1, where $E_i > 0$ is preferred and $E_i < 0$ is avoided. *Galaxea* found and used in the analysis was *G. fascicularis*, the genus *Pavona* was exclusively *P. varians* and *Pocillopora* was both *P. damicornis* and *P. verrucosa*.

Statistical analysis

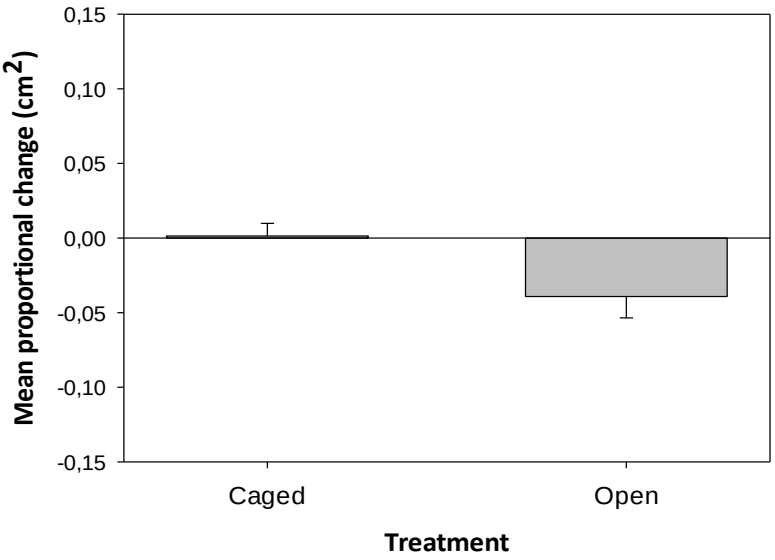
Difference in surface area (cm^2) between open and caged transplants (summed) as well as differences between the genera within caged transplants and within open treatments were analyzed using Mann-Whitney and Kruskal-Wallis Tests. The observed feeding preferences of corallivores were compared to available food sources by χ^2 test. Kruskal-Wallis Tests were used to demonstrate any differences in coral abundance, grazing incidence and in electivity index values between genera and between the growth forms massive and branching. To evaluate if grazing incidence was correlated with abundance linear regression analysis was conducted, in which percentage grazing was the independent variable and abundance was the dependent variable.

Results

Predator exclusion experiment

Some of the transplants in the open treatment could be distinguished from the caged transplants by signs of grazing, either from damaged or missing tissue or branches. While the experiment started with 7 replicates, some transplants ended up with 4 to 6 replicates because of missing transplants. The missing transplants were unlikely to be consumed because sometimes the whole coral including nail and glue was missing; these were therefore excluded in the analysis. There was a significant difference in predation effect between the caged and open transplants overall (Fig. 2A) (Mann-Whitney, p = 0.023); transplants open to predation had on average 3.9 % loss in area (cm^2) and the caged transplants a positive change of 0.15 %. There was no significant difference in proportional change in area (cm^2) between the different genera within caged transplants (Kruskal-Wallis Test = 16.56, df = 14, p = 0.280) nor between the genera within open treatments (Kruskal-Wallis Test = 10.29, df = 14, p = 0.740) (Fig. 2B).

A)



B)

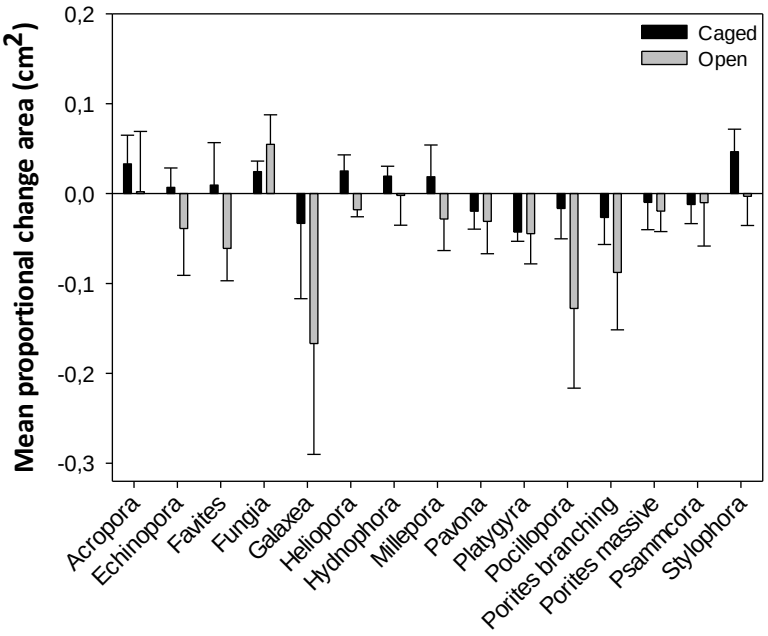


Fig. 2. Mean proportional change (+ SE) in area (cm^2) of A) all transplants summed for caged (n = 101) and open (n = 94) and B) all transplants separated by genera and treatment.

Fish transects

A total of 17 species within 5 families (i.e. Scaridae, Chaetodontidae, Zanclidae, Tetraodontidae and Balistidae) of corallivores were recorded in the belt transects with a total mean density of 20 individuals/250 m^2 (Fig. 3). *Scarus sordidus* was most abundant with 4.5 ± 0.77 individuals/250 m^2 followed by *B. undulatus, S. frenatus* and *Calotomus carolinus* having mean densities of 2.5 ± 0.72, 2.2 ± 0.98 and 2.0 ± 0.77 individuals/250 m^2 respectively.

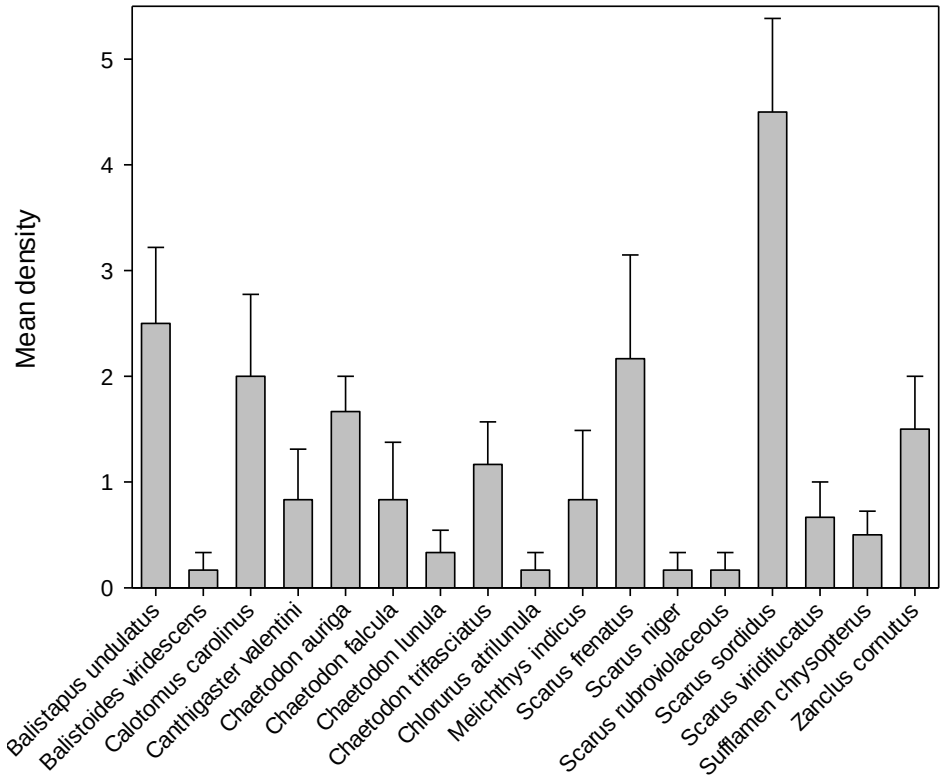


Fig. 3. Mean fish density (individuals per 250 m^2) (+ SE), n = 6.

Feeding observations

Feeding behavior of 4 species from the family Chaetodontidae i.e. *Chaetodon auriga, C. falcula, C. lunula* and *C. trifasciatus* and 5 species belonging to Scaridae i.e. *Chlororus strongylocephalus, S. frenatus, S. niger, S. rubroviolaceus* and *S. sordidus* was studied. The available food sources estimated in the grazing survey i.e. turf, soft coral, hard coral and coralline (ratio 0.36 : 9.6 : 0.21 : 0.18 respectively) were significantly different from the observed values (χ^2 values listed in Table 1, $p < 0.001$). All species from the family Chaetodontidae consumed hard corals (Fig. 4). *C. trifasciatus* fed almost exclusively on hard corals (> 98 %). *C. lunula, C. auriga* and *C. falcula* had a mixed diet including various amount of living hard coral (78, 23 and 20 % respectively). I did not observe any species within family Scaridae feeding on hard coral, all species consumed between 99-100 % turf algae.

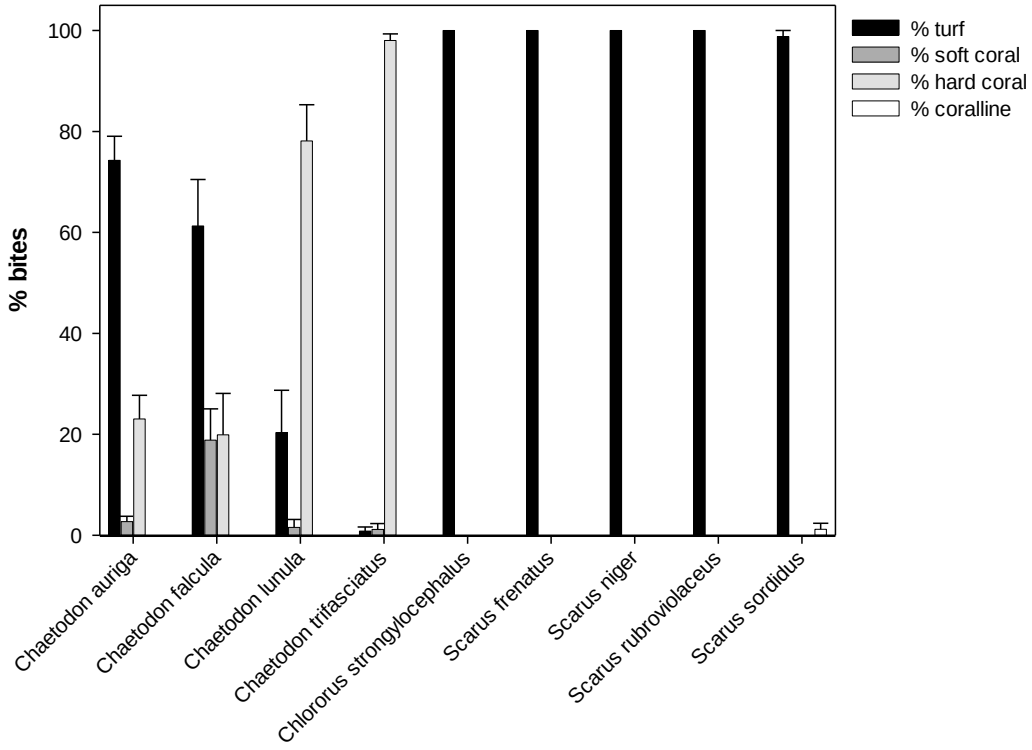


Fig. 4. Mean percentage bites taken (+ SE) on turf, soft coral, hard coral and coralline by different species.

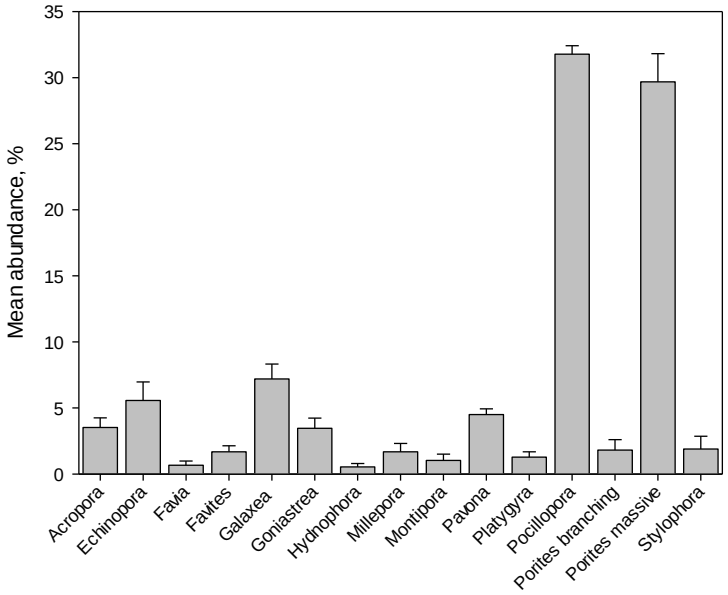
Table 1. Chi square values for the corallivores feeding on turf, soft coral, hard coral and coralline algae. Star (*) represent significance ($p < 0.001$).

Species	χ^2
Chaetodon auriga	50.7 *
Chaetodon falcula	34.7 *
Chaetodon lunula	159.3 *
Chaetodon trifasciatus	293.0 *
Chlororus strongylocephalus	132.6 *
Scarus frenatus	132.6 *
Scarus niger	132.6 *
Scarus rubroviolaceus	132.6 *
Scarus sordidus	127.2 *

Grazing incidence and coral abundance

There was a significant difference in the abundance of the coral genera (Kruskal-Wallis Test = 56.08, df = 14, p < 0.0001) (Fig. 5A). The branching *Pocillopora* and the massive form of *Porites* were highly abundant in the surveyed area representing 31.8 and 29.7 % of the total number of colonies respectively. *Galaxea, Echinopora* and *Pavona* species were also common corals on the reef in Malindi MNP representing 7.2, 5.6 and 4.5 % of all coral colonies respectively. 11 of the 15 genera were grazed, with *Montipora, Pocillopora*, branching *Porites* and *Acropora* having the highest percentage grazed i.e. 31.7, 27.6, 25.3 and 20.1 % of the total number of colonies infested respectively (Fig. 5B). The other genera grazed were *Millepora, Stylophora, Pavona*, massive *Porites, Echinopora, Galaxea* and *Goniastrea* having between 15 and 3 % (decreasing order). *Favia, Favites, Hydnophora* and *Platygyra* were not grazed at all. There was a significant difference in percentage grazed between the coral genera (Kruskal-Wallis Test = 30.11, df = 14, p = 0.007).

A)



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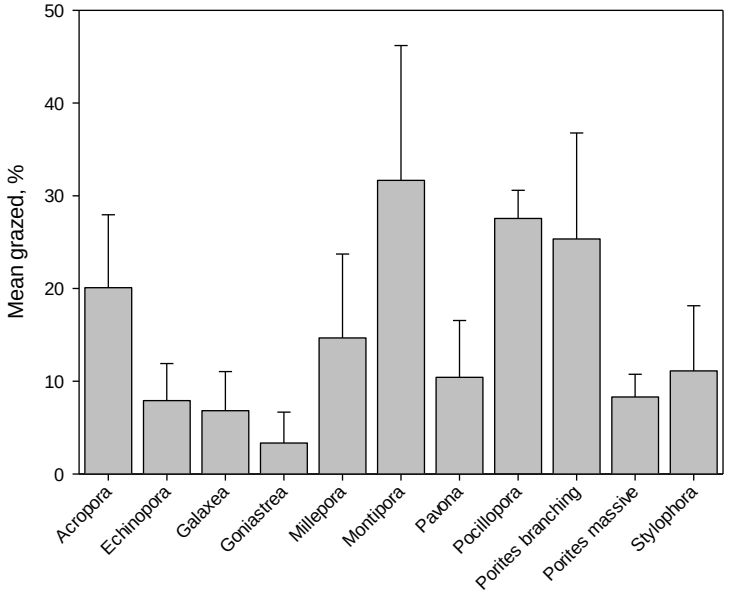


Fig. 5. (A) Mean percentage abundance (+SE) (n = 5) and (B) mean percentage of the colonies grazed (+SE) (n = 5).

Linear regression showed that there is no significant correlation between percentage abundance and percentage grazed for each genus (Fig. 6) (R^2 = 0.0358, p = 0.104).

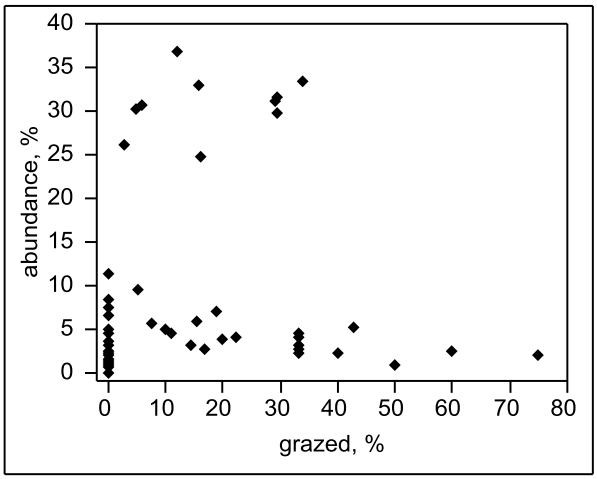


Fig. 6. Linear regression of the relationship between abundance and colonies grazed (%), y = 0.11x + 5.16, n = 74, R^2 = 0.0358, p = 0.104.

Grazing selectivity

The branching growth form of *Porites* was much more grazed than the massive growth form. To examine if there was any differences in selection between coral growth forms, I grouped the corals into branching, massive (including submassive) and encrusting. The branching group included *Acropora, Millepora, Pocillopora, Porites* (branching) and *Stylophora,* the massives included *Favia, Favites, Goniastrea, Hydnophora, Platygyra, Pavona* and *Porites* (massive) and the encrusting *Echinopora, Galaxea* and *Montipora*. There was a significant difference in selection between the three groups (Kruskal-Wallis Test = 16.07, df = 2, p < 0.001) and the difference was between the branching and the massive group (Dunn´s Multiple Comparison). The branching corals (n = 20) was positively selected and the massive corals (n = 29) were negatively selected (avoidance) (E_i = 0.49 and -1 respectively). There was a significant difference in selectivity between the different genera (Kruskal-Wallis Test = 33.23, df = 14, p = 0.003) (Fig. 7, Table. 2). The differences in selectivity were largely explained by the strongly preferred *Monitpora* and branching *Porites* (E_i = 0.93 and 0.85 respectively) and the strongly negative selected *Favia, Favites, Hydnophora* and *Platygyra* (E_i = -1) and *Porites* massive (E_i = -0.58) (Dunn´s Multiple Comparison).

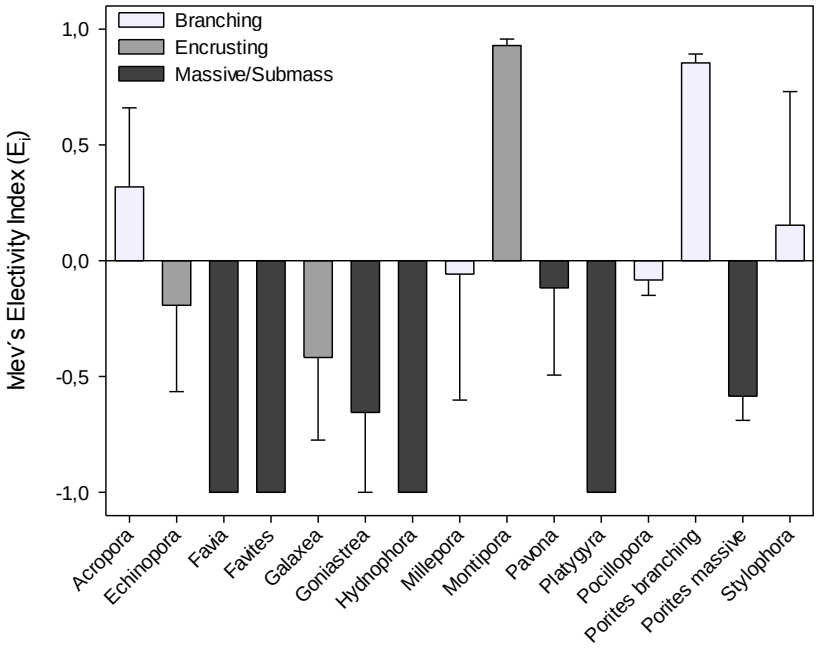


Fig. 7. Feeding selectivity for coral genera based on proportion grazed and relative abundance. Mean values of Ivlev´s electivity index (+ SE), where $E_i > 0$ is preferred, $E_i < 0$ is avoided, n = 5. Light bars represent branching, dark grey represent encrusting and black bars represent massive and submassive corals.

Table 2. Summary table of mean percentage abundances (based on number of colonies), colonies grazed and Ivlev's electivity index (E_i).

Genus	mean % abundance	mean % grazed	mean E_i
Montipora	1.03	31.67	0.93
Porites branching	1.82	25.33	0.85
Acropora	3.53	20.1	0.32
Stylophora	1.89	11.11	0.15
Millepora	1.68	14.67	-0.06
Pocillopora	31.77	27.55	-0.08
Pavona	4.5	10.43	-0.12
Echinopora	5.57	7.91	-0.19
Galaxea	7.19	6.83	-0.42
Porites massive	29.68	8.31	-0.58
Goniastrea	3.47	3.33	-0.66
Favia	0.67	0	-1
Favites	1.68	0	-1
Hydnophora	0.54	0	-1
Platygyra	1.28	0	-1

Discussion

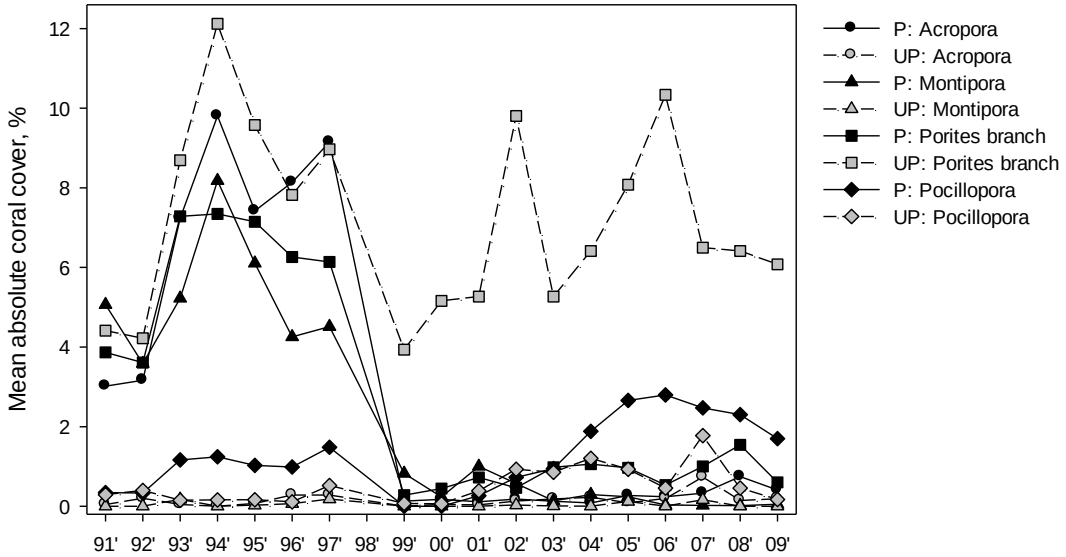
This study shows that some corals can be significantly affected by fish predation. A loss of 3.9 % surface area in 18 days exposed to fish suggests high predation pressure, since a loss of 4 % in this study (coral area varied from 10 - 60 cm^2) represented between 4 and 24 mm in 18 days i.e. 81 - 487 mm/year. Taking into consideration that annual coral growth rates vary between 5-200 mm/year (dependent on species and region; Roth 1979, Baker & Weber 1975, Edinger *et al.* 2000) predation is likely an important factor influencing coral growth. Both visual observations of the coral transplants and the significant loss in surface area between caged and open plots

demonstrated that not only coral tissue but also underlying calcium carbonate skeleton was removed. Recent studies have also shown that fish predators can have consequences for coral fitness (Rotjan & Lewis 2008, Cole *et al.* 2008, Jayawardene *et al.* 2009) and decrease coral growth rates (McClanahan *et al.,* 2005).

Linear regression showed that there is no significant correlation between abundance and grazing indicating potential selection between the coral genera. Massive *Porites* was highly abundant (representing 30 % of the total number of colonies) and the percentage grazing was relatively low (8 % of the colonies) indicating that the genus is not preferred by predators. This is also in agreement with the significant negative value of Ivlev's electivity index (E_i = -0.58). Other massive corals, such as *Favia, Favites, Hydnophora* and *Platygyra* also showed a strong avoidance (E_i = -1). *Pocillopora* had the highest abundance (32 %), with 28 % of the colonies being grazed, resulting in a non-preferred value of E_i = -0.08. Interestingly, three genera with some of the lowest abundances in this study, had high percentage grazed colonies i.e. *Acropora* (abundance 3.5 %, 20 % grazed), branching *Porites* (abundance 1.8 %, 25 % grazed) and *Montipora* (abundance 1.0 %, 32 % grazed) and of these branching *Porites* and *Montipora* demonstrated high preferences (E_i = 0.85 and 0.93 respectively).

Branching forms of *Montipora* species seems to be very rare since none were seen on the reef in Malindi MNP during this study (personal observations). Long-term data from protected and un-protected reefs in Kenya show the history of absolute percentage cover for some common genera (CRCP, unpublished data) (Fig. 8). The branching and encrusting genera; *Acropora, Montipora, Porites* and *Pocillopora* showed a sharp drop in percentage cover following the 1998 bleaching event (Fig. 8A). Consistently for branching *Porites, Acropora* and *Montipora,* the recovery was lower on the protected reefs (un-fished), while *Pocillopora* recovered well on both protected and unprotected reefs. The massive and submassive *Porites, Echinopora, Favia* and *Platygyra* show different responses in absolute coral cover to the bleaching event and also in recovery rates (Fig. 8B). *Echinopora, Favia* and *Platygyra* declined in abundance after 1998 and have recovered on both protected and un-protected reefs, all with a higher abundance on protected reefs. Massive *Porites* increased in abundance during 1998 on both protected and un-protected reefs and has since then remained high in abundance, with a higher abundance on protected reefs.

A)



B)

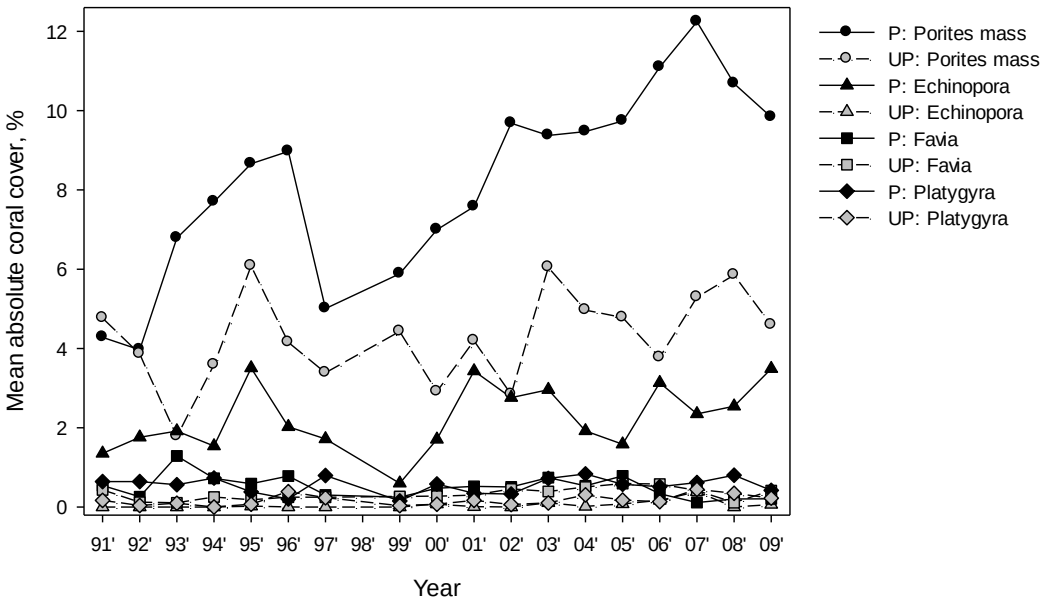


Fig. 8. Time series of mean absolute coral cover on protected (Mombasa, Watamu and Malindi MNP) and un-protected reefs (Diani, Kanamai, Vipingo and RasIwatine) with A) representing branching/encrusting *Acropora, Montipora, Porites* and *Pocillopora* and B) massive/submassive *Porites, Echinopora, Favia* and *Platygyra*. Black symbols and solid lines represent protected reefs (P) and grey symbols and dashed lines represent un-protected reefs (UP).

Kenya's un-protected reefs have much lower abundance of *Acropora,* possibly due to coral collection and trampling by fishermen (McClanahan & Mutere 1994, McClanahan *et al.* 1996, Mangi & Roberts 2006). The protected reefs have a high abundance and biomass of fish compared to heavily fished reefs (McClanahan & Arthur, 2001) and predation by corallivores is one possible explanation for why branching *Porites, Acropora* and *Montipora* have lower recovery on protected compared to un-protected reefs. Predators can influence diversity and structure of communities in a variety of ways (Almany 2003, Addicott 1974, Kelley *et al.* 2003) e.g. by consuming the most abundant prey (keystone predator) and thereby allowing existence of less compatible species (Estes & Duggings, 1995) or by selective predation; consuming a prey not necessarily most abundant (Saage *et al.*, 2009). Feeding selectivity can consequently have negative effect on preferred species, especially if the abundance of the species is already low. McClanahan *et al.* (2005) showed that *B. undulatus* and *Chlorurus strongylocephalus* limited the growth and survival of 4 genera of experimental coral transplants; *Pavona*, branching *Porites*, massive *Porites* and *Pocillopora*. Evidence of selectivity for branching *Porites* was also detected. The fact that branching *Porites* and *Montipora* are selected is likely to explain the pattern that the genera have recovered slower on protected reefs. Remarkably, *Montipora* showed the highest incidence of grazing scars and furthermore the electivity index value indicates that *Montipora* is highly preferred by predators, suggesting that corallivores might limit the abundance and recovery of the genus. This high electivity score is likely influenced by the extremely low abundances of *Montipora* recorded in Malindi MNP. Since the total loss of surface area was 3.9 % for all coral transplants, the predation pressure of the preferred coral genera (i.e. *Montipora* and branching *Porites*) is possibly higher in natural communities. In this study *Pocillopora* and *Echinopora* were not preferred by predators (-0.08 and -0.19 respectively) and this may explain why these genera are more common on protected reefs. Electivity values of massive *Porites, Favia* and *Platygyra* indicated strong avoidance and this may also explain why these genera are more common and/or recover faster within marine reserves. Even though *Acropora* showed a high percentage of infested colonies the variance in electivity values were large (Fig. 7) and the resulting mean value (E_i = 0.32) did not indicate

strong selection. The reason why this genus has not recovered on protected reefs remains unclear. Low growth rates or limitation by other factors are areas of future research.

In contrary to my prediction, I did not observe any species of Scaridae feeding on hard corals during my feeding observations, though observations did confirm corallivory within the family Chaetodontidae (Pratchett, 2005, Rotjan & Lewis, 2008). *C. trifasciatus* is an obligate corallivore (feed exclusively on living coral) and *C. lunula, C. auriga* and *C. falcula* are all consuming a mixed diet including various amount of hard and soft corals (Rotjan & Lewis, 2008). Since these species are only consuming coral tissue and mucus (Rotjan & Lewis, 2008), it is unlikely that this group stands for the observed amount of loss in coral skeleton. McClanahan *et al.* (2005) also showed that corallivores of Chaetodontidae species are of minor importance to coral survival compared to larger predators such as Balistidae, Scaridae and the starfish *Acanthaster planci*. Particularly large individuals of Scaridae and particularly males are more commonly observed feeding on corals (McClanahan, 2002). Only 13 of the studied individuals of Scaridae in the feeding study were males (total n = 34) which might explain that we observed female Scaridae predominantly feeding on turf. However, larger fishes can consume live coral occasionally (personal observations of Balistidae (i.e. *Sufflamen chrysopterus, B. undulatus*) and Scaridae (i.e. *S. niger, S. tricolor*)). Predation events are rare (Rotjan & Lewis, 2006) and it seems to be difficult to quantify feeding preferences of corallivores using behavioral observations. Therefore it is possible that the grazing quantifications may give a better representation of overall grazing pressure. *S. frenatus, S. sordidus, C. carolinus* and *B. undulatus* are the most abundant species on the studied site. These species have all been reported to consume live coral tissue, with *B. undulatus* and *C. sordidus* also removing coral skeleton in the African-Indian Ocean regions (Rotjan & Lewis, 2008). *S. frenatus* has also been recorded to consume coral skeleton but has not yet been studied in other regions but the Indo-pacific (Hoey & Bellwood, 2008). The high abundance of corallivores, on average 20 individuals/250 m^2, makes it possible to believe that these species could have an impact of corals in Malindi MNP, although I was not able to observe direct consumption.

Although there was a significant difference between the treatments in the predator exclusion experiment, variation within each genus was large and I did not find any significant differences between genera. One possible explanation could be that the coral transplants exposed to fish constituted of a too small part of the total area and number of colonies in the whole area to attract corallivores. This in combination with a low treatment replication (n = 4-7) may have limited the statistical power required to detect a significant difference.

Coral reefs have low growth rates and as severe coral bleaching events are predicted to be more common within the next 20 years (Hoegh-Guldberg, 1999), understanding of recovery and growth after disturbances is becoming increasingly important. Studies focusing on coral recovery, such as this, are very important to identify factors driving changes in the abundance of corals and to make appropriate action to restore high diversity in communities. If selective corallivory limits the recovery of predator-preferred coral species, caging of new recruits and/or transplants could be a successful management strategy to allow these species to establish on reefs with high abundance of corallivores. Coral transplantation has been developed to restore degraded coral reef habitats and successful restoration efforts have been proven to increase diversity and abundance of corals, fish and invertebrate species (Yap, 2009).

Branching *Porites* is still abundant on the reefs in Kenya even though it is a preferred genus. This suggests that different species are not equally sensitive to predators and/or that other factors such life-history characteristics of growth rates, generation time and reproductive mode can also affect coral distribution and abundance. Management strategies should not be general but are suggested to be selected based on important factors affecting coral growth such as life-history and predation sensitivity. Even though it is difficult to identify

the exact mechanisms leading to coral decline, this study has enabled a better understanding of recovery patterns of certain coral species on protected and unprotected coral reefs in Kenya. Grazing selectivity was also reflected on coral growth form, as branching species were significantly selected over massive corals. Another study investigating the coral eating snail (*Drupella cornus*) has also demonstrated preference for branching coral forms in Kenya (McClanahan, 1997). More studies on growth and recovery rates from invertbrate and fish grazing are needed to pinpoint the effects of grazing on corals. It could be important in further coral preference studies to examine the predation effect on coral growth forms on a more evolutionary level, relating to adaptations. A recent study has shown that fish predation determines growth form of Caribbean coral reef sponge (*Mycale laevis*) (Loh & Pawlik, 2009). The grazing pattern between thick branching corals (e.g. *P. verrucosa*) and thinner branching corals (e.g. *P. damicornis*) and their distribution on fished and un-fished reefs is an interesting area for further investigation.

The combination of low abundance, the high percentage of grazed colonies, high electivity index value and the high abundance of coral eating fishes suggests that predators may be limiting the recovery of *Montipora* in Malindi MNP. Corallivores on the Kenyan reefs and on other reefs in the Indian Pacific can limit the recovery of *Montipora* and perhaps other rare, predation-sensitive coral genera.

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