

Trophic cascades result in large-scale coralline algae loss through differential grazer effects

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Abstract. Removal of predators can have strong indirect effects on primary producers through trophic cascades. Crustose coralline algae (CCA) are major primary producers worldwide that may be influenced by predator removal through changes in grazer composition and biomass. CCA have been most widely studied in Caribbean and temperate reefs, where cover increases with increasing grazer biomass due to removal of competitive fleshy algae. However, each of these systems has one dominant grazer type, herbivorous fishes or sea urchins, which may not be functionally equivalent. Where fishes and sea urchins co-occur, fishing can result in a phase shift in the grazing community with subsequent effects on CCA and other substrata. Kenyan reefs have herbivorous fishes and sea urchins, providing an opportunity to determine the relative impacts of each grazer type and evaluate potential human-induced trophic cascades. We hypothesized that fish benefit CCA, abundant sea urchins erode CCA, and that fishing indirectly reduces CCA cover by removing sea urchin predators. We used closures and fished reefs as a large-scale, long-term natural experiment to assess how fishing and resultant changes in communities affect CCA abundance. We used a short-term caging experiment to directly test the effects of grazing on CCA. CCA cover declined with increasing fish and sea urchin abundance, but the negative impact of sea urchin grazing was much stronger than that of fishes. Abundant sea urchins reduced the CCA growth rate to almost zero and prevented CCA accumulation. A warming event (El Niño Southern Oscillation, ENSO) occurred during the 18-year study and had a strong but short-term positive effect on CCA cover. However, the effect of the ENSO on CCA was lower in magnitude than the effect of sea urchin grazing. We compare our results with worldwide literature on bioerosion by fishes and sea urchins. Grazer influence depends on whether benefits of fleshy algae removal outweigh costs of grazer-induced bioerosion. However, the cost-benefit ratio for CCA appears to change with grazer type, grazer abundance, and environment. In Kenya, predator removal leads to a trophic cascade that is expected to reduce net calcification of reefs and therefore reduce reef stability, growth, and resilience.

Key words: coral reef; coralline algae; echinoderms; ENSO; herbivorous fish; marine protected areas; marine reserves; red algae; trophic cascades.

INTRODUCTION

Species interactions are integral to understanding ecological systems and frequently drive ecosystem function. When predator-prey interaction strengths are high, alterations at the predator level can have indirect effects on the rest of the ecosystem through trophic cascades (Hairston et al. 1960, Wootton 1994, Estes et al. 1998). For example, in most U.S. terrestrial systems, the extirpation or displacement of numerous top predators has resulted in overgrazing by ungulate populations and major negative impacts to woody plant communities (Beschta and Ripple 2009). Trophic cascades occur in all ecosystems, but tend to be

particularly important in structuring marine benthic systems (Shurin et al. 2002). When trophic cascades extend to the benthos, there may be large changes at the base of the food chain that effect primary production and result in further alteration of ecological function (Shurin et al. 2002, Newman et al. 2006). Because fisheries can indirectly alter unharvested benthic communities through trophic cascades, long-term fisheries closures provide an unprecedented opportunity to understand community-level effects of alterations to food webs (Côte et al. 2001, Halpern 2003). Comparisons between fished and closed areas are approximately analogous to classic marine experiments using caging (e.g., Paine 1974), though at a much larger spatial and temporal scale.

In coral reef systems, reef structure is built through primary production (via carbon fixation) by two groups: hard (scleractinian) corals and crustose coralline algae (CCA). A large body of research has focused on corals,

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with very few studies concentrating on CCA ecology (Miller et al. 2003) despite the fact that they are major primary producers worldwide (Aguirre et al. 2000). In tropical reefs, CCA play four key roles: (1) they create reef material through calcification, (2) they stabilize reefs by binding coral rubble (Bak 1976), (3) they help prevent the biological destruction (bioerosion) of coral substratum, and (4) some species chemically induce recruitment of corals and octocorals (Morse et al. 1996, Heyward and Negri 1999, Harrington et al. 2004).

Given the important role of CCA in reef ecology, understanding the factors that influence their abundance is critical, and can inform how human-induced trophic cascades can alter ecological processes and reef structure. CCA are widely cited as having a positive association with grazing herbivores (Steneck 1983, 1986, Stachowicz and Hay 1996, Littler and Littler 2007). Grazers indirectly increase CCA abundance by removing competitively dominant fleshy algae (Steneck 1986). The importance of grazing for enhancing CCA abundance has also been used in commonly cited models (e.g., Littler et al. 2006), despite the fact that studies have shown that at high densities, some grazers can bioerode CCA (e.g., Glynn et al. 1979). The lack of a comprehensive analysis of potential negative grazer effects on CCA may be due to the fact that the most commonly cited studies on the interactions between CCA and grazers have been carried out in temperate systems and in the tropical Caribbean, each of which has only one major herbivorous functional group.

The dominant algal grazers in temperate systems are sea urchins; herbivorous fishes are absent or uncommon (Sala and Boudouresque 1997). Removal of top predators, often through fishing, results in high numbers of sea urchins that denude reefs of fleshy macro-algae and drive the system toward a CCA dominated substrate (Lawrence 1975, Harrold and Reed 1985, Estes et al. 1998). Temperate areas with sea urchin predators (often fisheries closures) have few sea urchins and abundant fleshy algae that results in lower CCA cover (Underwood et al. 1991, Micheli et al. 2005, Guidetti 2006), even when CCA monopolizes understory space (Irving and Connell 2006).

The dominant grazers in Caribbean systems are herbivorous fishes (Mumby et al. 2006). Caribbean systems currently have few sea urchins that feed on exposed surfaces due to a devastating sea urchin disease in 1983 that killed most *Diadema antillarum* (Lessios 1988). Like temperate sea urchins, tropical herbivorous fishes have been shown, in most cases, to increase CCA abundance by removing fleshy algae (Lewis 1986, Belliveau and Paul 2002). CCA cover tends to be high in fisheries closures where fish grazers are abundant and low in fished reefs that are dominated by fleshy algae (Williams and Polunin 2001).

A more thorough examination of the effects of trophic cascades and grazers on CCA abundance is warranted because (1) the direct effects of tropical sea urchin

grazing on CCA cover has been investigated in only a few cases, (2) tropical fishes and sea urchins may have differential effects on CCA when both are present in the same system, and (3) data collected overtime from long-term fisheries closures allows evaluation of how human induced trophic cascades and environmental disturbances can alter the grazer-CCA relationship. The coral reefs along the coast of Kenya in the Western Indian Ocean have abundant herbivorous sea urchins and fishes, and thus provide an opportunity to study the relative effects of these grazer types. The dominant grazers in Kenyan fisheries closures are fishes (especially surgeonfish and parrotfish); due to loss of fish predators, the dominant grazers on fished reefs are sea urchins (McClanahan and Shafir 1990, McClanahan et al. 1999). There are numerous well-enforced closed reefs (patrolled day and night) interspersed with heavily fished reefs (Appendix A), providing true replicates of fish predator exclusions (fished reefs) and inclusions (closed reefs).

We investigated long term trends in CCA cover in Kenyan fisheries closures and fished reefs between 1987 and 2005. We evaluated the causes of trends in these data with a short-term experiment where we excluded fishes, sea urchins and both in a fisheries closure and a fished reef. Using these data sets, we tested the following hypotheses: (1) fish grazing has a positive effect on CCA cover by removing competitive fleshy algae, (2) high-density sea urchin grazing lowers CCA cover through bioerosion, and (3) differences in fish and sea urchin grazing in fisheries closures and fished reefs explain long-term, large-scale patterns in CCA abundance. Because our data spanned a major El Niño Southern Oscillation (ENSO) event (McPhaden 1999), we were also able to assess the relative contributions of a climatic change vs. grazer differences in establishing patterns of CCA abundance.

METHODS

Study areas

The studied Kenyan reef system is a back-reef lagoon protected by an uninterrupted fringing reef spanning 450 km of the coastline and located 100–1000 m from shore (McClanahan and Arthur 2001). The lagoon is shallow, ranging from 0.5 to 3 m at low tide, and is dominated by patch reefs though larger continuous reef structures exist in some locations. Three areas have been protected from all fishing since 1968–1972 (Malindi, Watamu, and Kisite National Parks), and a fourth area (Mombasa National Park) has been protected since 1991 and appears to be still recovering from previous fishing impacts (McClanahan et al. 2007).

Reefs closed to fishing have more complex topography, higher coral cover and diversity, much higher fish biomass (by two orders of magnitude), and much lower sea urchin densities (by two orders of magnitude) than on fished reefs (McClanahan 1997, 2008). In the closed areas, about 20 species of herbivorous surgeonfish (Acanthuridae) and parrotfish (Scaridae) account for

TABLE 1. Results of principal-components analyses, listing variables contributing to each factor and coefficients.

(-) Variables	(+) Variables
Factor 1	
<i>Echinometra mathaei</i> (-0.17)	Labridae (0.26)
Sand (-0.16)	Pomacentridae (0.25)
	Scaridae (0.13)
	Pomacanthidae (0.13)
	Chaetodontidae (0.11)
	Acanthuridae (0.05)
	Lutjanidae (0.05)
	Calcareous (erect) algae (0.04)
	Balistidae (0.0004)
Factor 2	
Algal turf (-0.32)	Soft coral (0.34)
Fleshy algae (-0.24)	Hard coral (0.28)
Factor 3	
<i>Diadema setosum</i> (-0.27)	Lutjanidae (0.07)
<i>Diadema savignyi</i> (-0.26)	
<i>Stomopneustes variolaris</i> (-0.25)	
Sponge (-0.19)	
<i>Toxopneustes pileolus</i> (-0.14)	
<i>Tripneustes gratilla</i> (-0.13)	
<i>Echinothrix diadema</i> (-0.10)	

Note: Variables were included using a loading threshold of $\geq \pm 0.5$ and coefficients are listed in parentheses.

most algal grazing. Low sea urchin biomass is due mainly to predation by one triggerfish, *Balistapus undulatus* (Balistidae), with a few wrasses (Labridae) and emperors (Pomacanthidae) as subordinate predators. Outside the four closed areas, artisanal fishing with seine nets, hook and line, and spears is intense. Fished reefs areas are topographically simpler, with low coral cover and diversity largely due to bioerosion by nine species of sea urchins (McClanahan and Shafir 1990, McClanahan 2000, 2008, McClanahan et al. 2008). Kenyan reefs and fish communities are described in detail in McClanahan and Arthur (2001).

Annual surveys

We assessed abundances of major organisms using three types of surveys (benthic, fish, and sea urchin) in 1987, then annually over a 15-year period from 1991 to 2005 at three fished reefs (Diani, Kanamai, and Vipingo), the more recent fisheries closure (Mombasa), and two long-term fisheries closures (Malindi and Watamu). Data at an additional fished site (Ras Iwatine) was collected in every survey year except 1987 and 1992. Data was collected at the third long-term fisheries closure (Kisite) in 2004 and 2005.

On each reef, one to two sites (approximately 30×30 m) were permanently marked in shallow (<2 m deep at low tide) back-reef environments. For reefs with two sites, data were averaged for that reef in that year. All surveys were done during the northeast monsoon season between November and March (McClanahan and Shafir 1990).

Benthic surveys.—We estimated abundances of CCA and eight other substratum groups (Appendix B) along 9–12 haphazardly placed, 10 m long line–intercept transects at each site (McClanahan and Shafir 1990).

Fish surveys.—We conducted visual fish censuses during neap tides along two to five replicate 5×100 m belt transects per site (McClanahan and Kaunda-Arara 1996). Each fish was identified to species and its length was estimated to the nearest 10 cm. Small or cryptic taxa such as blennies and gobies were not included in analyses. Biomass (wet mass; kg/ha) was estimated for 11 families (Appendix B) from length–weight correlations previously measured at local fish landing sites in Kenya (McClanahan and Kaunda-Arara 1996).

Urchin surveys.—We estimated sea urchin density and biomass in nine nonoverlapping, circular, 10-m^2 areas per site (McClanahan and Shafir 1990). The center of each area was determined haphazardly by tossing a weight. Nine sea urchin species were counted and identified (Appendix B). Biomass (g/m^2) of each species was estimated by multiplying the average density by the average wet mass of 20–200 haphazardly selected individuals per species (depending on abundance). Biomass samples were collected only at fished reefs as we have not observed large differences in urchin size among reefs (T. McClanahan, unpublished data).

Relationships between CCA, reef substrate, and grazers

We explored relationships between CCA cover, substratum, fish and sea urchin abundances, and time with a multiple regression analysis to determine whether fish and sea urchin abundance are the main factors affecting CCA cover. We transformed the data as necessary to meet assumptions of normality (Appendix B). We excluded the most recently closed reef (Mombasa) from our analysis because there are no replicate reefs in this category.

One underlying assumption of regression analyses is that independent variables do not covary, but given 28 variables (11 fish families, 9 urchin species, and 8 non-CCA substrates; Appendix B), covariance is likely. Covariance was evaluated using tolerance values and condition indices resulting from a general linear model that included the 28 variables independently with CCA as the dependent variable. We found that most species exceeded acceptable covariance limits. This high amount of covariance suggests an ecological phase shift due to fishing that is not easily evaluated by single species and univariate methods that assume non-independence. Therefore, we used a principal-components analysis (PCA, with varimax rotation). PCA extracts a few uncorrelated variables that capture most of the variability in the data set while preserving the orthogonality of these new composite factors. If composite factors can be created using PCA, such factors, by definition, do not covary (Quinn and Keough 2002). The PCA yielded three important factors (eigenvalues > 1 , meaning that each factor explained more of the variance than would be

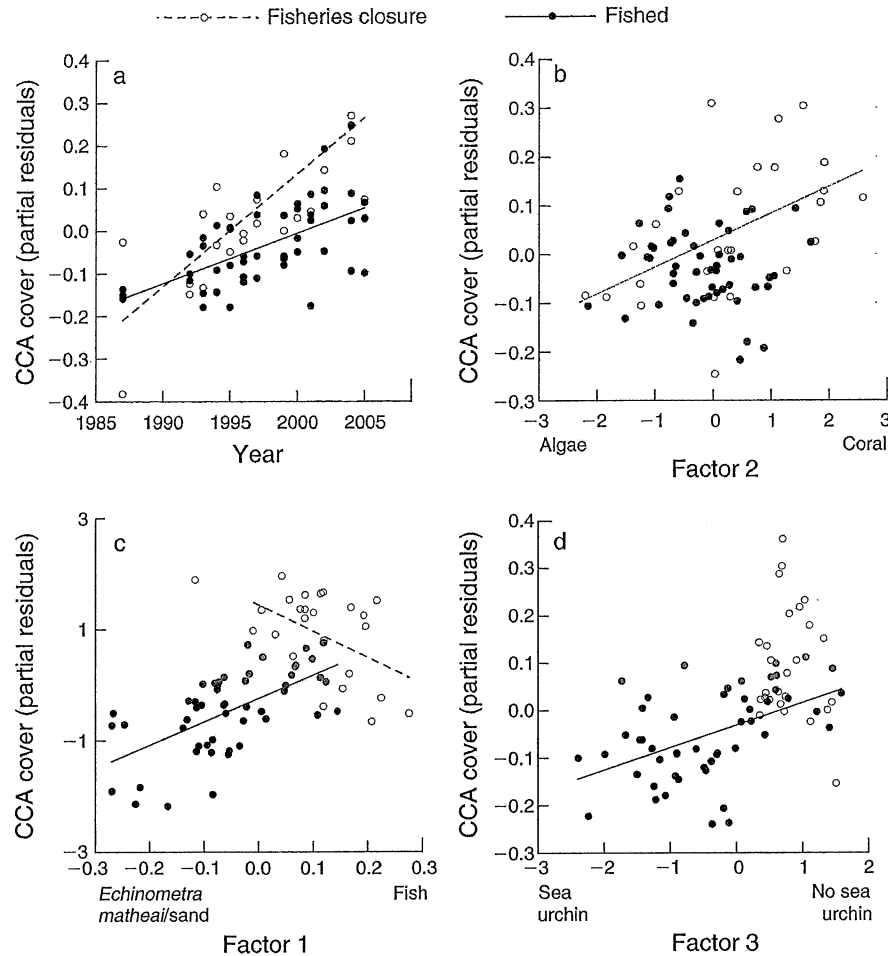


FIG. 1. Individual components of the multiple regression model plotted against crustose coralline algae (CCA) partial residuals from the analysis. Only significant relationships are shown with best-fit lines: (a) CCA partial residuals vs. time; (b) CCA partial residuals vs. principal-component factor 2; (c) CCA partial residuals vs. principal-component factor 1; and (d) CCA partial residuals vs. principal-component factor 3.

expected; Table 1). We determined which variables were important contributors to each PCA factor by using a loading cut off, excluding variables with loadings of less than the absolute value of 0.5. We use the term loading to indicate the strength of relationship between the original variable and the derived variable (factor). The term “coefficient” (listed in Table 1) indicates the slope of that relationship.

In the multiple regression analysis, we used CCA as the dependent variable with time and the three PCA factors as independent variables. We wanted to distinguish between trends in closed and fished reefs, as these reefs have different grazing communities (domination by fishes in closed reefs and sea urchins in fished reefs). We present these results in four graphs plotting the variables time and PCA factors 1–3 against the partial residuals for CCA from the multiple regression analysis (Fig. 1). Graphs using partial residuals show the relationship between a given independent variable (time or PCA factors) and the response variable (CCA) after account-

ing for the variance explained by other independent variables in the model. Because we recognize that plots using partial residuals and PCA factors are not always intuitive, we have also plotted the raw data of biomass of the dominant sea urchin *Echinometra mathaei*, six other sea urchin species, and fishes against CCA percent cover (Appendix C). Plotting of raw data does not account for variance explained by other variables, but we have included these plots as the resulting trends are highly similar to those of the multiple regression.

To statistically analyze the results from the multiple regression analysis (shown in Fig. 1), an ANCOVA could be used when the x-values in each management type spanned a similar range. The independent variables time (Fig. 1a) and PCA factor 2 (substrate variables; Fig. 1b) met this criterion. The independent variables PCA factor 1 (*E. mathaei* and fishes) and PCA factor 3 (other sea urchin species) did not have overlapping x-values because fished and closed reefs had values in different ranges along the x-axis (Fig. 1c, d).

For time and PCA factor 2 (substrate variables), we used partial residuals of CCA cover from the regression model as the dependent variable in two separate ANCOVAs, with management as the independent variable, and the appropriate variable (year or factor 2) as a covariate. For PCA factor 1 (sea urchins and fishes) and PCA factor 3 (sea urchins), the ranges of x values did not overlap, so we plotted the factors against the appropriate partial residuals, with management type (closed or fished) superimposed on them (Fig. 1c, d). Within each management category, we investigated the relationships shown in the figure plots using regression analyses to determine if the trends were significant.

Experimental test of fish and sea urchin grazing effects on CCA cover

We investigated direct effects of fish and sea urchin grazing on CCA cover in experiments on a closed reef (Mombasa) and a nearby fished reef (Ras Iwatine, 3 km away). Sites were selected to maximize differences in fish and sea urchin biomass and to minimize physical differences. Both reefs are in the shallow (<2 m deep at low tide) back-reef environment typical of the Kenyan coast and have similar morphologies and currents. Mombasa Marine Park (closed in 1991) now has high fish and moderate sea urchin biomasses (though there are more sea urchins on this reef than in longer-term fisheries closures). The fished Ras Iwatine reef has low fish and high sea urchin biomasses.

We surveyed fish and urchin abundances at the experimental sites in 2004 during the annual surveys. Fishes were censused visually along five 5×100 m belt transects on each reef, and converted to biomass (McClanahan and Kaunda-Arara 1996). Sea urchins were counted in 18 (Mombasa closed) and nine (Ras Iwatine, fished) nonoverlapping 10-m^2 circular areas, respectively. More urchin counts were done on the closed reef to cover the larger coral-dominated reef area. Urchin abundances were converted to biomass as described above. We used ANOVAs to compare total fish and sea urchin biomass, the biomass of the major predator and herbivore fish families (triggerfish and parrotfish), and common sea urchin species between our experimental sites.

Our experiment measured direct effects of grazing by fishes and sea urchins on growth of a common and easily identified CCA species, *Neogonolitheon fosliei* (Heydrich) Setchell & Mason. This species is a good indicator of total CCA cover on both closed and fished reefs (J. O'Leary, unpublished data). The experiment had three treatments at each site: cages (excluding fishes and sea urchins); fences (allowing access to fishes while excluding sea urchins); and open areas without cages or fences (allowing access by all grazers). It was not feasible to construct cages that allowed sea urchin grazing but excluded fish grazing. We constructed circular cages and fences of plastic garden mesh with 2-cm^2 openings. Cages and fences were approximately 30 cm in diameter

and 20 cm high. We placed six replicates of each treatment at each reef on flat, horizontal surfaces adjacent to naturally occurring *N. fosliei*. During the experiment, we cleaned cages and fences weekly to remove fouling algae on both inner and outer surfaces, but we did not remove any fleshy or turf algae that accumulated on the substratum.

We chipped CCA pieces of $\sim 64\text{ cm}^2$ area from the substratum with hammer and chisel, and discarded any pieces with large fouling or boring organisms (e.g., algae or terebellid worms). To allow measurement of CCA lateral growth rate, we killed half of the surface area of each sample with a soldering iron, and used a hacksaw to mark the intersection of live and dead coralline tissues with an ~ 2 mm deep incision. After marking the CCA pieces, we kept them in mesh bags in the lagoon for 24 hours to ensure that there was no CCA death behind the hacksaw line. We then returned the pieces to their original sites and randomly allocated five pieces to each replicate of the three treatments.

We fixed samples to the substratum in the various treatments between 25 August and 6 October 2004 with a 50/50 mixture of masonry cement and sand mixed with sea water. During the course of the experiment, some CCA pieces and entire replicates were lost due to strong currents; whenever possible, these were replaced with new pieces in new replicates within their treatment type, allowing us to keep track of amount of time samples were in the field.

CCA samples were removed from the field between 3 and 12 December 2004 and air dried. Due to CCA loss and subsequent replicate addition, final numbers of replicates and CCA samples per replicate differed from the original design (of five CCA pieces per replicate; six replicates per treatment per reef). The closed Mombasa reef ended with six cages, six fences, and five open controls, and an average of four CCA pieces/replicate (range = 3–5); the fished Ras Iwatine reef ended with eight cages, nine fences, and seven controls, and an average of 4.5 pieces/replicate (range = 2–5).

We measured lateral CCA expansion (growth) or contraction (erosion) of each CCA piece as distance from the hacksaw line, with measurements taken at 5-mm intervals along the line, scoring loss of living tissue as a negative value. We averaged CCA cover change measurements for all samples within each replicate and divided by the time exposed to estimate a monthly growth rate per replicate. We used ANOVAs to compare growth rates among treatments independently for the closed and fished reefs, with CCA growth rate as the dependent variable and treatment as the independent variable. We then used one-degree of freedom a priori contrasts to compare treatments (or treatment combinations).

Magnitude of ENSO vs. grazing effects on CCA cover

Because the major ENSO event in 1997–1998 caused large declines in coral cover (McClanahan 2008), we

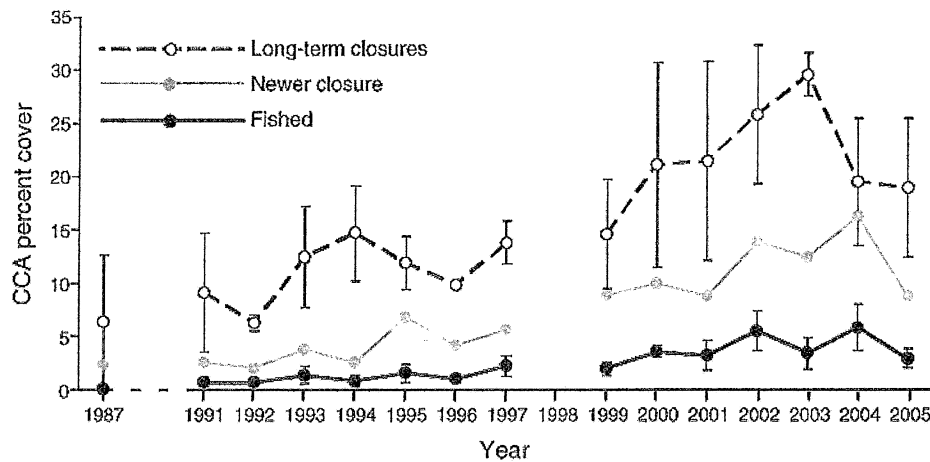


FIG. 2. Time-series plot of crustose coralline algae (CCA) in Kenya in the three management categories in 1987 and from 1992 to 2005 with standard error bars. The more recently closed reef is shown to demonstrate trends even though there is no replication in this category.

investigated whether this ENSO event altered CCA cover and if so, how the magnitude of its effects compared with differences in CCA cover attributable to grazers. We examined CCA trends before and after the ENSO in two long-term fisheries closures (Malindi and Watamu) and four fished reefs.

To understand the nature of CCA cover trends before the ENSO, we used data from five continuous years prior to the ENSO (1991–1997) to test for (1) temporal trends in CCA cover in closed and fished reefs (using a regression) and (2) differences between CCA cover in closed and fished reefs (using an ANOVA). We then used pre-ENSO period data to project what CCA cover for the post-ENSO time period (1998–2005) might have been in the absence of ENSO influence. To do this, we used the slopes and intercepts of best-fit linear regressions fitted to the data from the pre-ENSO period. We then estimated changes in CCA cover due to the ENSO event by subtracting the projected CCA estimates from the observed mean CCA cover for each year during the post-ENSO period (1998–2005) for fished reefs and fisheries closures. For all analyses above, we used transformed CCA data.

We calculated an annual grazer effect as the difference between CCA cover in fisheries closures and fished sites in a given year. We then pooled the annual differences to get an average grazer effect. Similarly, we pooled differences between the actual CCA cover and projected (non-ENSO) CCA cover to get an average ENSO effect, calculating separate effects for fished reefs and fisheries closures. We then compared average differences in CCA cover due to grazing and ENSO during the post-ENSO period (1998–2005). We examined the relative magnitude of grazer and ENSO effects on CCA (1) on average, (2) when the ENSO effect was at its peak in 2003, and (3) at the end of our study (2005).

RESULTS

CCA abundance

CCA cover was highest in long-term fisheries closures and lowest in fished reefs throughout the study (Fig. 2). CCA cover in newer closures appears to be intermediate (although statistical tests of newer closures could not be performed because there was no replication in this category). CCA cover increased between 1999 and 2003 (Fig. 2) especially in fisheries closures, then decreased through 2005. In 2005, CCA cover was $19.0\% \pm 6.5\%$ on reefs in fisheries closures, 8.9% on reefs in the more recently closed MPA, and $3.0\% \pm 0.9\%$ on fished reefs.

Relationships between CCA, reef substrate, and grazers

The PCA analysis used data from annual surveys in the three older fisheries closures and four fished reefs. The PCA reduced the initial 28 independent variables to three factors that each explained more than the expected variance in the independent variables (Table 1). The PCA factors included 22 of the 28 independent variables. The excluded species were not included in the subsequent multiple regression analysis. Excluded sea urchins (*Echinothrix calamaris* and *Echinostrephus molaris*) and one excluded fish (Diodontidae) are uncommon in Kenya. Two other excluded fish (Mullidae and Siganidae) are unlikely to have any influence on CCA cover because they feed in sand and seagrass habitats. The excluded substrate, seagrass, occurs in sand and rubble habitat and therefore should not influence CCA cover on hard substrate.

PCA factor 1 explained 44.3% of the variance in the independent variables and was comprised of an abundant sea urchin, *Echinometra mathaei*, and sand loaded opposite of eight fish families (including herbivores and carnivores and erect calcareous algae). PCA factor 2 explained 11.9% of the variance in independent variables and was comprised of substrate categories, with algal

TABLE 2. Multiple regression model with crustose coralline algae (CCA) percent cover (arcsine-square-root transformed) as the dependent variable and year and the three PC factors as independent variables.

Effect	SS	df	Coefficient	<i>t</i>	<i>P</i>	Partial r^2
a) ANOVA						
Regression	1.095	4			<0.001	
Residual	0.860	71				
b) Regression						
Year			0.018	6.920	<0.0001	0.22
PCA factor 1			0.074	5.933	<0.0001	0.16
PCA factor 2			0.036	2.887	<0.0001	0.03
PCA factor 3			0.070	5.610	<0.0001	0.14

Note: For ANOVA, $r^2 = 0.55$, $n = 76$.

turf and fleshy algae loading opposite of soft and hard coral. PCA factor 3 explained 7.6% of the variance in independent variables and was comprised of 6 sea urchin species (and sponge cover) loaded opposite of a fish family (Lutjanidae). We considered PCA factor 3 to be essentially sea urchins/no sea urchins because neither sponges nor Lutjanidae are likely to affect CCA cover: sponges are not abundant in Kenya and Lutjanidae do not feed on the substratum.

The subsequent multiple regression analysis explained 55% of variation in CCA cover, and all four independent variables were significant (year, PCA factor 1, factor 2, and factor 3; Table 2). From partial residuals, time explained 22% of the CCA variance in the model, PCA factor 1 (*E. mathaei* vs. fishes) explained 16%, and factor 3 (other sea urchins vs. no sea urchins) explained 14%. PCA factor 2 (algae vs. corals) had the smallest contribution, only explaining 3% of CCA cover variation.

We present the results of the multiple regression analysis using partial residual plots with fisheries closures and fished reefs shown (Fig. 1). Considering changes over time (year), the rate of change in CCA cover was different in closures and fished reefs (ANCOVA interaction between time and management, $F = 10.80$, $df = 1, 72$, $P = 0.002$; Fig. 1a). CCA cover increased over time at a greater rate in closures (slope = 0.026) than in fished reefs (slope = 0.012). Considering PCA factor 2 (substrate), CCA increased with decreasing turf and fleshy algae cover and increasing hard and soft coral cover, but only in closed reefs (ANCOVA interaction between management and PCA factor 2, $F = 0.36$, $df = 1, 72$, $P = 0.008$; Fig. 1b). For both PCA factor 1 (sea urchins and fishes) and factor 3 (sea urchins vs. no urchins), increasing sea urchin biomass was strongly correlated to decreasing cover of CCA in fished reefs, where sea urchin grazing dominates (regression factor 1, slope = 0.088, $t = 5.28$, $P < 0.0001$; regression factor 3, slope = 0.047, $t = 3.89$, $P < 0.0001$; Fig. 1c, d). For PCA factor 1 (sea urchins and fishes), in the range where fishes become important grazers (closed reefs with scores from 0.05 to 0.25), there was a decrease in CCA cover with increasing fish biomass (regression, slope = -0.057,

$t = -3.00$, $P = 0.006$; Fig. 1c). However, the CCA cover decrease associated with the increasing fish biomass was not as extreme as the decrease in CCA caused by increasing sea urchin biomass (fished reefs with factor scores of 0.05 to -0.25).

Experimental test of fish and sea urchin grazing effects on CCA growth rate

Total fish biomass was significantly higher at Mombasa closure than in fished Ras Iwatine (Appendix D: Table D3). Scarids (parrotfish), the fish family most likely to cause bioerosion through grazing, also had significantly higher biomass in the closed than in the fished reef (Appendix D: Tables D1 and D3). Balistids (triggerfish), the major predator of sea urchins in Kenya, were rare in the fished site and had a moderate biomass in the protected reef (Appendix D: Tables D1 and D3). Total sea urchin biomass was much higher in the fished reef (Appendix D: Tables D2 and D3). *E. mathaei* is the most abundant sea urchin in many Kenyan fished areas, but at our experimental sites, there was no significant difference in *E. mathaei* biomass. Four other sea urchins were relatively abundant in our experiment, and all had higher biomass at the fished than the closed reef (Appendix D: Tables D2 and D3).

Cages and fences were effective in excluding sea urchins; CCA in open treatments clearly exhibited sea urchin scars on that were not seen on CCA in fenced and caged treatments. Fences, while excluding sea urchins, successfully allowed access to fish: small and medium sized scarids and acanthurids were observed entering the fenced area and grazing, and some CCA samples inside fences had scarid bite scars.

Effects of grazers can be determined by differences in growth rates between treatments within a site. At each reef (closed and fished), CCA growth rate differed among treatments (Table 3a). At the closed reef (Mombasa), the highest CCA growth rate was in the caged treatment that excluded both fishes and sea urchins and was ~3 mm/month (Fig. 3a). Allowing fish grazers (the fenced treatment) significantly reduced the CCA growth rate to almost half that of the caged treatment (Table 3a, Fig. 3). Adding sea urchin grazing (the open treatment)

TABLE 3. Results of ANOVA and treatment comparisons (contrasts) for CCA growth rates under caged (no grazing), fenced (fish but not sea urchin grazing), and open (fish and urchin grazing) treatments.

Source	SS	df	F	P
a) Closed reef (Mombasa)				
Treatment	11.89	2	5.81	<0.0001
Closed vs. fenced	5.52	1	24.00	<0.0001
Fenced vs. open	1.20	1	5.22	0.038
Error	3.22	14		
b) Fished reef (Ras Iwatine)				
Treatment	15.58	2	14.02	<0.0001
Closed vs. fenced	0.23	1	0.42	0.53
Fenced vs. open	15.47	1	27.83	<0.0001
Error	10.56	19		

caused an additional significant decline in CCA growth rate to approximately a third of that in the caged treatment (Table 3a, Fig. 3). At the fished reef (Ras Iwatine), the highest growth rate of CCA also occurred when fishes and sea urchins were both excluded (i.e., cages; Fig. 3b). However, in contrast to our results in the closed reef, allowing fish grazing did not cause any reduction in CCA growth (Table 3b, Fig. 3b), but adding sea urchin grazers (the open treatment) caused a highly significant reduction in CCA growth (Table 3b, Fig. 3b). CCA growth at the fished site, where grazing is predominantly due to sea urchins, was only 0.1 ± 0.1 mm/month in the open treatment; a 95% decrease in the CCA growth rate. The open treatment at the fished site thus had significantly lower CCA growth compared to any other treatment in the study, with the CCA growth rate near zero.

Magnitude of ENSO vs. grazing effects on CCA cover

In the pre-ENSO period (1991–1997), there were no temporal trends indicating change in CCA cover in either fisheries closures (regression slope = 0.08, $t = 1.45$, $P = 0.16$) or fished reefs (slope = 0.014, $t = 1.44$, $P = 0.18$). There was a significant difference in CCA cover by management type with more CCA in closed reefs (ANOVA, $df = 1, 39$, $F = 118.10$, $P < 0.0001$). The equation for the projection line for closed reefs was $CCA\ cover = 0.732(\text{year}) + (-1449.3)$, and for fished reefs was $CCA\ cover = 0.192(\text{year}) + (-384.12)$. The ENSO effect was calculated as the difference between actual and estimated CCA cover in fished reefs and fisheries closures (Fig. 4). CCA cover increased due to the ENSO effect until 2003, and then decreased until 2005. In 2005, the actual and estimated CCA cover values converged in both the closed reefs (with 19% and 18% cover, respectively) and the fished reefs (with 3% and 1% cover, respectively). The average post-ENSO grazer effect (difference between projected CCA cover in closed and fished reefs) caused a CCA cover difference of 13.9%, while the average ENSO effect (actual minus projected CCA cover) caused a difference of 5.5% in

closed and 1.6% in fished reefs. The maximum ENSO effect on CCA occurred in 2003 and caused a difference of 12.7% in closed reefs and 3.3% in fished reefs. In this same year, the estimated effect of grazers was a difference of 14.4% CCA cover between closed and fished reefs.

DISCUSSION

There is a strong trophic cascade in Kenya where removal of predatory fishes, such as triggerfishes and wrasses, results in a proliferation of sea urchins (McClanahan 2000). We predicted that herbivorous fishes would have a positive influence on CCA cover and growth by removing shading macroalgae, that abundant sea urchins would reduce CCA growth through bioerosion (McClanahan 1997), and that therefore fishing would result in decreased CCA abundance. We found large differences in CCA cover between fisheries closure and fished treatments that appear to support these hypotheses. CCA cover is very low where sea urchins are abundant in fished reefs and increases with decreasing sea urchin biomass. Our long-term data thus indicate that sea urchins have a strong negative association with CCA that persists over long time periods at numerous Kenyan reefs. Our experimental manipulation confirms that sea urchins can greatly decrease CCA net growth rates. Sea urchins reduced the net growth of CCA to almost zero at our fished experimental site. Thus, as we predicted, sea urchins seem to prevent CCA accumula-

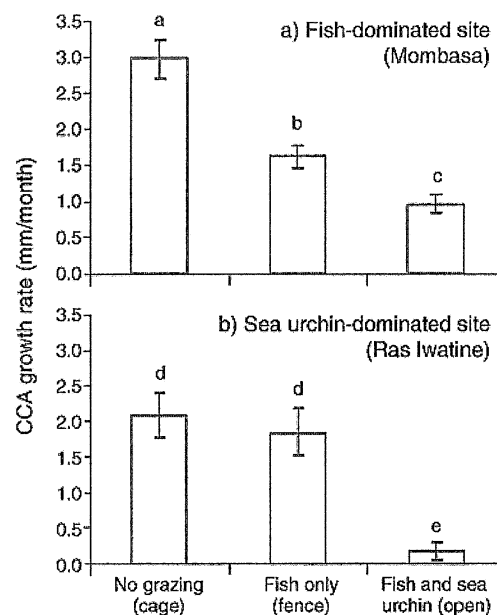


FIG. 3. CCA growth rates (mm/month; mean \pm SE) at (a) a reef with abundant fishes and few sea urchins (Mombasa fisheries closure) and (b) a reef with abundant sea urchins and few fishes (fished Ras Iwatine) in three treatments: total grazer exclusion cages, urchin exclusion fences, and open (fish and urchin grazing). Within each plot, different letters above bars indicate significant differences.

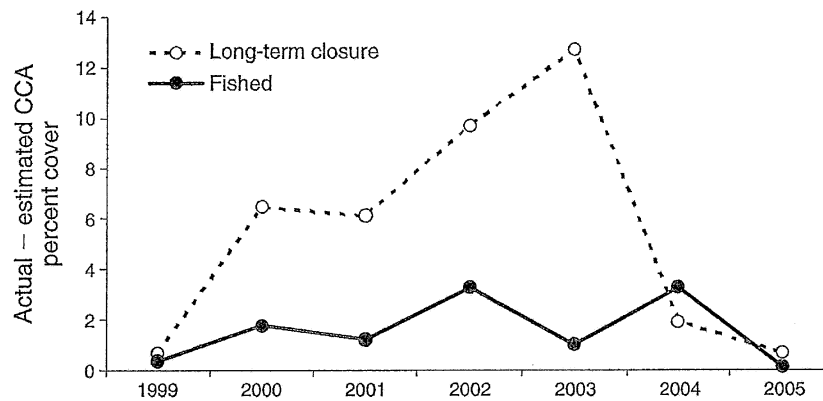


FIG. 4. Effect of the 1997–1998 El Niño Southern Oscillation (ENSO) determined by subtracting the projected CCA cover estimate (the best-fit line from pre-ENSO CCA cover) from the observed CCA cover over the post-ENSO period, 1999–2005. Fished reefs are depicted with solid circles and lines, and fisheries closures are depicted with open circles and dashed lines.

tion in reefs throughout Kenya. Contrary to our expectations, fishes also reduced CCA cover in our analysis and experiment. However, fishes had a much lower magnitude of impact than sea urchins. Consequently, fish-dominated grazing in fisheries closures resulted in a relatively high cover of CCA.

CCA cover appeared to increase over time at all reefs in Kenya between 1999 and 2003, and at a much higher rate in older fisheries closures (Figs. 1a and 2). In our regression model, time explained a large amount of variance in CCA cover. A reasonable hypothesis would be that change over time is due to changes in grazer abundance; however, neither fish nor sea urchin abundance is changing greatly over time in either older fisheries closures or fished reefs (McClanahan and Graham 2005). Furthermore, the change in CCA cover over time does not appear to be linear: there was an increase in CCA cover following the 1997–1998 ENSO (Fig. 2). After the ENSO, corals died (Appendix F), followed by a preliminary increase in fleshy and turf algae (Appendix F), and finally an increase in CCA cover as it colonized dead coral substratum (McClanahan 2008). CCA do not rely on symbiotic algae and may therefore be more resistant to increased temperatures than corals, giving them a competitive advantage during periods of climate disturbances and warming (Baker et al. 2004, Hoegh-Guldberg et al. 2007) such as ENSO events.

In the five-year period prior to the ENSO, CCA cover did not change significantly over time in either closed or fished reefs, but was significantly higher in the closed reefs. The long-term closures were established ~25 years prior to the start of the study. This time period appears to have been long enough for these closed reefs to establish different grazing communities and more CCA cover than fished reefs.

The ENSO had a strong, positive, but temporary effect on CCA cover from 1998 to 2005. The ENSO effect on CCA was much stronger in closed than in fished reefs. This is likely due to two factors: (1) there

was less coral cover prior to the ENSO in fished reefs, so less new open space was created by coral bleaching (Appendix F), and (2) sea urchins prevented an increase in CCA in fished reefs due to bioerosion. During the post-ENSO period, on average, the grazer effect in closed reefs was 2.5 times greater than the ENSO effect. At its peak, the ENSO effect in closed reefs was approximately equal to the grazer effect on CCA cover. However, after 2003, CCA cover declined and differences in CCA cover between management types were attributable to grazing differences. The reasons behind the decline in CCA after 2003 are unclear, as coral cover, though recovering, had not returned to pre-ENSO levels in closed reefs (Appendix F). Regardless, the ENSO effect on CCA cover did not persist, while the differential effects of fish and sea urchin grazers remained strong and relatively consistent over time.

Because grazers differentially affect CCA, the impacts of the fishing-induced trophic cascade in Kenya (Fig. 5) extends to reef benthos and results in major changes in CCA abundance over a large spatial and temporal scale. CCA cover in fisheries closure was equal to coral cover at the end of the study period, making CCA a major component of the benthic substratum in Kenyan fisheries closures, as in many undisturbed coral reefs. CCA may be an important indicator of reef recovery status. Reefs recently closed to fishing appear to have an intermediate cover of CCA between that of older closures and fished reefs, suggesting that time after closure impacts CCA cover (Fig. 2).

The grazing influence of fishes and sea urchins on CCA has been widely cited as positive because of their important role in removing fouling macroalgae (Steneck 1983, 1986, Littler and Littler 2007). In contrast, here we found that both fishes and sea urchins can negatively impact CCA cover and growth rates. Where grazer abundance is high and grazing intense, the negative effect of grazer bioerosion outweighs the benefit of fleshy algae removal, resulting in reduction of CCA. CCA and fleshy/turf algae compete for space in Kenya:

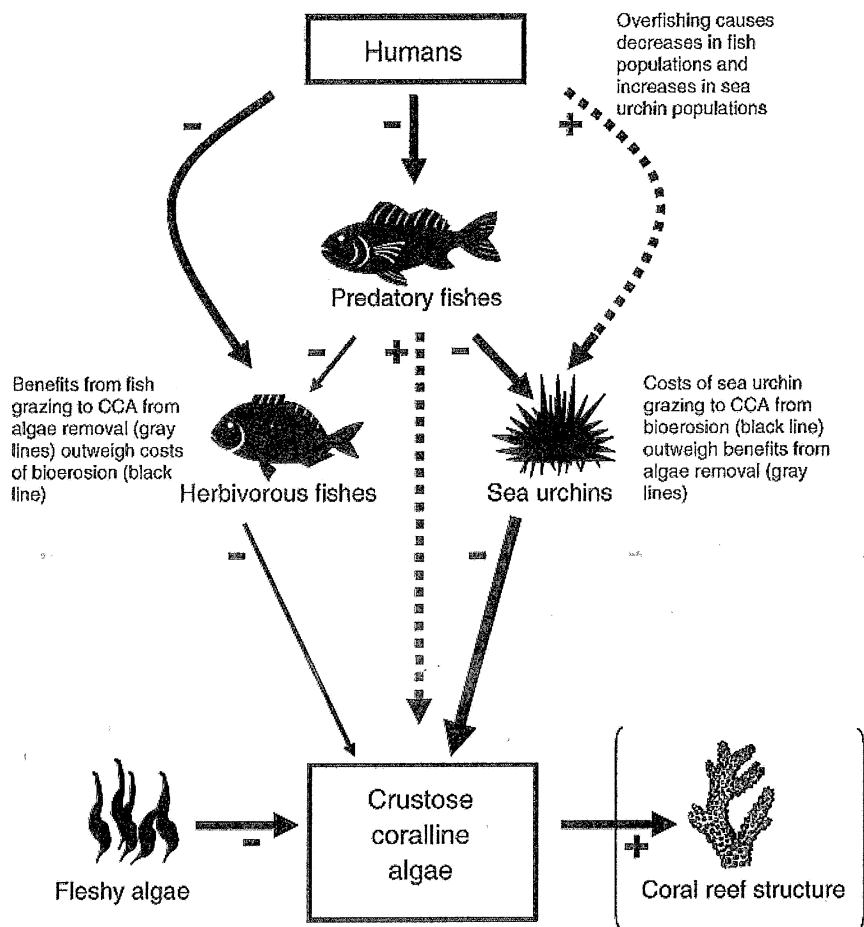


FIG. 5. Diagram of trophic interactions demonstrating cascade whereby fishing indirectly affects crustose coralline algae (CCA) abundance. Solid lines indicate direct effects, and dotted lines indicate indirect effects. Positive and negative symbols indicate impact to the target organism in the next trophic level. Gray lines (from herbivorous fishes and sea urchins to CCA) show the effects of algal removal. Coral reef structure is in brackets, as there is a hypothesized positive relationship between CCA and reef structure through induction of coral settlement and reef stabilization, but this relationship was not tested as part of this paper.

CCA increases as a function of decreasing fleshy and turf algae, and increasing hard and soft coral (Fig. 1b). However, associations between CCA and fleshy and turf algae were only found in fisheries closures; CCA cover is likely too low in fished reefs to respond significantly to potential competition for space. More importantly, substrate variables (fleshy/turf algae and hard/soft corals) had the weakest association with CCA in our regression analysis (Table 3b). In both fished and closed reefs, abundant grazers (fishes or sea urchins) maintain macroalgae at low levels except when impacted by ENSO (Appendix E). In our experiment, some fleshy algae did accumulate in the caged treatments, but did not seem to affect CCA growth rates. Our experimental manipulation was likely long enough to show a negative effect of bioerosion, but too short to show a positive indirect effect of removal of fleshy algae. If grazer abundance were reduced over longer time scales, fleshy algae would likely slow CCA growth. However, given the current high abundance of either fish or urchin

grazers in Kenyan reefs, fleshy algae cover is consistently low, and sea urchin bioerosion is more important than competitive interactions between algae in explaining CCA abundance.

Neither our correlative study nor our experiment considered environmental factors apart from ENSO. However, it is unlikely that general environmental differences were strong given the highly significant relationships between CCA and sea urchin abundance in our multiple regression model and the response of CCA to grazing in our experiment. CCA has been shown to have higher growth rates in high flow and unshaded conditions (Adey and Vassar 1975). While we did not measure flow or light levels in our experiment, the highest growth rates were in the fully caged treatment, which potentially had the lowest flow and light levels. We also did not measure nutrients, but CCA has a weak response to nutrients (Belliveau and Paul 2002, McClanahan et al. 2003, Burkepille and Hay 2006). Thus differences in CCA observed can likely be

attributed to differences in grazing rather than physical parameters.

Because our results contrast with commonly cited models regarding the influence of grazers on CCA, we surveyed the literature for studies reporting bioerosion rates or associations between tropical fishes and temperate/tropical sea urchin grazers and CCA (Appendices E, G, H). This approach was limited by three shortcomings: (1) most authors did not report size class (or biomass) for sea urchins, which for large-bodied sea urchins is likely more important than density in predicting impacts on CCA (Bak 1994); (2) where bioerosion rates were reported, they are typically for coral, not coralline; and (3) a variety of methods (yielding different estimates) were used in bioerosion calculations (Mallela and Perry 2007). We have nonetheless attempted to relate population density to bioerosion rates to determine locations where sea urchins may have a negative effect on CCA cover similar to that found in this study.

Tropical investigations citing high CCA cover under high grazing pressure come primarily from the present day Caribbean, where densities of the dominant sea urchin *Diadema antillarum* are low (often <0.01 sea urchins/m²; Williams and Polunin 2001) due to a devastating disease in 1983 (Lessios 1988). We found no recent Caribbean studies where sea urchins were abundant enough to cause CCA bioerosion. Another major reef system, the Great Barrier Reef, also shows no evidence of negative effects of sea urchin grazing on CCA, but this system naturally has low sea urchin abundances (Done et al. 1991). However, negative associations between CCA and sea urchins have been found in Japan (Appendix G: Table G1). In the Indo-Pacific and Hawaii, *Echinometra* have relatively high numbers (Appendix G: Tables G2 and G3), comparable to those in Kenya and Japan where negative associations with CCA have been found (Appendix G: Table G1). Some pre-disease Caribbean reef habitats also had sufficient sea urchin densities to negatively impact CCA cover.

Diadema antillarum has been recovering in some Caribbean areas since the late 1990s. At densities up to 9 sea urchins/m², this urchin is currently associated with decreased macroalgae and increased CCA and coral recruitment (Carpenter and Edmunds 2006). Based on our literature survey, Caribbean *D. antillarum* populations have positive associations with CCA at densities up to 15 sea urchins/m² (Appendix G: Table G1). However, at approximately 20 sea urchins/m² (Appendix G: Table G2), bioerosion begins to occur and CCA should be negatively affected. Thus, as sea urchins continue to recover in the Caribbean, whether the recovery process enhances or depletes reef substrate will depend on the extent of recovery. It may be that in years since the 1983 urchin disease, further reduction of sea urchin predators has occurred (Paddock et al. 2009). Continued decline of fish predators along with a

recovery in sea urchins in the Caribbean may result in overpopulation of sea urchins, as has occurred in fished Kenyan reefs (McClanahan 1999).

We did not find bioerosion rates reported for temperate sea urchins, but in all temperate studies CCA cover appears to increase with sea urchin abundance (Appendix H). It is possible that CCA simply becomes more evident as macroalgae are removed, as CCA is relatively common in the understory of macroalgae habitats. However, one study found that percent cover of CCA is reduced under algal canopies compared to open areas (Daume et al. 1999) and another study demonstrated that absolute (not just visible) CCA abundance increased with temperate sea urchin grazing (Fletcher 1987). There is strong evidence from the literature that temperate CCA cover does not decline with high numbers of sea urchins, as CCA cover often approaches 100% in dense sea urchin areas.

The positive effects of abundant sea urchins on CCA in temperate systems contrast with the apparently negative effects of abundant tropical sea urchins. The discrepancy may be due to greater nutrient availability and net algal production in temperate systems. Even within CCA dominated sea urchin barrens in temperate systems, it is likely that sea urchins are obtaining more food from abundant diatom biofilms, dissolved organic material, and drift kelp (Lawrence 1975, Himmelman et al. 1983). Though CCA is not a preferred sea urchin food, they are known to consume non-preferred food items when other food sources are unavailable (Lawrence 1975). In Kenya, the dominant sea urchin species, *Echinometra mathaei*, is known to be food limited (McClanahan and Kurtis 1991) and may be consuming CCA as a non-preferred food source. It may be that in tropical regions with abundant sea urchins, nutrient limitation and high grazer abundance depletes other food sources and sea urchins consume CCA at a greater rate than in high nutrient temperate systems. Some additional possibilities are: that tropical CCA are structurally less able to handle grazing, that tropical sea urchins are more destructive grazers than temperate sea urchins, or that underlying substrate strength (rock vs. coral) results in different bioerosion capacities. It seems improbable that tropical CCA are structurally less defended, given that most tropical algae have been shown to have greater defenses against herbivores compared to temperate algae (Bolser and Hay 1996).

Most of the tropical studies we reviewed indicate a positive association between herbivorous fishes and CCA. Seven studies on parrotfish grazing in the Caribbean, Indo-Pacific, and Western Indian oceans showed positive associations between CCA cover and fish biomass, where densities ranged from 4.5 to 44 fish/100m² (Appendix E). Similarly, our multiple regression analysis indicated that areas dominated by fish grazing have high CCA cover. However, we found that fishes can have a negative effect on CCA growth due to bioerosion. Parrotfishes are known to bioerode calcium

carbonate substrates (Appendix E: Table E2). Erosion rates for tropical herbivorous parrotfishes are either lower or in the same range of bioerosion rates reported for sea urchins where negative urchin-CCA associations have been found. Steneck and Adey (1976) report that in a Caribbean algal ridge system, CCA transplants were grazed away by abundant parrotfish (Scarids, density/biomass were not reported). Similarly, in our study, fishes associated with bioerosion of CCA are likely parrotfishes.

Grazer effects appear to be density or, more likely, biomass dependent. The influence of grazers is positive when grazer abundance is low, but harmful when high. In Kenya, sea urchins are highly abundant in fished areas and reduce CCA cover. Fishes also reduce CCA cover, but their abundance, even in Kenyan fisheries closures, was not high to outweigh the positive influence of fleshy algae removal and fish grazing resulted in overall high CCA cover (Fig. 5). Thus, intermediate grazer abundances appear to promote CCA cover. A similar effect has been shown for temperate limpet grazers, where intermediate densities of limpets promoted growth of a CCA (*Clathromorphum*) and were required to remove fouling epiphytes, but high densities caused partial mortality of crusts (Steneck 1982).

Conclusions

Fish and sea urchin grazers indirectly benefit CCA by removing fleshy algae but have direct negative effects on CCA through bioerosion. In Kenyan fished reefs, intense sea urchin grazing results in a major net loss of CCA. The negative effect of sea urchin grazing was generally stronger and more ubiquitous than even an intense ENSO event. Climatic changes such as ENSO may increase CCA cover but only where grazing pressure is moderate, such as in fisheries closures.

Where CCA is abundant, it should have a major influence on reef calcification and growth rate and have many indirect effects on reef ecology including coral recruitment (Fig. 5). Fisheries management practices that enhance CCA cover should have indirect benefits for reef structure and function. In Kenya, CCA appear to be a good indicator of reef recovery status, with increasing CCA cover over time when fishing is excluded.

Our results demonstrate that grazing communities can determine CCA abundance over large spatial and temporal scales. Furthermore, our findings and literature survey contrast with the commonly cited idea that grazers are ubiquitously beneficial to CCA cover. The response of CCA to grazing is not consistent across systems and depends on the abundance of grazers, the grazer type, and possibly other factors, such as ambient nutrient and disturbance levels. In any ecosystem, community or ecosystem level responses to small-scale species interactions cannot be predicted by simply knowing the species involved. We must understand how the strength and direction of interactions change

with changing densities and with the changing environment.

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APPENDIX A

Map of Kenya showing fisheries closures (Marine Protected Areas) and study sites (*Ecological Archives* E091-252-A1).

APPENDIX B

Variables from annual surveys and transformations used (*Ecological Archives* E091-252-A2).

APPENDIX C

Raw data showing trends for biomass of *E. matheai*, the six sea urchins in PC factor 3, and total fish plotted against CCA percent cover (*Ecological Archives* E091-252-A3).

APPENDIX D

Biomass of the major grazing family (Scaridae) and the major predator family (Balistidae) as well as for all fish at the experimental sites in 2004, biomass of common urchins in our experiment at closed and fished reef study sites in 2004, and results of one-way ANOVAs comparing biomass between sites (*Ecological Archives* E091-252-A4).

APPENDIX E

Survey of world-wide studies reporting herbivorous fish associations with CCA and parrotfish (Scaridae) bioerosion rates (*Ecological Archives* E091-252-A5).

APPENDIX F

Temporal trends in hard coral and fleshy algae percent cover in fisheries closures and fished reefs (*Ecological Archives* E091-252-A6).

APPENDIX G

Survey of tropical studies reporting sea urchin associations with CCA, sea urchin bioerosion rates, and sea urchin densities (*Ecological Archives* E091-252-A7).

APPENDIX H

Survey of temperate studies reporting associations between sea urchins and crustose coralline algae (*Ecological Archives* E091-252-A8).