



Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic

Emily S. Darling,¹ Timothy R. McClanahan,² & Isabelle M. Côté¹

¹ Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada

² Marine Programs, Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA

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Correspondence

Emily S. Darling, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada. Tel: +1-778-782-3989; fax: +1-778-782-3496. E-mail: edarling@sfu.ca

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Abstract

A challenge for conservation science is predicting the impacts of co-occurring human activities on ecological systems. Multiple anthropogenic and natural stressors impact ecosystems globally and are expected to jeopardize their ecological functions and the success of conservation and management initiatives. The possibility that two or more stressors interact synergistically is of particular concern, but such nonadditive effects remain largely unidentified in nature. A long-term data set of hard coral cover from Kenyan reefs was used to examine the independent and interactive effects of two stressors: fishing and a temperature anomaly in 1998 that caused mass coral bleaching and mortality. While both stressors decreased coral cover, fishing by 51% and bleaching by 74%, they did not interact synergistically. Instead, their combined effect was antagonistic or weakly additive. The observed nonsynergistic response may be caused by the presence of one dominant stressor, bleaching, and cotolerance of coral taxa to both bleaching and fishing stressors. Consequently, coral bleaching has been the dominant driver of coral loss on Kenyan reefs and while marine reserves offer many benefits to reef ecosystems, they may not provide corals with a refuge from climate change.

Introduction

The potential for interactions among anthropogenic and natural disturbances is one of the largest uncertainties for predicting ecological change and effective conservation policy (Sala *et al.* 2000; Didham *et al.* 2007; Brook *et al.* 2008). Climate change, habitat loss, invasive species, pollution, disease, and overexploitation are typically studied and managed in isolation, although it is becoming increasingly clear that a single-stressor perspective is inadequate when ecosystems are threatened by multiple, co-occurring stressors (Sala *et al.* 2000; Breitburg & Riedel 2005; Halpern *et al.* 2008a, b). If such stressors interact nonadditively, the result can be “ecological surprises” that precipitate sudden and accelerated declines in biodiversity and ecological function (Paine *et al.* 1998; Folke *et al.* 2004), which are difficult to predict and, therefore, to manage.

Synergies are one type of nonadditive interaction between two or more stressors that occur when the combined impact of the stressors is greater than the simple sum of their individual impacts (Folt *et al.* 1999; Breitburg & Riedel 2005). Here, a stressor is defined as any environmental or biotic factor that exceeds natural levels of variation to cause a detrimental effect in a response variable (Bertness & Callaway 1994; Breitburg & Riedel 2005; Crain *et al.* 2008; Darling & Côté 2008). Two recent meta-analyses evaluating multiple stressor interactions in terrestrial, freshwater, and marine systems suggest that synergies may not be as common as expected and that other forms of stressor interactions are equally likely (Crain *et al.* 2008; Darling & Côté 2008). For example, a nonadditive antagonistic interaction can occur when the combined impact of two stressors is less than the sum of individual impacts or the effect of multiple stressors can be additive, where the combined impact

is simply equal to the sum of the impacts of individual stressors (Folt *et al.* 1999; Breitburg & Riedel 2005). Despite the importance of quantifying the nature of stressor interactions for effective management and conservation policy (Didham *et al.* 2007; Crain *et al.* 2008; Darling & Côté 2008; Halpern *et al.* 2008b), explicit evaluations of stressor interactions (e.g., synergy vs. antagonism vs. additive effects) in natural systems remain limited, likely because most stressors occur simultaneously and it can be difficult to distinguish the independent and combined effects of multiple stressors (Mora *et al.* 2007; Halpern *et al.* 2008a, b).

Coral reefs are a model ecosystem to evaluate the cumulative impacts of multiple stressors. Coral reefs are in decline around the world (Gardner *et al.* 2003; Bruno & Selig 2007) and widespread losses of live coral cover and phase shifts from coral- to algae-dominated communities are frequently assumed to be driven by the synergistic impacts of overfishing, eutrophication, sedimentation, and rising sea surface temperatures associated with climate change (Nyström *et al.* 2000; Bellwood *et al.* 2004; Pandolfi *et al.* 2005; Knowlton & Jackson 2008; Mora 2008). In this study, we investigated the independent and interactive effects of fishing and climate change-induced coral bleaching on Kenyan coral reefs. Coral bleaching is a stress response, primarily caused by anomalously high water temperatures associated with climate change, that leads to the expulsion of symbiotic dinoflagellate algae (*Symbiodinium* spp.) from coral tissue, causing the coral to turn white or “bleach” and can lead to coral mortality (reviewed in Hoegh-Guldberg *et al.* 2007). In 1998, the El Niño-Southern Oscillation (ENSO) coincided with the Indian Ocean Dipole (IOD), which resulted in the warmest water temperatures on record for the Western Indian Ocean and led to unparalleled levels of coral bleaching and mortality throughout the region (McClanahan *et al.* 2007a; Graham *et al.* 2008). The 1998 bleaching event did not, however, occur in isolation but against a background of on-going human pressures, particularly fishing. With the exception of reefs within no-take marine reserves that exclude fishing, a small-scale reef fishery heavily exploits marine resources on Kenya reefs. Fisher densities range from 5 to 30 fishers km⁻² and use gill nets, hand lines, spear guns, beach seines, and traps as the primary fishing gears and where fisher densities range from 5 to 30 km⁻² (McClanahan *et al.* 2008). Other major coral reef stressors, such as sedimentation and eutrophication can occur periodically, but are spatially limited along the Kenyan coast due to strong currents and tidal flushing, and are expected to influence both fished and unfished reefs (Obura 2001).

A synergistic interaction between fishing and coral bleaching could occur if fishing reduces the resilience of

exploited reefs to bleaching (Nyström *et al.* 2000; Hughes *et al.* 2003; Mumby *et al.* 2007) and a number of mechanisms are possible. At the physiological level, physical damage from fishing could require coral colonies to spend energy on tissue and skeleton repair, which may reduce the ability of corals to resist and recover from co-occurring thermal stress and bleaching (Anthony *et al.* 2002, 2009). At the coral community level, fishing could increase the abundance of corals that are tolerant of trampling and breakage caused by fishers and fishing gear (Mangi & Roberts 2006) but intolerant of thermal stress. At the ecosystem level, fishing could reduce the abundance of grazing herbivorous fishes such that benthic assemblages on fished reefs are more likely to become overgrown by fleshy erect algae that may out-compete corals for space, reduce coral recruitment, and potentially increase coral disease, all of which have been suggested to increase the vulnerability of reef corals to bleaching (Knowlton & Jackson 2008).

Here, we evaluate the independent and combined impacts of fishing and bleaching on live coral cover by comparing ecological changes on fished and unfished reefs before and after a major coral-bleaching event. We test the hypothesis that exposure of coral reefs to both fishing and climate change-induced bleaching mortality will intensify the loss of coral cover in a synergistic manner.

Methods

Ecological surveys were carried out between 1987 and 2008 at 12 sites along an approximately 150 km stretch of Kenyan coastline. Previous analyses of these data have focused on the short- and medium-term effects of bleaching on coral reef communities (McClanahan *et al.* 2001; McClanahan 2008), but have not considered the potential for synergy between fishing and bleaching. In this study, we focus particularly on 2 years of this time series: 1997 and 1999, i.e., 1 year before and after the 1998 bleaching event. Seven sites were located on intensively fished reefs (Diani, two sites; Kanamai, two sites; Ras Iwatine, one site; Vipingo, two sites) and five sites were located on reefs inside unfished, no-take marine reserves (Malindi Marine National Park, two sites; Mombasa Marine National Park, two sites; Watamu Marine National Park, one site); fished and unfished sites are interspersed along the coast (for map, see McClanahan & Obura 1995). Fishing prohibition is enforced in all Marine National Parks while artisanal fishers intensively exploit the nonpark reef sites (McClanahan *et al.* 2008). All sites were located in shallow back-reef lagoons typical of Kenya's coral reef systems. Benthic cover was surveyed annually at each site using nine to 12 haphazardly

placed 10 m line-intercept transects. The lengths of major benthic components (hard coral, soft coral, turf algae, and erect fleshy algae) underlying each transect line were measured to the nearest centimeter. Percent coral cover was calculated as the sum of the lengths of the hard coral components divided by the total transect length. Site-specific mean (\pm standard error) percent coral cover was calculated for each year from the average of the individual transect values and used in all following analyses. There was no evidence for spatial autocorrelation of coral cover either before or after the 1998 bleaching event (Moran's I : 1997, $P = 0.53$; 1999, $P = 0.49$; Mantel test: 1997, $P = 0.54$; 1999, $P = 0.88$), confirming that the estimates of coral cover at each site were independent.

Change in coral cover following bleaching was quantified using an effect size metric which estimates gains or losses in coral cover relative to a baseline coral cover (equivalent to C_A in Gardner *et al.* 2003; Côté *et al.* 2005). This effect size provides estimates of change that are comparable across all sites and accounts for initial prebleaching differences in coral cover on fished and unfished reefs (Côté *et al.* 2005; Graham *et al.* 2008). We compared changes in coral cover on fished and unfished reefs across the 1998 bleaching event to quantify the independent and combined effects of fishing and bleaching on live coral cover. For clarity, we use the absolute values of these effect sizes to estimate coral loss associated with fishing and bleaching.

The independent effect of fishing was calculated as:

$$Fishing = (\bar{X}_{Fished,1997} - \bar{X}_{Unfished,1997}) / \bar{X}_{Unfished,1997} \quad (1)$$

where $\bar{X}_{Fished,1997}$ is the mean percent cover of hard corals on fished sites ($n = 7$) in 1997 and $\bar{X}_{Unfished,1997}$ is the mean percent coral cover at unfished sites ($n = 5$) in 1997. We calculated the variance of the fishing effect size from the delta method, which is a mathematical method used to calculate the variance of a function from the variances of the individual input variables (see Oehlert 1992; Casella & Berger 2001). Here, the variance of the fishing effect size is calculated as:

$$\begin{aligned} \text{var}_{Fishing} = & s_{Fished,1997}^2 * \left(\frac{1}{\bar{X}_{Unfished,1997}} \right)^2 \\ & + s_{Unfished,1997}^2 * \left(\frac{-\bar{X}_{Fished,1997}}{(\bar{X}_{Unfished,1997})^2} \right)^2 \end{aligned} \quad (2)$$

where $s_{Fished,1997}^2$ and $s_{Unfished,1997}^2$ are the variances of the 1997 coral cover estimates at fished and unfished sites, respectively. The 95% confidence interval (95% CI) was calculated using the t -distribution, which is more appropriate for small sample sizes (Zar 1999), and using pooled degrees of freedom ($df = 10$), as $95\% \text{ CI}_{Fishing} = 2.228 * \sqrt{\text{var}_{Fishing}/12}$. Evaluating the effect of fishing as

the difference in coral cover between the fished and unfished sites in 1997 removes any influence of the 1998 bleaching event, which occurred 1 year later. However, if habitat quality were higher in unfished reserves prior to implementation of protection (i.e., better quality habitats were chosen as reserve sites), our estimate of the difference in coral cover between fished and unfished reefs would be artificially inflated (Halpern 2003). To address this potential problem, we compared coral cover in 1987 on the Mombasa reef before this site was established as a marine reserve, to coral cover in the same year on six fished reefs that later remained unprotected. No preprotection data were available for the Malindi or Watamu reserves, which were established in 1968 and 1972, respectively. Similarity between the Mombasa site (prior to its enforcement as a reserve) and other fished sites would suggest that bias caused by natural differences in site quality was limited. We also performed a post-hoc power analysis on the effect size of fishing, as detailed below.

The independent effect of bleaching was calculated from the average change in coral cover on unfished sites before and after the 1998 bleaching event:

$$Bleaching = \frac{\sum_i^5 (X_{Unfished,1999} - X_{Unfished,1997}) / X_{Unfished,1997}}{5} \quad (3)$$

where $X_{Unfished,1999}$ and $X_{Unfished,1997}$ are the percent cover of hard corals at each unfished site, i , ($n = 5$) in 1999 and 1997, respectively. Evaluating the effect of bleaching from only the unfished sites removed any influence of fishing. The variance of the mean bleaching effect size was calculated from the variation of the individual bleaching effect sizes calculated for each protected site ($n = 5$) and used to quantify 95% confidence limits, also using the t -distribution ($df = 4$), as $95\% \text{ CI}_{Bleaching} = 2.776 * \sqrt{\text{var}_{Bleaching}/5}$. [Correction added after online publication 15 January 2010: Equation 3 originally read as $(X_{Unfished,1999} - X_{Fished,1997})$.]

The independent effect sizes of fishing and bleaching were then combined to produce an additive expectation, which was used as a null hypothesis against which we compared the observed combined effect of fishing and bleaching. The additive null expectation was generated from a multiplicative risk model, such that:

$$Fishing + Bleaching = F + B - (F * B) \quad (4)$$

where F and B are the absolute values of the Fishing and Bleaching effect sizes, respectively. Multiplicative risk models correct for over-inflated mortality estimates of simple additive sum models (Soluk & Collins 1988; Sih *et al.* 1998). For example, if stressors X and Y kill 60%

and 70% of a population, respectively, a simple additive expectation ($X + Y$) would predict an unattainable mortality of 130% while the multiplicative risk model generates a more realistic expectation of 88% mortality. For clarity, we refer to the prediction of the multiplicative risk model as the “additive” or null expectation. The variance of the null expectation was again calculated using the delta method to combine the variances of the independent fishing and bleaching effect sizes:

$$\text{var}_{F+B} = \text{var}(F) * (1 - B)^2 + \text{var}(B) * (1 - F)^2 \quad (5)$$

where $\text{var}(F)$ and $\text{var}(B)$ are the variances of the fishing and bleaching effect sizes, respectively. The 95% CI was then calculated using the t -distribution (pooled $df = 10$), as $95\% \text{CI}_{F+B} = 2.228 * \sqrt{\text{var}_{F+B}/12}$.

To evaluate the nature of the interaction between fishing and bleaching, we compared the additive null expectation to the observed change in coral cover on reefs that were exposed to both fishing and bleaching, quantified as,

$$\begin{aligned} & \text{Fishing} \times \text{Bleaching} \\ & = (\bar{X}_{\text{Fished},1999} - \bar{X}_{\text{Unfished},1997}) / \bar{X}_{\text{Unfished},1997} \quad (6) \end{aligned}$$

where $\bar{X}_{\text{Fished},1999}$ is the mean coral cover on fished sites in 1999 and $\bar{X}_{\text{Unfished},1997}$ is the mean coral cover on unfished sites in 1997. The variance of the interaction between fishing and bleaching ($F \times B$) was calculated using the delta method to combine the variances of coral cover on fished sites in 1999 and unfished sites in 1997: [Correction added after online publication 15 January, 2010: this sentence originally read “... fished sites in 1997 and unfished sites in 1999:.”.]

$$\begin{aligned} \text{var}_{F \times B} = & s_{\text{Fished},1999}^2 * \left(\frac{1}{\bar{X}_{\text{Unfished},1997}} \right)^2 \\ & + s_{\text{Unfished},1997}^2 * \left(\frac{-\bar{X}_{\text{Fished},1999}}{(\bar{X}_{\text{Unfished},1997})^2} \right)^2 \quad (7) \end{aligned}$$

where $s_{\text{Fished},1999}^2$ and $s_{\text{Unfished},1997}^2$ are the variances of the coral cover estimates from fished sites in 1999 ($n = 7$) and unfished sites in 1997 ($n = 5$), respectively. The 95% confidence limit of the fishing \times bleaching interaction was calculated using the t -distribution for small sample sizes (pooled $df = 10$) as $95\% \text{CI}_{F \times B} = 2.228 * \sqrt{\text{var}_{F \times B}/12}$. If the observed $F \times B$ change in coral cover was greater than the additive null expectation in absolute terms (i.e., no overlap of 95% CIs), the interaction between fishing and bleaching was classified as synergistic. If the observed change in coral cover was less than the additive null expectation (with no overlap in 95% CIs), the interaction between fishing and bleaching was classified as antagonistic. If the 95% CI of the additive null expectation overlapped with the 95% CI of the observed fishing \times

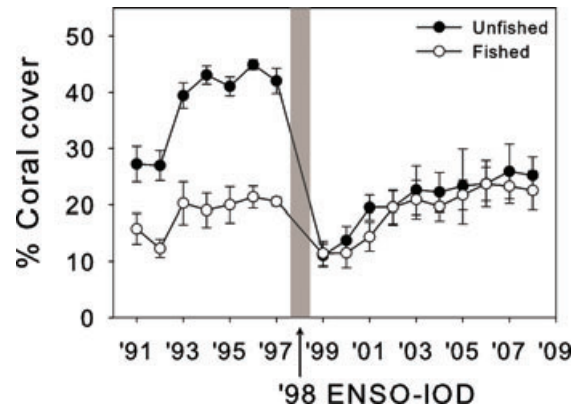


Figure 1 The lack of fishing pressure in unfished marine reserves did not ameliorate the effects of a coral bleaching event in 1998. Values shown are percent coral cover on fished (open circles) and unfished (filled circles) Kenyan reefs between 1991 and 2008. The gray bar indicates the 1998 ENSO-IOD (El Niño Southern Oscillation-Indian Ocean Dipole) bleaching event. Mean coral cover is shown \pm 1 SEM.

bleaching effect size, the interaction was classified as additive. [Correction added after online publication 15 January, 2010: Equation 7 original read as $s_{\text{Fished},1997}^2$ in the second part of the Equation.]

To test whether the interaction type was robust to changes in the calculated independent effect sizes, we performed a post-hoc power test by independently increasing and decreasing the fishing and bleaching effect sizes by 10%, increasing both effect sizes by 10% and decreasing both effect sizes by 10% (e.g., Sala et al. 2000). We then recalculated the additive expectation for each scenario and retested with the 95% CIs of the new expectations against the 95% CI of the observed interaction, reclassifying each outcome as antagonistic, additive, or synergistic. We also compared annual rates of change in coral cover on fished and unfished reefs across the bleaching event (between 1997 and 1999) and quantified the subsequent postbleaching recovery trajectories (between 1999 and 2008) using a geometric rate of change, which is appropriate for nonlinear time series, as $C_{RG} = 100 * [(C_{end}/C_{start})^{1/d} - 1]$, where C_{end} and C_{start} are the percent coral cover at the start and end years, respectively, and d is the number of years between the start and end years (Côté et al. 2005).

Results

Coral cover declined on both fished and unfished reefs following the El Niño-Southern Oscillation and Indian Ocean Dipole (ENSO-IOD) event of 1998 (Figure 1). Percent hard coral cover was higher on unfished reefs (mean coral cover \pm SEM: $42.0 \pm 1.6\%$) than on fished reefs ($20.6 \pm 1.3\%$) in 1997 before the bleaching event

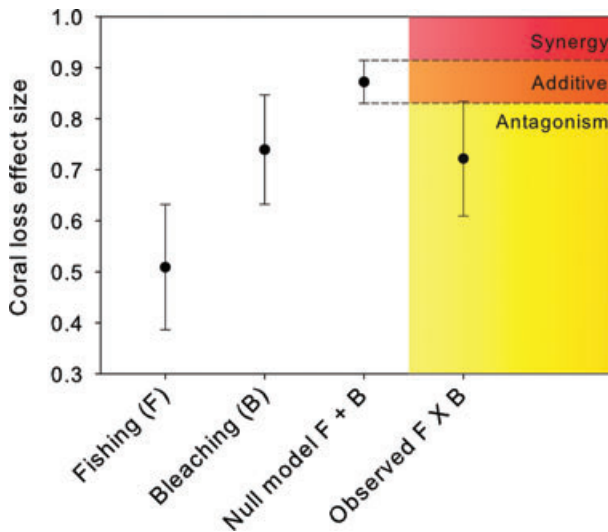


Figure 2 The impact of the 1998 bleaching event was significantly greater than fishing impacts on the loss of coral cover on Kenyan reefs. The observed decline in coral cover from the combined effect of the two stressors was antagonistic or weakly additive, not synergistic; bleaching appears to override the benefits of local protection from fishing in no-take marine reserves. Mean effect sizes are shown with 95% confidence intervals and the dashed line indicates the 95% confidence interval of the additive (null) expectation (see Methods).

(two-sample t -test, $t_{10} = -10.4$, $P < 0.0001$; Figure 2). This difference does not appear to be due to the selection of high-quality reefs for reserve establishment since coral cover on the Mombasa reef in 1987, before it was protected, was not significantly different from coral cover in the same year on reefs that remained unprotected (mean 1987 coral cover \pm SEM: Mombasa: $6.8 \pm 5.5\%$, fished reefs: $12.4 \pm 3.2\%$; one-sample t -test, $t_5 = 0.61$, $P = 0.57$). Following the 1998 bleaching event, there was no difference in coral cover between fished and unfished reefs (mean 1999 coral cover \pm SEM: unfished reefs: $11.1 \pm 2.4\%$, fished reefs: $11.4 \pm 2.0\%$; two-sample t -test, $t_{10} = 0.12$, $P = 0.91$). Overall, live coral cover declined more on unfished reefs (mean coral loss per year \pm SEM: $49.6 \pm 3.7\%$ per year) than on fished reefs ($28.0 \pm 7.3\%$ per year) following the bleaching event and coral cover between 1999 and 2008 has been recovering along similar trajectories on unfished reefs ($9.9 \pm 1.8\%$ per year) and fished reefs ($8.1 \pm 1.6\%$ per year) (see also McClanahan 2008).

Fishing on its own was associated with a 50.9% decline in relative coral cover (95% CI = 38.6%–63.1%, Figure 2), as revealed by the comparison of fished and unfished sites prior to bleaching. Bleaching was associated with a 74.0% decline in relative coral cover (95% CI = 63.2%–84.7%, Figure 2). The observed combined effect of fishing and bleaching was a relative decline of

72.2% (95% CI = 60.9%–83.4%) in coral cover, which was less, in absolute terms, than the predicted additive expectation of the combined stressors (null model $F + B = 87.2\%$, 95% CI = 83.0%–91.4%), suggesting an antagonistic interaction between fishing and bleaching (Figure 2). However, the small overlap in the 95% CIs (0.4%) indicates that the additive null hypothesis cannot be fully rejected. Our classification of the fishing \times bleaching interaction as nonsynergistic was confirmed in all scenarios of the post-hoc power test. Increasing any or all of the stressor impacts by 10% resulted in antagonistic interactions and decreasing the stressor impacts by 10% resulted in additive interactions. Since none of these scenarios resulted in the reclassification of the fishing \times bleaching interaction as synergistic, our finding of a nonsynergistic interaction appears to be robust.

Discussion

The potential for interactive effects between co-occurring stressors has been highlighted as a severe threat to biodiversity and ecosystem function (Sala *et al.* 2000; Folke *et al.* 2004; Brook *et al.* 2008). Empirical evaluations of the cumulative impacts of multiple stressors and predictions of future ecological change are, however, challenged by a poor understanding of the nature and interaction of the impacts (Didham *et al.* 2007; Halpern *et al.* 2008a; Mora 2008). Here, parts of a long-term data set of coral cover on Kenyan reefs were used to quantify the nature of the interaction between two common stressors on coral reefs, fishing and thermal-stress-associated coral bleaching. Fishing and bleaching were predicted to interact synergistically and an accelerated decline of live coral cover on fished reefs was expected following bleaching (relative to an additive expectation). This prediction was not empirically supported and we conclude that the interaction between fishing and bleaching on Kenyan coral reefs is antagonistic or weakly additive, both of which are nonsynergistic. Immediately following the 1998 bleaching event, hard coral cover declined less on fished (-28.0% per year) than on unfished reefs (-49.6% per year) (Figures 1 and 2). The larger decline of live coral cover on unfished reefs was not solely a function of higher absolute coral cover on unfished reefs in 1997 (Figure 1) because our effect size metric takes into account prebleaching differences in initial cover on fished and unfished reefs (Gardner *et al.* 2003; Côté *et al.* 2005; Graham *et al.* 2008).

While the mechanisms that cause coral mortality from coral bleaching and thermal stress are well studied (reviewed in Hoegh-Guldberg *et al.* 2007), the impacts of fishing on coral decline are less well understood and

could greatly influence the outcomes of the interactive responses. Fishing disturbances may directly damage living corals from trampling by fishers or damage by fishing gear (Cros & McClanahan 2003; Mangi & Roberts 2006). Fishing may also indirectly influence corals through the loss of predatory fishes. For example, the loss of fish predators can increase the abundance of coral-eating starfish (Dulvy *et al.* 2004), but fishing also removes coral-eating fishes, which can reduce the predation pressure on corals such that fast-growing corals released from corallivory could increase in abundance on fished reefs (McClanahan *et al.* 2005; Cole *et al.* 2008; Green *et al.* 2008; Rotjan & Lewis 2008). Fishing could also influence interactions between corals and algae through the removal of grazing herbivorous fishes (Bellwood *et al.* 2004; Mumby *et al.* 2007), and it may increase the abundance of sea urchins that can reduce algal cover and impact corals via settlement success and bioerosion (Sammarco 1980; Carreiro-Silva & McClanahan 2001). However, the impacts of fishing on total coral cover and the structure of coral assemblages have not been fully explored.

Why do fishing and bleaching have a nonsynergistic effect on coral cover? The answer may partly depend on the asymmetric effects of the two stressors considered. For example, Folt *et al.* (1999) suggested that the dominant stressor could drive the magnitude of combined stressor effects. We found that greater declines in coral cover were associated with bleaching compared to fishing; the average coral mortality from the 1998 bleaching event (74%) was nearly 25% higher than mortality from fishing (51%, Figure 2). The dominant effect of coral bleaching on Kenyan reefs may therefore drive the magnitude of the fishing \times bleaching interaction, potentially overriding a synergistic interaction with fishing. The mechanisms causing such an effect are not currently known but, nonetheless, confirmation of this result in other parts of the world would indicate that a global strategy to mitigate climate change should provide more benefits to corals than local management efforts to reduce fishing pressure (see also Graham *et al.* 2008).

Covariation in the response of coral species to the two stressors could also greatly influence the interaction observed. For example, if the tolerance of a species to one stressor is associated with tolerance to another stressor (positively correlated tolerances or cotolerance), the cumulative impact of both stressors should be less than the sum of both effects, resulting in an antagonistic interaction (Vinebrooke *et al.* 2004). By contrast, negatively correlated tolerances due to trade-offs in stress tolerance, or no relationship between sensitivities to different stressors may result in synergistic or additive effects, respectively (Vinebrooke *et al.* 2004). Species-diverse communities are expected to be composed of species with both

positively and negatively correlated tolerances such that the net effect may depend on the abundance and dominance of tolerant or sensitive species within the community. The similarity in postbleaching coral cover on fished and unfished reefs is consistent with the idea of positively correlated tolerances to fishing and bleaching effects. If fishing pressure has already removed coral species that are sensitive to bleaching stress, then the fishing-sensitive species that had become abundant within marine reserves are also the bleaching-sensitive taxa that were mostly lost in the 1998 bleaching event. The combination of fishing and bleaching may therefore reduce assemblages on both fished and unfished reefs to a few species that are both fishing- and bleaching-resistant. These similar postbleaching assemblages would be expected to recover at the same rates and this may explain the similar recovery trajectories in fished and unfished sites.

Direct empirical evidence for community tolerance or sensitivity to different stressors in reef corals is currently lacking. Nevertheless, based on independent observations of coral assemblages inside and outside of fishing-protected areas and their responses to bleaching (e.g., McClanahan *et al.* 2001, 2007b; McClanahan 2008), assemblages dominated by foliaceous *Montipora* and various branching taxa such as *Acropora*, *Stylophora*, *Seriatopora*, and *Pocillopora* are likely to be sensitive to both fishing and coral bleaching; conversely, assemblages dominated by massive and submassive taxa, such as faviids (e.g., *Favia*, *Favites*, *Platgyra*) and massive *Porites*, are expected to show cotolerance to bleaching and fishing. Predicting cotolerance and consequences for coral assemblages is complicated, however, because fishing pressure may also favor "weedy" branching coral species with fast-growing and short-lived life histories that might be more tolerant of subsequent and continuous disturbances (Knowlton 2001; McClanahan *et al.* 2006; Green *et al.* 2008). Thus, if the selection pressure exerted by fishing leads to the replacement of disturbance-sensitive individuals or species with disturbance-tolerant ones, the tolerance of the entire assemblage to a future disturbance, such as bleaching, would effectively be increased (Odum 1985; Blanck & Wängberg 1988). Ultimately, it should be relatively simple to test for species tolerances or sensitivities to different stressors. Identifying these life-history attributes will make it easier to identify species of special conservation concern for both *in situ* and *ex situ* conservation actions. Furthermore, the prevalence and role of correlated tolerances is critically important for predicting future ecological changes on coral reefs and developing management priorities.

Can our results be generalized to future stressor events and to other combinations of stressors on coral reefs in other regions? Interactive effects that depend on the

relative effects of contributing stressors may be both context- and magnitude-dependent. For example, if our fished sites had experienced coral mortality from more destructive fishing gears, such as cyanide poisoning or bomb fishing, we may have reached different conclusions. In addition, if herbivorous sea urchins were not abundant on fished reefs, which they are on Kenyan reefs (McClanahan 2008), then the fishing effects of reduced herbivorous fishes might have been considerably greater. Similarly, interactive effects that are explained by species cotolerance may also be context dependent (Vinebrooke *et al.* 2004). For example, if the background stressor had selected for species assemblages that are more sensitive to thermal stress, we might have detected a synergistic response. As such, managing interactions will likely require an understanding of the underlying mechanisms of the individual stressors, their combined effects, the magnitude of the impact, and the ecosystem context.

While ours is the only study that found a nonsynergistic interaction between two stressors, it adds to the growing evidence that antagonistic and additive effects may be as common as synergies (Crain *et al.* 2008; Darling & Côté 2008). This evidence suggests that synergies are neither pervasive nor inevitable. Instead, quantifying the nature of stressor interactions and identifying the dominant drivers of change can improve future forecasts of ecological change and inform successful management and mitigation of multiple stressors.

In the context of coral reef conservation, the finding that the impacts of fishing and bleaching are not synergistic is hopeful news given future predictions for coral reefs. However, our results also suggest that marine reserves are not enough to protect Kenyan corals in a changing climate. This conclusion challenges the commonly held belief that managing local stressors, such as fishing, will mitigate global stressors, such as climate change. While there is some evidence for a reduction of climate change impacts through local protection on Caribbean coral reefs (Carilli *et al.* 2009), an exclusive focus on local stressor management in Kenya, where climate change is the dominant driver of coral loss, may lead to unrealistic expectations of reef resilience. This is, of course, not to say that local protection efforts should be abandoned. Marine reserves provide a myriad of well-documented benefits for coral reef ecosystems and fisheries (Halpern 2003; Russ *et al.* 2004; Knowlton & Jackson 2008). However, to fulfill their important role as refuges and recolonization sources for disturbance-sensitive coral species (McClanahan 2008), marine reserves will need to be located in areas that are not vulnerable to thermal stress (Graham *et al.* 2008; Maina *et al.* 2008). Through judicious placement in areas of climate refugia, marine reserves can

help to protect coral reefs by reducing additional anthropogenic disturbances.

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