

Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks

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Abstract

The red-lined triggerfish (*Balistapus undulatus*) is a major predator of sea urchins and the loss of this species, along with other less influential sea urchin predators, has resulted in the proliferation of sea urchin populations on the coral reefs of East Africa. I studied the recovery of *B. undulatus* and the associated demise in their sea urchin prey in five Marine Protected Areas (MPAs) which differed in their age, such that the data collected spanned a 30-year range in the age of protection. Results suggest that predation on sea urchins and *B. undulatus* dominance recovered on a time scale of 5–10 years, but sea urchin populations were not reduced below 1000 kg/ha for more than 10 years, and *B. undulatus* populations may require > 30 years to recover. In a new MPA, *B. undulatus* competitively excluded a subordinate wrasse predator, *Cheilinus trilobatus*, at baited sites in < 8 years. A second triggerfish, *Balistoides viridescens*, was the competitive dominant to *B. undulatus* in direct interference interactions, but *B. viridescens* was not found in 2.7 ha of sampling and rarely seen eating sea urchins at baited sites. An even longer estimate of top predator recovery would occur if *B. viridescens* is the dominant sea urchin predator. This study suggests that short and temporary closures of < 10 years will not fully restore reef ecology, and that fully protected and permanent MPAs are a necessary part of coral reef conservation programs. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Predators at or near the top of ecological food webs are of special concern to conservation because they can influence the ecological state, process and diversity of their ecosystems. Severe reductions or losses of their populations can, therefore, have cascading influences on ecosystems (Steneck, 1998). For example, the ecology of East African coral reefs is greatly influenced by the relationship between sea urchins, their predators, and fishing of these sea urchin predators (McClanahan, 1995a; McClanahan et al., 1995, 1999). Dominant sea urchin predators are finfishes in the triggerfish (Balistidae), wrasse (Labridae) and emperor (Lethrinidae) families with snails, starfishes and other invertebrates being of lesser importance (McClanahan and Muthiga, 1989; McClanahan, 1995b). The red-lined triggerfish (*Balistapus*

undulatus) has been shown to be the dominant predator in Kenyan marine protected areas (MPAs) often eating, in experiments, >75% of Kenya's numerically and competitive dominant sea urchin *Echinometra mathaei* (McClanahan, 1995b, 1998). Consequently, I have suggested that *B. undulatus* is a keystone predator because it appears to be the most important predator among a suite of predators that control the populations of sea urchins (McClanahan, 1995b, 2000). Sea urchin abundance, in turn, influences reef ecology including coral and algae interactions, the abundance of other grazers, and erosion of reef substratum (McClanahan, 1995a; McClanahan et al., 1995; Eakin, 1996). Maintaining reef ecology undisturbed by fishing may, therefore, depend on the relationship between levels of fishing on *B. undulatus* and, in the case of MPAs, on the rate of recovery of *B. undulatus* from fishing (McClanahan et al., 1999).

Marine protected areas, fisheries reserves or other types of closed area management are management tools used to conserve fisheries and natural resources (Roberts and Polunin, 1993; Bohnsack and Ault, 1996; Allison et

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al., 1998). Ecosystem and species management of closed areas may be permanent or rotated with periods of resource use followed by closures and ecological recovery. Deciding among management options and predicting the period of recovery requires knowing the rates of recovery of important species and their successional ecology. In East Africa, the recovery rate of *B. undulatus* from fishing and the associated reduction in their sea urchin prey are important ecological variables for planning MPA recovery or fishery reserves or reef management closure and recovery plans.

This study explores the recovery of *B. undulatus* in East Africa's MPAs, the potential influence of this predator on predation intensity and subsequent sea urchin abundance and the interactions between *B. undulatus* and other predatory species in five MPAs of East Africa. These MPAs compositely had a 30-year range in the time since their closure to fishing (Table 1). I studied *B. undulatus*, other triggerfish and wrasse species which feed on sea urchins, their abundance, feeding and interspecific competitive behavior in these parks and unprotected reefs. Additionally, the abundance of sea urchins and predation intensity were measured annually in a new park over an 8-year period and less periodically in four additional parks. I hypothesized that the elapsed time since the exclusion of fishing would be a dominant factor in predicting the abundance of sea urchin predators, their interspecific interactions, and the abundance of their prey.

2. Methods

2.1. Study sites

Observations and field measurements were made in the five fully protected MPAs of East Africa which include Malindi, Watamu, Mombasa, Kisite and Chumbe Marine Parks (Table 1) and four unprotected areas which included Vipingo, Kanamai, Ras Iwatine and Diani. These reefs differ geomorphologically in being platform, fringing and rock island reefs but share species common to the East African region (Smith and Heemstra, 1986). Study sites were similar in being shallow-water reefs (< 3 m deep at low tide) and having a high abundance

and diversity of corals and fishes. Measurements were made between 1991 and January 1999. Measurements were most frequently made in four sites in Mombasa and one site in Malindi followed by Kisite, Watamu and Chumbe protected areas. These MPAs eliminated fishing between 1968 (Malindi MNP) and 1993 (Chumbe) which allowed comparison of *B. undulatus*, predation and sea urchin populations over ~30 year range of protection. Data from the four unprotected reefs were pooled and given a value of zero for the age of protection.

2.2. Field measurements

Population measurements included estimates of triggerfish, predatory wrasses, and sea urchin population densities. Triggerfish and wrasses were identified to species and counted in three to four 100×5 m belt transects established in each of the study sites during each sampling period (McClanahan, 1994). A total of 54 belt transects were completed during the eight-year study. Sea urchins were identified to species and counted in nine to 18 10 m² circular quadrats per site. Estimates of sea urchin wet weights were estimated by multiplying the average weight wet (McClanahan et al., 1999) of each species by their population density and summing the weight of each species to obtain a total sea urchin wet weight.

An estimate of predation intensity on sea urchins at each site was made by tethering 30–60 individuals of the sea urchin *Echinometra mathaei*. Experimental sea urchins were pierced with a hypodermic needle, threaded with monofilament fishing line and tied to nylon lines attached to the reef (McClanahan and Muthiga, 1989). Tethered urchins were visited daily for three days and the last day that an urchin was seen alive on the tether was recorded for three consecutive days. A measure of predation intensity, the Predation Index (PI), was calculated as $PI = (3-S)/3$ where *S* was the last day the urchin was observed alive (McClanahan, 1998). Sea urchin wet weights, *B. undulatus* abundance and the Predation Index were plotted against the age of the protected areas and the unprotected reefs given an age of zero.

Predator identification and competitive interactions among predators were made by baiting sites with the sea urchin *E. mathaei*. Whole adult *E. mathaei* (test lengths

Table 1

Description of study sites, measurements, sampling dates and measurements. Kenya's national parks are government parks while Chumbe Island is a privately leased park

	Malindi MNP	Watamu MNP	Mombasa MNP	Kisite MNP	Chumbe Island Coral Reef Park
Year fishing restricted	1968	1972	1991	1973	1993
Reef type	Platform reef	Reef outcrop	Fringing Reef	Platform reef	Rock Island Reef
Reef location	Lagoon	Lagoon	Back-reef lagoon	Back-reef lagoon	Reef edge
Sampling periods	1987–1998	1987–1999	1991–1999	1992–1993	1997

between 1.5–6.5 cm) were collected from reef platforms or rocky shores near the study sites and kept in a floating bucket. At a variety of sites in each reef a small number of urchins (4–15) were placed on the ground. The observer then hid behind a coral head or floated on the surface at a distance of 5–10 m from the baited area. In some cases the time spent observing was reduced by tossing one or two urchins from the surface towards the baited site as the splash and sinking frequently attracted predators and scavengers. A minimum of three different baited sites were studied in each of the MPAs per sampling period. This technique was unsuccessful in the unprotected reefs because no predators were observed eating the sea urchin bait after more than 2 h of observation.

The observer recorded the number of individuals of each species of predator that killed and opened whole *E. mathaei* (using the nomenclature of Smith and Heemstra, 1986). A total of 273 observations of predation were made during the 8 years of this study. In some cases, predators carried the urchin into a crevice and the observer later examined these crevices for carcasses to confirm that the urchins had been eaten. Studies in each area required a minimum of 12 observations of predation for calculating the percentage of predators. In the Mombasa MNP I studied five sites in the same location (Mombasa 4) every year between November and January and plotted the frequency of observed predators with time.

Interactions between and among species at the baited area were recorded. In most cases one individual attacked and displaced another from the baited area and the species and sex of the aggressor and aggrieved were recorded. Male *B. undulatus* were distinguished from females in that males were larger than females. Terminal-male wrasses were distinguished from females: coloration was used as the distinguishing characteristic in the genus *Coris* and caudal and dorsal fin extensions for the genus *Cheilinus* (Smith and Heemstra, 1986).

3. Results

Scatter plots of the Predation Index and the wet weight of sea urchins against time indicate that predation on sea urchins is variable for new parks, but increases during the first 10 years of protection and then levels out, but does not entirely stop rising at the 30-year period of our data set (Fig. 1a). Sea urchin wet weights decrease rapidly during the initial stages of park protection but are probably not reduced below 1000 kg/ha until after 10 years of protection (Fig. 1b). A plot of the density of *B. undulatus* with the age of protection is variable but rises in a straight-line manner with no indication of levelling in population densities up to the 30-year limit of the data (Fig. 2). *B. undulatus* is about twice as abundant as the two next most abundant predators, *Coris formosa*

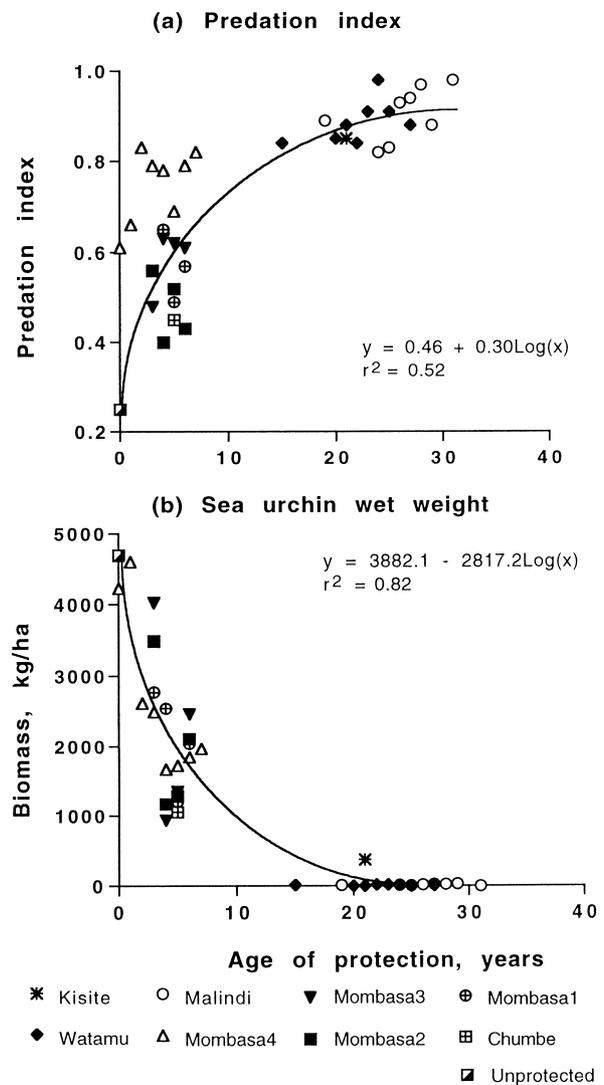


Fig. 1. The relationship between the age of the five MPAs and (a) the Predation Index on tethered *Echinometra mathaei* and (b) the wet weight estimates of all sea urchin species. The equation for (a) is $y = 0.23 + 0.48\log(x)$; $r^2 = 0.86$ if the Mombasa 4 data is removed.

and *Cheilinus trilobatus* (Table 2). *Pseudobalistes fuscus* was seldom seen while *Balistoides viridescens* was not seen in the 2.7 ha sampled area (Table 2).

Plots of the frequency of observations of different predators eating baited *E. mathaei* in the Mombasa park between 1993 and 1998 (Fig. 3) showed that the wrasse *Cheilinus trilobatus* was the dominant predator in the early stages of the park, but their frequency at baited sites consistently decreased over time. In contrast the frequency of *B. undulatus* predation increased from 20 to 100% of the observations during the 7-year interval. The *Coris* wrasses (largely *C. formosa*) increased during the first 3 years and then decreased during the last 3 years, while lethrinids were seldom observed eating *E. mathaei* and showed no trend with time. Plotting the percentage of *B. undulatus* predation with time since protection (Fig. 4a) and with the actual observation

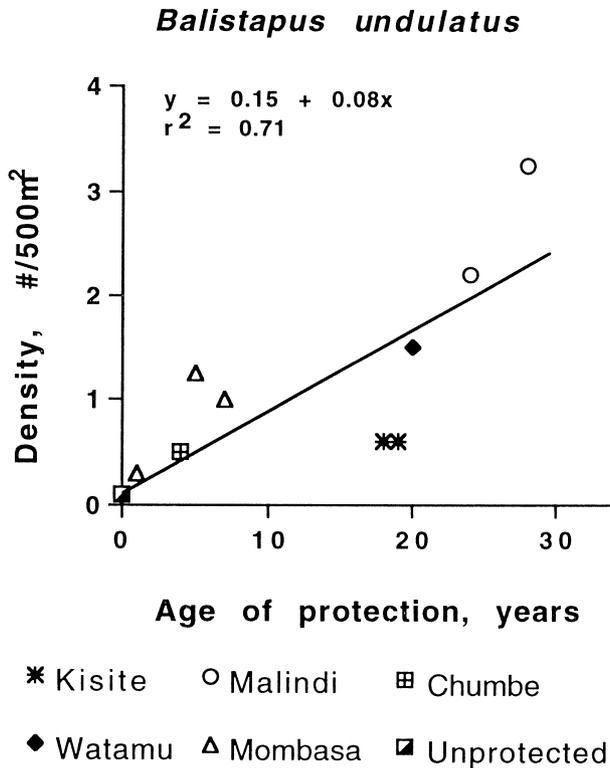


Fig. 2. Scatter-plot relationship between the age of the five MPAs with population density estimates of *Balistapus undulatus* during census periods.

Table 2

Population densities (No./500 m²) of triggerfish and wrasses that predate on sea urchins in the marine protected areas of East Africa. Based on 54 500 m² transects in the five MPAs of East Africa

Predatory species	\bar{x}	S.D.
<i>Balistapus undulatus</i>	0.94	1.12
<i>Coris formosa</i>	0.35	0.70
<i>Cheilinus trilobatus</i>	0.28	0.49
<i>Coris gaimardi africana</i>	0.22	0.46
<i>Coris aygula</i>	0.11	0.32
<i>Pseudobalistes fuscus</i>	0.09	0.40
<i>Balistoides viridescens</i>	0.00	0.00

date (Fig. 4b) indicate that predation by *B. undulatus* has increased very rapidly in the new Mombasa MNP compared to the older parks. The older parks do, however, show a rise in *B. undulatus* dominance in predation from around 75–95% of the total observed predation events.

Interspecific observations at baited sites (Fig. 5) indicate that *B. undulatus* is the most common predator (Fig. 5a), comprising 82% of the 273 predation observations, and also the species with the most competitive interactions (Fig. 5b). *B. undulatus* was involved in 42 of the 55 interspecific competitive interactions and was the superior in all interactions except for the four interactions with *Balistoides viridescens* (Titan triggerfish). *B. viridescens* and the other triggerfish predator, *Pseudo-*

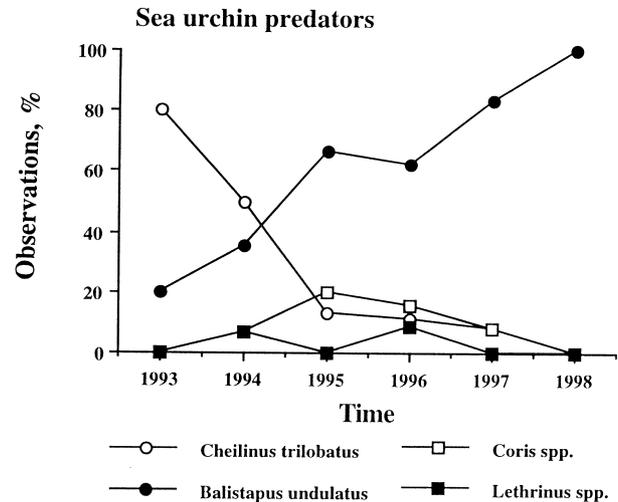


Fig. 3. Time series plot of the predator observations at baited sites in the Mombasa MNP which closed fishing in 1991. Each point represents 12–35 observations.

balistes fuscus, were not frequently seen eating at the baited sites, together eating <2% of the experimental urchins, or interacting with other predators. The wrasses *Coris formosa*, *Cheilinus trilobatus*, *Coris aygula* and *Coris gaimardi africana* were observed eating 14% of the urchins with *C. formosa* and *C. trilobatus* being the dominant wrasse predators. Ten interactions were observed among wrasses and these observations suggest that *C. formosa* was the most competitively interactive species, but the less interactive *C. trilobatus* won all observed aggressive interactions. Observations suggest that the outcome of the wrasse–wrasse interactions were, however, not entirely predictable based on species, but, like *B. undulatus*, terminal males frequently displaced females regardless of species. Species of lethinids were the least commonly observed predators, eating <3% of the urchins, and were also subordinate in all interspecific interactions.

4. Discussion

4.1. Species interactions

It is clear that *Balistapus undulatus* plays a dominant role, both competitively and numerically, on the predation of sea urchins, particularly *Echinometra mathaei*. Despite the high frequency of agonistic interactions by *B. undulatus*, the less common *Balistoides viridescens* is the competitive dominant in direct interactions. *B. viridescens* was not seen in relation censuses and when seen at baited sites it was usually solitary, moving, and not associated with the opposite sex, a nest, or an obvious territory. When seen feeding apart from baited sites, it was often consuming starfish or sea urchins in the Diademidae (personal observation). *B. viridescens*

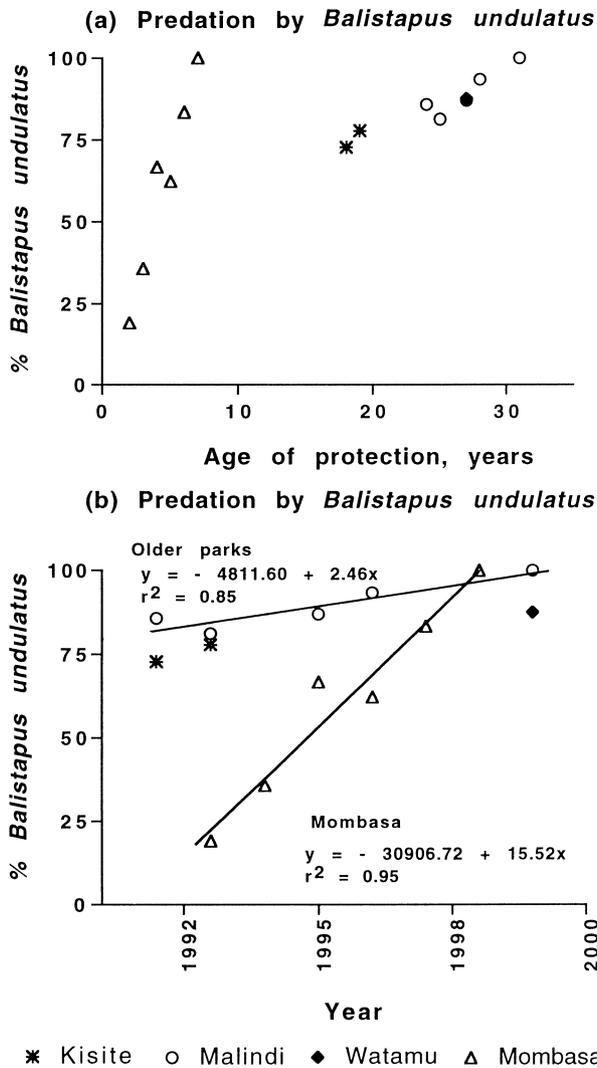


Fig. 4. Plots of the percentage of *Balistapus undulatus* predation on the sea urchin *Echinometra mathaei* at baited sites in the studied parks. Data plotted as (a) the age of the park and (b) the year of the observations. Data in (b) separate the new Mombasa MNP from the older parks for regression statistics.

also appears to have one of the most rudimentary of triggerfish egg nests and may not breed, like many triggerfish, in permanent pairs, leks or harems (Fricke, 1980; Gladstone, 1994) but few published studies or observations on this species are available. Although *B. undulatus* was subordinate to *B. viridescens* in the agonistic interactions, *B. undulatus* did, by far, eat the most *E. mathaei* and successfully defended its prey most often against other predators and scavengers. Consequently, *B. undulatus* is the most common sea urchin predator, while not the dominant interference competitor.

The top interference competitor among the wrasses appeared to be *Cheilinus trilobatus*, which was only numerically dominant to *B. undulatus* at baited sites during the first 3 years after the Mombasa park's formation. It was not seen eating sea urchins in the older parks or

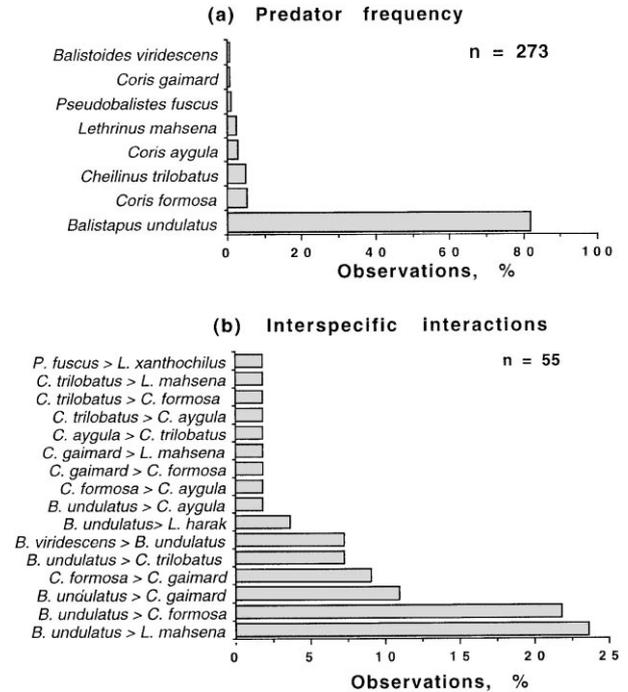


Fig. 5. (a) Frequency of observed predation by predatory species and (b) outcome of interspecific competition (displacement or chasing = >) interactions at the baited sites. One species was considered superior (>) if it chased or displaced another.

in Mombasa after the seventh year of protection. A combination of species interaction observations and their change over time in Mombasa MNP suggest that *B. undulatus* is the slow colonizing species but competitively dominant, and *C. trilobatus* the fast colonizing but subordinate species. Coexistence among this guild of predators may, therefore, be partly attributable to species-level trade offs where the competitive dominance of species is inversely related to the recovery time of species after a disturbance (Tilman, 1988, 1990). I did, however, see *C. trilobatus* temporarily entering undefended *B. undulatus* territories and feeding on their eggs, so complex interactions between these two species may be possible.

This is one of the first long-term studies to show an asymmetrical successional species interaction in coral reef fish population, which many have suggested to be more dependent on the timing and spatial distribution of settlers rather than on deterministic competitive interactions (Doherty and Williams, 1988; Sale, 1991; Doherty and Fowler, 1994). My observations suggest that species interactions and relationships may not always be hierarchical and deterministic based on species alone as terminal males often dominated female wrasses, irrespective of species. Among the wrasse and lethrinid species, there were not enough observations of all possible terminal-male interactions and other species-sex combinations to develop or fully understand the interspecific competitive organization of the wrasse guild.

Species in the genus *Coris* were competitively subordinate to *C. trilobatus*, but showed more predation during the transition from *C. trilobatus* to *B. undulatus* dominance at the baited sites and not a straight reduction over time, which would be the prediction for the most subordinate species. It should be appreciated that *C. formosa* and other *Coris* wrasses are scavengers of *E. mathaei* carcasses (McClanahan, 1995a) and triggerfish eggs, and may, therefore, often scavenge carcasses or eggs left undefended by *B. undulatus*. Some of the observed agonistic interactions could, therefore, be construed as a weak predator/scavenger attracting a stronger predator in order to increase the possibility of getting some scraps or distracting it with prey, in order to feed on the predator's undefended eggs, or both. *Coris* species were probably competitively superior to lethrinids but these groups were infrequently seen agonistically interacting. *Coris* wrasses and lethrinids may be the most common predators in heavily fished East African reefs as these species are a common part of the catch while balistids are uncommonly caught in mature coral reef fishing grounds (personal observation).

4.2. Recovery time

The data were variable, but there appeared to be a lag between the various peaks or stabilizing points of the various measures of predation including sea urchin abundance, *B. undulatus* dominance, the Predation Index and population abundance in this study. The Predation Index recovered most quickly followed by *B. undulatus* dominance, the demise of sea urchins, and lastly *B. undulatus* population densities. The Predation Index was quite variable within the first 10 years of protection varying between 0.4 and 0.85, but after 9 years of protection, all sites were above 0.80 and suggested a slight increase during the latter 10–30-year period. Sea urchin wet weights were not below 1000 kg/ha for any sites < 9 years old, and the reduction of sea urchins by their predators may, therefore, require periods in excess of 10 years, but probably < 17 years. In the Mombasa MNP study sites, dominance of predation on *E. mathaei* by *B. undulatus* was complete in < 8 years, despite the fact that *B. undulatus* population densities were half those of the oldest park, Malindi MNP. Consequently, the recovery time of reefs from heavy fishing disturbances may depend on the objectives of management, recovery of *B. undulatus* dominance and reduction on small sea urchins, on the scale of 5–10 years, reduction in sea urchins on the scale of 10–15 years, and recovery of *B. undulatus* populations on a scale greater > 15 years.

The above conclusions assume that there were not large site, poaching or habitat differences in the different MPAs that I studied or that they had a greater influence on the data than the temporal trajectories of recovery suggested by the scatter plots with the age of MPAs.

This study, like most large-scale ecological studies of MPAs, is not abundantly replicated in space, with a total of only five parks, only two recent parks, a lack of sites for park ages between 9 and 17 years, and the likely possibility that perfect management is not achieved (Muthiga et al., 2000). These weaknesses are unavoidable, as these MPAs, represent all the functioning MPAs in East Africa. Census data and observations in the recovering Mombasa MNP indicate that the area I studied when baiting *E. mathaei* (Mombasa 4) had the fastest recovery rates of *B. undulatus* compared to other areas in the park. This is probably due to the sites nearness to the centre of the park, the occurrence of a shallow tidal channel connecting the lagoon and deeper reef edge, a high relief and abundance of corals and particularly large massive *Porites* that were often the location of *B. undulatus* dens. Consequently, I suggest that the recovery of *B. undulatus* was near the maximum rate in this area and probably indicates an upper limit to recovery for this species.

Despite the fast recovery of *B. undulatus* at the Mombasa site 4 there were still abundant *Echinothrix diadema* that, despite the demise of most other species of sea urchin, changed little from the opening of the park (McClanahan, T. unpublished data). *E. diadema* is among the most resistant sea urchins to predation (McClanahan, 1998) and it may be that *B. undulatus* and other predators select less well-defended prey in the early stages of their population recovery. Sites dominated by less predator-resistant sea urchins should recover more quickly. An additional limitation is that the Predation Index is only a relative measure of predation and is dependent on the sea urchin species used in the experiments. *E. mathaei* is one of the most predator-susceptible sea urchins and will, therefore, not be able to distinguish predation intensity at the highest levels of predation, as may be expected in MPAs (McClanahan, 1998).

The lack of saturation in *B. undulatus* with the age of the MPAs may indicate that *B. undulatus* never reached its maximum population density before 30 years. The most likely alternative explanation is that site differences and their suitability to *B. undulatus* produced this pattern. Observations of *B. undulatus* behaviour and movements during this study suggest that male-female pairs regularly patrol and defend areas on the order of 100–200 m² (Kiambo, R. and McClanahan, T. unpublished data). Consequently, a population density of > 5 individuals/500 m² may be the expected carrying capacity of this species, where habitat and environmental conditions are appropriate. The present average population of one *B. undulatus* per 500 m² overall and a maximum of ca 2.7 per 500 m² in Malindi suggests that MPAs still have the potential for greater *B. undulatus* populations. Further studies on *B. undulatus* territory size, habitat associations and food requirements will be needed to improve predictions for their population

numbers in time and space, but our data and observations suggest populations short of carrying capacity in MPAs.

The low population densities of *B. undulatus* in the Kisite MNP compared to Malindi may be habitat or resource limitations or difficulties in accurately counting *B. undulatus*. It should be appreciated that *B. undulatus* are often found hiding in dens or burrows, and this behavior may make accurate censusing of these species difficult and result in underestimates of population sizes in some of the MPAs. Alternatively, sea urchin predators may have slow recovery times and even after 30 years of protection these parks may not have reached their limits to colonization and growth. For example, there is a possibility that *B. viridescens* or another slow-colonizing predator have not recovered to levels where they are common enough to dominate *B. undulatus* and predation at baited sites. The very large humphead wrasse (*Cheilinus undulatus*) is another possibility for top predator as it is a very large and likely sea urchin predator that is present in the region. Nonetheless, terminal males are very uncommon in either fished or MPA reefs and were never observed eating the baited urchins. If this is the case, than there may still be further serial species replacements among the sea urchin predators, in which case the recovery time of reefs from heavy fishing may even exceed 30 years. It may also be that low but chronic levels of poaching are affecting population densities and the recovery rate of these MPAs.

This study suggests that the complete recovery of coral reef ecology after heavy fishing can be slow to the order of 5 to, perhaps, > 30 years depending on the measure of recovery. Ecological functions like predation appeared to recover faster than species or community ecology factors such as sea urchin dominance or the recovery of the dominant predatory species. Temporary closures of coral reefs from fishing may result in rapid increases in the numbers and sizes of many of the fished species (Roberts, 1995; McClanahan and Kaunda-Arara, 1996; Russ and Alcala, 1998) and even in indirect factors such as coral cover and the calcium carbonate balance (McClanahan and Mutere, 1994), but this study suggests that the recovery time of some critical species may be considerably slower. Common to many ecosystems, the recovery of ecological processes, such as productivity and predation, and gross trophic groups may be considerably faster than recovery of certain key, slow growing, colonizing or competitively dominant species. Studies that focus on processes or gross trophic recovery can give the false impression that ecological succession and recovery are complete and that human or other disturbances can be relatively frequent and still maintain biological diversity or ecosystems in a state largely undisturbed by humans. This impression can encourage and justify a management policy that maintains frequent to moderate human disturbances. This study

suggests that short and temporary fisheries closures may be useful for the management of fisheries and ecosystem functions, but are less valuable for conserving important species and undisturbed reef ecology. Permanent MPAs or areas permanently closed to resource extraction are, therefore, a necessary part of the management of biological diversity and coral reef ecosystems.

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References

- Allison, G.W., Lubchenco, J., Carr, M.H., 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* 8, S79–S92.
- Bohnsack, J.A., Ault, J.S., 1996. Management strategies to conserve marine biodiversity. *Oceanography* 9, 73–82.
- Doherty, P., Fowler, T., 1994. An empirical test of recruitment limitation in a coral reef fish. *Science* 263, 935–939.
- Doherty, P.J., Williams, D.M., 1988. The replenishment of coral reef fish populations. *Oceanography and Marine Biology Annual Review* 26, 487–551.
- Eakin, C.M., 1996. Where have all the carbonates gone. A model comparison of carbonate budgets before and after the 1982–1983 El Niño at Uva Island in the eastern Pacific? *Coral Reefs* 15, 109–120.
- Fricke, H.W., 1980. Mating systems, maternal and biparental care in triggerfish (Balistidae). *Zeitschrift für Tierpsychologica* 53, 102–122.
- Gladstone, W., 1994. Lek-like spawning, parental care and mating periodicity of the triggerfish *Pseudobalistes flavimarginatus* (Balistidae). *Environmental Biology of Fishes* 39, 249–257.
- McClanahan, T.R., 1994. Kenyan coral reef lagoon fish: effects of fishing substrate complexity, and sea urchin. *Coral Reefs* 13, 231–241.
- McClanahan, T.R., 1995a. A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. *Ecological Modelling* 80, 1–19.
- McClanahan, T.R., 1995b. Fish predators and scavengers of the sea urchin *Echinometra mathaei* in Kenyan coral-reef marine parks. *Environmental Biology of Fishes* 43, 187–193.
- McClanahan, T.R., 1998. Predation and the distribution and abundance of tropical sea urchin populations. *Journal of Experimental Marine Biology and Ecology* 221, 231–255.
- McClanahan, T.R., 2000. Coral reef use and conservation. In: McClanahan, T.R., Sheppard, C.R.C., Obura, D.O. (Eds.), *Coral Reefs of the Indian Ocean: Their Ecology and Conservation*. Oxford University Press, New York, pp. 39–80.
- McClanahan, T.R., Kamukuru, A.T., Muthiga, N.A., Gilgaber Yebio, M., Obura, D., 1995. Effect of sea urchin reductions on algae, coral and fish populations. *Conservation Biology* 10, 136–154.
- McClanahan, T.R., Kaunda-Arara, B., 1996. Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology* 10, 1187–1199.

- McClanahan, T.R., Mutere, J.C., 1994. Coral and sea urchin assemblage structure and interrelationships in Kenyan reef lagoons. *Hydrobiologia* 286, 109–124.
- McClanahan, T.R., Muthiga, N.A., 1989. Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. *Journal of Experimental Marine Biology and Ecology* 126, 77–94.
- McClanahan, T.R., Muthiga, N.A., Kamukuru, A.T., Machano, H., Kiambo, R., 1999. The effects of marine parks and fishing on the coral reefs of northern Tanzania. *Biological Conservation* 89, 161–182.
- Muthiga, N.A., Riedmiller, S., van der Elst, R., Mann-Lang, J., Horrill, C., McClanahan, T.R., Carter, E., 2000. Management status and case studies. In: McClanahan, T.R., Sheppard, C.S., Obura, D. (Eds.), *Coral Reefs of the Indian Ocean: Their Ecology and Conservation*. Oxford University Press, New York, pp. 473–505.
- Roberts, C.M., 1995. Rapid build-up of fish biomass in a Caribbean marine reserve. *Conservation Biology* 9, 815–826.
- Roberts, C.M., Polunin, N.V.C., 1993. Marine reserves: simple solutions to managing complex fisheries? *Ambio* 22, 363–368.
- Russ, G.R., Alcala, A.C., 1998. Natural fishing experiments in marine reserves 1983–1993: community and trophic responses. *Coral Reefs* 17, 383–397.
- Sale, P.F., 1991. Reef fish communities: open nonequilibrium systems. In: Sale, P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, pp. 564–598.
- Smith, M.M., Heemstra, P.C., 1986. *Smiths' Sea Fishes*. Springer-Verlag, New York.
- Steneck, R.S., 1998. Human influences on coastal ecosystems: does overfishing create trophic cascades? *Trends in Ecology and Evolution* 13, 429–430.
- Tilman, D., 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, New Jersey.
- Tilman, D., 1990. Constraints and tradeoffs: towards a predictive theory of competition and succession. *Oikos* 58, 3–15.