



How effective are MPAs? Predation control and 'spill-in effects' in seagrass–coral reef lagoons under contrasting fishery management

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ABSTRACT: Marine protected areas (MPAs) are heavily promoted as a panacea for marine conservation, but lagging and sometimes idiosyncratic protection effects bring their overall effectiveness into question. In Kenyan lagoons, seagrass overgrazing by the sea urchin *Tripneustes gratilla* has been linked to removal of predators, but overgrazing has also been observed within well-protected MPAs. In this study we investigated the effectiveness of Kenyan MPAs in facilitating predation control over sea urchins, particularly *T. gratilla*, in relation to system (seagrass or coral reef), distance to reefs, and seagrass presence. A strong protection effect on urchin densities on reefs and a negative correlation between *T. gratilla* density and predation pressure (from sea stars, fish and gastropods) in seagrass beds ($r^2 = 0.345$) confirmed the importance of top-down control. Yet there were no clear effects of protection or distance to reefs in seagrass beds, most likely due to (1) low predator densities in the recently established Mombasa MPA; (2) 'spill-in' of aggregated *T. gratilla* into the older Watamu MPA (potentially facilitated by low predation pressure on the large urchins and nutrient enrichment); and (3) a potential buffering effect of seagrass canopies on predation, regardless of distance to reefs. Effects of seagrass presence differed between areas, but indicated that overgrazing in some areas could be self-regulated by inducing higher urchin mortality. As MPA effects appear to be system-, time- and site-specific, managers should also assess other more holistic approaches (e.g. banned fishing of urchin predators and reduced nutrient input from land runoff) to protect seagrasses.

KEY WORDS: Marine protected areas · Indirect effects · Trophic cascades · Seagrass · *Tripneustes gratilla* · *Thalassodendron ciliatum* · Kenya · Shelter

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INTRODUCTION

Coastal fisheries supply a crucial food source for humans, but have frequently been found to drive depletion of target and non-target species, weaken trophic cascades, and indirectly cause community shifts associated with reduced ecosystem functioning (Jennings & Kaiser 1998, Pinnegar et al. 2000, Jackson et al. 2001). Consequently, implementation of marine protected areas (MPAs) has become heavily promoted as a global man-

agement 'panacea' (e.g. Kelleher & Kenchington 1992, Agardy 1994, NRC 2001). MPAs can indeed provide a number of benefits, e.g. protection of target stocks (Polunin & Roberts 1993), 'spill-over' to adjacent fisheries (McClanahan & Mangi 2000) and strengthening trophic cascades (McClanahan & Shafir 1990, Guidetti & Sala 2007). At the same time, however, protection effects can be spatially idiosyncratic (Guidetti & Sala 2007), show considerable time lags (McClanahan & Graham 2005, Guidetti & Sala 2007), and when poorly designed and managed

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conflict with local livelihoods (Sale et al. 2005). This makes it imperative to investigate in closer detail under what circumstances MPAs produce the benefits with which they are so often associated (e.g. Sale et al. 2005).

Seagrasses are rhizomatous marine angiosperms that form inter- and sub-tidal beds in coastal areas around the world (Green & Short 2003). By supplying a range of ecosystem services to society (e.g. fisheries production and nutrient filtering), seagrass beds are one of the most valuable coastal ecosystems (Costanza et al. 1997). The 'bottom-up' paradigm (i.e. that resources limit production) has dominated seagrass ecology and management, but is currently questioned by accumulating evidence of the importance of 'top-down' (consumer) control over seagrasses and associated macroalgae (see Valentine & Duffy 2006 for review). As many seagrass communities display features that generally promote cascading effects of top predators, e.g. strong interactions between few keystone species or functional groups at each trophic level (Valentine & Duffy 2006, Moksnes et al. 2008), it has been suggested that overharvest of top predators could be a major driver behind seagrass loss (Heck & Valentine 2007, Moksnes et al. 2008). At the same time, however, many seagrass systems demon-

strate features that normally buffer cascading effects (Borer et al. 2005) — e.g. feeding on multiple trophic levels (Heck et al. 2000), and buffering effects of habitat structural complexity and prey size (Heck & Valentine 1995, Farina et al. 2009) — that can override protection effects (Prado et al. 2008).

In East Africa, seagrass beds constitute diverse and productive ecosystems (Ochieng & Erftemeijer 2003) that are highly important fishing grounds (de la Torre-Castro & Rönnbäck 2004). Grazing by parrotfish and sea urchins is a common natural disturbance in most areas (Alcoverro & Mariani 2004), known to enhance seagrass production (Eklöf et al. 2008). Over the last decades, however, highly dense aggregations of the urchin *Tripneustes gratilla* has overgrazed entire beds of the dominating seagrass *Thalassodendron ciliatum* (Fig. 1a) in a number of areas along the Kenyan coast (Eklöf et al. 2008). On adjacent coral reefs, protection of sea urchin predators (primarily the triggerfish *Balistapus undulatus* and the wrasse *Cheilinus undulatus*) indirectly reduces densities of sea urchins (McClanahan & Muthiga 1989, McClanahan & Shafir 1990). It has therefore been suggested that coral reef fisheries could contribute to high densities of urchins in sea-

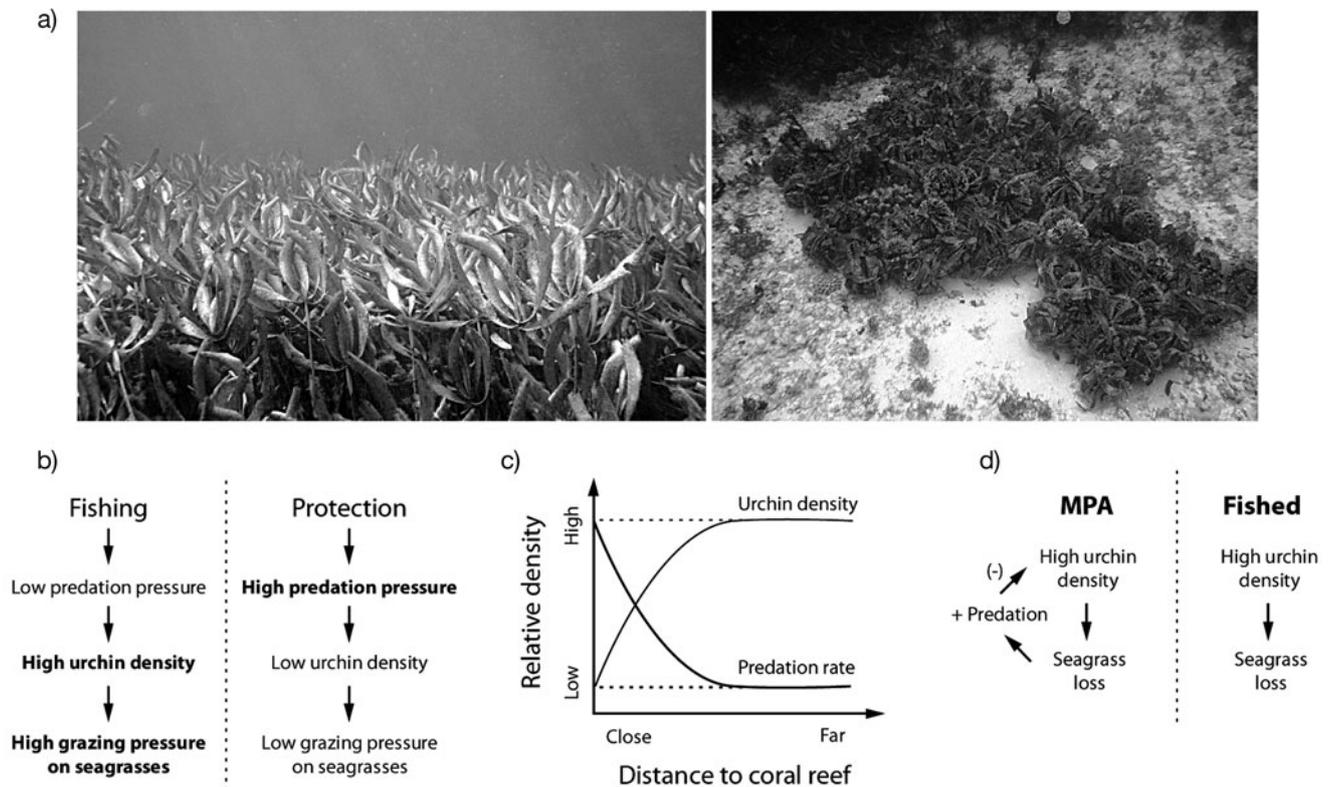


Fig. 1. (a) *Thalassodendron ciliatum* seagrass beds. Left panel: healthy bed with low urchin density. Right panel: overgrazed bed in Watamu Marine Park with aggregation of the herbivorous sea urchin *Tripneustes gratilla*. Photos: Maria Asplund and Annika Lindvall. (b) Hypothesized effects of protection on predation on urchins, urchin densities, and urchin grazing on seagrasses. (c) Hypothesized effects of distance to coral reefs on predation rates on urchins (solid lines: protected areas; dashed lines: fished areas). (d) Hypothesized self-regulated sea urchin overgrazing in protected but not in fished areas

grass beds as well (Alcoverro & Mariani 2004). At the same time, several of the overgrazing events have occurred within old and well-protected MPAs (Alcoverro & Mariani 2002, Zanre & Kithi 2004). Consequently, there is an obvious need to investigate to what extent these MPAs actually facilitate predation on seagrass-residing sea urchins and thereby control their grazing pressure on seagrasses (Fig. 1b).

In many tropical areas seagrass beds subsidize adjacent coral reef food webs, as many reef-associated predators (often large finfish) feed on seagrass-associated grazers and other primary consumers (Heck et al. 2008). In East Africa, such feeding migrations seem to be restricted to seagrass areas closest to reefs (Dorenbosch et al. 2005). Consequently, if reef-associated predators control sea urchins close to reefs, urchin densities should increase with increasing distance from reefs, at least in areas where reef predators are abundant (Fig. 1c).

Structural habitat complexity can mediate predator-prey interactions, e.g. between predatory fish and sea urchins (Hereu et al. 2005), and even override protection effects (Guidetti & Sala 2007). As seagrass leaves form dense canopies that can shelter invertebrates (e.g. Heck et al. 2003) and seagrass protection seems to 'buffer' predation on sea urchins (Heck & Valentine 1995, Farina et al. 2009), it has been suggested that urchin overgrazing could be self-regulated, since loss of the protective canopy should increase predation pressure on urchins (Heck & Valentine 1995). However, if predation is the important controlling factor, this feedback should only be present where predators are abundant enough (Fig. 1d).

Here we report on a study investigating the relative and interactive effects of protection, system, distance to coral reefs, and seagrass presence on sea urchins in seagrass beds and coral reefs in Kenyan lagoons. We used multiple techniques in multiple habitats to test the hypotheses that (1) there is a negative relationship between predation pressure and densities of the seagrass herbivore *Tripneustes gratilla*; (2) protected areas display higher predation control and lower densities of urchins than fished areas; (3) seagrass sites close to reefs (at least in MPAs) display higher predation pressure and lower densities of urchins than sites far away; and (4) sites with seagrasses (at least in MPAs) demonstrate lower predation pressure and higher densities of urchins than those without.

MATERIALS AND METHODS

Study area. The Kenyan coastline (600 km from 1 to 5° S) is characterized by inter- and subtidal lagoons and a fringing coral reef located 0.5 to 3 km from the shore. Tides are semi-diurnal with amplitudes ranging from

1.5 to 4 m, and surface water temperature ranges from 25 to 31°C (Obura 2001). Seagrass beds are a dominating feature of the lagoons, with 12 species encountered in mixed and monospecific beds (Ochieng & Erftemeijer 2003). The dominant seagrass is *Thalassodendron ciliatum* L., found subtidally from the shore to the reef flats (Obura 2001) in densities of ~ 700 shoots m^{-2} and with leaf biomass of ~ 150 g DW m^{-2} (Uku & Bjork 2005).

Survey 1. Survey design: Effects of protection and area on sea urchins on coral reefs were estimated during low water spring tides in Feb to March 2006 by sampling in 4 fished and 4 protected coral reef areas along a 200 km stretch of the southern Kenyan coast (Fig. 2). The 4 MPAs (from north to south) were Malindi, Watamu, Mombasa and Kisite Marine National Parks, gazetted in 1968, 1971, 1991 (fully protected in 1995) and 1978, respectively (Obura 2001). In these parks fishing and extraction of other natural resources (e.g. invertebrate collection) is banned, resulting in higher diversity, density and biomass of predatory fish inside than outside parks (e.g. Obura 2001, McClanahan & Graham 2005). The 4 fished areas were (from north to south) Vipingo, Kanamai, Ras Iwatine and Diani, where fishermen use a combination of traditional traps ('malema'), hook-and-lines, and drag nets (McClanahan & Mangi 2004). In addition, gastropods, sea cucumber, and sea stars are collected as part of the ornamental tourist and export trade (McClanahan

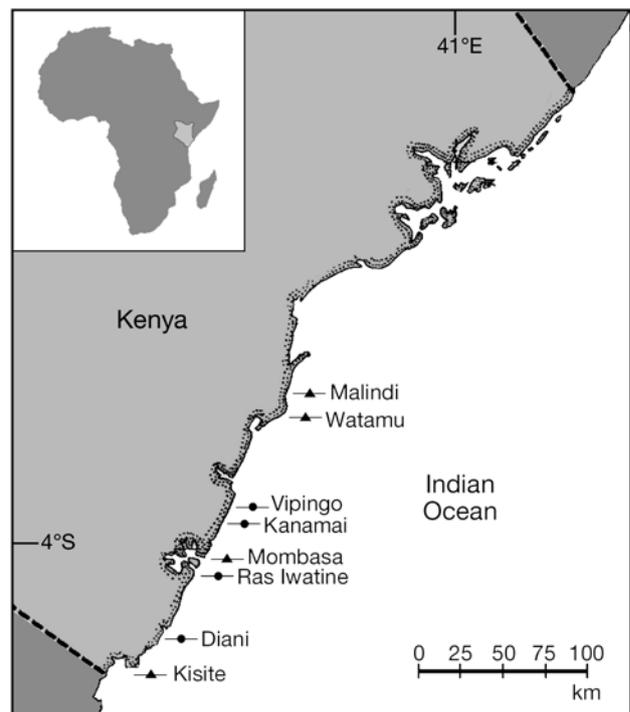


Fig. 2. Kenyan coastline, with 8 sampling areas highlighted. ▲ = Protected (Marine National Parks), ● = fished (including reserves)

2002). In each area, sea urchin density (to species level) was estimated on reef flats by counting all urchins within 10 m² circular plots (n = 9).

Data analysis: The effects of protection and area on density of (1) all urchins and (2) *Tripneustes gratilla* alone were analyzed using nested 2-way ANOVAs with 'Protection' (fixed, 2 levels: Fished and Protected) and 'Area' (random, 4 levels, nested in Protection) as factors. The assumption of homogenous variances was tested using Cochran's C-test. As many 0-values made it impossible to appropriately transform the data, the transformations yielding the lowest C (log2[x+2] and log[x+1], respectively) were applied. Significant main effects were further analyzed using Tukey's HSD post hoc test. Significance levels were set at $\alpha = 0.05$, and all analyses were run using the Generalised Linear Model (GLM) module in STATISTICA v. 7.1 (StatSoft®).

Survey 2. Experimental design: To investigate the effects and interactions of protection, distance to reefs and seagrass presence on sea urchins in seagrass beds, a field survey was conducted in 2 of the protected (Watamu and Mombasa) and 2 of the fished areas (Ras Iwatine and Diani, Fig. 1) during spring tides between October and November 2006. The effect of distance to the coral reef was investigated by sampling in 2 *Thalassodendron ciliatum*-dominated sites (100 × 100 m) within each area; site 'Close' (17 to 134 m from the reef) and site 'Far' (>500 m shoreward from the seagrass-reef transition zone). To investigate the effects of seagrass presence, an 'Unvegetated' site (100 × 100 m, <10% vegetation cover, placed >100 m from the Far site and 570 to 1200 m from the reef) was also sampled and compared with site Far. The sites were characterized by estimating the percent benthic cover of seagrass (to species level), macroalgae, poriferans, ascidians, coral rubble, stone and sand (to nearest 5%) within 0.25 m² frames (n = 15). The average benthic substrate composition can be found in Table 1.

Predation rates and predator types: Tethering of urchins is frequently used to assess relative predation potential (e.g. McClanahan & Muthiga 1989, Sala & Zabala 1996, Guidetti 2006). This method has been criticized for potential artifacts that may interact with treatment effects (Peterson & Black 1994), but was chosen because (1) we wanted to compare our results with those from previous studies (all using tethering) in the area (e.g. McClanahan 1998), and (2) it is the simplest and least time-consuming method available to assess relative predation pressure (Aronson & Heck 1995). *T. gratilla* randomly collected within each study area (23 to 89 mm test diameter) were tethered using a 2 × 80 mm hypodermic needle through the arboreal ventral region, and tied using a 0.5 m nylon monofilament line (0.5 mm). An aquaria trial showed 6% tethering-induced mortality after 3 d (n = 16), which was regarded as being acceptably low. Five tethered urchins were tied every 1.2 m along a 7 m transect line (5 mm nylon rope). Because these 5 urchins are dependent, each transect line was treated as a replicate. Replicated transects (n = 8) were randomly placed within sites (5 m from each other and edges to other substratum categories), anchored using wooden poles (Ø = 2 cm, length = 40 cm), and revisited every 24 h over 3 consecutive days to check for predation. Three transects (2 in Diani Unvegetated and 1 in Mombasa Close; 3% of total) were lost due to strong currents and/or fishing. A relative Predation Index (PI = (3 - S) / 3) was then calculated, where S is the average survival of the urchins in days and the number 3 represents the total length of the experiment or the maximum possible survival in days. Values range from 0 to 1, where 0 indicates 100% survival over 3 d and 1 indicates that 0% survived the first day (McClanahan 1998). The reason for using the PI was to allow for comparison with earlier studies in the areas (McClanahan 1998). Since there was a small difference in *T. gratilla* test diameter between areas (see 'Results'), we assessed whether size could have affected

Table 1. Benthic substrate composition (percent cover, to nearest 5%) in protected and fished areas, and at 3 sites within each area (C: seagrass Close; F: seagrass Far; U: Unvegetated) along the Kenyan coast (mean ± SE, n = 15)

Category	MPA						Fished					
	Watamu			Mombasa			Ras Iwatine			Diani		
	C	F	U	C	F	U	C	F	U	C	F	U
<i>Thalassodendron ciliatum</i>	75±5	90±2	5±2	70±11	85±4	–	75±6	60±7	–	30±8	60±9	–
<i>Thalassia hemprichii</i>	–	–	6±2	5±3	–	<5	<5	10±3	<5	10±5	<5	<5
<i>Halophila decipiens</i>	–	–	–	–	–	<5	–	–	<5	–	–	<5
<i>Syringodium isoetifolium</i>	–	–	–	10±6	–	<5	–	–	–	–	–	–
<i>Cymodocea</i> spp.	–	–	–	–	–	–	–	–	<5	–	–	–
Macroalgae	–	<5	5±1	<5	5±3	<5	5±3	<5	–	<5	–	–
Porifera	–	–	–	–	–	–	–	<5	–	<1	–	–
Ascidea	–	–	–	–	<5	–	–	10±2	–	–	–	–
Coral rubble	–	–	5±3	–	–	5±1	–	–	–	10±3	–	–
Stone	–	–	15±6	–	–	–	–	–	–	–	–	–
Sand	25±5	10±2	65±6	15±6	10±3	95±2	20±5	20±4	95±2	55±7	40±9	95±2

predation. The lack of a difference in size between urchins that were predated or not (t -test; $p = 0.9$, $n = 130$ per group) suggested that the difference in size had little overall effect.

The predators responsible for predation were identified by examining predation wounds on the remaining tests (following McClanahan & Muthiga 1989). The categories used—including all the major predators that have been previously identified—were (1) triggerfish (Balistidae): broken tests without the Aristotle's lantern; (2) wrasse (Labridae): broken test with intact Aristotle's lantern; (3) snail (Gastropoda): tests with a single perforation wound on the test; and (4) sea star (Asteroidea): intact test and Aristotle's lantern but missing spines. In addition, urchins dying of other causes ('unknown') or lost during the experiment ('missing') were noted.

Urchin density and size frequency distribution: Sea urchin density was estimated by identifying and counting all urchins in 10 m² circular plots ($n = 15$). The method was chosen to allow for comparisons with previous surveys (McClanahan 1998, Alcoverro & Mariani 2004), but could have underestimated the densities of juvenile urchins, as we did not sieve sediments or coral rubble, or excavate and search through rhizome mats, (Farina et al. 2009). A potential underestimation should, however, affect all areas and sites similarly. Finally, size frequency distribution of *Tripneustes gratilla* was estimated within Close and Far sites (because few urchins were encountered in Unvegetated sites) by measuring test diameter of urchins ($n = 40$) with callipers (0.5 mm accuracy).

Urchin grazing: To estimate effects on sea urchin grazing pressure, a herbivory assay using natural shoots of the 2 most common species (*Thalassodendron ciliatum* and *Thalassia hemprichii*) was used (see Alcoverro & Mariani 2004). Shoots ($n = 20$ per site) were collected in Close and Far sites, presence/absence of urchin bite marks was noted for each leaf, and grazing pressure was expressed as proportion of leaves with bite marks (per shoot). Prior to analysis, the data was arcsin-transformed (Quinn & Keough 2002).

Data analysis: To investigate to what extent top-down control actually regulates *Tripneustes gratilla* densities, we first tested if there was a negative correlation between relative predation pressure on and density of *T. gratilla*. Since these 2 variables were not sampled at the exact same points, we conducted a Pearson correlation analysis using site means ($n = 12$).

The main and interactive effects of 'Protection', 'Distance' (to reefs) and 'Seagrass' were investigated using mixed-model nested ANOVAs (Quinn & Keough 2002). Since a comparison of Close and Unvegetated sites would be confounded by seagrass presence/absence and the distance to reefs, data was separated

into 2 groups of analyses. The first, 'Protection and Distance' (comparing Close and Far sites), tested effects of protection and distance to patch reefs on all variables using an ANOVA model with 'Protection' (fixed, 2 levels: Protected vs. Fished), 'Area' (random, 4 levels, nested under Protection), 'Distance' (fixed, 2 levels: Close vs. Far) as main factors, and 'Protection × Distance' and 'Distance × Area(Protection)' as interaction terms. The second, 'Protection and Seagrass' (comparing Far and Unvegetated sites), tested effects of protection and seagrass presence on sea urchin density and predation rates using a similar ANOVA design, but with 'Seagrass' (fixed, 2 levels: Far vs. Unvegetated) replacing 'Distance' and respective interaction terms. When factor(s) were non-significant at $\alpha > 0.25$, they were pooled and the analysis was run again (Quinn & Keough 2002). Significant main effects were tested as described above. Before the analyses, the assumption of homogeneity of variances was tested using Cochran's C -test, and when necessary, data were appropriately transformed. For some variables the large number of treatment groups and replicates resulted in unavoidable violations of the assumption. In these cases, the analysis was run on data with the transformation resulting in the lowest $C_{\text{calculated}}$, and the violation was reported. In figures and tables, non-transformed data is presented for all variables.

RESULTS

Survey 1: Effects of protection and area on sea urchins in coral reefs

Nine sea urchin species were encountered in the 8 coral reef areas (Table 2). *Echinometra mathei* dominated (80% of all urchins encountered), particularly in the fished areas (23 to 99%); it was followed by *Diadema savigny* (5.8%), *Echinostrephus molaris* (4.6%) and *Tripneustes gratilla* (3.2%).

The density of all sea urchin species pooled, as well as that of *Tripneustes gratilla* alone (Fig. 3), were 14 and 127 times higher in fished than in protected coral reef areas; 88.5 vs. 5.8, and 3.25 vs. 0.02 ind 10 m⁻², respectively (Table 3, Tukey's, $p < 0.001$ for both comparisons). There were also differences between areas within each level of protection (Table 3). In the protected Mombasa area, densities of all urchins pooled were higher than in Malindi and Watamu, and in Malindi and Kisite, densities were higher than in Watamu ($p < 0.05$ for all comparisons; Table 3). For *T. gratilla* densities, however, there were no differences between the 4 protected areas ($p > 0.05$ for all comparisons). In the fished Diani and Kanamai areas, the total urchin density was higher than in Ras Iwatine

Table 2. Densities of sea urchins (mean $10\text{ m}^{-2} \pm \text{SE}$) in 8 coral reef areas (4 protected and 4 fished; $n = 9$, except for Watamu and Ras Iwatine, where $n = 12$) along the Kenyan coast. Species listed in decreasing order according to percent contribution to total density (across all areas)

	Protected				Fished			
	Malindi	Watamu	Mombasa	Kisite	Vipingo	Kanamai	Ras Iwatine	Diani
<i>Echinometra mathei</i>	1.8±0.55	0.1±0.09	2.0±0.71	0.11±0.12	19±3.3	89.5±14.8	7.6±1.8	186±27.3
<i>Diadema savigny</i>	–	–	0.56±0.26	0.22±0.16	5.1±1.4	3.89±0.74	12.2±4.4	0.33±0.35
<i>Echinostrephus molaris</i>	1.89±0.8	0.58±0.37	8.22±1.54	6.0±2.54	–	–	0.67±0.27	–
<i>Tripneustes gratilla</i>	–	0.08±0.09	–	–	4.0±1.27	1.56±0.92	5.83±3.42	0.78±0.29
<i>Diadema setosum</i>	–	–	–	–	4.33±1.43	3.44±1.13	1.83±0.99	–
<i>Echinothrix diadema</i>	–	–	2.11±0.41	0.78±0.61	–	0.11±0.12	3.5±0.8	0.22±0.24
<i>Toxopneustes pileolus</i>	–	–	0.22±0.24	–	–	–	0.58±0.27	–
<i>Echinothrix calamaris</i>	–	–	0.11±0.12	–	–	–	0.25±0.19	–
<i>Stomopneustes variolaris</i>	0.11±0.12	–	–	–	–	–	0.08±0.09	–

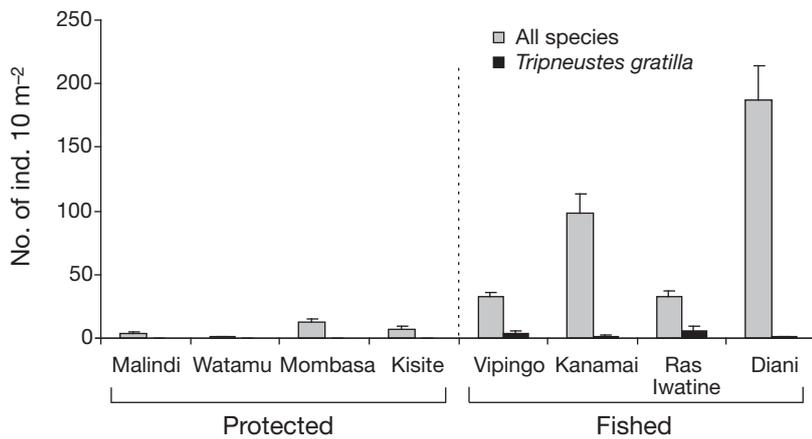


Fig. 3. Sea urchins. Densities in 4 protected and 4 fished Kenyan coral reef areas (mean $10\text{ m}^{-2} \pm 1\text{ SE}$; $n = 9-12$)

Table 3. Summary of mixed-model nested ANOVAs on effects and interactions of 'Protection' (fixed, 2 levels) and 'Area' (random, 4 levels, nested in Protection) on density of (1) all urchin species pooled and (2) *Tripneustes gratilla* alone, in Kenyan coral reefs. Bold values indicate significant main effects ($\alpha = 0.05$)

Source	df	MS	F	p
1. Density of all urchin species				
Protection	1	601.5	77.8	0.005
Area(Protection)	6	7.8	20.04	<0.001
Error	70	0.38		
2. Density of <i>Tripneustes gratilla</i>				
Protection	1	34.15	15.12	0.008
Area(Protection)	6	2.27	3.27	0.007
Error	70	0.69		

and Vipingo ($p < 0.05$ for all comparisons). For *T. gratilla* alone, however, densities in Vipingo were higher than in Diani and Kanamai ($p = 0.014$ and 0.44 , respectively).

Survey 2: Effects of protection, distance to reefs and seagrass presence

Relationship between predation pressure on and densities of *T. gratilla*.

The relationship between mean densities of *Tripneustes gratilla* and mean relative PI is presented in Fig. 4. A Pearson correlation showed a significant negative relationship ($p = 0.045$), indicating that predation explained 34.5% of variation in *T. gratilla* density.

Predation rate and predator type.

Predation rates (PI), ranging from 0.016 (in Diani Far) to 0.39 (in Watamu Close), were within the range of those previously observed on adjacent coral reefs (McClanahan 1998).

The 'Protection and Distance' analysis showed no effects of 'Protection' or 'Distance' to the reef, but a clear 'Area(Protection)' effect (Fig. 5a, Table 4); predation rates in Watamu Marine Park were 2.5, 3.5 and 6 times higher than in Mombasa, Ras Iwatine and Diani, respectively (Tukey's, $p < 0.05$ for all comparisons).

The 'Protection and Seagrass' analysis showed that predation rates in protected areas were 3 times higher than in fished (Fig. 5a, Table 4) areas and that there was a 'Seagrass \times Area(Protection)' interaction: seagrass presence (Far vs. Unvegetated) decreased predation pressure in Mombasa with ~50% ($p = 0.012$) but had no effect in Watamu, Ras Iwatine and Diani ($p > 0.05$ for all comparisons).

Inspection of urchin carcasses indicated that sea stars (Asteroidea) were the most important predators (Table 5), with 44 and 18 urchins preyed upon in Watamu and Mombasa MPAs, respectively (69 to 100% and 45 to 100% of total predation, respectively). In the fished areas Ras Iwatine and Diani, 14 and 4 sea

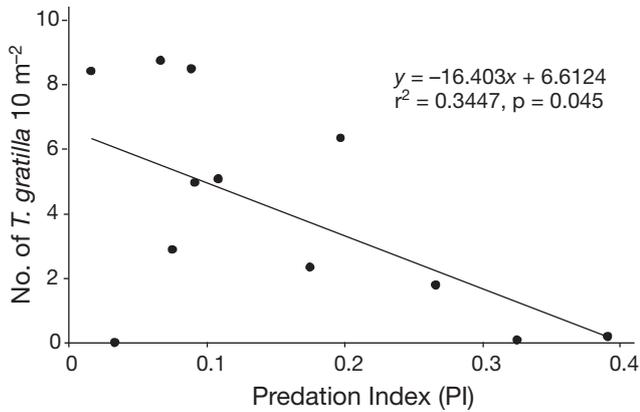


Fig. 4. *Tripneustes gratilla*. Correlation between relative predation pressure (PI) and density (no. of ind. 10 m⁻²; n = 12; means for each site)

urchins were eaten by sea stars, respectively (83 to 100% of total predation). Visual observations of ongoing predation suggested that the main species was *Protoreaster linki* (Oreasteridae). Fish (triggerfish *Balistidae* and wrasse *Labridae*) was numerically the second most important predator group in protected areas, with 1 and 6 urchins preyed upon in Watamu and Mombasa, respectively (Table 5). In the Mombasa, 5 were preyed upon in the Unvegetated site. In the 2 fished areas, however, only 1 out of the 230 tethered urchins was eaten by a fish (a Balistid). Gastropods, the third most important group, preyed upon 3 and 4 urchins in protected and fished areas, respectively. Urchin mortality was also caused by unknown factors: in Diani Far and Unvegetated, 8 (20%) and 28 (94%) of the tethered urchins died, respectively, and 13 urchins disappeared (Missing) in all the 12 sites.

Sea urchin density and size. *Tripneustes gratilla* was the most common urchin species of the 9 encountered

Table 4. Summary of 3-way mixed-model ANOVAs on effects of 'Protection' (fixed, 2 levels), 'Area' (random, 2 levels, nested in Protection) and (1) 'Distance' to reefs (fixed, 2 levels) or (2) 'Seagrass' (fixed, 2 levels) on relative predation pressure on *Tripneustes gratilla* in Kenyan seagrass beds (n = 8). Bold values indicate significant main effects ($\alpha = 0.05$)

Source	df	MS	F	p
1. Protection and distance				
Protection: P	1	0.29	3.01	0.22
Area(Protection): A(P)	2	0.096	6.93	0.002
Distance: D	1	<0.01	0.11	0.77
P × D	1	<0.01	<0.01	0.99
A(P) × D	2	0.04	2.9	0.06
Error	56	0.01		
2. Protection and seagrass				
Protection: P	1	0.36	19.6	0.047
Area(Protection): A(P)	2	0.018	1.8	0.18
Seagrass: S	1	<0.01	<0.01	0.99
P × S	1	<0.01	0.06	0.83
A(P) × S	2	0.12	11.4	<0.001
Error	53	0.01		

(Table 6; 0.1 to 8.4 ind. 10 m⁻²; 73% of all urchins encountered), followed by *Echinometra mathaei* (12%) and *Diadema setosum* (10%).

The 'Protection and Distance' analysis on total sea urchin density showed no significant effects of any factors, whereas the analysis on *Tripneustes gratilla* densities alone showed a significant 'Area(Protection) × Distance' interaction (Fig. 5b,c, Table 7). This was most likely caused by higher density of *T. gratilla* in Ras Iwatine Far than Close (Tukey's, p = 0.08), as there were no differences in any other areas (p >> 0.05 for all comparisons).

The 'Protection and Seagrass' analyses revealed slightly different patterns. For densities of all urchins as well as of *Tripneustes gratilla* alone, there were no

Table 5. Mortality (total ind.) and predator types determined by urchin test conditions after tethering experiment in protected (Watamu and Mombasa) and fished (Ras Iwatine and Diani) areas, and at 3 sites within areas (C: seagrass Close; F: seagrass Far; U: Unvegetated). Figures in brackets are percent contribution to the total number of urchins preyed upon, except for 'total predation,' 'unknown mortality,' 'missing' and 'survival,' where figures in brackets are percent contribution to total number of tethered urchins

	Protected						Fished					
	Watamu			Mombasa			Ras Iwatine			Diani		
	C	F	U	C	F	U	C	F	U	C	F	U
Tethered urchins (n)	40	40	40	40	40	35	40	40	40	40	40	30
Total predation	16 (40)	21 (53)	12 (30)	12 (30)	6 (15)	9 (26)	6 (15)	4 (10)	5 (13)	3 (8)	4 (10)	1 (3)
Asteroidea	11 (69)	21 (100)	12 (100)	12 (100)	4 (68)	4 (44)	5 (83)	4 (100)	5 (100)	3 (100)	-	1 (100)
Gastropod	2 (13)	-	-	-	1 (16)	-	1 (16.5)	-	-	-	3 (75)	-
Balistidae	1 (6)	-	-	-	-	1 (11)	-	-	-	-	1 (25)	-
Labridae	-	-	-	-	1 (16)	3 (33)	-	-	-	-	-	-
Balistidae/Labridae	-	-	-	-	-	1 (11)	-	-	-	-	-	-
Unknown predator	2 (13)	-	-	-	-	-	-	-	-	-	-	-
Unknown mortality	4 (10)	5 (12)	5 (12)	-	-	1 (3)	-	-	-	1 (2)	8 (20)	28 (94)
Missing	1 (2)	-	-	-	2 (5)	9 (25)	-	-	-	1 (2)	-	-
Survival	19 (47)	14 (35)	23 (57)	28 (70)	32 (80)	16 (45)	34 (85)	36 (90)	35 (87)	35 (87)	28 (70)	1 (3)

Table 6. Densities of sea urchins (mean $10\text{ m}^{-2} \pm \text{SE}$) in 4 seagrass areas (2 protected and 2 fished), and at 3 sites within each area (C: seagrass Close; F: seagrass Far; U: Unvegetated; $n = 15$) along the Kenyan coast. Species listed in decreasing order according to percent contribution to total density (across all areas)

	Watamu			Mombasa			Ras Iwatine			Diani		
	C	F	U	C	F	U	C	F	U	C	F	U
<i>Tripneustes gratilla</i>	1.8±5.9	0.2±0.4	6.3±5.2	2.3±7.1	4.9±6.8	0.1±0.3	5.1±9.2	8.7±7.4	2.9±7.9	8.4±10	8.5±17	–
<i>Echinometra mathaei</i>	–	–	0.5±1.8	–	–	–	–	0.1±0.3	–	2.6±4	5.1±10	–
<i>Diadema setosum</i>	–	–	–	–	–	–	6.6±14	0.1±0.3	–	–	–	–
<i>Echinothrix diadema</i>	–	–	–	–	0.1±0.3	–	–	1.4±1.9	–	–	–	–
<i>Toxopneustes pileolus</i>	0.1±0.3	–	–	–	0.1±0.3	–	–	–	–	0.5±1.2	0.1±0.5	–
<i>Diadema savignyi</i>	–	–	–	–	–	–	–	0.1±0.3	–	0.2±0.8	0.1±0.5	–
<i>Stomopneustes variolaris</i>	–	–	–	–	–	–	–	–	–	–	0.3±0.8	–
<i>Salmacis bicolor</i>	–	–	–	–	0.1±0.3	–	–	–	–	–	–	–
<i>Salmaciella dussumieri</i>	–	–	–	–	0.1±0.3	–	–	–	–	–	–	–

Table 7. Summary of mixed-model ANOVAs on effects and interactions of 'Protection' (fixed, 2 levels), 'Area' (random, 2 levels, nested in 'Protection') and (1) 'Distance' to the reef (fixed, 2 levels), and (2) 'Seagrass' (fixed, 2 levels) on (A) total urchin density, (B) density of *Tripneustes gratilla*, and (C) mean test size of *T. gratilla* in Kenyan seagrass beds. Values in **bold** indicate significant main effects ($\alpha = 0.05$)

	df	MS	F	p	F_{pool}	p_{pool}
1. Protection and distance						
(A) Density all urchin species						
Protection: P	1	44.78	13.4	0.17		
Area(Protection): A(P)	2	3.34	2.71	0.07	2.74	0.068
Distance: D	1	0.86	0.23	0.67		
P × D	1	0.26	0.07	0.81		
A(P) × D	2	3.61	2.93	0.57	2.96	0.055
Error	112	1.22				
Pool	114	1.219				
(B) Density <i>Tripneustes gratilla</i>						
Protection: P	1	21.11	8.06	0.10		
Area(Protection): A(P)	2	2.62	2.40	0.09	2.40	0.09
Distance: D	1	1.70	0.25	0.66		
P × D	1	0.04	0.006	0.94		
A(P) × D	2	6.62	6.06	0.003	6.08	0.003
Error	112	1.09				
Pool	114	1.087				
(C) Size <i>Tripneustes gratilla</i>						
Protection: P	1	2118	2.6	0.25		
Area(Protection): A(P)	2	824.4	14.1	<0.001		
Distance: D	1	395.9	3.1	0.22		
P × D	1	0.64	0.01	0.95		
A(P) × D	2	127	2.2	0.11		
Error	312	58.7				
2. Protection and seagrass						
(A) Density all urchin species						
Protection: P	1	2.08	0.63	0.51		
Area(Protection): A(P)	2	3.31	4.32	0.015		
Seagrass: S	1	13.93	0.87	0.45		
P × S	1	22.42	1.41	0.35		
A(P) × S	2	15.93	20.79	<0.001		
Error	112	0.76				
(B) Density <i>Tripneustes gratilla</i>						
Protection: P	1	0.89	0.188	0.70		
Area(Protection): A(P)	2	4.75	6.17	0.002		
Seagrass: S	1	7.92	0.61	0.51		
P × S	1	14.88	1.14	0.39		
A(P) × S	2	13.01	16.9	<0.001		
Error	112	0.76				

'Protection' effects but significant 'Area(Protection)' effects and, most importantly, significant 'Area(Protection) × Seagrass' interactions (Fig. 5b,c, Table 7). These were caused by higher densities of all urchins and those of *T. gratilla* alone in Far than in Unvegetated sites in Mombasa, Diani and Ras Iwatine, but lower densities in the Far than the Unvegetated site in Watamu ($p < 0.05$ for all comparisons).

The size (test diameter) of *Tripneustes gratilla* ranged from 16.5 to 94.5 mm (across areas and sites), and 97% of all individuals were larger than 50 mm. All 8 populations (4 areas × 2 sites) showed a normally distributed size–frequency distribution (Fig. 6). There were no effects of 'Protection' or 'Distance', but an 'Area(Protection)' effect; urchins in Watamu were 9 to 13% larger than in the three other areas (Table 7; $p < 0.001$ for all comparisons).

Sea urchin grazing pressure. The *Thalassodendron ciliatum* leaf grazing assays (Fig. 5d) showed no effect of 'Protection' or 'Distance', but a significant 'Distance × Area(Protection)' interaction (Table 8); in Ras Iwatine the grazing pressure was twice as high in the Close as in the Far site ($p < 0.001$), but there were no such effects in Watamu, Mombasa and Diani ($p > 0.05$ for all comparisons).

Also for *Thalassia hemprichii* leaf assays (Fig. 5e) only the 'Distance × Area(Protection)' interaction was significant (Table 8). This was caused by a 3 times higher grazing pressure in Watamu Far than Close ($p = 0.018$) but a lack of effect in the three other areas ($p > 0.05$ for all comparisons).

DISCUSSION

Predation on *Tripneustes gratilla*

Results from research on the causes of intense sea urchin consumption of 'founder' species like perennial macroalgae and hard corals gradually resulted

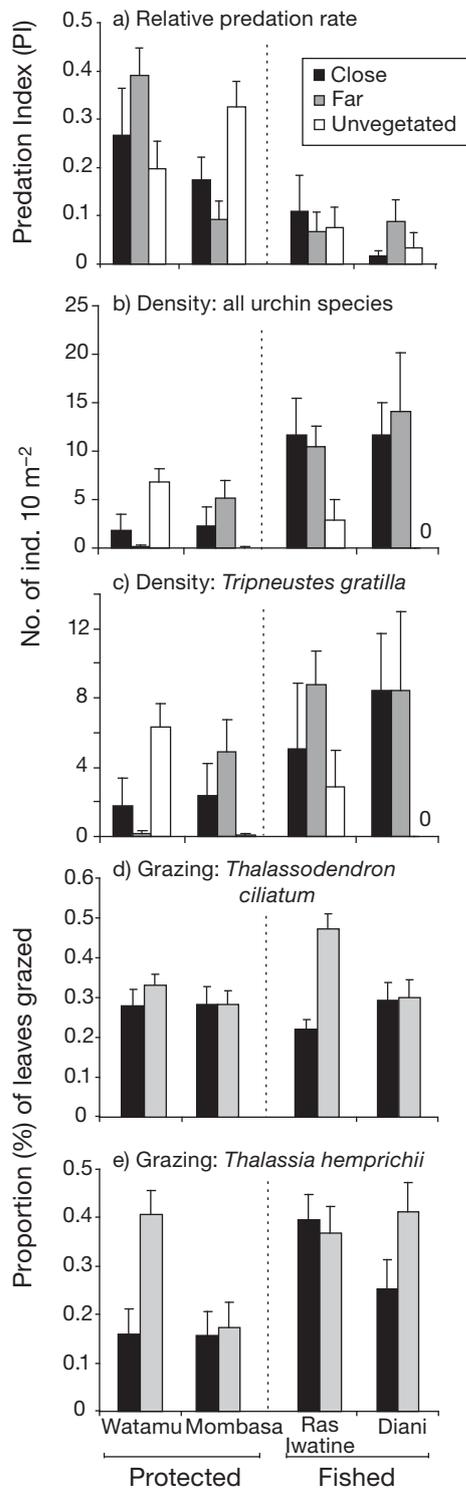


Fig. 5. Sea urchins in seagrass beds. (a) Predation rate on tethered *Tripneustes gratilla* (n = 8), (b) total sea urchin density (n = 15), (c) density of *T. gratilla* (n = 15), and proportion of leaves per shoot of (d) *Thalassodendron ciliatum* and (e) *Thalassia hemprichii* grazed by urchins, in 2 protected (Watamu and Mombasa) and 2 fished (Ras Iwatine and Diani) areas, and 3 sites within those areas: Close, Far and Unvegetated (mean ± SE)

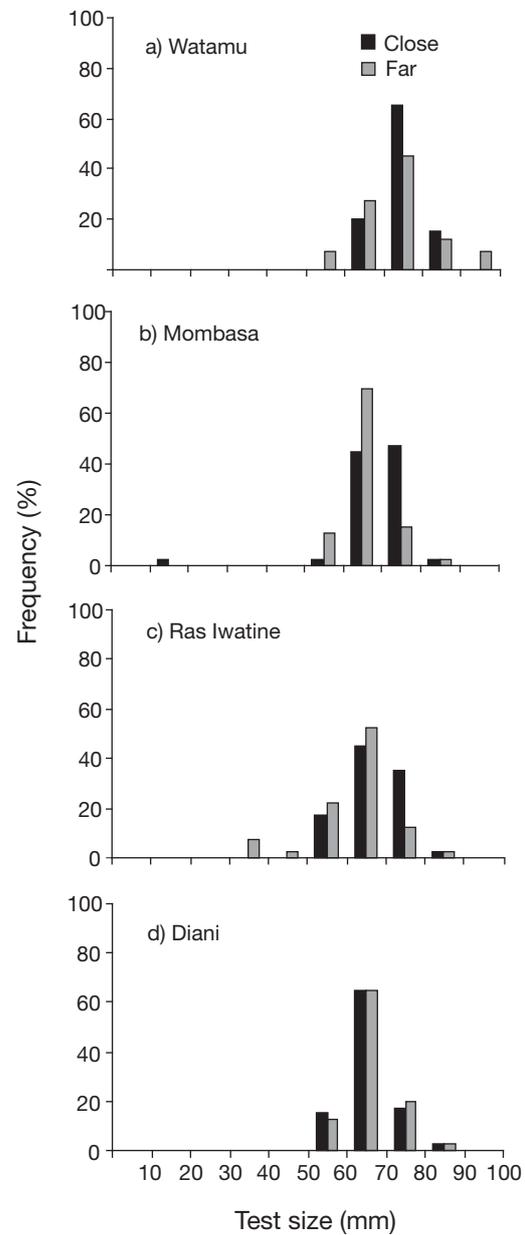


Fig. 6. *Tripneustes gratilla*. Size frequency distribution in (a) Watamu, (b) Mombasa, (c) Ras Iwatine, and (d) Diani, and 2 sites in each area: Close and Far (n = 40 per area)

in an 'overfishing paradigm' in the early 1980s, identifying removal of predators as the main driving factor (see Elner & Vadas 1990 for overview). This paradigm has since received considerable critique for simplifying the complexity of marine food webs, ignoring the obvious roles of other factors (e.g. pollution, temperature, disease) and lacking adequate experimental testing (Elner & Vadas 1990, Sala et al. 1998). In Kenyan coral reefs, however, long-term surveys and experiments provide compelling evidence that overfishing of

Table 8. Summary of 3-way mixed-model ANOVAs on effects and interactions of 'Protection' (fixed, 2 levels), 'Area' (random, 2 levels, nested in 'Protection') and 'Distance' to reefs (fixed, 2 levels) on sea urchin grazing pressure (% of leaves with bite marks) on shoots of (A) *Thalassodendron ciliatum* and (B) *Thalassia hemprichii* in Kenyan seagrass beds. **Bold** values indicate significant differences ($\alpha = 0.05$)

Source	df	MS	F	p	F_{pool}	P_{pool}
(A) Sea urchin grazing on <i>Thalassodendron ciliatum</i>						
Protection: P	1	0.04	1.16	0.39		
Area(Protection): A(P)	2	0.04	1.10	0.34		
Distance: D	1	0.28	1.45	0.35		
P × D	1	0.14	0.73	0.48		
A(F) × D	2	0.19	6.01	<0.001		
Error	152	0.03				
(B) Sea urchin grazing on <i>Thalassia hemprichii</i>						
Protection: P	1	0.81	3.73	0.19		
Area(Protection): A(P)	2	0.22	2.96	0.06	2.85	0.06
Distance: D	1	0.56	2.02	0.29		
P × D	1	0.04	0.13	0.75		
A(F) × D	2	0.28	3.82	0.02	3.67	0.03
Error	152	0.07				
Pool	154	0.08				

predators is indeed a major driver behind high sea urchin densities (e.g. McClanahan & Muthiga 1989, McClanahan & Shafir 1990). To test if lack of predation explains high densities of sea urchins that have been shown to overgraze seagrasses, we first of all hypothesized that there should be a negative correlation between predation pressure on and densities of *T. gratilla*. An observed significant relationship ($r^2 = 0.345$, Fig. 4)—very similar to that previously found in adjacent coral reefs (McClanahan 1998)—indicates that predation is at least a contributing factor to the distribution of *T. gratilla*. This is the first study to demonstrate such a relationship in seagrass ecosystems, which strengthens the hypothesis that lack of predation contributes to seagrass overgrazing (Eklöf et al. 2008).

The main predator type seemed to be sea stars (primarily *Protoreaster linki*), which at first glance may seem striking since fish are usually the major urchin predators in protected hard-bottom areas (McClanahan & Muthiga 1989, Sala & Zabala 1996, Shears & Babcock 2002). Results from a recent study, however, indicate that predatory sea stars can play a key role by controlling sea urchins also within reserves (Bonaviri et al. 2009). Based on our survey, we cannot exclude that tethering overestimated the relative importance of these slow-moving predators (McClanahan & Muthiga 1989, Aronson & Heck 1995). However, recent observations in the study area of predation on untethered urchins also confirm that *P. linki*, as well as 2 other sea star species (*Culcita schmideliana* and *Pentaceraster mammilatus*), prey upon juvenile and adult *Tripneu-*

stes gratilla (J. Eklöf unpubl. data). These large predatory sea stars are exploited for ornamental trade (Gossling et al. 2004) and for use as fish bait (Jiddawi & Ohman 2002), and in the Caribbean, densities of the closely related sea urchin predator *Oreaster reticulatus* are reduced by collection (Guzman & Guevara 2002). Ongoing surveys of sea star densities in fished and protected Kenyan seagrass beds and coral reefs will undoubtedly shed more light on this interesting issue.

Predation by fish, the second most important group, seemed to be relatively more common in protected than in fished areas (Table 5). Protection is known to benefit Kenyan reef-associated populations of urchin predators such as triggerfish and wrasse, that at least weakly control *Tripneustes gratilla* on reefs (McClanahan 1998). The seemingly lower levels of predation by fish than seastars (Table 5) was most likely due to the size of the urchins (97% > 50 mm), as fish predation pressure is much lower on adult than juvenile *T. gratilla* (Dafni & Tobol 1987) and other urchins (e.g. Sala & Zabala 1996, Guidetti 2006). Dominance of one

age cohort (as reported here) is common and can be caused by sporadic extreme recruitment success and/or ontogenetic habitat shifts (Fernandez et al. 2001). However, while Kenyan *T. gratilla* populations seem to have continuous reproduction (Muthiga 2005) they appear to have been dominated by adults for the past decade (Alcoverro & Mariani 2002, Muthiga 2005). In the nearby Red Sea, *T. gratilla* juveniles hide in crevices and beneath boulders until they reach a size that protects them from predation (Dafni & Tobol 1987). Since our urchin survey did not include such detailed sampling, we cannot rule out the possibility that we (and others before) underestimated juvenile densities and that protection effects on juveniles may be stronger. It is therefore crucial that future studies specifically target recruit and juvenile distribution using more fine-scale sampling (e.g. larval collectors, sediment sieving, searching in crevices and beneath boulders) in various habitats and seasons. However, in support of our results, recent studies from Mediterranean seagrass beds indicate a lack protection effects on juvenile urchins as well (Prado et al. 2008), partly because of the sheltering effect from seagrass leaves and rhizomes (Farina et al. 2009).

The least important predator group, gastropods, can be major predators on seagrass-residing sea urchins (Hughes & Hughes 1971, Keller 1983) and anecdotes suggest that intense gastropod collection for ornamental trade has contributed to urchin outbreaks in East Africa (Richmond & Rabesandratana 1997). We, however, could not show any major protection effects on predation pressure from these species, most likely

because intense collection outside parks is counterbalanced by predation inside parks (McClanahan 2002).

Are protection effects system-, site- and time-dependent?

We hypothesized that MPAs should display higher predation control and lower densities of sea urchins than fished areas by harboring higher densities of predators. In coral reefs (Survey 1) densities of sea urchins, including *Tripneustes gratilla*, were indeed much lower in protected areas. This pattern, almost identical to those previously found in the study area (McClanahan & Muthiga 1989, McClanahan & Shafir 1990), indicates that *T. gratilla* are controlled by highly abundant reef predators and, consequently, that overfishing reduces predation control (see also Alcoverro & Mariani 2004). As many urchins, including *T. gratilla*, show ontogenetic migrations from hard-bottom reefs to seagrass beds in search of food (Ogden et al. 1973, Dafni & Tobol 1987, Fernandez et al. 2001), it is possible that overfishing of coral reef-associated urchin predators could induce overgrazing of adjacent seagrass beds. Such 'cross-system' cascades have been previously observed in linked oceanic–nearshore systems (Estes et al. 1998), but must be studied in closer detail before taken as a fact (e.g. Valentine et al. 2008).

In contrast, we found no protection effects on any of the investigated variables in the seagrass beds (Survey 2). A survey design with more than 2 areas per level of protection would undoubtedly have had higher statistical power (Quinn & Keough 2002), but a study conducted in the same areas in 1997 (with 3 areas per level) also failed to demonstrate a protection effect on urchins (Alcoverro & Mariani 2004). Based on the history of the 2 investigated marine parks (Mombasa and Watamu), we propose 3 separate but potentially interacting mechanisms explaining the lack of protection effects.

(1) Insufficient time of protection. While full recovery of Kenyan keystone urchin predator populations takes 30 to 40 yr (McClanahan & Graham 2005), the Mombasa MPA has been protected only since 1995 (Obura 2001) and lacks predation control (McClanahan & Graham 2005). This is supported by relatively high densities of sea urchins on the Mombasa coral reefs compared to the 3 other parks (Fig. 3), as well as documented seagrass overgrazing by hyperabundant *Tripneustes gratilla* in the park (Alcoverro & Mariani 2002, 2004). Similar time-lagged protection effects, which have been observed in Mediterranean rocky reefs, are generally caused by non-linear predator–prey relationships (Guidetti & Sala 2007) and must be considered when assessing MPA effects.

(2) 'Spill-in' effects. The other MPA (Watamu) was, on the other hand, gazetted in 1971 and harbors highly abundant reef-associated predators (McClanahan & Graham 2005) that appear to control *Tripneustes gratilla* on the coral reefs (Table 2). The predation rates on urchins in the 2 seagrass areas (Close and Far) were also higher than in Mombasa, Ras Iwatine and Diani (Table 4). In the Unvegetated Watamu site, however, the pattern was strikingly different from that in the other areas; predation rates were very low, while *T. gratilla* density (6.3 ind. 10 m⁻²) was comparable to those in the 2 fished areas (Table 2, Fig. 5). This is surprising given the long time of protection (~38 yr), but is probably explained by the fact that the Unvegetated site consisted of a previously overgrazed *Thalassodendron ciliatum* bed (~10% seagrass cover, see Table 1). Historical notes show that in 2001, large aggregations of *T. gratilla* (up to 37 ind. m⁻²) formed and overgrazed seagrasses in the fished reserve surrounding the Watamu marine park (Zanre & Kithi 2004). Contrary to what was expected the aggregations grew in size over time and progressively invaded the marine park and overgrazed several *T. ciliatum* beds. Removal of 66 000 urchins 2 yr later (2003) decreased grazing pressure in the short term (Zanre & Kithi 2004), but several aggregations were still present at the time of this study (2006). This interesting chain of events, which we label a 'spill-in effect', is most likely explained by a combination of the low predation pressure from fish (see Table 5 and discussion above) caused by the large size of the urchins (Fig. 6); the aggregation behavior of the urchins, which is known to reduce predation pressure (e.g. Bernstein et al. 1981); and the high structural complexity of the bottom (consisting of dead rhizome mats and exposed gravel and boulders), which offers protection from predation.

(3) Interactions with eutrophication. Not only low predation pressure but also eutrophication can stimulate urchin growth and recruitment (Sala et al. 1998, Eklöf et al. 2008). In the larger Watamu area, loads of land-derived sediments have increased for the past century due to runoff from coastal agriculture (Fleitmann et al. 2007). Consequently, increased sedimentation and elevated nutrient levels (Ohowa 1996) have caused high coral mortality (van Katwijk et al. 1993) and induced growth of large, leathery macroalgae (McClanahan et al. 2002). As nutrient addition is known to stimulate the growth of *Tripneustes gratilla* at the individual (Dafni 1992) and population levels (Mergner 1982), eutrophication could be a contributing factor to the observed sea urchin outbreaks. In strong support, experimental short-term (6 wk) nutrient enrichment increased the size of *T. gratilla* and their grazing impact on *Thalassodendron ciliatum* growth (J. Eklöf unpubl. data).

No effects of distance to patch reefs

We hypothesized that seagrass sites situated close to reefs should display higher predation pressure and lower densities of urchins than sites far away, at least in protected areas. We found no such 'Distance' or 'Distance × Protection' effects, which could be due to several factors. First, the large size of the urchins could have reduced predation by reef-associated fish (see discussion above) and therefore diminished any distance-related effects. In Mombasa, however, fish preyed upon 5 urchins in the Unvegetated site but only 1 in the vegetated Far site (Table 5)—both situated >500 m from the reef. This demonstrates that fish can consume urchins far away from reefs, but potentially only when shelter is lacking (see Heck & Valentine 1995, Farina et al. 2009). In support, a study of rocky reef–seagrass interactions showed that the distance to reefs explained densities of invertivorous fish, whereas the structural complexity of the seagrass beds explained predation rates on tethered invertebrates (Vanderklift et al. 2007).

Importance of seagrasses as shelter

Finally, we hypothesized that sites with seagrasses should, by being more structurally complex, demonstrate lower predation pressure and higher urchin densities than unvegetated sites, at least in protected areas. Such 'buffering' effects of shelter have been observed elsewhere (Heck & Valentine 1995, Farina et al. 2009) and could potentially buffer overgrazing (Fig. 1d). We found no clear effects of 'Seagrass' or 'Protection × Seagrass' interactions, partly because the patterns in Watamu were opposite to expected (with lower predation rate and higher density in the Unvegetated than in the Far site) and partly because of much lower urchin densities in Unvegetated than in Far sites in the 2 fished areas (Ras Iwatine and Diani; Fig. 5a–c). The unexpected pattern in Watamu was most likely caused by the fact that the Unvegetated site was an overgrazed *Thalassodendron ciliatum* bed with unnaturally high urchin densities and low predation pressure (see discussion above). The lower densities of urchins in Unvegetated than Far sites in the 2 fished areas were equally unexpected, as shelter from seagrass leaves (at least from predation) should be less important than in protected areas. Even though predation rates were indeed very low, the overall mortality was higher in Unvegetated than Far sites, particularly in Diani (where 94% of all tethered urchins died from unknown causes; Table 5). The cause(s) of this high mortality were not further investigated, but seagrass presence may—depending on site-specific con-

ditions—be important for other reasons than predation. Lack of food (seagrass or detritus) is unlikely to have an effect over such a short time span, but exposure to sunlight and high temperatures are well-known and rapid stressors on *Tripneustes gratilla* (Lawrence & Agatsuma 2007). These mechanisms must undoubtedly be tested using manipulations of seagrass cover (see e.g. Farina et al. 2009) in relation to predation, but the results clearly show that habitat characteristics exert strong influence on *T. gratilla* populations even when predation pressure is low.

Cascading effects from MPAs in seagrass beds?

A number of recent publications hypothesize that protection of top predators is crucial for seagrass ecosystem functioning (e.g. Valentine & Duffy 2006, Heck & Valentine 2007, Moksnes et al. 2008). However, even though cascading effects from unexploited intermediate predators have been demonstrated on epiphytes (Moksnes et al. 2008) and seagrasses (Douglass et al. 2007), and protection seems to increase densities of exploited grazers and their consumption on seagrasses (Alcoverro & Mariani 2004, Prado et al. 2008), evidence for cascading effects from top predators to seagrasses (via sea urchins or other grazers) is so far lacking (Alcoverro & Mariani 2004, Valentine et al. 2007, 2008, Prado et al. 2008, present study). Proposed explanations include insufficient time of protection and/or the buffering capacity of seagrasses as shelter (Vanderklift et al. 2007, Prado et al. 2008). Undoubtedly, there is need for further studies including exploited top predators using e.g. correlations in time and space, enclosure/exclosure experiments, and manipulations of habitat complexity in relation to time of protection (see e.g. McClanahan & Graham 2005) to draw safe conclusions about the 'primacy' of top predators (see Heck & Valentine 2007).

Implications for management

Even though predation rates partly explained densities of *Tripneustes gratilla* and protection appears to have beneficiary cascading effect on coral reefs, the relatively large Mombasa and Watamu MPAs appear to provide inadequate protection for seagrasses from sea urchin overgrazing (Alcoverro & Mariani 2002, Zanre & Kithi 2004, present study). Even though these results are striking, they are not unique; similar lack of protection effects on urchin populations have been observed in seagrass beds in the well-protected Chumbe Island Coral Park, Tanzania (F. Lanshammar pers. comm.) and in Spain (Prado et al. 2008). The explana-

tion is probably complex and—at least in Kenya—most likely involves a combination of (1) insufficient time of protection in some areas; (2) ‘spill-in’ of aggregated urchins more or less protected from predation by their size; (3) interactions between low predation pressure and nutrient enrichment from land runoff; and (4) the protection effect of seagrass leaves on urchins. As these factors act across ecosystem and MPA borders (Eklöf et al. 2008, present study), our results indicate the need for more holistic and adaptive management approaches. Most likely, site-specific combinations of MPAs, banned fisheries on and collection of keystone predators, co-managed fishery reserves, and reduction of nutrient input from land runoff will be needed to safeguard the future of seagrass ecosystems and the crucial services they provide.

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