Differential impacts of coral reef herbivores on algal succession in Kenya

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ABSTRACT: In shallow-water systems, fisheries management influences herbivory, which mediates ecosystem processes by regulating algal biomass, primary production, and competition between benthic organisms, such as algae and corals. Sea urchins and herbivorous fishes (scrapers, grazers, browsers) are the dominant herbivores in Kenya's fringing coral reef and their grazing influences coral–macroalgal dynamics and dominance. Using experimental substrata and grazer exclusions, we tested the hypothesis that herbivores differentially affect algal composition and succession using 3 levels of fisheries management: fished reefs, community-managed closures (<10 yr old, <0.5 km²), and government-managed closures (20 to 40 yr old, 5 to 10 km²). In fished reefs and government closures, herbivores facilitated maintenance of early successional algal species, such as turfs, associated with sea urchins in the former and scraping fishes in the latter. Crustose coralline algae were only abundant in government closures, and video recordings showed that fish grazing was greatest at these sites, most notably for parrotfishes (scrapers). A combination of sea urchins and small grazing and detritivorous fishes was present in community closures, which allowed macroalgae to quickly develop from turf into early then late successional stages. These reefs may represent an intermediate or transitional system of herbivore dominance characterized by macroalgae. Consequently, reefs in heavily fished seascapes initially protected from fishing may require additional management efforts to facilitate the recovery of larger-bodied scraping fishes, including bans on capturing parrotfishes and restricting gear (e.g. spearguns) that target these species.

KEY WORDS: Animal–plant interactions · Community-based management · Marine protected area and reserves · Niche replacement · Phase shift · Primary succession · Resilience

INTRODUCTION

In both terrestrial and aquatic systems, herbivory is a key top-down process that mediates the abundance of primary producers and hence overall community composition (Jones 1992, Schmitz et al. 2000, Scheffer et al. 2001, Mumby et al. 2006). On tropical coral reefs, macroalgae compete with corals for space, nutrients, and light, and herbivores may mediate antagonistic interactions between these 2 primary space occupiers (Hay 1997, McCook et al. 2001). A critical factor governing coral reef growth and sustainability

is the maintenance of suitable recruitment space for coral larvae, which is often achieved through high herbivore abundance and low abundance of foliose macroalgae (Mumby 2006). However, herbivore communities are increasingly being affected by overfishing, potentially undermining the ability of reefs to resist a phase shift to dominance by macroalgae (Hughes 1994, McClanahan et al. 2011a) and recover from disturbances (Nugues & Bak 2006, Hughes et al. 2007). Here, transitions to macroalgae generally progress from filamentous turf algae and crustose coralline algae (CCA) to corticated and fleshy macroalgae,

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then to leathery and coarsely branched macroalgae or calcified algae that are unpalatable to most herbivores (Hixon & Brostoff 1996, McClanahan 2000, Diaz-Pulido et al. 2007). Thus, it is important to identify how different herbivores influence algal composition and succession on coral reefs, and what this means in the context of preventing shifts to macroalgal dominance (Hughes 1994, McClanahan et al. 2001, Hoey & Bellwood 2009).

The functional roles herbivores play on coral reefs may reflect their mobility (Sandin & McNamara 2012), feeding preferences (Mantyka & Bellwood 2007), life-history characteristics (Russ & Alcala 1998), or resistance and recovery responses to disturbances, such as fishing and coral bleaching (McClanahan et al. 2007, Graham et al. 2011, McClanahan & Humphries 2012). These traits ultimately affect competition, size, and predation risk, all of which are important factors that influence the distribution and functional role of a herbivore in an ecosystem (Werner & Anholt 1993, Dulvy et al. 2004). In Kenya, scrapers and grazers are fishes that may play similar roles in contributing to coral reef resilience by preventing the establishment of macroalgae and providing areas of clean substratum for coral recruitment (Cheal et al. 2010). Their activities can also facilitate the establishment of CCA, which are important for reef growth (Steneck 1983, McClanahan 1997, O'Leary & McClanahan 2010). Scrapers feed primarily on epilithic algal turf while closely cropping or scraping the reef surface (Bellwood & Choat 1990). Grazers feed on a similar diet to scrapers, and detritivores on a combination of turf, sediment, and plankton; however, grazers and detritivores can have similar impacts on algal dynamics (Marshell & Mumby 2012).

As sea urchins are spatially constrained organisms with different feeding properties from fish, the patterns in algal and coral composition that they are able to mediate may be different from those maintained by fish (O'Leary & McClanahan 2010, O'Leary et al. 2012). Fish are vagile consumers and more wide ranging than sea urchins, with relatively large home ranges (75 to 300 m^2 in the Caribbean; Mumby & Wabnitz 2002), whereas an individual sea urchin may forage within an area of just 1 m^2 on coral reefs (Carpenter 1984). Fish may be selective foragers in these larger areas and select algae based on properties of palatability (Burkepile & Hay 2008), while sea urchins are less selective and select algae primarily on the basis of accessibility (Ogden & Lobel 1978, Sandin & McNamara 2012). This can create a dynamic mosaic of intensely grazed and ungrazed areas on a reef that reflects patchiness in sea urchin

abundance. Overall, herbivorous fishes and sea urchins will likely have quite different effects on community structure and ecosystem functioning on coral reefs.

In Kenya, all herbivorous fish species are heavily and indiscriminately exploited while sea urchins are not (McClanahan et al. 2008). Fisheries closures in Kenya represent a management tool intended to prevent overfishing, which will create reefs with variable herbivore abundances and species assemblages (McClanahan et al. 2007). In this study, we used the rapidly emerging establishment of community-managed fisheries closures together with older government closures and fished reefs as a 'natural experiment' to examine the differential influence of herbivore assemblages on algal succession. To do this, we used survey techniques coupled with regular estimates of algal abundance (percentage cover) on experimental substrata over a ~390 d period. We tested 2 hypotheses: (1) that sea urchins and fishes affect algal abundance differently because of differences in feeding mode, and (2) that algal succession will trace similar paths across fisheries management regimes because herbivorous fishes will gradually replace sea urchins as fishing is eliminated on reefs.

MATERIALS AND METHODS

Study sites

Kenya's coastline is paralleled by a fringing reef and experiences predictable seasonality. The northeast monsoon season occurs from September to March and is characterized by drier weather and moderate rainfall, river discharge, and wind energy, while solar insolation and air temperatures are high (McClanahan 1988). The southeast monsoon season occurs from April to August and is characterized by thick cloud cover, heavy rains, strong winds, large waves, and fast currents.

Data were collected at 6 sites representing 3 fisheries management types along a ~150 km stretch of Kenyan coast: 2 younger and smaller community-managed fisheries closures, 2 older and larger government-managed closures, and 2 heavily fished reefs (Fig. 1). Sites representing these treatments were interspersed. The community closures, Kuruwitu and Mradi, have been protected from fishing since 2005 and 2010, respectively, and are both ~0.3 to 0.4 km^2 in size. The government closures, Mombasa and Malindi, have been protected from fishing since 1991 and 1968, respectively; Mombasa is
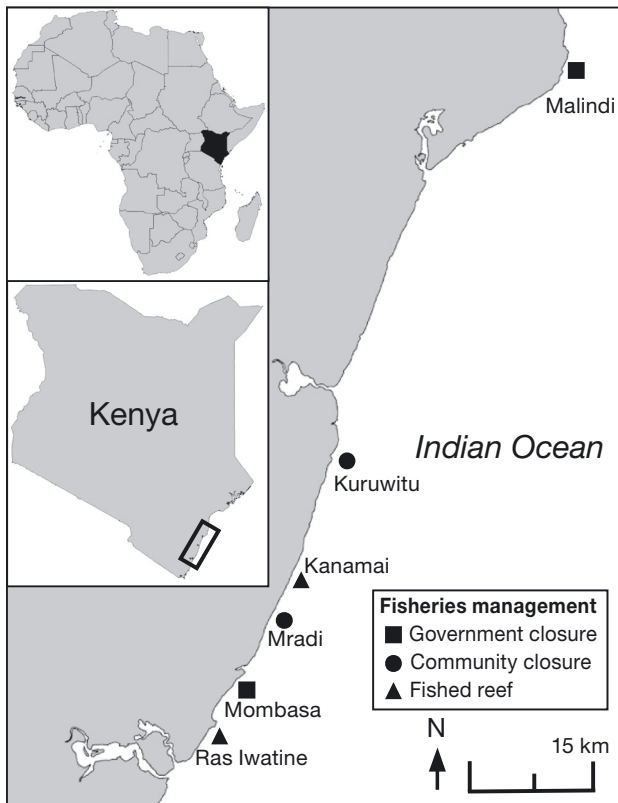
Fig. 1. Study sites located along the coast of east Africa in Kenya. Different shapes represent fisheries management: government closures are no-take zones managed by the Kenya Wildlife Service, community closures are no-take zones managed by fishers, and fished reefs are year-round open access areas

~6 km^2 in size, whereas Malindi is 10 km^2. At the fished reefs, Kanamai and Ras Iwatine, fishing is intense and highly unselective with a variety of gear types being used (e.g. spearguns, nets, traps), while beach seines are not used at Ras Iwatine. Sites included coral and algae-dominated areas in back-reef lagoons that are protected from strong waves.

Existing herbivore and benthic community composition

Sea urchins were identified to the species level and counted in 10 m^2, haphazardly placed plots (n = 9 to 18 site^{-1}). Wet weight was estimated by multiplying average numbers of individuals by average wet weights per species using values from McClanahan & Shafir (1990). Non-herbivorous fishes were counted and identified to family, and size (total length, TL) estimated to the nearest 10 cm by underwater visual census (via snorkel) using 2 to 4 haphazardly placed replicate belt transects (5 × 100 m) per site. Herbivorous fishes were counted and identified to species, and size estimated to the nearest 5 cm TL in separate passes along the same transects. Scarid species (parrotfishes) <10 cm TL were grouped together as 'juveniles' due to the difficulty of identifying them to species in the field. Transects were conducted during neap tides when the water was between ~1 and 4 m deep. Small and cryptic taxa, such as blennies, tobies, and gobies, were recorded but probably underestimated (Ackerman et al. 2004). Mass was determined by converting fish counts to biomass using published length–weight relationships (Letourneur et al. 1998, Froese & Pauly 2006). Herbivorous fishes were assigned to feeding groups (scrapers, grazers, browsers) based on published information on diets (Froese & Pauly 2006, Green et al. 2009). Grazers and detritivores were combined into one functional group because they have been shown to have similar influences on algae (Marshell & Mumby 2012). There were no excavating fishes (parrotfishes >45 cm) at these reefs and therefore all parrotfishes were considered scrapers.

Benthic cover was surveyed using haphazardly placed, 10 m line-intercept transects (n = 9 site^{-1}). The distances covered by major benthic components (hard coral, turf algae, CCA, and erect macroalgae) underlying each transect line were measured to the nearest centimeter. Macroalgae were further identified to the genus level, and percentage cover was calculated as the sum of the lengths divided by the total transect length.

Algal dynamics and succession on experimental substrata

Experimental substrata (algal growth plates) were made from ~2.5 cm cross-sections of dead massive *Porites* coral (mean plate size ± SE was 184 ± 11 cm^2; n = 288 plates). Plates had flat surfaces but irregularly shaped edges. Holes were drilled in individual plates allowing them to be attached to plastic cage flooring. Plates were deployed in sets of 4, attached at least 5 cm apart to the same piece of flooring to form a single replicate. To allow access to the plates by different groups of herbivores, 3 experimental treatments were created: (1) cage treatments, which represented a control (for site-specific differences in environmental variables), or plates that are not grazed by fishes or sea urchins, (2) fence treatments that allowed herbivory only by fishes, and (3) open

treatments that allowed herbivory by both fishes and sea urchins. Cages and fences were made from plastic mesh material (2.5 × 2.5 cm square holes) and attached to bare substratum using U-bolts. Cages were approximately 1 × 1 × 0.5 m (L × W × H) in size. Previous work showed that cages similar to these had no significant effect on algal standing crop or species composition other than the effect of excluding grazers (Scott & Russ 1987). At each reef site, treatments were deployed in 4 blocks, each including 1 replicate from each cage, fence, and open treatment (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m504p119_supp.pdf). Blocks were placed >20 m apart from one another, and treatments within blocks were <3 m apart. Areas for deployment were typical of the larger reef areas and away from damselfish territories.

The experiment began during the northeast monsoon season between September and October 2011. This is a time when bare substratum is most likely to occur because it is just after the seasonal peak in wave energy and most likely to resemble the natural seasonal process of succession (McClanahan 1988, 1997).

The algal communities growing on the plates were digitally photographed at each site every 6 to 8 wk; samples were taken a total of 7 times over the ~390 d duration of the experiment. Photographs were processed and percent composition of algal turf, fleshy algae, calcareous algae, and CCA was determined using a stratified random point-intercept method (n = 50 points plate^{-1}) with digital photography software. Fleshy algae were further identified to the genus level as being *Sargassum*, *Padina*, *Hypnea*, *Dictyota*, *Turbinaria*, *Cystoseira*, or placed in an 'other' category. The approach involved sacrificial pseudoreplication (Hurlbert 1984), and average values of algal cover for the 4 plates within a replicate were subsequently used in the analyses.

Fish feeding impact

To quantify feeding on the algal growth plates, stationary underwater video cameras (GoPro) were used. Cameras were deployed at each site and positioned 1 to 2 m from a haphazardly selected open treatment. Filming commenced and continued without disturbance for ~4 h, and between 15 and 20 repetitions were conducted at each site using different replicates (15 to 20 repetitions × 4 h = 60 to 80 h footage site^{-1}). All video footage was viewed, and the number of bites taken on the plates by each fish species and the sizes (TL) of these fish was recorded and standardized to bites taken per hour. Estimates of fish size were calibrated by placing an object of known length in front of the treatment at the beginning of each video. To account for body size-related variation in the impact of individual bites, a mass-standardized bite impact was calculated as the product of fish body mass and number of bites taken by each fish (Hoey & Bellwood 2009).

Statistical analyses

We used separate 1-way analyses of variance (ANOVAs) to test for an effect of fisheries management (fished, community closure, government closure) on: total fish biomass, herbivorous fish biomass, sea urchin biomass, and herbivorous fish functional group biomass (scrapers, browsers, grazers). Using 2-way ANOVAs, we tested for an effect of fisheries management and treatment (cage, fence, open), and their interaction, on the percentage cover of algal groups on the experimental substrata. Algal groups tested were: algal turf, upright macroalgae (all macroalgal species combined), CCA, *Dictyota*, *Padina*, *Sargassum*, *Turbinaria*, *Hypnea*, and *Cystoseira*. The 'other' macroalgae category was excluded from analyses because it accounted for <3% of overall abundance. Data used in these models were from the first (Day 0) and last sampling event (~Day 390). Site was nested within fisheries management for all models, and where necessary, data were log-transformed to improve the spread of the data and to meet model assumptions of normality and homoscedasticity. We also used 1-way ANOVAs to test for an effect of fisheries management on the feeding impacts of herbivorous fishes (scrapers, browsers, grazers). These models were based on the proportion of mass-standardized bites taken per hour from stationary underwater video recordings. All model diagnostics were performed visually using frequency histograms, funnel plots, and quantile-quantile (Q-Q) plots, and the final models met the assumptions of normality and homogeneity of residuals. Significant models were followed by individual contrasts using Tukey tests to identify pairwise differences.

We estimated grazing strength on upright macroalgae using the natural log-response ratio (LRR; Osenberg et al. 1997). LRRs are a commonly used effect metric because they are amenable to biological interpretation, are proportionally symmetrical, and have a sampling distribution that approximates normality (Hedges et al. 1999). Here, LRRs were calculated as:

$$LRR = \ln\left(\frac{A_C}{A_T}\right) \qquad (1)$$

where A_C is the abundance (% cover) of the cage treatment and A_T is the abundance (% cover) of either the fence or open treatment. Positive LRR values indicate a reduction of macroalgae by consumption, while negative values of LRR indicate that grazers promoted the abundance of macroalgae through fertilization. Zero values of LRR indicate no difference in macroalgal abundance from control (cage) treatments, or no grazing or fertilization effect. We then used 1-way ANOVAs of the LRR values to determine whether there was a significant grazing or fertilization effect at the fence and open treatments.

To determine how treatment and fisheries management affected algal community structure through time, we used a multivariate randomization procedure to create a matrix of Bray-Curtis similarity measures (for the final sampling event as well as one in the middle of the experiment; ~180 and 390 d). We analyzed these distance matrices using permutational analysis of variance (PERMANOVA; n = 999 permutations) and used non-metric multidimensional scaling (MDS) ordination to visualize similarities in algal community structure. We then used correlation-based principal component analysis (PCA) on Euclidean distances with data from the open treatments at the final sampling event. Multivariate homogeneity of the treatments was confirmed using Levene's test for equality of variances (Levene 1960). All data analyses were performed using the program 'R' (v. 2.15.1; R Development Core Team 2013).

RESULTS

Existing herbivore and benthic community composition

The fished reefs, Kanamai and Ras Iwatine, had low abundances of fish, total fish biomass being only 70.6 and 96.5 kg ha^{-1}, respectively. For Kanamai, herbivores comprised 4.6 kg ha^{-1}, or 7.8%, of total fish biomass; for Ras Iwatine they contributed 12.9 kg ha^{-1}, or 13.4% (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m504p119_supp.pdf). Sea urchins were abundant at these 2 sites with a mean biomass of 6095 kg ha^{-1} and 4401 kg ha^{-1} at Kanamai and Ras Iwatine, respectively. At Kanamai, most urchins were *Echinometra mathaei* (4530 kg ha^{-1}), whereas at Ras Iwatine most were *Echinothrix diadema* (2956 kg ha^{-1}).

The community closures, Kuruwitu and Mradi, had more fish biomass but fewer urchins than the fished reefs. Kuruwitu had a total fish biomass of 364 kg ha^{-1} and a sea urchin biomass of 2591 kg ha^{-1}, whereas Mradi had 440 kg ha^{-1} of fish and 2664 kg ha^{-1} sea urchin biomass. At Kuruwitu, herbivores accounted for 49% of the total fish biomass, or 178 kg ha^{-1}. The majority of these herbivores were grazers with <10% being browsers or scrapers. Sea urchins at Kuruwitu were mostly either *Diadema* spp. or *Echinometra mathaei*. Mradi had 209 kg ha^{-1} of herbivorous fishes, forming 47% of its total fish biomass. Much like Kuruwitu, the majority of the herbivorous fishes at Mradi were grazers, with <5% being browsers or scrapers. The sea urchin community at Mradi consisted of mostly *Echinothrix diadema* (1272 kg ha^{-1}).

Mombasa and Malindi, the government closures, had the highest fish biomass and lowest sea urchin biomass. Mombasa had a mean fish biomass of 954 kg ha^{-1}, with 460 kg ha^{-1} of that being herbivores, or 48%. Herbivorous fishes at Mombasa were dominated by browsers (187 kg ha^{-1}), followed by grazers (161 kg ha^{-1}), and scrapers (112 kg ha^{-1}). Malindi had the highest fish biomass of all sites with 1165 kg ha^{-1}, of which 578 kg ha^{-1}, or almost 50% were herbivores. Herbivorous fish functional groups were somewhat evenly distributed at Malindi, with biomass ranging between 120 and 172 kg ha^{-1}. The sea urchin community at Mombasa was composed of mostly *Echinothrix diadema* and had an overall biomass of 1411 kg ha^{-1}. With a total biomass of 60 kg ha^{-1}, Malindi had the fewest sea urchins of any site.

Existing benthic cover varied among sites and fisheries management, with the highest hard coral and lowest macroalgal cover at Mradi and Kanamai (hard coral: 46 and 34.8%, macroalgae: 8.5 and 0.9%, respectively; Table 1). Ras Iwatine had the lowest hard coral abundance with 7.1%, and Mombasa had the highest macroalgal abundance with 25.7%. CCA was highest at Malindi with 20.4% cover. Algal turf abundance was highest at the fished reefs, Kanamai and Ras Iwatine, with >42% cover. Macroalgal genera varied by site and management; *Sargassum* was most abundant at Mombasa (23.2%) and *Turbinaria* was most abundant at Malindi (9%). Other macroalgal genera comprised never >5% of cover at sites.

Model results indicated significant differences among all fisheries management types for the biomass of all fish and herbivorous fish (p < 0.01 in all cases; Table 2). Although sea urchins generally decreased in biomass as fish increased, the difference was only statistically significant when comparing fished reefs to government closures (p = 0.021).
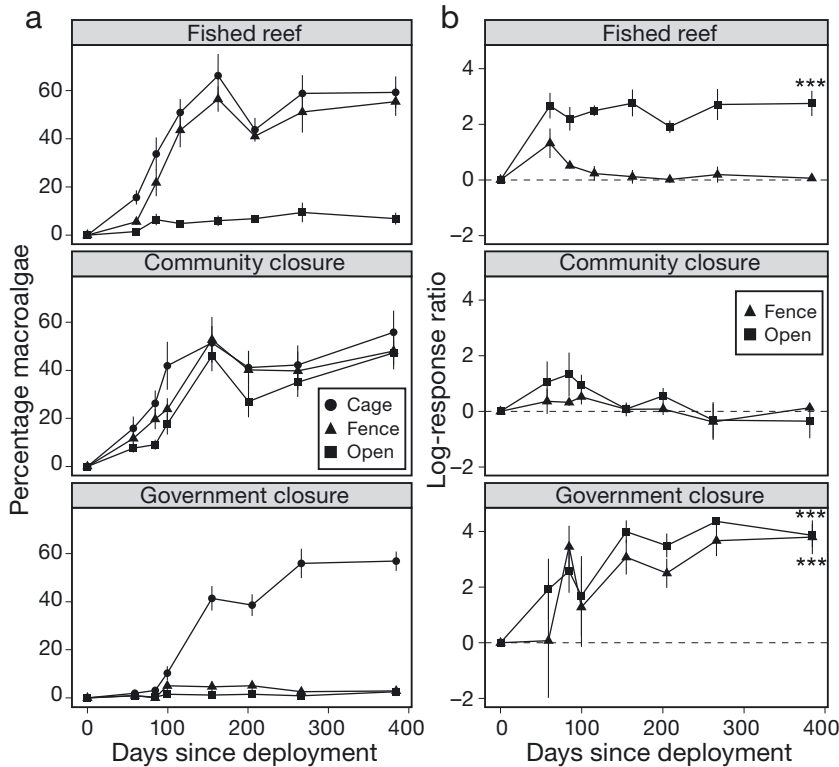
Fig. 2. Time series of the mean (±SE) (a) percentage cover of macroalgae and (b) log-response ratio (LRR) on the experimental substrata over ~390 d by treatment (cage, fence, open) and fisheries management type. Positive values of LRR indicate a reduction of macroalgal abundance by consumption, negative values of LRR indicate that grazers promote the abundance of macroalgae through fertilization, and zero values indicate no difference in macroalgal abundance from control (cage) treatments. ***p < 0.001 (from ANOVAs of the final sampling event)

Scraper and browser fish biomass was significantly higher at government closures, but there was no difference between fished reefs and community closures (Table 2). Grazer fish biomass was significantly

higher at government closures and community closures when compared with fished reefs, but there was no significant difference between government and community closures (Table 2). Fisheries management was a poor predictor (p > 0.05) for most benthic categories, with the exception of algal turf (which was more abundant at fished sites than in both types of closures), and CCA (which was more abundant at government closures than in other management types) (Table S2). Macroalgal genera did not differ by management type except for *Turbinaria*, which was more abundant at government closures.

Algal dynamics and succession on experimental substrata

Percentage cover and LRRs of total upright macroalgae showed distinct trends through time among treatments and fisheries management types (Fig. 2); however, responses of individual macroalgal genera were less clear through time (Fig. 3). CCA cover (open treatments only) was significantly greater at the government closures than other management types (p < 0.001) and increased through time to reach an overall percentage cover >20% (Fig. 4).

Two-way ANOVAs revealed a significant interaction term for 6 of the 9 algal groups, indicating that

Table 1. Mean abundance (% cover ± SE) of the major substratum categories and macroalgal genera at each of the 6 study sites and by fisheries management type

| | Fished reef | | Community closure | | Government closure | |
	Kanamai	Ras Iwatine	Kuruwitu	Mradi	Mombasa	Malindi
Major substratum						
Hard coral	34.77 ± 6.79	7.1 ± 4.56	26.17 ± 8.38	46.01 ± 13.12	20.23 ± 10.08	27.17 ± 14.77
Algal turf	42.6 ± 9.48	42.80 ± 12.77	37.33 ± 13	21.05 ± 16.59	33.18 ± 12.60	24.86 ± 15.49
Macroalgae	0.93 ± 2.01	13.88 ± 11.62	12.44 ± 7.82	8.50 ± 6.27	25.73 ± 7.95	9.30 ± 6.34
Crustose coralline algae	1.77 ± 2.06	8.56 ± 2.61	3.18 ± 2.47	10.21 ± 5.35	13.16 ± 6.17	20.44 ± 7.94
Macroalgal genus						
Cystoseira	0 ± 0	0 ± 0	1.57 ± 1.24	0.25 ± 0.25	0 ± 0	0 ± 0
Dictyota	0.03 ± 0.05	1.25 ± 1.40	0.75 ± 0.54	1.21 ± 0.02	0.45 ± 0.35	0.09 ± 0.13
Hypnea	0.04 ± 0.06	1.35 ± 0.54	0.41 ± 0.37	3.62 ± 2.53	0 ± 0	0.1 ± 0.0
Padina	0.25 ± 0.16	3.63 ± 0.37	1.00 ± 0.81	1.24 ± 0.20	0.03 ± 0.04	0 ± 0
Sargassum	0.07 ± 0.10	7.11 ± 1.37	4.93 ± 1.37	0.67 ± 0.67	23.17 ± 2.66	0 ± 0
Turbinaria	0.50 ± 0.53	0.52 ± 0.37	1.00 ± 0.11	0.83 ± 0.83	1.95 ± 0.03	9.04 ± 2.24

Table 2. Pairwise comparisons of fish and sea urchin communities by fisheries management type (fished reefs, community closures, government closures) from ANOVAs of biomass (kg ha^{-1}) data. All fish represent both herbivorous and non-herbivorous fishes. Sea urchin data were log-transformed to meet assumptions of normality and homoscedasticity. *p < 0.05, **p < 0.01, ***p < 0.001

	Estimate	Z	p
All fish			
Fished vs. government	−976.00	−12.87	***
Community vs. government	−657.28	−8.67	***
Community vs. fished	318.72	4.20	**
Sea urchin			
Fished vs. government	2.93	3.46	*
Community vs. government	2.26	2.47	0.088
Community vs. fished	−0.67	−0.73	0.751
Herbivorous fish			
Fished vs. government	−508.76	−14.83	***
Community vs. government	−324.34	−9.45	***
Community vs. fished	184.42	5.38	***
Scraper			
Fished vs. government	−111.01	−7.71	***
Community vs. government	−106.83	−7.42	***
Community vs. fished	4.18	0.29	0.955
Browser			
Fished vs. government	−183.65	−6.38	***
Community vs. government	−165.58	−5.75	***
Community vs, fished	18.07	0.63	0.809
Grazer			
Fished vs. government	−214.10	−6.91	***
Community vs. government	−51.93	−1.68	0.266
Community vs. fished	162.17	5.23	***

significant effects (p < 0.05) of treatment type on the abundance of algal groups depend on the fisheries management regime (Table S3). This trend was true for all groups except *Turbinaria*, *Hypnea*, and *Padina*.

At the fished reefs, succession of macroalgal genera in the cage and fence treatments mostly began with *Padina* and *Hypnea* dominating the assemblage, but transitioned into a more mixed assemblage with increasing cover of *Sargassum* as the experiment progressed (Fig. 3). Total upright macroalgae in the cage and fence treatments reached and remained around or above 40% cover after ~100 d (Fig. 2a). The open treatment at these sites developed very little macroalgal cover through time, remaining consistently at or below ~10%. There were slight fluctuations in percentage cover in the cage and fence treatments around ~210 d, when the stronger winds and currents of the southeast mon-

soon season may have caused a reduction in the already established macroalgal community. The ANOVA by treatment for percentage cover of total upright macroalgae was significant (F = 19.31; p < 0.01), and pairwise comparisons indicated that the fence and cage treatments at the fished reefs were not significantly different from one another (p = 0.894); however, open treatments were significantly lower than both fence and cage treatments (p < 0.001; Table S4). The ANOVAs of LRRs corroborated these findings with a significant grazing effect on total upright macroalgae at the open treatment (F = 36.31; p < 0.001), but not the fence treatment at the fished reefs (F = 0.62; p = 0.443; Fig. 2b).

Padina and *Hypnea*, with *Sargassum* and *Cystoseira*, dominated succession of macroalgal genera for all treatments at the community closures and increased through time (Fig. 3). Total upright macroalgae in all treatments traced similar successional trajectories; there was an immediate increase in total upright macroalgae at all treatments that reached the highest levels around ~150 d, and then again at the end of the experiment at ~50% cover (Fig. 2a). Similar to the fished reefs, there was a slight decrease in percentage cover between ~200 and ~300 d, most likely due to seasonal monsoon effects. The ANOVA by treatment for percentage cover of total upright macroalgae was not significant (F = 1.16, p = 0.532; Table S4), and LRRs corroborated this finding with no significant grazing or fertilization effect (open: F = 0.33, p = 0.577; fence: F = 1.46, p = 0.247; Fig. 2b).

At the government closure sites, succession of macroalgal genera in cage treatments began mostly with *Padina*, *Cystoseira*, and *Hypnea*, then transitioned into a mixed assemblage, with *Sargassum* becoming dominant and *Turbinaria* present (Fig. 3). Total upright macroalgae in the cage treatments increased and were at or above ~40% cover after ~150 d (Fig. 2a). Total upright macroalgae in the fence and open treatments remained low for the duration of the experiment, and percentage cover never exceeded ~10%. The ANOVA by treatment for percentage cover of total upright macroalgae was significant (F = 30.87; p < 0.001), and pairwise comparisons indicated a significant difference between both the open and fence treatments with the cage treatment (p < 0.001); however, fence and open treatments were not significantly different from one another (p = 0.997; Table S4). The ANOVAs of LRRs corroborated these findings and indicated a significant grazing effect of total upright macroalgae in both fence (F = 38.97; p < 0.001) and open treatments (F = 83.22; p < 0.001; Fig. 2b).
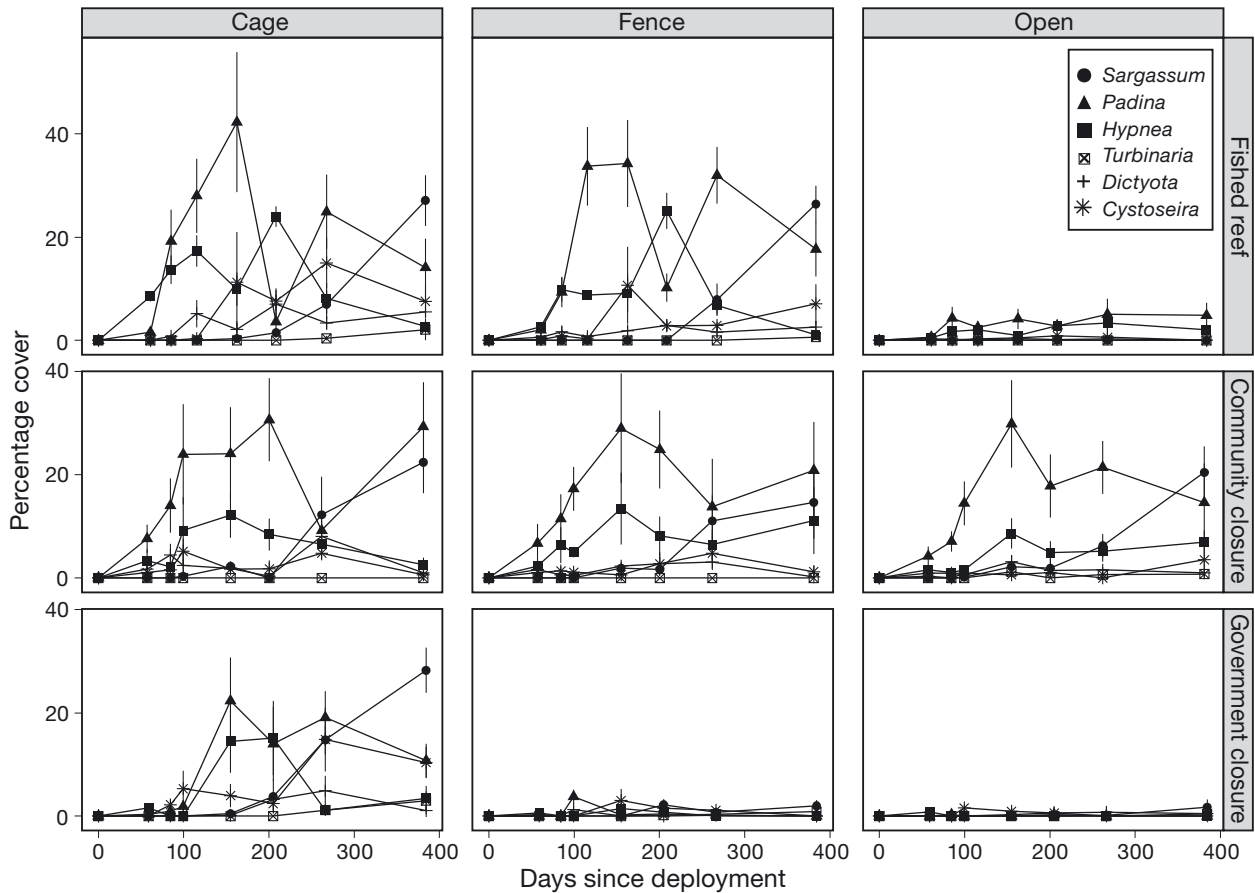
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Fig. 3. Time series of mean percentage cover (±SE) of macroalgal genera by treatment type (cage, fence, open) and fisheries management type (fished reefs, community closures, government closures) on experimental substrata at 6 study sites in Kenya over ~390 d. If the total percentage cover is <100, the remaining algal cover is turf
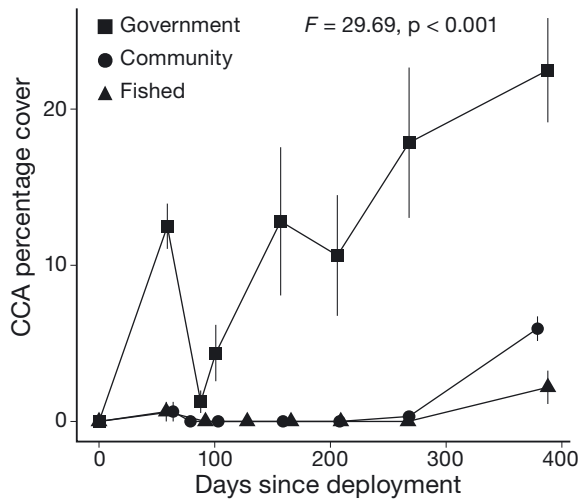

Fig. 4. Time series of mean percentage cover (±SE) of crustose coralline algae (CCA) by fisheries management type (fished reefs, community closures, government closures) on experimental substrata over ~390 d. Data are from open treatments only. ANOVA results from the comparison of management types are for the final sampling event

Results from MDS showed that algal community structure in the cage treatment had a high variance and sites failed to cluster by fisheries management in axis space at either ~180 or ~390 d (Fig. S2). Model results indicated poor explanatory power of these plots, and the results were not significant (~180 d: $R^2 = 0.123$, p = 0.205; ~390 d: $R^2 = 0.120$; p = 0.203). For the fence treatment, there was a differentiation among all 3 fisheries management types at both ~180 and ~390 d. This was driven by the presence of turf algae at government closures, and macroalgae at community closures and fished reefs. These plots explained >40% of the variation in the models and, although explanatory power was low, both were significant (~180 d: $R^2 = 0.407$, p < 0.001; ~390 d: $R^2 = 0.464$, p < 0.001). The open treatment showed the clearest effect of management type. Government closures and fished reefs tended to cluster together, being characterized by algal turf and, in the case of government closures, CCA, whereas community closures were different, with a high abundance of

macroalgae at both ~180 and ~390 d. Model results indicated stronger explanatory power for these plots, with >50% of the variance explained by the model (~180 d: R^2 = 0.562, p < 0.001; ~390 d: R^2 = 0.498, p < 0.001; Fig. S2).

The first principal component axis (PC1) of the PCA differentiated fisheries management by herbivore group, with fishes (scrapers, browsers, grazers) at negative PC1 scores and sea urchins at positive PC1 scores (Fig. 5). The second principal component axis (PC2) differentiated fisheries management along a gradient from algal communities, with turf and CCA at negative PC2 scores, to those with macroalgae at positive PC2 scores. PCA results show overlap and suggest fisheries management mediated algal assemblages through herbivore composition: turf algae were representative of fished reefs because of sea urchins; turf algae and CCA were representative of government closures because of scrapers (and browsers); and macroalgae dominated in community closures because of intermediate levels of sea urchins and the presence of very few scrapers and browsers.

Fish feeding impact

Feeding on the algal growth plates was dominated by grazers, which accounted for 75% of all mass standardized bites (Fig. S3). Most bites occurred at the government closures, where fish of 16 to 20 cm TL had the greatest contribution. Scrapers accounted for nearly 22% of all mass standardized bites, and these were caused primarily at the government closure sites by fish between 16 and 25 cm TL. Browsers accounted for <3% of all mass standardized bites on the plates. Model results indicated a significant effect of fisheries management on the bite impact of scrapers (F = 195.15; p < 0.001) and grazers (F = 66.18; p < 0.001), but not browsers (F = 0.61; p = 0.434). However, it should be pointed out that the algal growth plates within government closures experienced high rates of grazing by scraping and grazing fishes and thus had little upright macroalgae. Even though browsing herbivorous fishes were abundant within the government closures, one would expect low rates of herbivory by browsers under such circumstances (i.e. due to a lack of preferred food), so the lack of effect of management on browser herbivory would be expected. Pairwise comparisons showed that all contrasts between fisheries management types were significant for both scrapers and grazers (p < 0.05; Table S5).
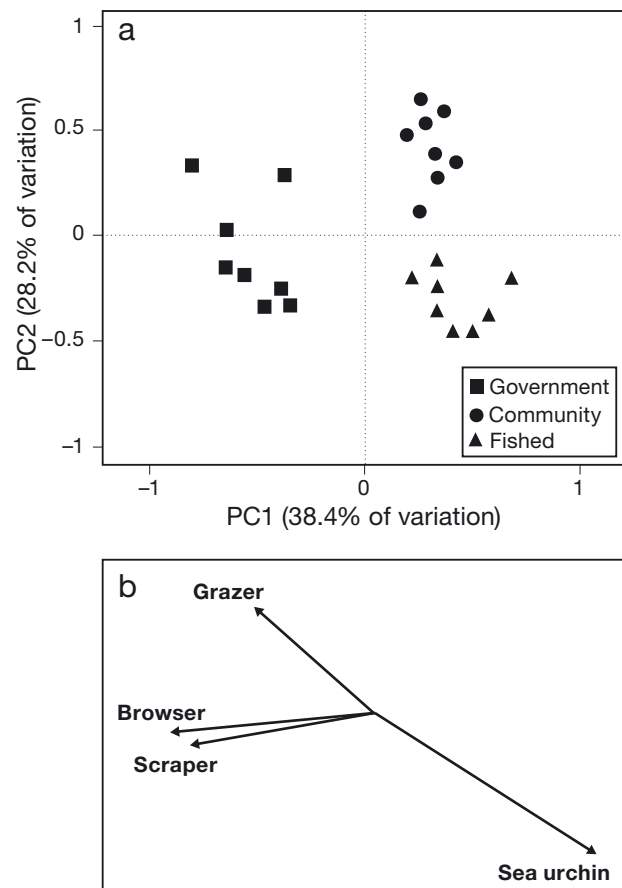

Fig. 5. (a) Spatial variation in algal composition on experimental substrata and (b) relative contribution of herbivores using principal component analysis (PCA) on Euclidean distances. Data points represent open treatments (herbivory by sea urchins and fishes) ~390 d after deployment, and different shapes represent fisheries management type (fished reefs, community closures, government closures). Points that are closer together in ordination space are more similar in terms of algal community

DISCUSSION

Patterns of algal succession on the experimental substrata followed different trajectories in the presence and absence of herbivores and according to management type. Specifically, the results were linked to the grazer assemblages found at the sites under different management regimes: larger scraping (and browsing) fishes were associated with algal turfs and CCA at the older and larger government closures, and sea urchins co-occurred with turfs at the fished reefs. The younger community-managed fisheries closures had intermediate levels of sea urchins and mostly grazer fishes, which allowed algae to quickly transition from turf into assemblages

dominated by fleshy macroalgae. Here, macroalgae that became established early primarily comprised *Hypnea* and *Padina*, followed by a late stage dominated by *Sargassum* and some *Turbinaria*. These particular reefs may represent a transitional system of herbivore dominance that exists prior to the full recovery of fish biomass and larger-bodied scrapers in no-take fisheries closures. These results provide further support for other studies that have identified differential grazing effects between sea urchins and fishes (Ogden & Lobel 1978, McClanahan 1997, O'Leary & McClanahan 2010). This study also highlights the importance of herbivore species composition, biomass, and feeding impact in preventing algal turf from transitioning to early and then late successional macroalgae species that may be detrimental to coral growth (Rasher & Hay 2010). Furthermore, creating a complementary grazing guild that is able to prevent macroalgae proliferation (Burkepile & Hay 2010) may not be achieved immediately after establishment of fisheries closures.

In the absence of sea urchin and fish grazing, as well as in treatments with low levels of grazing, algal succession over the ~390 d generally progressed from turf to an early dominance by blades and finely branched brown and red algae, including *Padina* and *Hypnea*. Following these macroalgae were coarsely branched and leathery macroalgae, such as *Sargassum* and *Turbinaria*. This trend is mediated by competitive interactions and life-history characteristics of algae that reflect a species' growth, reproduction, and survival rate (Grime 1977, Huston & Smith 1987, Duffy & Hay 1990). The results here agree with life-history theory and findings from similar experiments in other regions (e.g. Carpenter 1986, Hixon & Brostoff 1996, Ceccarelli et al. 2011), indicating that early successional algae invest energy in continuous rapid growth and invade newly opened space first, rather than investing in costly structural and chemical defenses that may mean slower rates of establishment (Duffy & Hay 1990). A concern for reefs containing a high abundance of these late successional species is that stabilizing feedbacks will strengthen the macroalgae state because they are unpalatable to the majority of herbivores (Hay 1991). This may prevent successful coral recruitment (Kuffner et al. 2006) and compromise reef growth and sustainability (McCook et al. 2001). Preventing algal shifts to dominance by unpalatable macroalgae in this experiment was ultimately dependent on the ability of sea urchins or groups of large-bodied fishes (i.e. scrapers) to maintain a surface of cropped or calcified algae.

In this study, macroalgae colonized substrates rapidly in all treatments where grazing was absent, and reached levels of ~55 % cover within 100 d. These rates are similar to, or slightly greater than, those found in previous experiments at Australian (Great Barrier Reef) and Hawaiian reefs (Hatcher & Larkum 1983, Scott & Russ 1987, Hixon & Brostoff 1996, Smith et al. 2010), but ~20 % lower than those at Caribbean reefs (Carpenter 1986, Morrison 1988, Sotka & Hay 2009, Ferrari et al. 2012). The number of macroalgal genera also remained relatively high in this experiment at ungrazed treatments, even at the end of the sampling period, compared with other studies. Differences among regions and reefs most likely occur because of biogeographic differences in algal species composition, or differential rates of algal recruitment mediated by surrounding conditions (e.g. UV radiation), propagule dispersal, and herbivore community composition (Stiger & Payri 1999, Vermeij et al. 2013). Differences in physical forces, such as waves and tides, may also contribute to the heterogeneity between regions, as these factors can sometimes have a stronger effect than herbivory on algal communities (Gaylord et al. 2002, Lefèvre & Bellwood 2010, Ferrari et al. 2012). Therefore, the specific herbivory levels needed to prevent shifts to macroalgal dominance may be region or site specific, and dependent on local physical and spatial factors (Lefèvre & Bellwood 2010, Roff & Mumby 2012).

While the mechanisms by which fishing structures communities may differ among harvesting methods, regions, or ecosystems, understanding the recovery patterns of herbivores can help with conservation and harvest models aimed at increasing reef resilience to phase shifts (Halpern & Warner 2002, Gaylord et al. 2005). At the reefs in this study area, herbivore composition is primarily a function of fishing intensity (McClanahan et al. 2007). For instance, at heavily fished reefs, sea urchins have few predators and biomass can exceed 4000 kg ha^{-1} (McClanahan 1997). The absence of urchin predators is mediated by the removal of large invertebrate-feeding fish species, such as the triggerfish *Balistapus undulatus* (McClanahan 2000). When fishing is reduced or eliminated, fish biomass may exceed 1200 kg ha^{-1}, and sea urchins can drop to <60 kg ha^{-1} (McClanahan 1997). At these 2 extremes of fisheries management and herbivore dominance, we found herbivory to be high on the experimental substrata, which were dominated by algal turf (and CCA at the older government closures). We did, however, find that relatively young (<10 yr since protection) and small (<0.5 km^2) community closures had herbivore com-

munities somewhere between the extremes, with a mixture of sea urchins and fishes. The slow recovery of herbivorous fish biomass, and in particular scraping parrotfishes, in these younger closures led to herbivory levels that were insufficient to prevent macroalgae from establishing and overtaking algal turf, eventually resulting in >50% cover. This does not necessarily mean community closures are ineffective management tools and may never have the grazing potential to prevent macroalgal dominance, but they may need more time to develop to be efficient conservation strategies in this area.

If results from these experiments represent reefscale patterns, then *in situ* algal abundance should be low at the fished sites and within the government closures (due to high sea urchin and fish grazing, respectively), and should be high within the community closures. Fleshy algae, however, developed on experimental substrata at sites where they were uncommon on existing substratum (Kuruwitu, Mradi), and vice versa (Mombasa). Mradi had only 8.5% macroalgal cover at the site, but macroalgae quickly established on the experimental plates and moved into a late-successional assemblage consisting of larger, canopy-forming species such as *Sargassum* by the end of the experiment. This discrepancy may be a result of the extremely high coral cover at Mradi (it was more than double that of most of the other study sites) and indicates the site is nearing a threshold where any increase in substratum availability has the potential to enter a macroalgae-dominated state (Steneck & Dethier 1994, Williams et al. 2001). At Mombasa, experimental plates experienced very little macroalgal cover throughout the experiment, which is in contrast to existing conditions of 25% macroalgal cover, consisting primarily of *Sargassum*. Such discrepancies could be a result of previous events at the site where macroalgae were released from grazing pressure and able to develop into a late successional stage consisting of species resistant to herbivory (e.g. 1998 mass coral-bleaching event; McClanahan et al. 2001). Both of these examples stress the importance of the interaction between the histories of sites and existing herbivore assemblages, and how the timing of disturbances may be especially important in determining benthic conditions (Graham et al. 2013). Additionally, algal growth studies such as this one may reflect processes that can establish patterns and not processes that maintain algal distributions.

Grazing by sea urchins in this study prevented the development of fleshy macroalgae; however, sea urchins can have reef erosion rates greater than herbi-

vory rates (Carreiro-Silva & McClanahan 2001) and prevent the establishment of CCA (O'Leary & McClanahan 2010). This can result in the loss of key services such as the creation of new reef material through calcification, stabilization of reefs through the binding of coral rubble, and a reduction in chemical cues important for coral recruitment (Bak 1976, Morse & Morse 1996, O'Leary et al. 2012). In this study, fishing on fished reefs may have increased the ability of reefs to resist the establishment and proliferation of macroalgae; however, trade-offs with increased rates of bioerosion should also be considered in the context of reef sustainability and growth.

The establishment of fisheries closures with no additional management action (e.g. gear restrictions) may be insufficient to facilitate the recovery of herbivore populations in some areas, and fishing intensity around closures is likely to be a major factor in the success of closures (Côté et al. 2001, Lester et al. 2009, McClanahan et al. 2009, Pollnac et al. 2010, Daw et al. 2011). Large herbivores have slow recovery times from fishing (Abesamis & Russ 2005, McClanahan et al. 2007), and these fish are particularly important for herbivory on a reef (Lokrantz et al. 2008). For example, parrotfishes (family Scaridae) >20 cm take more than 20 yr to recover (McClanahan et al. 2007) and have a disproportionate impact on algal grazing (Lokrantz et al. 2008). Thus, it is not possible to infer the full benefits of community closures from this study since both study sites (Kuruwitu and Mradi) are <10 yr old and parrotfish populations have not fully recovered. One solution to prevent macroalgal phase shifts here could be to complement fisheries closures with alternative management strategies (e.g. gear restrictions), especially when the herbivorous fish communities have already been decimated. For example, removal of certain types of nets (i.e. beach seine) may aid in fish recovery by allowing juveniles and adults time to disperse and shorten the period required for fish to return to reefs in surrounding fisheries closures (Öhman et al. 1998). The herbivore community would then only be able to maintain a macroalgae-free reef once it is beyond a grazing threshold, and this threshold will vary amongst locations (Williams & Polunin 2001, Mumby et al. 2007).

The recovery of herbivores in fisheries closures may have lasting effects on coral reef functioning by influencing algal succession (Hoey & Bellwood 2011, McClanahan et al. 2011b). Our data show that large-bodied parrotfishes are vital in preventing dominance by unpalatable macroalgae where fishing is prohibited. However, if a reef has only large scraping

herbivores and no sea urchins or small grazing fishes, macroalgae may still become established (Cheal et al. 2010). Consequently, each herbivore has an important role on the reef that contributes to complementary grazing and the prevention of macroalgal phase shifts (Burkepile & Hay 2008, 2010, 2011); while large-bodied scraping herbivores are important (Mumby 2006), so are small ones and other functional groups, such as grazers and sea urchins (Ogden & Lobel 1978, McClanahan & Shafir 1990, Ceccarelli et al. 2011). At reefs where smaller grazers and sea urchins are dominant, such as the community closures in this study, additional time or management strategies (e.g. gear restrictions) may be necessary to prevent a transition from turf to early and then late successional macroalgae that are better defended against herbivory and erode reef functioning.

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Differential impacts of coral reef herbivores on algal succession in Kenya

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Supplement. Additional survey data for herbivore communities, as well as model results, study sites, and experimental design.

Table S1. Mean (with SE) herbivorous fish biomass (kg ha^{-1}) at each study site by fisheries management type. Fish family, species, and functional grouping are also shown. Detritivores were grouped with grazers because their influence on algae is similar (Marshell & Mumby 2012).

Family	Species	Functional group	Fished reefs		Community closure		Government closure	
			Kanamai	Ras Iwatine	Kuruwitu	Mradi	Mombasa	Malindi
Acanthuridae	*Ctenochaetus striatus*	Grazer	0 (0)	3.7 (0.1)	89.1 (8.5)	105.2 (2.6)	39.8 (4.5)	123.2 (9.8)
	Acanthurus nigrofuscus	Grazer	0 (0)	0.9 (0.9)	0 (0)	67.7 (4.1)	38.8 (38.8)	56.1 (22.8)
	Zebrasoma scopas	Grazer	0 (0)	0 (0)	0 (0)	1.5 (1.5)	56.4 (21.1)	26.9 (17.4)
	Naso annulatus	Browser	0 (0)	0 (0)	0 (0)	2.5 (2.5)	3.5 (3.5)	22.5 (10.2)
	Acanthurus triostegus	Grazer	0.9 (0.9)	0 (0)	57.3 (2.1)	0 (0)	0 (0)	0 (0)
	Zebrasoma veliferum	Grazer	0 (0)	0 (0)	0 (0)	0 (0)	5.5 (5.5)	0 (0)
	Acanthurus leucosternon	Grazer	0 (0)	0 (0)	0 (0)	7.1 (7.1)	9.1 (2)	55.3 (15.9)
	Ctenochaetus strigosus	Grazer	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)
	Acanthurus nigricauda	Grazer	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	7.3 (2.6)
	Acanthurus dussumieri	Grazer	0 (0)	0 (0)	0 (0)	0 (0)	5.5 (5.5)	9.7 (0.2)
	Naso lituratus	Browser	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	15.8 (2.8)
	Naso unicornis	Browser	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	10.5 (6.8)
Labridae	*Chlorurus sordidus*	Scraper	0 (0)	0 (0)	13.5 (13.5)	2.1 (2.1)	95.1 (25.5)	29.7 (2.6)
	Scarus ghobban	Scraper	0 (0)	3.5 (2.1)	0 (0)	0 (0)	0 (0)	29.2 (11.2)
	Calotomus carolinus	Browser	0 (0)	0 (0)	0 (0)	5.6 (1.4)	92.2 (46.9)	46.4 (10.2)
	Scarus frenatus	Scraper	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	9 (9)
	Scarus psittacus	Scraper	0 (0)	2.8 (2.8)	0 (0)	0 (0)	0 (0)	12.6 (3.6)
	Scarus niger	Scraper	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	16.6 (7.6)
	Scarus rubroviolaceus	Scraper	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	22.1 (14)
	Hipposcarus harid	Scraper	0 (0)	0 (0)	0 (0)	0 (0)	15.1 (15.1)	0 (0)
	Leptoscarus vaigiensis	Browser	0 (0)	0 (0)	7.8 (0.8)	3.5 (3.5)	24.9 (9.9)	26.1 (10)
	Juvenile sp (< 10cm)	Scraper	3.7 (3.3)	0.2 (0.1)	1.4 (1)	1.6 (0.5)	2 (0.9)	0.8 (0.5)
Pomacanthidae	*Centropyge multispinis*	Grazer	0 (0)	0 (0)	0 (0)	4.9 (1.4)	6.3 (3.2)	7.4 (1.9)
Siganidae	*Siganus sutor*	Browser	0 (0)	1.8 (1.8)	8.7 (5)	2.8 (0.9)	0 (0)	24 (24)
	Siganus argenteus	Browser	0 (0)	0 (0)	0 (0)	0 (0)	61.2 (26.9)	15 (15)
Ephippidae	*Platax teira*	Browser	0 (0)	0 (0)	0 (0)	2.1 (2.1)	1.1 (1.1)	0 (0)
Kyphosidae	Kyphosus vaigiensis	Browser	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	9.7 (3.4)
Total			4.6 (4.2)	12.9 (5.8)	177.7 (24.7)	208.6 (2)	456.6 (44.7)	578.9 (23.6)

Table S2. Results from ANOVAs used to evaluate the effect of fisheries management type (fished reefs, community closure, government closure) on the existing abundance of major substratum groups and macroalgae genera. $*p < 0.05$.

Major substratum	F-value	p-value
Hard coral	1.64	0.247
Algal turf	7.55	*
Macroalgae	1.51	0.272
CCA	6.22	*

Macroalgal genus	F-value	p-value
Cystoseira	2.90	0.107
Dictyota	1.85	0.212
Hypnea	1.62	0.248
Padina	2.53	0.135
Sargassum	1.23	0.337
Turbinaria	4.90	*

Table S3. Results from 2-way ANOVAs used to evaluate the effects of fisheries management type (fished reefs, community closures, government closures) and treatment (cage, fence, open) on algal percentage cover at the dead-coral plates using algal percentage cover data on experimental substrata. Data used in the models were from the first (day 0) and last sampling events (~day 390). ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

Algal turf	df	F-value	p-value	Upright macroalgae	df	F-value	p-value	CCA	df	F-value	p-value
(Intercept)	1	1029.02	***	(Intercept)	1	413.67	***	(Intercept)	1	23.21	***
Management	2	14.11	***	Management	2	26.70	***	Management	2	11.72	***
Treatment	2	27.20	***	Treatment	2	39.15	***	Treatment	2	5.22	**
Management x Treatment	4	9.51	***	Management x Treatment	4	12.54	***	Management x Treatment	4	2.57	*

Hypnea	df	F-value	p-value	*Dictyota*	df	F-value	p-value	*Padina*	df	F-value	p-value
(Intercept)	1	15.69	***	(Intercept)	1	40.11	***	(Intercept)	1	42.65	***
Management	2	4.88	**	Management	2	11.43	***	Management	2	8.17	**
Treatment	2	0.21	0.810	Treatment	2	8.84	***	Treatment	2	3.19	*
Management x Treatment	4	1.79	0.142	Management x Treatment	4	6.18	***	Management x Treatment	4	0.58	0.681

Sargassum	df	F-value	p-value	*Turbinaria*	df	F-value	p-value	*Cystoseira*	df	F-value	p-value
(Intercept)	1	120.13	***	(Intercept)	1	6.67	*	(Intercept)	1	20.56	***
Management	2	4.22	**	Management	2	0.95	0.392	Management	2	1.50	0.230
Treatment	2	14.69	***	Treatment	2	1.68	0.195	Treatment	2	4.30	*
Management x Treatment	4	6.06	***	Management x Treatment	4	0.84	0.504	Management x Treatment	4	3.78	**

Table S4. Pairwise comparisons between treatments (cage, fence, open) by fisheries management type (fished reefs, community closures, government closures) of total upright macroalgae (% cover) on experimental substrata. Data are from the final sampling event (~390 days since deployment). ***p < 0.001, **p < 0.01, *p < 0.05

Fished reefs	Estimate	Z-value	p-value
Fence vs. Cage	-2.81	-0.45	0.894
Open vs. Cage	-54.35	-8.74	***
Open vs. Fence	-51.54	-8.28	***

Community closure	Estimate	Z-value	p-value
Fence vs. Cage	-11.18	-1.35	0.370
Open vs. Cage	-10.68	-1.28	0.404
Open vs. Fence	0.51	0.06	0.998

Government closure	Estimate	Z-value	p-value
Fence vs. Cage	-53.35	-14.40	***
Open vs. Cage	-53.59	-15.39	***
Open vs. Fence	-0.24	-0.07	0.997

Table S5. Pairwise comparisons between fisheries management types (fished reefs, community closures, government closures) by herbivorous fish functional group (scrapers, browsers, grazers) of mass standardized bite impact (kg $\times$ bites h^{-1}) on experimental substrata using stationary underwater video. Data were log-transformed to satisfy the assumptions of homogeneity of variances and normality of residuals. *p < 0.05, **p < 0.01, ***p < 0.001

Scraper	Estimate	Z-value	p-value
Fished vs. Government	-2.90	-16.92	***
Community vs. Government	-2.49	-16.60	***
Community vs. Fished	0.41	2.37	*

Browser	Estimate	Z-value	p-value
Fished vs. Government	-2.56	-1.79	0.173
Community vs. Government	-2.40	-1.73	0.194
Community vs. Fished	0.16	0.11	0.993

Grazer	Estimate	Z-value	p-value
Fished vs. Government	-2.53	-11.46	***
Community vs. Government	-1.17	-5.71	***
Community vs. Fished	1.36	5.91	***

Fig S1. Schematic of experimental design with replicate numbers

Fisheries Management
n=3

| Open access fished reef | Community closure | Government closure |

Sites (Reefs)
n=2 per management

| Kanamai | Ras Iwatine | Kuruwitu | Mradi | Mombasa | Malindi |

Blocks (Replicates)
n=4 per site

| Block 1 | Block 2 | Block 3 | Block 4 | (> 20 m apart) |

Treatment
n=1 per block

| Cage (no herbivory) | Fence (fish herbivory) | Open (fish & sea urchin herbivory) | (< 3 m apart) |

Algal Growth Plates
n=4 per treatment

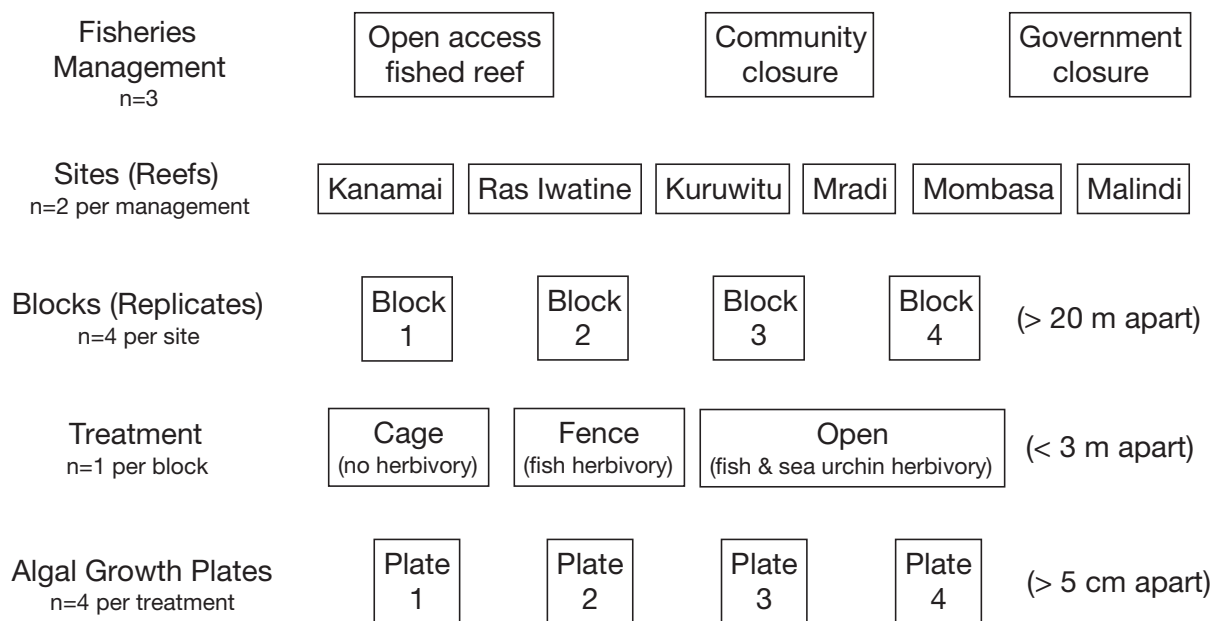| Plate 1 | Plate 2 | Plate 3 | Plate 4 | (> 5 cm apart) |

Fig. S2. Non-metric multidimensional scaling (MDS) describing the similarity of the algal communities by treatment (cage, fence, open). Data are for (a) ~180 days and (b) ~390 days since deployment. Different shapes represent different fisheries management (fished reefs, community closures, government closures). Associated R^2 and p-values from PERMANOVAs are displayed in the upper corner of each plot. Points that are closer together in ordination space are more similar in terms of algal community and individual algae are overlaid to visualize dominant assemblages. Stress for all plots was < 0.16.
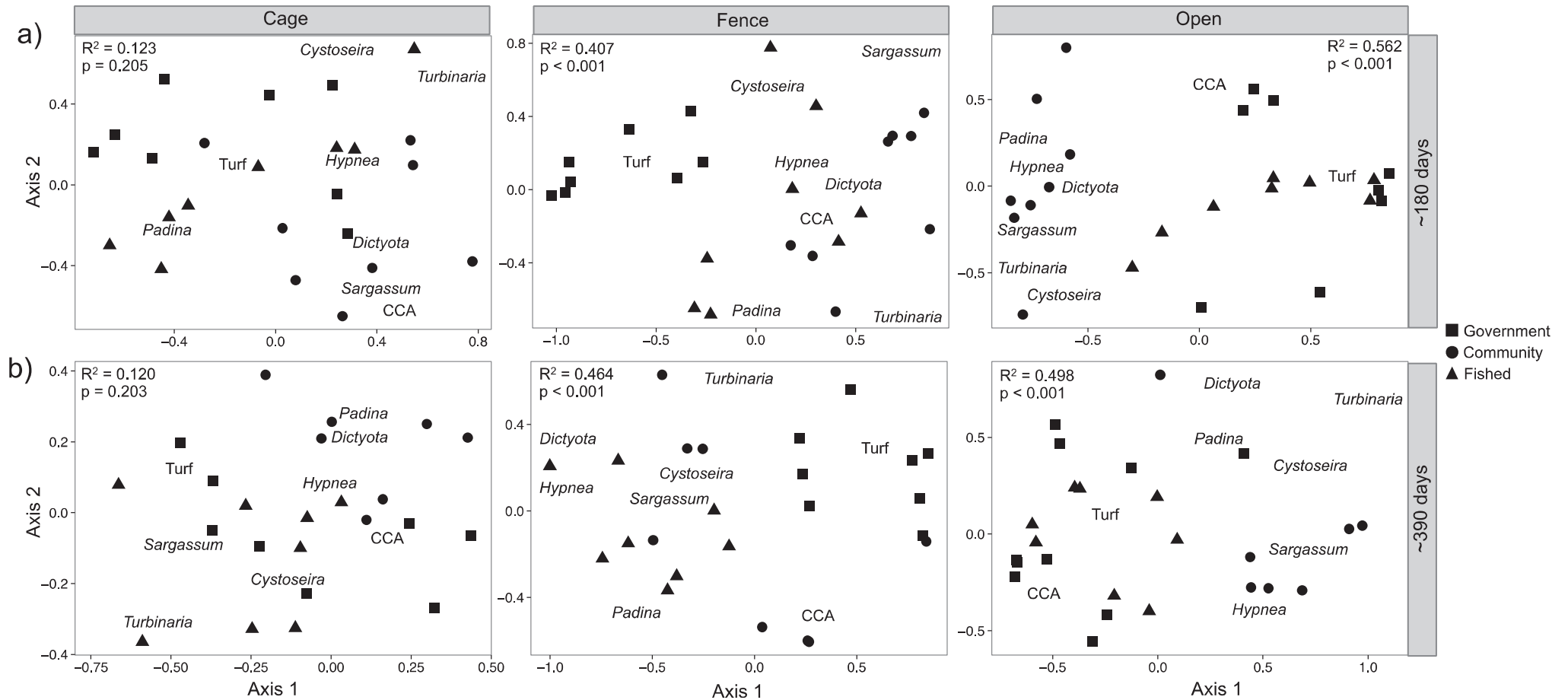
Fig. S3. Mass standardized bite impact (kg × bites h^{-1}; mean + SE) by size class (total length; cm; estimated to the nearest 5 cm) of herbivorous fishes (scraper, browser, grazer) by fisheries management type (fished reefs, community closures, government closures) on experimental substrata using stationary underwater video (n = ~160 h per management type)