

Corals in a Stressful World: Life Histories, Synergies, and Resilience

by

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Abstract

Diverse anthropogenic and natural disturbances affect ecosystems, with the potential to provoke synergies and other ‘ecological surprises’ that may impede our ability to predict and mitigate the impacts of multiple stressors. This thesis examines the impacts of stressors on populations and communities to establish the prevalence of synergies and identify ecological factors that influence interactions between stressors. First, I quantify the magnitude of multiple stressor interactions using a meta-analysis of published factorial studies, and find that synergies are as common as two other types of interactions, antagonisms and simple additive effects. Then, I turn my focus to coral reefs, an ecosystem that is expected to be particularly vulnerable to the impacts of synergies and stressor interactions. Using a long-term time-series of coral cover data in Kenya, I quantify the impacts of two common stressors, fishing and climate change-induced coral bleaching, and conclude that these stressors do not interact synergistically but instead have a weakly additive or antagonistic effect. The next two chapters investigate the impacts of multiple stressors on coral community dynamics in Kenya. I first propose a new approach to quantitatively classify the diversity of scleractinian corals into four life-history strategies based on species traits. I then apply these life-history groupings to Kenyan corals and show that the composition of life histories can, in part, explain the long-term impacts of fishing and coral bleaching, although life histories do overlook variability within coral communities. Finally, I discuss the implications of my results for our understanding of coral reef resilience to the cumulative impacts of stressors. Specifically, I consider how managing local impacts may have counterintuitive effects on the resilience of coral reefs to global climate change. This thesis highlights the importance of community dynamics for understanding the complex interactions among stressors and provides novel insights for conservation and management actions that attempt to mitigate the impacts of multiple stressors in an increasingly stressful world.

Keywords: Multiple stressors, climate change, coral reefs, life-history strategies, community disassembly, ecosystem resilience, East Africa

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Chapter 1.

General Introduction

The human footprint on global ecosystems is increasing as a consequence of climate change, overexploitation, habitat loss, pollution, and invasive species (Chapin et al. 2000; IPCC 2007; Newton et al. 2007; Halpern et al. 2008a). The diversity of anthropogenic pressures has raised concerns about the ability of ecosystems to absorb multiple, simultaneous disturbances (Novacek and Cleland 2001, Folke et al. 2004; Halpern et al. 2008a,b). In particular, the potential for multiple stressors to interact synergistically is provoking serious concern that such interactions will generate unpredictable 'ecological surprises' that can accelerate biodiversity loss (Sala et al. 2000; Brook et al. 2008) and impair the functioning of biological communities (Vinebrooke et al. 2004; Zavaleta et al. 2009) and ecosystems (Paine et al. 1998, Folke et al. 2004). Scientists have been nearly unanimous in declaring synergies a major challenge for conservation and management (Paine et al. 1998, Brook et al. 2008; Sutherland et al. 2009; Turner 2010), especially in the face of a rapidly changing climate (Harley et al. 2006; IPCC 2007, Hoegh-Guldberg and Bruno 2010).

One of the largest uncertainties for predictions of future ecological change is quantifying the cumulative impact of multiple stressors. Thus an important goal of modern ecology and conservation is to provide an explicit understanding of how multiple stressors interact to mitigate or exacerbate global change (Harley et al. 2006, Didham et al. 2007, Halpern et al. 2008b, Sutherland et al. 2009). It is often assumed that stressors act in synergy (e.g., Myers 1995, Dunne 2010), a type of non-additive interaction that occurs when the combined impact of several stressors is greater than the sum of the individual stressors (Folt et al. 1999). The alternatives to synergy are antagonistic interactions, where the combined stressor impact is less than the sum of the individual impacts, or simple additive effects where the combined effect is equal to the sum of the individual stressor impacts (Folt et al. 1999, Breitburg and Reidel 2005). However, the exact ways

in which multiple stressors interact to affect populations and communities remain largely untested, despite the fact that the ability to predict and mitigate the consequences of the human footprint depends, in part, on our understanding of these interactions (Halpern et al. 2008b; Hoegh-Guldberg and Bruno 2010).

There is a critical need to understand the impacts of multiple stressors on coral reef ecosystems. Coral reefs have been described as the 'rainforests of the sea' for the biodiversity they contain and ecosystem services they provide (Knowlton and Jackson 2008). However, coral reefs are in ecological crisis due to the combined effects of climate change, overexploitation, pollution, sedimentation, invasive species, and disease (Bellwood et al. 2004; Hoegh-Guldberg et al. 2007; Newton et al. 2007; Halpern et al. 2008). Widespread losses of live coral cover and architectural complexity (Roberts et al. 1995; Gardner et al. 2003; Pandolfi et al. 2003; Bruno and Selig 2007; Alvarez-Filip et al. 2009) are commonly assumed to be driven by synergies (Hughes and Connell 1999; Nyström et al. 2000; Bellwood et al. 2004; Knowlton and Jackson 2008). However, the combined impacts of multiple stressors on coral reefs and the ecological mechanisms that may mediate these impacts remain poorly understood (Dunne 2010).

This thesis explores how multiple stressors interact to affect ecological systems, with a focus on tropical coral reefs. In Chapter 2, I quantify the prevalence and magnitude of stressor interactions using a meta-analysis of factorial experiments that assessed the impacts of multiple stressors on mortality rates of terrestrial and aquatic animals. I find that synergies, antagonisms and additive interactions are equally common, suggesting that while synergies may not be the overriding interaction, non-additive ecological surprises (synergies, antagonisms) may be more common than simple additive effects. In Chapter 3, I test how two common stressors on coral reefs, fishing and thermal stress owing to climate change, interact to affect reef-building scleractinian corals using a 20-year time series of coral dynamics in Kenya. I find no evidence that a fishing x bleaching synergy has driven recent declines of coral cover on Kenyan reefs. However, I identify coral bleaching as the dominant stressor on Kenyan reefs, which suggests that marine reserves may not always provide corals with a refuge from climate change. In Chapter 4, I propose a quantitative approach for evaluating the response of coral communities to multiple stressors – I assemble a global database of coral species traits to provide a conceptual framework of major life-history strategies for scleractinian corals. I then apply

this framework to Kenyan coral reefs in Chapter 5 to evaluate the roles of life history and co-tolerance on the long-term responses of coral assemblages to fishing and bleaching. Finally in Chapter 6, I consider the direct relevance of my findings for conservation and management policy by highlighting how multiple stressors affect how we attempt to manage ecosystems for resilience to climate change. I conclude that the placement of Marine Protected Areas may need to be strategically reconsidered to combat the overriding effects of a rapidly changing climate.

Interactions between multiple stressors, and synergies in particular, are of critical ecological and conservation concern, yet are rarely quantified in the ecological literature (Dunne 2010; but see Folt et al. 1999; Christensen et al. 2006; Crain et al. 2008). As a whole, this thesis takes a data-driven approach to understand the impacts of multiple stressors and their potential interactions. I have focused on coral reefs, which may be one of the first ecosystems to reach a 'tipping point' of cumulative impacts (e.g., Folke et al. 2004, Hughes et al. 2010). However, this thesis also contributes to a more general understanding of the ecological impacts of multiple stressors and their interactions for marine, freshwater, and terrestrial ecosystems. Understanding and quantifying interactions between stressors can support ecosystem-based management actions and climate-adaptation policies that explicitly consider, evaluate and attempt to mitigate human impacts in a rapidly changing world.

Chapter 2.

Quantifying the evidence for ecological synergies¹

Abstract

There is increasing concern that multiple drivers of ecological change will interact synergistically to accelerate biodiversity loss. However, the prevalence and magnitude of these interactions remain one of the largest uncertainties in projections of future ecological change. We address this uncertainty by performing a meta-analysis of 112 published factorial experiments that evaluated the impacts of multiple stressors on animal mortality. We found that, on average, mortalities from the combined action of two stressors were not synergistic and this result was consistent across studies investigating different stressors, study organisms and life-history stages. Furthermore, only one-third of relevant experiments displayed truly synergistic effects, which does not support the prevailing ecological paradigm that synergies are rampant. However, in more than three-quarters of relevant experiments, the outcome of multiple stressor interactions was non-additive (i.e. synergies or antagonisms), suggesting that ecological surprises may be more common than simple additive effects.

¹ A version of this chapter is appears as, Darling E.S. and I.M. Côté (2008) Quantifying the evidence for ecological synergies. *Ecology Letters* 11, 1278 – 1286.

Introduction

Diverse natural and anthropogenic disturbances are impacting global ecological systems (Chapin et al. 2000, Sala et al. 2000, Halpern et al. 2008a). While natural disturbance regimes are important for biodiversity (Connell 1978) and the structure of ecological communities (Levin and Paine 1974), increasing anthropogenic pressure (e.g. overexploitation, pollution and climate change) is raising concerns about the capacity of systems to absorb multiple disturbances that occur simultaneously (Novacek and Cleland 2001, Folke et al. 2004). Recent reviews suggest that multiple stressors will interact synergistically to accelerate biodiversity loss (Sala et al. 2000, Sala and Knowlton 2006), exacerbate the impacts of climate change (Harley et al. 2006, IPCC 2007) and amplify the negative effects of existing anthropogenic stressors (Chapin et al. 2000, Halpern et al. 2008a). While true synergies have the potential to drive future trends in biodiversity and ecosystem function, the prevalence and magnitude of such interactions remain unclear (Sala et al. 2000, Mora et al. 2007, Didham et al. 2007).

An important goal of modern ecology and conservation is a quantitative understanding of how multiple drivers will interact to mitigate or exacerbate global environmental change (Harley et al. 2006, Sutherland et al. 2006, Didham et al. 2007, Mora et al. 2007). If multiple stressors have interactive effects that are not predictable from single stressor impacts (e.g. "ecological surprises", Paine et al. 1998), this represents a major source of uncertainty for projections of biodiversity (Sala et al. 2000) and ecosystem resilience (Folke et al. 2004). Furthermore, if drivers of climate change interact synergistically (e.g. Harley et al. 2006, Didham et al. 2007, IPCC 2007), making predictions based on additive expectations will underestimate the ecological impacts of global environmental change (Hoffman et al. 2003, Przeslawski et al. 2005). However, if multiple stressors act independently in natural systems, additive models may be suitable and the predictive power of local and global forecast models would be greatly improved (e.g. Sala et al. 2000, Halpern et al. 2008a, Jetz et al. 2007).

It is often assumed that stressors typically act in synergy (e.g. Myers 1995, Sala et al. 2000, Sala and Knowlton 2006), however, it is important to note that synergies are one specific type of non-additive interaction, which occurs when the combined impact of several stressors is greater than the algebraic sum of the impacts of individual stressors

(Folt et al. 1999). The alternatives to synergy are either antagonistic interactions or simple additive effects. Antagonistic interactions, or “anti-synergies”, occur if the combined stressor impact is less than the sum of the individual impacts (Breitburg et al. 1998, Breitburg and Reidel 2005), effectively diminishing the combined impact of the stressors below what would be predicted from simple additive effects (Didham et al. 2007). The cumulative impact of multiple stressors can also be additive, where the combined effect is equal to the sum of the individual stressor impacts (Halpern et al. 2008b).

Few studies have explicitly evaluated the nature of interactions between stressors (but see Folt et al. 1999, Ross et al. 2004, Christensen et al. 2006, Mora et al. 2007). Our goal was therefore to examine the prevalence and magnitude of synergies using a meta-analysis of published studies. We do so by using an additive model as a null hypothesis to compare with an observed interaction effect because it is a relatively simple and straightforward method of evaluating interactions (e.g. Didham et al. 2007, Brook et al. 2008). We focused on mortality as a response to stressor action, because individual mortality governs population-level responses that can affect community- and ecosystem-level dynamics (Carpenter 1987, Power 1990, Taylor et al. 2006). Furthermore, population-level responses may be more sensitive to multiple stress effects than ecosystem-level variables (Schindler 1987, Folt et al. 1999). We broadly defined a stressor as any external environmental factor that causes a detrimental change in a response variable (Bertness and Callaway 1994, see Boone et al. 2007, Didham et al. 2007, Kawai and Tokeshi 2007). Specifically, we asked the following questions. (1) What is the overall impact of multiple stressors on mortality? (2) Is the magnitude of this impact consistent, on average, with synergies? (3) What is the prevalence of synergies compared to non-synergies? (4) Can we predict under which conditions synergistic and non-synergistic interactions will occur?

Methods

Study selection and data criteria

We searched the ecological literature for studies that experimentally manipulated two stressors in a factorial design. Literature searches were conducted using *ISI Web of Science* and *Scopus* databases (1965 through 2007) for relevant keywords: synergy, antagonism, additive, non-additive, multiple, stress, disturbance, factorial, ecology. In addition to database searches, we also hand-checked the reference lists of all studies retrieved to attempt to identify all relevant primary research (see Gates 2002). We restricted our literature search to controlled factorial experiments, which report the effect of two stressors individually and combined with a control treatment (Underwood 1997). We deemed this to represent the ideal experimental design to evaluate the nature of stressor interactions. Consistency of experimental design also reduced any bias potentially introduced by variable designs (Gates 2002).

To be included in our meta-analysis, each factorial experiment was required to report mortality from four experimental blocks: control (no stressor), two single stressor treatments, and the combined stressors treatment. Studies reporting survival were also included as $Mortality = 1 - Survival$. We only included studies that used two or more replicates within each experimental block and in which replicates consisted of closed populations (i.e. no reproduction or immigration occurred during the experiment). We recorded the sample size, mean and standard error of survival/mortality for each block within an experiment. We also recorded the species, life-history stage and type of stressors investigated in each experiment as possible categorical moderators in a meta-analytical model.

We included multiple experiments within a single study if separate factorial results were reported for each species, time period, or for each controlled combination of two stressors. If multiple results were presented for several species tested within the same replicate (e.g. individuals of two species within the same enclosure), we averaged mortality across species to avoid non-independence of effect-size estimates (Gurevitch and Hedges 1999). When mortality was reported as a time series, we recorded mortality

from the final time point. Experimental duration (days) was recorded for each experiment.

We considered a number of sources of potential bias (Gurevitch and Hedges 1999, Gates 2002). We evaluated the importance of publication bias using qualitative tests (weighted frequency histogram, funnel plots and Q-Q normality plots of effect sizes) and a quantitative rank correlation test (Spearman's rho). Bias towards publication of larger effects would be indicated by a significant correlation between effect size and sample size, i.e. the number of replicates, within experiments (Gurevitch and Hedges 1999). We further established the robustness of our results by calculating Rosenthal's fail-safe number, an indicator of the number of studies that would need to exist to overturn a significant result (Rosenthal 1979). A high fail-safe number relative to the number of experiments included in the meta-analysis indicates that the overall effect size of the meta-analysis is a robust estimate of the true effect size (Gurevitch and Hedges 1999). We also examined how sensitive our results were to the inclusion of studies that contributed more than 10 experiments to the dataset (see Gates 2002).

Data analysis

The effect of stressors on mortality was measured as the ln-transformed response ratio

$$RR = \ln \frac{\text{stress treatment}}{\text{control}} \quad (\text{eqn. 1})$$

where *stress treatment* and *control* are the percent mortality in the stress treatment (single or combined stressors) and in the control treatment, respectively. Response ratios are a commonly used effect metric in meta-analyses (Gurevitch and Hedges 1999, Hedges et al. 1999, Osenberg et al. 1999) because they are amenable to biological interpretation (proportional change in mortality when un-logged, see Shurin et al. 2002, Elser et al. 2007, Marczak et al. 2007). Response ratios are also proportionally symmetrical and have a sampling distribution that approximates normality (Hedges et al. 1999, Lajeunesse and Forbes 2003).

Traditional meta-analysis weights the contribution of an individual study to the overall mean effect size by the inverse of the sample variance (Gurevitch and Hedges 1999). However, recent ecological meta-analyses advocate weighting each study equally to avoid both underestimation of effect sizes and increased Type 1 errors (see Shurin et al. 2002, Elser et al. 2007, Marczak et al. 2007). We analyzed our overall dataset using both methods and found that the weighted and un-weighted mean effect sizes were not significantly different from each other (based on overlapping 95% confidence limits, see Results). We therefore use un-weighted effect sizes in all further analyses.

We calculated the overall effect of stressor experiments (the effect size of single and combined stressor treatments), as well as separate mean effect sizes for single and combined stressor treatments. We generated 95% confidence intervals for mean effect sizes by bootstrapping (N = 999 permutations) effect sizes and correcting for distribution bias (Rosenberg et al. 2000). Based on the sum of the individual stressor treatments for each experiment, we calculated a predicted ‘additive effect size’:

$$RR_{\text{additive}} = \ln \frac{(\text{Stressor 1} + \text{Stressor 2})}{\text{Control}} \quad (\text{eqn. 2})$$

We used an additive null model as our predicted combined-stressor expectation as this is a more conservative estimate than a multiplicative risk model (e.g. Soluk and Collins 1988, Sih et al. 1998). We did nevertheless also run all analyses using a multiplicative null expectation in which study-specific effect sizes were calculated as

$$RR_{\text{multiplicative}} = \ln \frac{(\text{Stressor 1} + \text{Stressor 2} - \text{Stressor 1} * \text{Stressor 2})}{\text{Control}} \quad (\text{eqn. 3})$$

The results were very similar and we therefore present only the analyses using the additive expectation. We present the mean predicted additive combined-stressor effect size for all experiments with bootstrapped (N = 999 permutations) 95% bias-corrected confidence intervals.

Heterogeneity in the overall mean effect size was evaluated using the test statistic Q_T (Rosenberg et al. 2000). Q_T evaluates the heterogeneity of effect sizes among experiments to determine whether all experiments share a common effect size, larger

values of Q_T indicate greater heterogeneity. If significant heterogeneity exists, experiments can be divided into biologically meaningful subgroups and overall effect sizes for each subgroup recalculated and compared using the Q_B statistic (Cooper and Hedges 1994, Gurevitch and Hedges 1999, Côté et al. 2005). Significance of the Q_T and Q_B test statistics is assessed using resampling tests (Gurevitch and Hedges 1999). We limited the number of pre-planned subgroup comparisons to three factors to guard against the possibility of increased Type 1 errors (Gates 2002). These three factors with potential influence on effect sizes were: (1) the type of stressors manipulated (two categories: physical or ecological), (2) the taxonomic level of the study organism (two categories: invertebrate or vertebrate), and (3) the life-history stage studied (three categories: embryo, juvenile, adult). Eight stressors were classified as physical: pollutant (N=72 experiments), thermal (N=32), UV (N=28), salinity (N=18), low food (N=10), pH (N=7), wave action (N=6), sedimentation (N=2), drought (N=1), two stressors were classified as ecological: predation (N=13) and competition (N=6). Within each factor, we calculated the mean response ratio and 95% confidence intervals for single, additive and observed interactions. We used MetaWin (version 2.1, Rosenberg et al. 2000) for all analyses.

Finally, we investigated whether differences among experiments could be used to predict the type of observed interaction. We classified each experiment as antagonistic, additive, or synergistic by calculating an experiment-specific additive response ratio with 95% confidence limits. Confidence limits were calculated for each additive mean from the variance of the single-stressor mean mortality in each experiment as

$$95\% \text{ CI} = 1.96 * \sqrt{(s_1)^2 + (s_2)^2} \quad (\text{eqn. 4})$$

where s_1 and s_2 are the standard deviations of the mean of Stressor 1 and Stressor 2, respectively. Experiments that did not report sample size or variance were excluded from this analysis (N=45 experiments excluded). We further excluded from this analysis 10 experiments where the additive expectation exceeded 100% as some authors have criticized the use of an additive-comparison approach if the mortality caused by single stressors sum to more than 100%, effectively biasing the classification of observed interactions towards antagonism (see Fournier et al. 2006). This left 57 experiments for

this analysis. We then compared the observed percent mortality from the combined stressor treatment to the calculated expected additive mortality. If the observed combined stressor mortality was less than the lower 95% confidence limit of the additive mortality, the experiment was classified as antagonistic. Similarly, if the combined stressor mortality was greater than the upper 95% confidence limit, we classified the experiment as synergistic. If the combined stressor mortality overlapped with the predicted additive 95% confidence limit, the experiment was classified as additive. We then plotted the predicted additive response ratio against the observed combined-stressor response ratio for each of the 57 experiments.

For the 57 experiments classified as synergistic or non-synergistic (a group containing the additive and antagonistic experiments), we used chi-square tests to evaluate differences in three categorical factors (taxon, life-history stage and stressor type) and nonparametric Wilcoxon signed rank tests to compare differences in four continuous variables (experiment duration, control mortality, mean single stressor mortality and the difference in mortality between the two stressors). Adult life-history stages were excluded from the chi-square analysis because of low sample sizes that violated assumptions of a 2x2 chi-square test (Field 2001). For the seven *a priori*-planned comparisons, we applied a Bonferroni correction and adjusted the α -significance level to 0.007.

Results

Overview

We included 112 experiments from 23 studies published in 13 peer-reviewed journals that manipulated diverse physical and ecological stressors (see Appendix A). The number of experiments contributed by each study ranged from one to 24 (mean 4.9, median 3). Three potentially influential studies contributed > 10 experiments to the dataset, the exclusion of these studies did not significantly change the overall mean effect size (mean RR = 1.42, 95% bias-corrected 95% CI= 1.18 - 1.65) or its significance (i.e. 95% confidence interval still does not overlap zero), justifying their inclusion. The variance-weighted overall effect size (RR=1.52, 95% bias CI: 0.50 to 2.45) was not

significantly different from the unweighted overall effect size (RR=1.56, 95% bias CI: 1.39 to 1.74) and all further analyses use unweighted effect sizes. We found no evidence of publication bias: visual assessment of weighted frequency histograms and funnel plots indicate effect sizes are normally distributed across studies and there was no correlation between effect size and sample size ($R_S = -0.05$, $P = 0.36$). An extremely large fail-safe number (Rosenthal's method: 100665.8) for the overall analysis also suggest that our results are robust to publication bias.

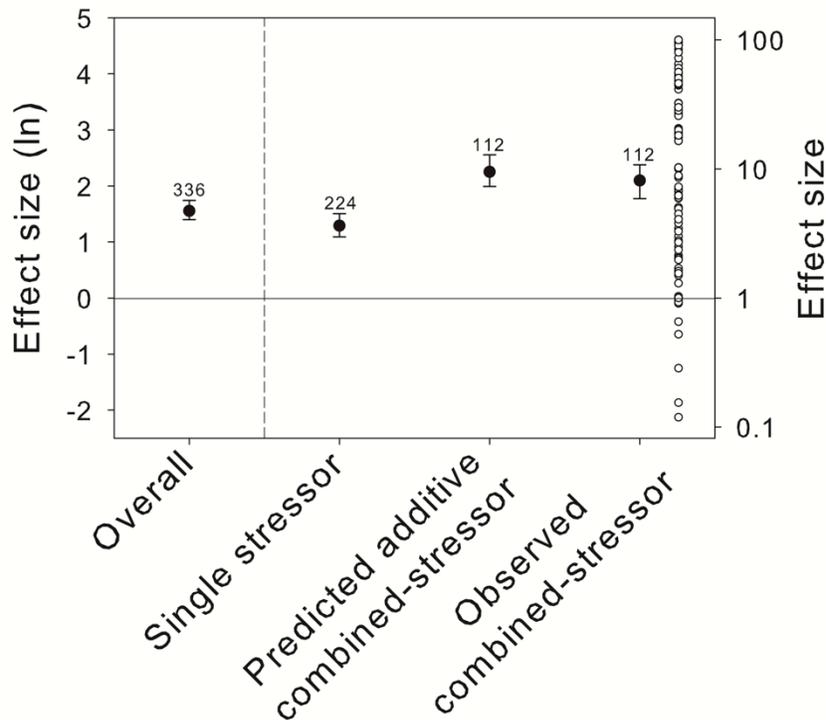


Figure 2.1. Mean effect sizes of stressor treatments on mortality. Means with 95% bootstrapped and bias-corrected confidence intervals are shown for all treatments combined (overall), single-stressor and combined-stressor effects. Predicted additive combined-stressor effects are calculated from the sum of the individual stressor mortalities from each experiment. Numbers above the means indicate the number of experiments from 23 studies. The open-circles are the observed combined-stressor effect sizes for each of the 112 experiments. The zero line indicates no effect of stressor on mortality.

Overall, the mortality rate of organisms experiencing experimental stressors was approximately six times higher than for organisms under control conditions (Figure 2.1). This effect is significant (i.e. the 95% CI does not overlap 0, Figure 2.1). There was significant heterogeneity in overall mortality among experiments ($Q_T = 951.57$, $df = 335$,

$P < 0.0001$), which is investigated below. Both single- and combined-stressor treatments enhanced mortality (Figure 2.1). The mean observed combined-stressor effect size was not significantly different from the mean predicted additive combined-stressor effect size ($Q_B = 0.98$, $P = 0.32$, Figure 2.1).

Explaining variation in stressor impacts

Although both physical and ecological stressors enhanced mortality of the study organisms, physical stressors increased mortality significantly more than ecological stressors (Fig. 2.2, $Q_B=7.19$, $df=1,222$, $P=0.007$). There was no difference between the observed mortality caused by the combined effect of two physical stressors (P x P) or one physical with one ecological (P x E) stressor (Fig. 2.2, $Q_B= 1.01$, $df=1,110$, $P=0.32$). Additionally, the observed combined-stressor effects, whether P x P or P x E, were not significantly different from their mean additive expectations (Fig. 2.2, P x P additive vs. observed: $Q_B=1.75$, $df=1,184$, $P=0.19$, P x E additive vs. observed: $Q_B=0.0013$, $df=1,36$, $P=0.97$).

Invertebrates were more susceptible to stressor treatments (mean RR = 1.92, 95% bias-corrected CI = 1.73-2.11) than vertebrates (mean RR = 1.28, 95% bias-corrected CI= 1.02 - 1.54, $Q_B=37.66$, $df=1,445$, $P<0.0001$). Juvenile (mean RR = 1.98, 95% bias-corrected CI = 1.78 - 2.17) and adult (mean RR = 2.46, 95% bias-corrected CI = 2.14 - 2.76) life-history stages were particularly susceptible to stressors, while embryonic life history stages displayed significantly lower mortality across all stress treatments, with the exception of the observed vertebrate combined-stressor treatment (mean RR across all treatments = 0.66, 95% bias-corrected CI = 0.43 - 0.91, $Q_B=169.98$, $df=2,444$, $P<0.0001$, Fig. 2.3).

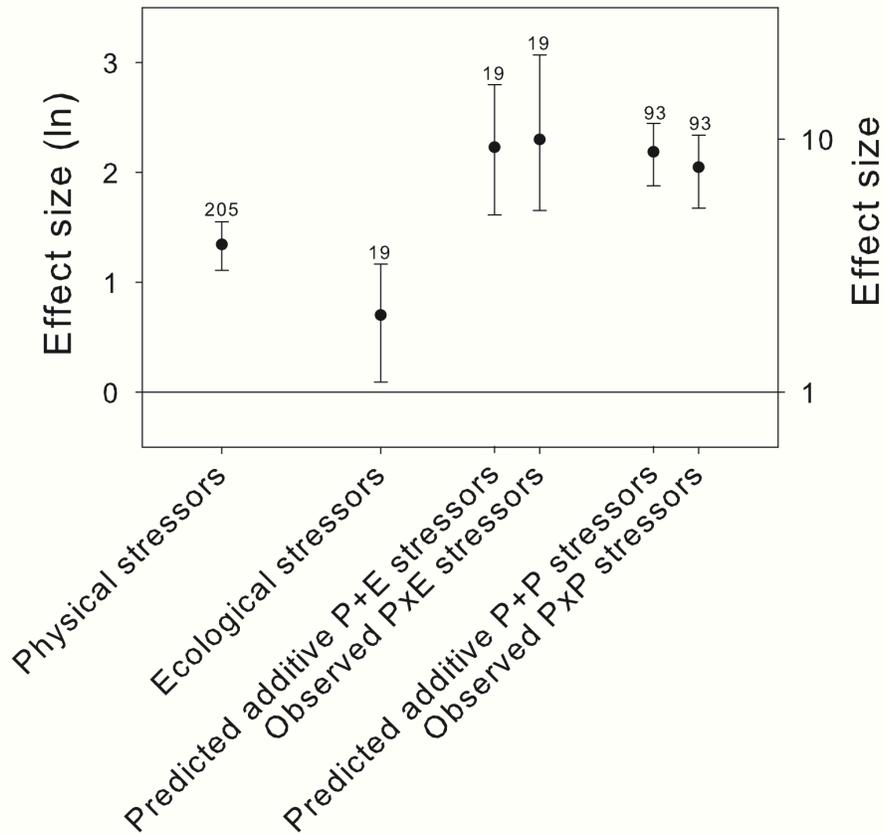


Figure 2.2. Mean effect sizes of physical and ecological stressors on mortality differ. Means with 95% bootstrapped and bias-corrected confidence intervals are shown for single physical and single ecological stressors, and for combined physical-ecological (P x E, N=9 studies) and physical-physical (P x P, N=16 studies) stressors. Predicted additive combined-stressor effects are described in Figure 2.1. Numbers above the means indicate the number of experiments. The zero line indicates no effect of stressor on mortality.

Predicting interaction types

When we considered only the observed combined-stressor effect sizes, there was considerable variation across experiments ($Q_T=313.62$, $df=111$, $P<0.0001$). Based on the experiment-specific comparison approach (N=57 experiments), we identified 20 synergistic and 37 non-synergistic experiments (24 antagonistic and 13 additive experiments) (Fig. 2.4). Similarly, we identified 13 additive and 44 non-additive (20 synergistic and 24 antagonistic) experiments. The 57 experiments came from 12 studies and each interaction-type group contained experiments from at least five separate studies (see Appendix A). These groups do not appear to be biased by the inclusion of

one study (Przeslawski et al. 2005) that contributed 24 experiments to the final subset of 57 experiments – this study yielded 18 non-synergistic experiments (out of 37 non-synergistic experiment) and 6 synergies (out of 20 synergistic experiments). Nine of 20 experiments identified as synergistic were contributed by a single study (Peachey 2005). Two studies (Folt et al. 1999 and Shaw et al. 2006) that contributed a large number of experiments to the full dataset of 112 experiments (N=12 and 20 experiments, respectively) were excluded from classification by interaction type because they failed to report standard deviation from their experiments.

Synergies were marginally more common in experiments involving invertebrates than those involving vertebrates, although this distinction became non-significant following Bonferroni correction (odds ratio: 3.9, $\chi^2_1=4.2$, $P=0.04$, Bonferroni $\alpha = 0.007$). There was no association between interaction type (synergy vs. non-synergy) and life-history stage (embryo vs. juvenile, adults excluded due to low sample size: $\chi^2_1=1.6$, $P=0.21$) or stressor type combination (physical x physical vs. physical x ecological: $\chi^2_1=1.1$, $P=0.29$). Synergistic experiments had, on average, shorter experimental durations than non-synergistic experiments (synergistic: 6.7 ± 3.9 d, non-synergistic: 17.1 ± 2.9 d, Wilcoxon signed-rank test: $Z= -3.93$, $P<0.0001$). There was no significant difference between synergistic and non-synergistic experiments in mean mortality of the control (mean = $8.36\% \pm 1.34\%$, $Z= -0.48$, $P= 0.63$) or single-stressor treatments (mean = $16.03\% \pm 1.87\%$, $Z= -2.25$, $P= 0.024$, Bonferroni $\alpha=0.007$), or in the difference in mortality between single stressors (mean = $18.73\% \pm 3.21\%$, $Z= -2.45$, $P= 0.014$, Bonferroni $\alpha=0.007$).

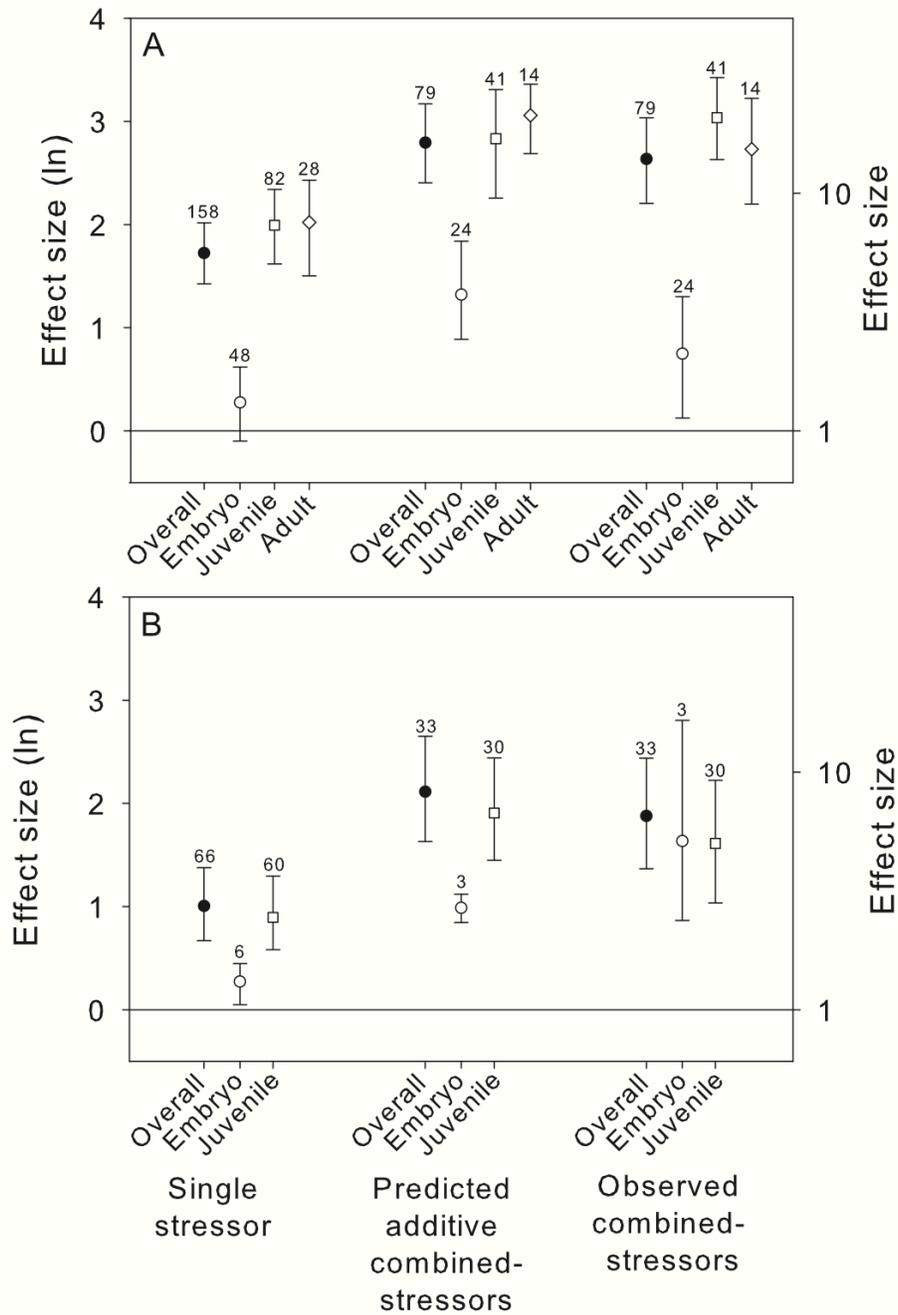


Figure 2.3. Mean effect sizes of stressor treatment on mortality vary across taxa (A: invertebrates, B: vertebrates) and life-history stage (embryo: open circles, juvenile: open squares, adult: open triangles). Overall effect sizes across all life-history stages are indicated by filled circles. Means with 95% bootstrapped and bias-corrected confidence intervals are shown for observed single- and combined-stressor effects. Predicted additive combined-stressor effects are described in Figure 2.1. Numbers above the means indicate the number of experiments from nine studies of invertebrates (embryo: N=1, juvenile: N=6, adult: N=4 studies) and 15 studies of vertebrates (embryo: N=2, juvenile: N=13 studies). The zero line indicates no effect of stressor on mortality.

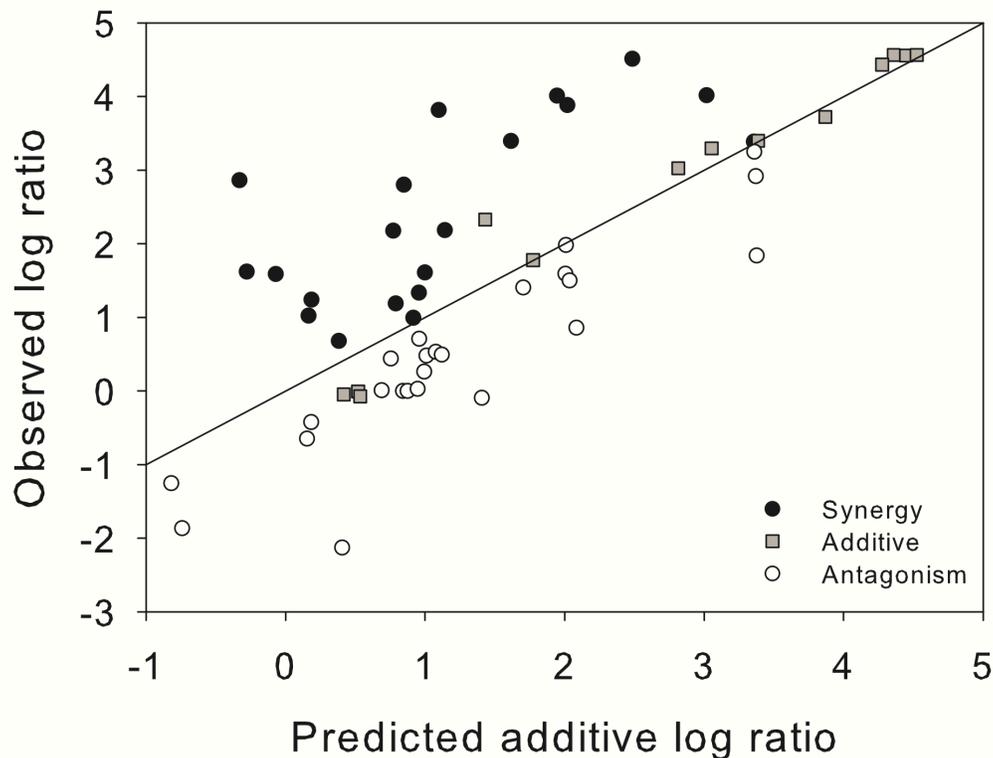


Figure 2.4. Predicted additive combined-stressor effect sizes in relation to observed combined-stressor effect sizes for each of the 57 experiments that reported standard deviation and could be classified as synergistic (filled circles), antagonistic (open circles) or additive (grey squares). The solid line shows the 1:1 predicted additive relationship.

Discussion

We found no evidence that the overall effect of multiple stressors on the mortality of various organisms was synergistic, i.e. greater than what is expected from the simple addition of the effects of individual stressors (Figure 2.1). This is not to say that synergies were never observed under experimental conditions. Examination of individual studies reveals that one-third of experiments (20 out of 57 or 35%) did yield truly synergistic interactions, but the majority (65%) of experiments did not (37 out of 57) (Figure 2.4). We conclude that synergies may be rarer than expected. However, the outcome of multiple interacting stressors was only predictable from the sum of the individual stressors (i.e. additive effects) in less than one-quarter of the experiments (13 out of 57 experiments, or 23%). We observed non-additive effects (i.e. synergies or antagonisms) in more than three-quarters of the experiments (44 out of 57 experiments,

or 77%), suggesting that multiple stressors may more commonly interact to generate ecological surprises (e.g. Paine et al. 1998) than simple additive effects.

As synergies were expected to be the most prevalent interaction type among multiple stressors (e.g. Myers 1995, Paine et al. 1998, Sala et al. 2000, Harley et al. 2006, Sala and Knowlton 2006, Brook et al. 2008), why did we observe synergies only in one-third of experiments? It is possible that experimental set-ups do not permit the widespread development of synergies. At the individual level, it is thought that synergies should be evident when physiologically stressed individuals are less likely to withstand additional stress compared to unstressed individuals (Myers 1995, Breitburg et al. 1998, Folt et al. 1999, Breitburg and Riedel 2005) or when individuals have particular life-history traits (e.g. large body size, long time to reproduction) that make them highly vulnerable to declines in population size (Davies et al. 2004, Harley and Rogers-Bennett 2004). At the population level, positive feedback loops between different stressors over time are expected to generate synergies that increase population extinction risk (e.g. Myers 1995, Sala and Knowlton 2006, Didham et al. 2007, Brook et al. 2008). In most experiments, the application of multiple stressors was simultaneous, rather than sequential, hence all subjects were unstressed until faced with a double dose of stressors. Neither the taxon, life-history stage, nor extent of experimental mortality was associated with the nature of the interaction between stressors. The only factor that was significantly associated with interaction type was experimental duration, experiments classified as non-synergistic were, on average, twice as long as experiments classified as synergistic, which goes against the notion that time is needed for synergies to develop. It is unclear how the length of the experiment could affect the type of interaction between stressors. There was large variation in experiment length across studies (2 to 134 d) and no standard methodology used to determine experiment duration – some studies were maintained until 100% mortality occurred (e.g. Metts et al. 2005) or a certain developmental stage of the study organism was reached (e.g. Long et al. 1995, Pahkala et al. 2002, Boone et al. 2007). Longer experiments provide scope for relatively higher mortality rates in control groups, which could decrease effect sizes and lead to apparent antagonistic interactions between stressors. Alternatively, the nature of interactions between stressors could vary over time. For example, Reich et al. (2006) found that the interaction between the effects of nitrogen availability and CO₂ enrichment on total plant biomass shifted from

antagonistic to synergistic over the course of a six-year experiment. In short, we currently cannot adequately predict the conditions under which interactions between stressors will be synergistic, even in well-controlled experiments.

Mortality was higher in experiments that manipulated single physical stressors compared to single ecological stressors. These results are of concern if extrapolated to the wild because many of the predicted consequences of global climate change entail increases in physical stressors (e.g. thermal stress, UV stress, pH stress) (IPCC 2007). Natural populations may therefore be particularly susceptible to isolated climate change stressors. However, climate-related stressors are most likely to be experienced in concert rather than in isolation by organisms. While combined stressors caused higher mortality than single stressors (Figures 2.1, 2.2), there was no difference between the effect of two physical stressors and that of one physical and one ecological stressor (Figure 2.2). Furthermore, the effects of both stressor combinations were consistent with simple additive effects (Figure 2.2). This suggests that in systems where two stressors are present, the combined effects of two stressors are independent and not moderated by the type of stressors. However, broadly classifying stressors as physical or ecological in origin may overlook interactions between specific stressors (e.g. thermal stress, acidification). Determining which specific stressors interact to generate non-additive effects remains an important area for future work (Harley et al. 2006).

In conservation and management science, ecological synergies have been implicated as generally having deleterious consequences (Paine et al. 1998, Harley et al. 2006, Sala and Knowlton 2006). They have the potential to produce amplified effects that either reduce ecosystem resilience or push systems into alternative states that would not have been reached with individual stressors (McClanahan et al. 2002, Folke et al. 2004). Our meta-analysis shows that interactions between stressors are not biased towards synergies, both in frequency (i.e. only 35% or 20 out of 57 experiments showed a truly synergistic effect) and in terms of overall effect on mortality (Figure 2.1). This result may be cause for cautious optimism and suggests that, more often than not, ecosystems may be spared from synergisms. However, our finding that synergies may be less common than predicted is not necessarily a complete reprieve for stressed populations. Recent reviews show multiple stressors impact many, if not all, terrestrial and marine systems (Harley et al. 2006, Halpern et al. 2008a,b, Brook et al. 2008). Even if stressors act

independently, single-stressor impacts that sum to more than 100% mortality will have catastrophic consequences for populations and will result in localized extinctions.

The potential for synergies remains one of the largest uncertainties facing predictions of future ecological change (Sala et al. 2000, Sutherland et al. 2006). From a species-based conservation perspective, only additive interactions have a predictable effect and a prevalence of these interactions would improve predictions of multiple stressor impacts. However, less than one-quarter of experiments (13 out of 57 experiments, or 23%) showed simple additive effects while the remainder (44 of 57 experiments, or 77%) displayed unpredictable non-additive effects, suggesting that predictable additive effects are less likely to occur than unpredictable non-additive ones. From the same perspective, antagonistic interactions that reduce cumulative impact should be less damaging for biodiversity and conservation objectives than synergistic interactions (Didham et al. 2007, Brook et al. 2008). Therefore, the use of an additive model would have been at least appropriate, if not a conservative (for the antagonistic experiments) estimate of combined-stressor impacts in 65% of the experiments (13 additive + 24 antagonistic = 37 out of 57 experiments). As most large-scale studies use an additive model for simplicity (e.g. Halpern et al. 2008a), such assumptions may be generally appropriate and may not always be a dangerous underestimation of the impacts of multiple stressors (e.g. Hoffmann et al. 2003, Halpern et al. 2008a,b). However, from a community- or ecosystem-based conservation perspective, the finding that more than three-quarters of stressors interactions were non-additive (i.e. synergies or antagonisms were found in 44 out of 57 experiments, or 77%) may be cause for concern as any non-additive interaction could alter species interactions or food web structure in ways that are unpredictable from the effects of individual stressors.

Our findings suggest that while non-additive effects may be common, synergies may not be the rule. However, our meta-analysis has examined the simplest situation of two superimposed stressors. Synergies may be more likely to occur if there are three or more stressors acting in the same system (e.g. Przeslawski et al. 2005, Mora et al. 2007, Crain et al. 2008). Furthermore, our meta-analysis has only included experiments that manipulated interactions across a range of study systems at the population level. Understanding how these effects scale up to natural communities and ecosystems remains a challenge for ecologists.

Chapter 3.

Combined effects of two stressors on Kenyan coral reefs are antagonistic or additive, not synergistic²

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 non-additive effects remain largely unidentified in nature. We used a long-term dataset of hard coral cover from Kenyan reefs 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 non-synergistic response may be caused by the presence of one dominant stressor, bleaching, and co-tolerance 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.

² A version of this chapter appears as, Darling E.S., McClanahan, T.R. and I.M. Côté (2010) Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. *Conservation Letters*, 3: 122-130.

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 and Reidel 2005, Halpern et al. 2008a,b). If such stressors interact non-additively, 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 non-additive 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 and Reidel 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 and Callaway 1994, Breitburg and Riedel 2005, Crain et al. 2008, Darling and Côté 2008; Chapter 2). 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 and Côté 2008; Chapter 2). For example, a non-additive antagonistic interaction can occur when the combined impact of two stressors is less than 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 and Reidel 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 and Côté 2008, Halpern et al. 2008b; Chapter 2), 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 and 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 and 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 (McClanahan et al. 2005a). Fisher densities range from 5 to 30 fishers km⁻² and primary fishing gears include gill nets, hand lines, spear guns, beach seines and traps (McClanahan et al. 2008a). 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 (McClanahan and Obura 1997, 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. 2007a) 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 and 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 and 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

Study sites

Ecological surveys were carried out between 1987 and 2008 at 12 sites along a ~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, McClanahan et al. 2008b), but have not considered the potential for synergy between fishing and bleaching. In this study, we focus particularly on two years of this time series: 1997 and 1999, i.e., one 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 O'Leary et al. 2012). Fishing prohibition is enforced in all Marine National Parks while artisanal fishers intensively exploit the non-park reef sites (McClanahan et al. 2005, McClanahan et al. 2008a). 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.

Effect sizes of individual and combined stressors

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 pre-bleaching 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:

$$Fishing = \left(\bar{X}_{Fished,1997} - \bar{X}_{Unfished,1997} \right) / \bar{X}_{Unfished,1997} \quad (\text{eqn.1})$$

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 and Berger 2001). Here, the variance of the fishing effect size is calculated as:

$$\text{var}_{Fishing} = s_{Fished,1997}^2 * \left(\frac{1}{\bar{X}_{Unfished,1997}} \right)^2 + s_{Unfished,1997}^2 * \left[\frac{-\bar{X}_{Fished,1997}}{(\bar{X}_{Unfished,1997})^2} \right]^2 \quad (\text{eqn. 2})$$

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 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 $95\%CI_{Fishing} = 2.228 * \sqrt{\text{var}_{Fishing} / 12}$.

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 one 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 pre-protection data were available for the Malindi or Watamu reserves, which were established in the 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:

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

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 $95\%CI_{Bleaching} = 2.776 * \sqrt{\text{var}_{Bleaching} / 5}$.

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:

$$\text{Fishing} + \text{Bleaching} = F + B - (F * B) \quad (\text{eqn. 4})$$

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 and 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:

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

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

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,

$$Fishing \times Bleaching = \left(\bar{X}_{Fished,1999} - \bar{X}_{Unfished,1997} \right) / \bar{X}_{Unfished,1997} \quad (\text{eqn. 6})$$

where $\bar{X}_{Fished,1999}$ is the mean coral cover on fished sites in 1999 and $\bar{X}_{Unfished,1997}$ 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 1997 and unfished sites in 1999:

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

where $s_{Fished,1999}^2$ and $s_{Unfished,1997}^2$ 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 $95\%CI_{F \times B} = 2.228 * \sqrt{\text{var}_{F \times B} / 12}$.

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% confidence intervals), 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% confidence intervals), the interaction between fishing and bleaching was classified as antagonistic. If the 95% confidence interval of the additive null expectation overlapped with the 95% confidence interval of the observed fishing \times bleaching effect size, the interaction was classified as additive.

Sensitivity analyses

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% confidence intervals of the new expectations against the 95% confidence interval of the

observed interaction, reclassifying each outcome as antagonistic, additive, or synergistic.

Post-bleaching recovery

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 post-bleaching recovery trajectories (between 1999 and 2008) using a geometric rate of change, which is appropriate for non-linear time series, as

$$CR_G = 100 * \left[\left(C_{end} / C_{start} \right)^{\frac{1}{d}} - 1 \right] \quad (\text{eqn. 8})$$

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 all reefs following the El Niño-Southern Oscillation and Indian Ocean Dipole (ENSO-IOD) event of 1998 (Figure 3.1). 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 (two-sample t -test, $t_{10} = -10.4$, $P < 0.0001$, Figure 3.2). 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 $\text{year}^{-1} \pm$ SEM: $49.6 \pm 3.7\% \text{ year}^{-1}$) than on fished reefs ($28.0 \pm 7.3\% \text{ year}^{-1}$) following the bleaching event and coral cover between

1999 and 2008 has been recovering along similar trajectories on unfished reefs ($9.9 \pm 1.8\% \text{ year}^{-1}$) and fished reefs ($8.1 \pm 1.6\% \text{ year}^{-1}$) (see also McClanahan 2008).

Fishing on its own was associated with a 50.9% decline in relative coral cover (95% CI = 38.6 to 63.1%, Figure 3.2), 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 to 84.7%, Figure 3.2). The observed combined effect of fishing and bleaching was a relative decline of 72.2% (95%CI = 60.9 to 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 to 91.4%), suggesting an antagonistic interaction between fishing and bleaching (Figure 3.2). However, the small overlap in the 95% confidence intervals (0.4%) indicates that the additive null hypothesis cannot be fully rejected. Our classification of the fishing \times bleaching interaction as non-synergistic 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 non-synergistic 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 dataset 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 non-synergistic. Immediately following the 1998 bleaching event, hard coral cover declined less on fished ($-28.0\% \text{ year}^{-1}$) than on unfished reefs ($-49.6\% \text{ year}^{-1}$) (Figures 3.1, 3.2). 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 3.1) because our effect size metric takes into account pre-bleaching differences in initial cover on fished and unfished reefs (Gardner et al. 2003, Côté et al. 2005, Graham et al. 2008).

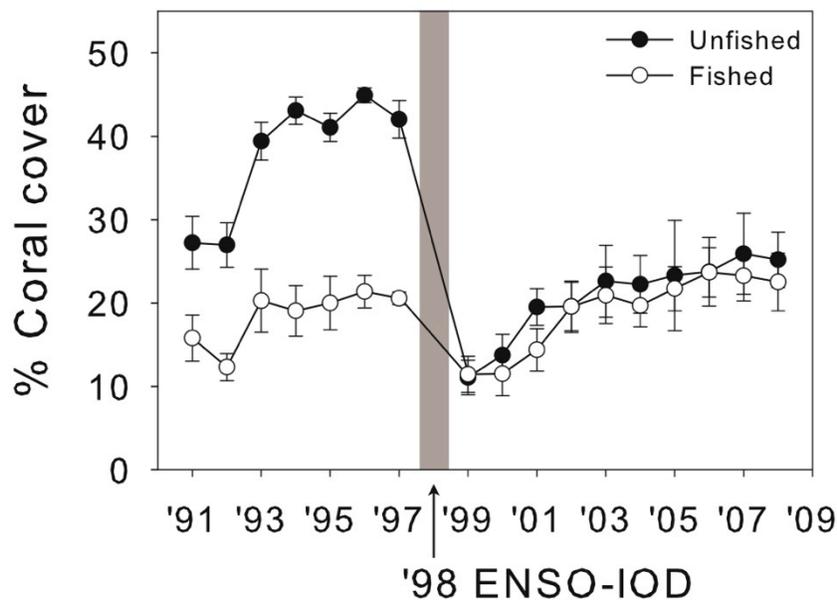


Figure 3.1. The lack of fishing pressure in unfished marine reserves did not ameliorate the effects of a coral bleaching event in 1998. Values shown are percent coral cover on fished (open circles) and unfished (filled circles) Kenyan reefs between 1991 and 2008. The grey bar indicates the 1998 ENSO-IOD (El Niño Southern Oscillation-Indian Ocean Dipole) bleaching event. Mean coral cover is shown ± 1 SEM.

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 and McClanahan 2003, Mangi and 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. 2005b, Cole et al. 2008, Green et al. 2008, Rotjan and 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. 2007b), 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 and McClanahan 2001). However, the impacts of fishing on total coral cover and the structure of coral assemblages have not been fully explored.

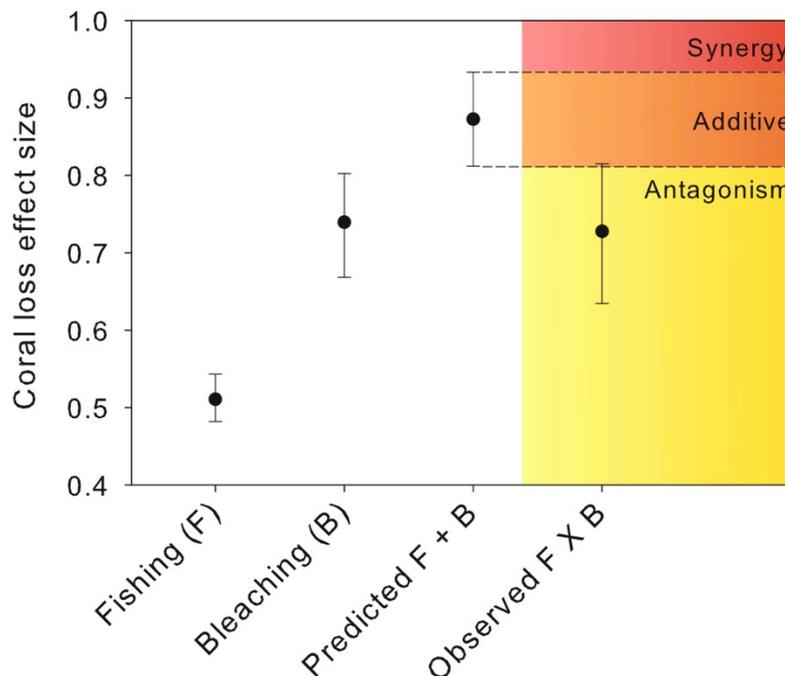


Figure 3.2. The impact of the 1998 bleaching event was significantly greater than fishing impacts on the loss of coral cover on Kenyan reefs. The observed decline in coral cover from the combined effect of the two stressors was antagonistic or weakly additive, not synergistic; bleaching appears to override 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).

Why do fishing and bleaching have a non-synergistic 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 3.2). 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).

Co-variation 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 co-tolerance), 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 post-bleaching 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 post-bleaching 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 co-tolerance to bleaching and fishing. Predicting co-tolerance and consequences for coral assemblages is complicated, however, because fishing pressure may also favour '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 and 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 co-tolerance 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.

This study adds to the growing evidence that antagonistic and additive effects may be as common as synergies (Crain et al. 2008, Darling and Côté 2008; Chapter 2). 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 and Jackson 2008). However, to fulfill their important role as refuges and re-colonization 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.

Chapter 4.

Evaluating life-history strategies of reef corals from species traits³

Abstract

Classifying the biological traits of organisms can test conceptual frameworks of life-history strategies and allow for predictions of how different species may respond to environmental disturbances. We apply a trait-based classification approach to a complex and threatened group of species, scleractinian corals. Using hierarchical clustering and random forests analyses, we identify up to four life-history strategies that appear globally consistent across 143 species of reef corals: competitive, weedy, stress-tolerant, and generalist taxa, which are primarily separated by colony morphology, growth rate and reproductive mode. Documented shifts towards stress-tolerant, generalist and weedy species in coral reef communities are consistent with the expected responses of these life-history strategies. Our quantitative trait-based approach to classifying life-history strategies is objective, applicable to any taxa, and a powerful tool that can be used to evaluate theories of community ecology and predict the impact of environmental and anthropogenic stressors on species assemblages.

³ A version of this chapter appears as, Darling E.S., Alvarez-Filip, L., Oliver, T.A., McClanahan, T.R. and I.M. Côté (2012) Evaluating life-histories strategies of reef corals from species traits. *Ecology Letters*, 15: 1378-1386.

Introduction

Ecologists are increasingly realizing that trait-based views of species assemblages may be more meaningful than comparisons of species richness or composition (Cadotte et al. 2011). Trait-based approaches can provide general and predictable rules for community ecology, as well as a more mechanistic understanding of community assembly and disassembly, habitat filtering and species coexistence, particularly in the context of global climate change and biodiversity loss (McGill et al. 2006). Species traits also provide important information about life-history strategies, which can broadly define how organisms interact with each other and their environment.

Life-history strategies describe consistent and context-independent characteristics of organisms. The classic two-strategy life-history framework of r - K models (Pianka 1970) is now generally seen as oversimplified as species can occur along a continuum of 'fast' (r) to 'slow' (K) life histories (Stearns 1977). Three-strategy frameworks resolve some difficulties of r - K models by adding a third 'beyond K ' group of stress-adapted species that can persist in unfavourable habitats (i.e., via adversity selection, Greenslade 1983). For example, Grime's C-S-R triangle describes three life-history strategies in plants, in which species are hypothesized to evolve strategies that promote competitive (C), stress-tolerant (S) or ruderal (R) life histories (Grime 1977, Grime and Pierce 2012). Similar triangular continuums of life-history strategies have also been proposed for insects (Greenslade 1983) and fishes (Winemiller and Rose 1992). Life-history models with three strategies are generally recognized as having more predictive power than the two-strategy r - K framework that can fail to recognize additional axes of life-history variation (Stearns 1977, Winemiller and Rose 1992). While more than two or three life history strategies likely exist in any given community, such multi-strategy frameworks are rarely quantitatively described. Moreover, many of these life-history frameworks are based on the responses of organisms to different environmental or habitat conditions, instead of on inherent characteristics of species (Westoby 1998). Furthermore, such classifications are often subjective (Gitay and Noble 1997), which can bias tests of evolutionary and ecological theories that are better addressed with quantitatively and objectively identified life-history strategies.

Here, we evaluate if life history strategies can be directly inferred from species traits in a complex and threatened group of organisms, scleractinian corals. Climate change, overexploitation, pollution and disease have resulted in global declines of coral cover and architectural complexity on coral reefs, one of the world's most complex and biodiverse ecosystems (Gardner et al. 2003, Pandolfi et al. 2003, Alvarez-Filip et al. 2009). Human impacts are altering coral communities in ways that are unprecedented from the historical record (Pandolfi and Jackson 2006, van Woesik et al. 2012) as historically dominant corals are replaced by more persistent and opportunistic species (Knowlton 2001, McClanahan et al. 2007b,c, Green et al. 2008, Alvarez-Filip et al. 2011). However, shifts in coral species can often be overlooked for a variety of reasons: they may be subtle – species-level coral identification is challenging – and changes may occur on decadal or millennial timescales (Pandolfi and Jackson 2006, van Woesik et al. 2012). Changes may also go unnoticed as the baseline for what is considered a 'normal' community composition is often unknown and shifts in species composition can occur slowly over time (Pauly 1995). More importantly, a general lack of long-term abundance information for individual coral species makes it difficult to identify species responses to environmental change and anthropogenic stress, and whether or not these responses are predictable.

There is currently no framework of life-history strategies for scleractinian corals, possibly because data on species traits are too sparse or scattered for classification or because corals do not fit well into existing frameworks (e.g., corals are clonal invertebrates with a complicated life cycle, Jackson and Hughes 1985). A few studies have considered how some coral traits may relate to life-history strategies. For example, small corals with brooding reproduction, fast growth rates and high population turnover are expected to be 'weedy' (Knowlton 2001), while large, slow-growing colonies of massive corals are expected to be more tolerant to chronically stressful or variable environments (Jackson and Hughes 1985, Soong 1993, Rachello-Dolmen and Cleary 2007). Similarly, variation in colony morphology and reproductive mode are thought to suggest three primary life histories (competitors, stress-tolerators and ruderals, Edinger and Risk 2000, Murdoch 2007). Observations of increasing abundances of 'weedy' species (Green et al. 2008) and the persistence of massive species on disturbed Caribbean (Alvarez-Filip et al. 2011) and Indo-Pacific reefs (McClanahan et al. 2007c, Rachello-Dolmen and Cleary

2007) suggests that life-history traits can predict which corals are ‘winners’ or a ‘losers’ in the face of environmental change (Loya et al. 2001, van Woesik et al. 2012). For example, branching and plating acroporid corals are dominant species that are very sensitive to stress and disturbance (i.e., ‘losers’), while massive species and ‘weedy’ species are more likely to be ‘winners’ and persist in unfavourable and disturbed environments (Loya et al. 2001, McClanahan et al. 2007c). However, the underlying species characteristics that may predict these responses are difficult to evaluate without a comprehensive understanding of coral traits and associated life-history strategies.

In this study, we describe a novel, quantitative method that can be used to evaluate and identify life-history strategies from species traits using hierarchical clustering and random forests analyses. We compile a global database of species traits for reef-building corals and classify taxa into life-history strategies that can be used to evaluate ongoing community shifts on coral reefs. Our approach to objectively classify life-history strategies is applicable to any species group and can be used to establish trait-based life-history frameworks, find general rules of community ecology, and predict the impacts of environmental and anthropogenic impacts on ecological communities.

Methods

Coral species traits

To evaluate life-history strategies in reef corals, we collected information on 11 commonly available species traits: colony growth form, solitary colony formation, reproductive mode and fecundity, maximum colony size, corallite diameter, depth range, generation time, growth rate, skeletal density and symbiotic zooxanthellae (*Symbiodinium*) associations (see Table 4.1, Appendix B). We specifically focused on traits that were expected to affect coral population dynamics, and for which quantitative data were available at a global scale. All life-history traits are variable and phenotypic plasticity within species is ubiquitous. Corals, in particular, have notoriously variable life-history traits and there can be extensive phenotypic plasticity within populations and species (Todd 2008). However, the goal of our study was to provide a broad, global comparison of life-history traits across species and not focus on intraspecific variation.

Thus we conducted an extensive literature survey in order to provide the most accurate ‘average’ description of species-specific traits and we leave in-depth assessments of intraspecific variability to future investigations.

Table 4.1. Summary of 11 species traits used to classify life-history strategies of scleractinian reef corals. Detailed descriptions and source references for each trait can be found in Appendix B.

Species trait	Description	Type of data
Colony growth form	Branching, plating, domed ^{1,2}	Categorical
Solitary colonies	Solitary or colonial colonies	Categorical
Reproductive mode	Brooding, broadcast spawning ¹	Categorical
Colony size	Largest recorded size of colony, cm	Continuous
Corallite diameter	Average size of corallites, cm	Continuous
Depth range	Median depth (m) of recorded depth range	Continuous
Fecundity	Number of eggs per polyp or mesentary	Continuous
Generation length	Number of years between generations	Continuous
Growth rate	Average annual growth rate, mm year ⁻¹	Continuous
Skeletal density	Average density of CaCO ₃ skeleton, g cm ⁻³	Continuous
Symbiont richness	Rarefaction curve of <i>Symbiodinium</i> genotypic richness corrected for sampling effort	Continuous

¹Colonies can have more than one characteristic

²Domed corals include massive, submassive and encrusting morphologies

We collected trait information for 847 scleractinian corals, comprising 101 western Atlantic and Caribbean (hereafter referred to as Atlantic) species and 746 Indo-Pacific species. This information came from 236 sources, including taxonomic monographs, regional identification guides, published literature, secondary sources and online databases (see Appendix B). Only taxa with information for more than 60% of the species traits were included in the analysis (i.e., species with data for at least 7 of 11 traits, N = 143 species: 32 Atlantic and 111 Indo-Pacific species from 51 genera and 19 families). Our cut-off of 60% trait coverage was a trade-off between the number of species included in the analysis and comprehensive trait information for each species. For example, only a small subset of species (N = 20, 8 Atlantic and 12 Indo-Pacific species) had complete (100%) trait information. We conducted a sensitivity analysis and found clusters to be qualitatively unchanged from 100% to 60% trait information. With

information on less than 60% of traits, clustering patterns became more variable, although generally similar to clustering analyses with more trait coverage.

Classifying life-history strategies

We took a data-driven approach to classify life-history strategies using a *posteriori* group classification of Ward's hierarchical clustering analyses (e.g., Gitay and Noble 1997), followed by random forests analyses to identify influential traits, and Principal Coordinates ordination to visually show species life-history strategies and traits in multivariate space.

We used hierarchical clustering and non-parametric multivariate analyses of variance (MANOVAs) as an objective and quantitative method to identify life-history strategies. First, we established a trait dendrogram of species relationships using Ward's hierarchical clustering of a Gower dissimilarity matrix. We chose the Gower dissimilarity index to compare the multivariate trait distance between species because it allows for mixed types of data, missing values and can weight individual traits differently (Laliberté and Legendre 2010). The 11 traits were independent characteristics (variance inflation factors < 5 for all continuous variables) and all traits were weighted equally in the analysis, except two traits, colony growth form and reproductive mode, which were each reclassified into separate binary variables (branching, plating and domed colony growth forms, brooding and spawning reproductive modes, see Appendix B). The three binary states for growth form were weighted by 0.33, and the two binary states for reproductive mode were weighted by 0.5, in order to avoid artificially inflating the effect of these traits (Laliberté and Legendre 2010). Dissimilarity indices and clustering were performed using the "FD" package (Laliberté and Legendre 2010) in R (2012).

We evaluated the 'best-fit' number of clusters by testing how many clusters maximized both within-cluster homogeneity and between-cluster dissimilarity. We used non-parametric multivariate analyses of variance (MANOVAs) to evaluate different groupings of species by comparing the coefficient of determination (R^2) across nine different clustering scenarios (between two and 10 clusters). We then identified a cut-off or 'elbow' where further clustering resulted in a sharp decrease (> 15%) in the amount of explained variance, clusters above this cut-off were deemed to be the 'best-fit' clusters

(Appendix B). This is comparable to the use of scree plots to evaluate the number of principal components to include in a principal components analysis. After identifying the number of 'best-fit' clusters, we calculated the mean and standard deviation of trait values within each cluster and tested for mean differences in multivariate traits across clusters using non-parametric MANOVAs. We also compared the variability of species strategies within life-history clusters using a multivariate homogeneity of variance test, which calculates the average distance of each species to median group trait values, followed by Tukey's Honestly Significant Differences tests to identify pairwise differences between groups (Oksanen et al. 2011).

In addition to classifying species into life-history strategies, we also wanted to identify traits that were the best predictors of coral life-history strategies. We used random forests analyses to evaluate the relative importance of different traits. Random forests are a machine-based learning method that estimates variable importance by combining many classification trees through bootstrap sampling and model averaging, and can also account for multicollinearity among variables (Cutler et al. 2007). During each iteration of the classification tree, a random subset of three traits (out of 11) was used to classify species into life-history groups and the final tree was then compared to the original 'blueprint' trait dendrogram produced by Ward's hierarchical clustering of the full set of 11 traits. After 20,000 iterations, we compared the increase in the cluster misclassification rate for each trait when it was excluded, and all other traits were held constant, in order to assess the relative importance of each trait, traits that resulted in the greatest increase in misclassifications when excluded were identified as the most important (Cutler et al. 2007). Prior to random forests analysis, missing species trait values were filled in using standard data imputation through proximity (Liaw and Wiener 2002, Cutler et al. 2007) – for each cluster, missing values of continuous traits were replaced with the median of the trait within the cluster, and missing values of categorical traits were replaced with the most frequent level of the trait in the cluster. In total, 288 missing values out of 2002 data points, or 14.4%, were replaced by imputation for the random forests analyses. We assessed the model accuracy of classification trees and random forests using standard metrics (e.g., out-of-bag error rate, Cutler et al. 2007). We used the 'randomForest' package (Liaw and Wiener 2002) in R (2012) for these analyses.

Finally, we used a Principal Coordinates Analysis (PCoA) ordination of the Gower dissimilarity matrix to visually show the life-history groups and species traits in multivariate space. However, this ordination is purely descriptive and does not provide statistical tests of clustering structure among species (Borcard et al. 2011). Following species ordination, we projected each trait onto the plot *a posteriori* using a double projection method based on correlations of the species traits with the PCoA axes, species traits were standardized prior to ordination and negative eigenvectors were adjusted using the Cailliez correction (Borcard et al. 2011). Multivariate analyses were performed using the ‘vegan’ (Oksanen et al. 2011) and ‘FD’ (Laliberté and Legendre 2010) packages in R (2012).

Results and Discussion

Life-history strategies of reef corals

Models with two, three and four clusters of coral species received the most support in the hierarchical clustering analyses (Table 4.2, Fig. 4.1, Appendix B). The two-cluster scenario identified a ‘fast’ life history of large, branching and plating corals and a ‘slower’ life history of smaller, slower-growing corals. The three-cluster scenario distinguished a third group of small, brooding corals, which would fit with a ruderal or opportunistic life history of three-strategy frameworks. (Grime 1977, Grime and Pierce 2012). The four-strategy clustering scenario (Table 4.2, Fig. 4.1) added a ‘generalist’ group of species that appear to have some traits of each life history identified in the three-cluster scenario. Here, we focus on the four-cluster scenario for a discussion of reef coral life histories. These four clusters describe significantly different groupings of species traits (non-parametric MANOVA, $P = 0.001$) and random forests analyses identified colony growth form, growth rate and reproductive mode as the most influential traits responsible for clustering the different groups (Fig. 4.2, Appendix B).

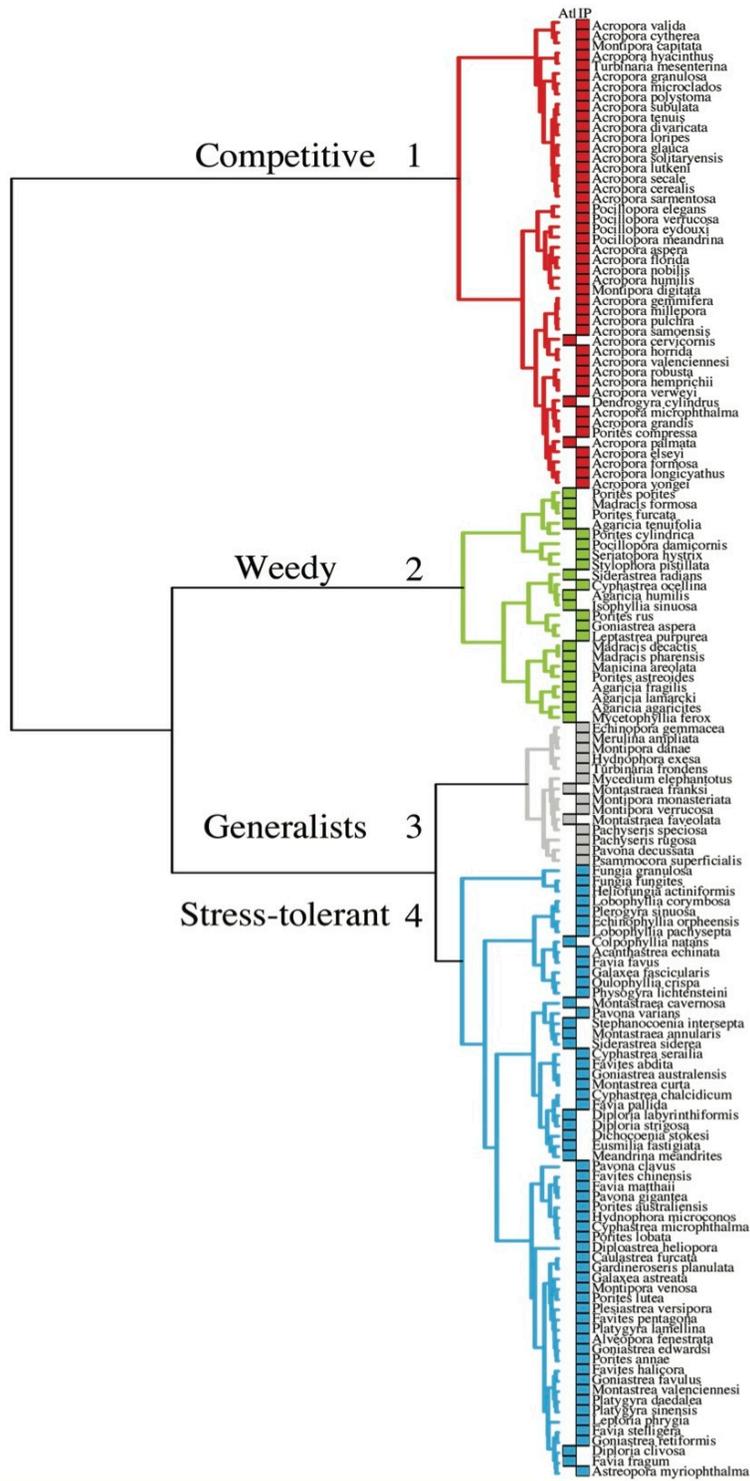


Figure 4.1. Hierarchical cluster analysis of global scleractinian corals based on species traits. The analysis includes 143 species with $\geq 60\%$ trait coverage (i.e., information for at least 7 out of 11 traits). Clustering scenarios with two, three and four groups received the strongest model support (see Appendix C); a four-cluster scenario is shown here. Boxes indicate Atlantic (Atl) or Indo-Pacific (IP) distributions.

Table 4.2. Summary of species traits across four life-history strategies of a) global, b) Atlantic, and c) Indo-Pacific reef corals. For categorical traits, we show the percent of species with each trait; mean (SD) are shown for continuous traits.

Life history	No. species	% Branching	% Domed	% Plating	% Solitary	% Brooding	% Spawning	Colony size (cm)	Corallite diameter (cm)	Depth range (m)	Fecundity (eggs polyp ⁻¹)	Generation length (years)	Growth rate (mm year ⁻¹)	Skeletal density (g cm ⁻³)	Symbiont diversity (m-value)
(a) Global															
1 - Competitive	46	95.7	0	39.1	0	0	100	259.32 (314.68)	2.70 (1.31)	12.53 (5.50)	20.04 (32.39)	9.72 (1.11)	49.83 (41.28)	1.51 (0.34)	1.78 (1.28)
2 - Weedy	23	39.1	56.5	21.7	0	100	18.2	105.54 (138.54)	4.45 (5.86)	20.58 (14.91)	19.70 (14.26)	9.41 (1.56)	11.35 (10.04)	1.73 (0.41)	1.70 (1.61)
3 - Generalist	14	35.7	100	100	0	0	100	248.77 (243.39)	3.56 (3.55)	17.95 (5.05)	18.46 (9.26)	10.00 (0.00)	19.18 (11.58)	1.62 (0.34)	1.79 (0.63)
4 - Stress-tolerant	60	0	100	1.7	5	3.4	100	137.81 (285.26)	8.57 (9.83)	19.50 (10.45)	372.45 (694.15)	10.17 (1.52)	7.98 (6.69)	1.54 (0.28)	1.42 (0.86)
(b) Atlantic															
1 - Competitive	3	100	0	0	0	0	100	304.80 (61.00)	2.52 (3.02)	21.10 (8.67)	63.34 (83.71)	10.00 (0.00)	71.09 (50.13)	1.45 (0.58)	1.07 (0.56)
2 - Weedy	15	26.7	60	33.3	0	100	0	69.80 (97.12)	5.30 (6.85)	26.26 (16.13)	23.00 (16.61)	10.00 (0.00)	6.99 (7.14)	1.72 (0.50)	1.19 (0.68)
3 - Generalist	2	0	100	100	0	0	100	166.97 (46.70)	2.58 (0.02)	23.88 (5.13)	17.31 (13.59)	10.00 (0.00)	7.40 (1.07)	1.31 (0.18)	2.50 (0.30)
4 - Stress-tolerant	12	0	100	8.3	0	0	100	105.75 (48.55)	7.15 (5.18)	32.42 (14.62)	100.68 (123.74)	10.00 (0.00)	5.53 (2.00)	1.51 (0.43)	1.26 (0.84)
(c) Indo-Pacific															
1 - Competitive	43	95.3	0	41.9	0	0	100	252.14 (338.70)	2.71 (1.15)	11.93 (4.82)	14.39 (16.31)	9.70 (1.15)	47.18 (40.52)	1.52 (0.32)	1.83 (1.30)
2 - Weedy	8	62.5	50	0	0	100	50	177.02 (186.01)	2.86 (3.24)	10.62 (2.37)	14.74 (9.76)	8.38 (2.33)	16.97 (10.90)	1.73 (0.27)	2.67 (2.37)
3 - Generalist	12	41.7	100	100	0	0	100	263.64 (263.22)	3.73 (3.86)	16.96 (4.50)	19.60 (8.20)	10.00 (0.00)	23.11 (10.65)	1.77 (0.30)	1.68 (0.60)
4 - Stress-tolerant	48	0	100	0	6.2	4.3	100	146.97 (322.75)	9.01 (10.89)	16.28 (5.82)	472.58 (790.45)	10.21 (1.70)	8.82 (7.53)	1.55 (0.19)	1.46 (0.87)

Cluster 1 describes large, branching and plating species that grow quickly, occur at shallow depths and reproduce by broadcast spawning (Table 4.2). This group includes the staghorn and bottlebrush corals in the genus *Acropora* in the Atlantic and Indo-Pacific, *Dendrogyra cylindricus* in the Atlantic and species of *Montipora*, *Pocillopora* and *Turbinaria* in the Indo-Pacific. We suggest that cluster 1 describes a 'competitive' life-history strategy that is typically efficient at using resources and can dominate communities in productive environments (Grime 1977, Grime and Pierce 2012). Branching and plating corals often grow quickly into large, arborescent colonies that can create canopies to shade out competitors for light and plankton prey, making them effective competitors in shallow, high light, and low water flow environments (Baird and Hughes 2000). However, these species are extremely sensitive to breakage and dislodgement during storms (Madin 2005), and often exhibit high mortality following temperature anomalies and coral bleaching (McClanahan et al. 2007c), suggesting they are only dominant in ideal environments. Interestingly, previous qualitative studies have classified species of *Acropora* and *Montipora* as a ruderal or weedy life history because of their fast-growth and good colonizing characteristics (Edinger and Risk 2000, Rachello-Dolmen and Cleary 2007). However, the ability of these species to competitively dominate coral assemblages in the Indo-Pacific (Baird and Hughes 2000, Hughes et al. 2012) and their sensitivity to environmental change and marked declines from historical dominance in the Atlantic (Alvarez-Filip et al. 2011) suggest, instead, that acroporids may be associated with a competitively dominant life-history strategy.

Species within cluster 2 can reproduce by brooding and have smaller colony sizes. This cluster includes branching *Porites* species in the Atlantic and Indo-Pacific, species of *Madracis* and *Agaricia* in the Atlantic, some pocilloporids (*Pocillopora damicornis*, *Stylophora pistillata*, *Seriatopora hystrix*) and some faviids (e.g., species of *Cyphastrea*, *Goniastrea* and *Leptastrea*) in the Indo-Pacific. Cluster 2 appears to describe a weedy or ruderal strategy of species that can opportunistically colonize recently disturbed habitats (Grime 1977, Grime and Pierce 2012). Ecological theory suggests that successful weeds reproduce faster and survive better than non-weedy species (Sutherland 2004). While species in cluster 2 displayed some traits of fast reproduction (e.g., shorter generation time, on average), they did not have higher fecundity (as measured by eggs per polyp) than the other clusters (Table 4.2). Moreover, this lack of a fecundity

advantage could be compounded by their smaller colony sizes (Table 4.2, Soong 1993). The reproductive advantage of weedy corals may instead lie in a correlate of their brooding reproductive mode. Although brooders produce relatively large offspring (Knowlton 2001), which is associated with high parental investment and would be an unusual characteristic of weeds, some brooding corals can reproduce by parthenogenesis (Ayre and Miller 2004). Parthenogenesis might allow for successful reproduction at low population densities, which may often occur on recently disturbed reefs. In contrast, many common broadcast spawning species are vulnerable to Allee effects and can fail to reproduce in small populations (Knowlton 2001). Furthermore, as population size increases, brooders can also disperse sexually produced larvae that may favour genetically diverse colonists (Ayre and Resing 1986). Weedy corals may also be better survivors than non-weedy corals because they show the most variation in their species traits compared the other life-history strategies (multivariate homogeneity of variances test, $P = 0.009$, Fig. 3), which may allow these taxa to colonize a variety of disturbed environments, such as heavily fished reefs or shallow back reef lagoons.

If clusters 1 and 2 describe competitive and weedy life-history strategies, theory would suggest that one of the remaining clusters (3 or 4) might represent a stress-tolerant strategy. Species in cluster 4 appear to be the best candidates for a stress-tolerant life history. This cluster includes slow-growing species that reproduce by broadcast spawning and have primarily domed morphologies, large corallites and high fecundity. Examples include the lobe and brain corals *Montrastraea annularis* and *M. cavernosa*, *Colpophyllia natans*, and species of *Diploria* in the Atlantic, and massive *Porites* species and many faviids (e.g., *Favia*, *Favites*, *Platygyra*, *Goniastrea*) in the Indo-Pacific. Slow growth, longer generation times, large corallites, which promote energy storage (van Woesik et al. 2012), and high fecundity during episodic spawning events may all be advantageous traits in chronically harsh environments with, for example, low light or high sedimentation. These traits have previously been assigned to a subdominant, stress-tolerant life history (Edinger and Risk 2000, Rachello-Dolmen and Cleary 2007). Long-lived corals can also persist in the absence of recruitment and can withstand sustained recruitment failure for decades, which may increase their long-term survival in stressful environments (Hughes and Tanner 2000).

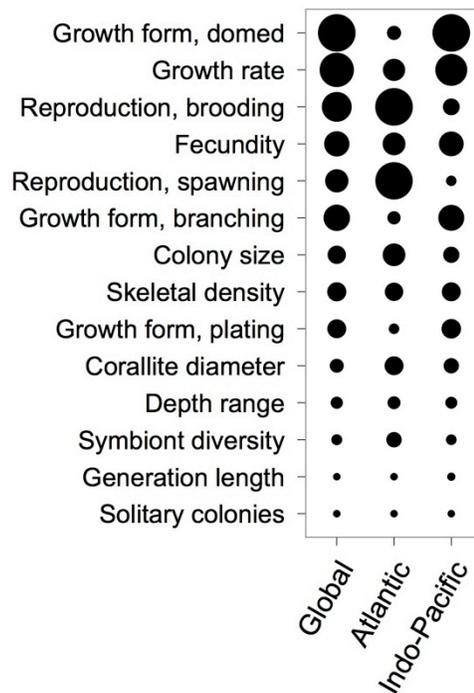


Figure 4.2. Importance of individual traits for differentiating the four clusters of global, Atlantic and Indo-Pacific reef corals as determined by random forests analyses (see also Appendix B). Circle size indicates rank of trait importance; larger circles represent more influential traits than smaller circles. A summary of species traits is given in Table 1.

The remaining group, cluster 3, includes an assortment of species that show some overlap with the competitive, weedy, and stress-tolerant life histories in the Principal Coordinates ordination (Table 4.2, Fig. 4.3). These taxa occur as domed and plating colonies (but can also have branching growth forms), with moderate growth rates and can reach large colony sizes. This group includes species of *Echinopora*, *Hydnophora*, *Montipora*, *Turbinaria* and *Pachyseris* in the Indo-Pacific, and two Atlantic species, *Montastraea faveolata* and *M. franksi*. These species may represent a ‘generalist’ life-history strategy that can do well in habitats where competition is limited by low levels of stress (Grime 1977, Winemiller and Rose 1992). Alternatively, this cluster may represent a subgroup of stress-tolerant taxa that are somewhat more competitive than average for that group, with horizontally spreading plating colonies and faster growth rates. For now, we label this cluster as a ‘generalist’ life-history strategy and more trait information is needed to discern whether species within this cluster are a separate life-history strategy,

a type of stress-tolerant life history, or even a slower-growing subset of 'subdominant' competitive taxa.

Three of the coral clusters emerging from our analysis resemble three-strategy life-history frameworks, such as Grime's triangle of primary plant life-history strategies (Grime 1977, Grime and Pierce 2012) (Fig. 4.3). It is perhaps not surprising that reef-building corals and plants can share some similarities in their life-history strategies. Corals and plants are both sessile and clonal organisms (Jackson and Hughes 1985), structured by competition for space (Lang and Chornesky 1990, Karlson and Hurd 1993), gradients of environmental productivity via light and food availability (Anthony and Connolly 2004), and disturbance (Connell 1978, Karlson and Hurd 1993). Previous studies investigating coral morphology and reproductive mode (Edinger and Risk 2000, Murdoch 2007), the recruitment of juvenile corals (Bak and Engel 1979) and the response of coral assemblages to depth gradients (Jackson and Hughes 1985), bleaching stress (Obura 2001b) and pollution (Rachello-Dolmen and Cleary 2007) have also suggested three major life-history strategies of reef corals, which are similar to those we describe quantitatively here, although with different species classifications (e.g., acroporids were classified as ruderal, and domed and plating species with moderate growth rates were classified as competitive).

Complexities of coral life histories

While Grime's triangle can reflect important life history patterns across species, this framework has been criticized for being too general and for failing to consider the many complexities associated with life-history strategies (e.g., the Grime-Tilman debate summarized by Aerts 1999, see also Westoby 1998). These drawbacks apply here, even though the C-S-R framework appears to have some application to reef corals. For example, 'faster' or 'slower' life histories, and competitive, stress-tolerant and weedy life histories, are end point life-history strategies (e.g., located at the 'tips' of Grime's triangle), but species can have suites of traits that place them along a continuum between primary strategies (Grime 1977, Winemiller and Rose 1992, Grime and Pierce 2012). This appears to be the case for species we have labeled as generalists (cluster 3), which display traits that occur in between competitive, weedy and stress-tolerant life

histories (i.e., “C-S-R” strategy, Grime 1977, Grime and Pierce 2012, Fig. 4.3). It is also the case for a few species that were placed in one of the three conventional strategies. For example, four stress-tolerant species (*Alveopora fenestrata*, *Favia fragum* and two fungiids, *Fungia fungites* and *Heliofungia actiniformis*) overlap with the weedy group, suggesting these species may be part of a secondary strategy of species adapted to lightly disturbed and unproductive habitats (i.e., “S-R” strategy, Grime 1977, Grime and Pierce 2012).

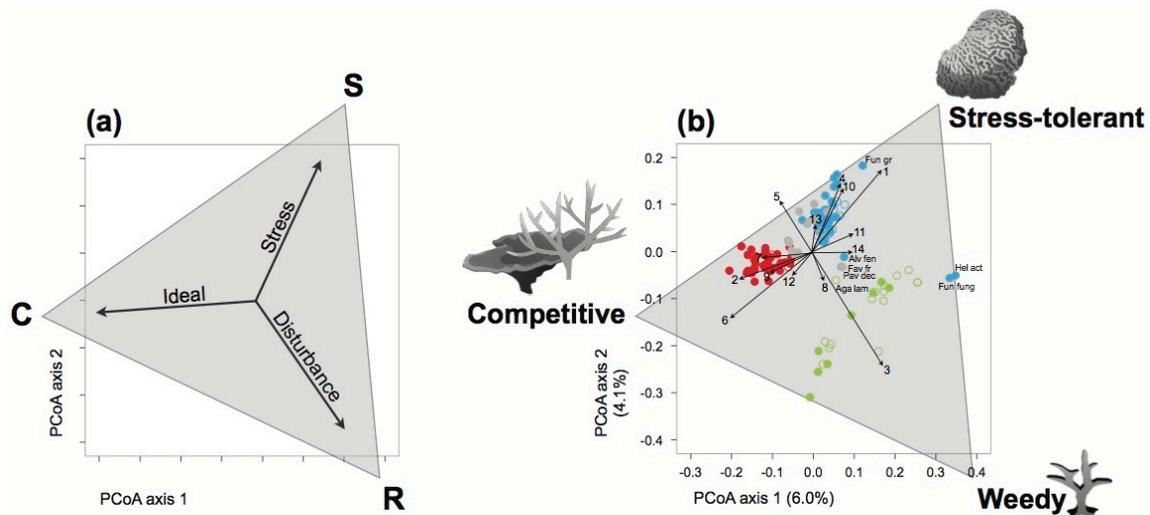


Figure 4.3. Grime’s triangle of life-history strategies applied to reef corals. (a) The conceptual framework of Grime’s three primary life-history strategies and the hypothetical environmental conditions associated with each strategy. (b) Principal Coordinates ordination of 143 coral species with four life-history strategies (red: competitive, green: weedy, blue: stress-tolerant, grey: generalist). Open circles are Atlantic taxa and filled circles are Indo-Pacific taxa. Arrows indicate trait loadings, traits are numbered from most important to least important in differentiating the life-history strategies: 1) domed morphology, 2) growth rate, 3) brooding reproduction, 4) fecundity, 5) broadcast spawning reproduction, 6) branching morphology, 7) colony size, 8) skeletal density, 9) plating morphology, 10) corallite diameter, 11) depth, 12) symbiont diversity, 13) generation length, 14) solitary colonies.

‘Mixing and matching’ of traits in the generalist life history, and overlap between primary strategies suggests there may be a variety of environmental selection pressures and trade-offs shaping life-history strategies in reef corals. This may explain why we observed some trait combinations in coral life histories that are not usually associated with these strategies. For example, fast growth and high fecundity are expected to be weedy traits (Grime 1977, Grime and Pierce 2012) but competitive corals have the fastest growth rates and stress-tolerant corals, the highest fecundities (Table 4.2).

Brooding reproduction is another example of an unusual trait in coral life histories. Brooding is associated with parental investment, which is usually considered a competitive (*K*) trait (Winemiller and Rose 1992). However, in reef corals, brooding predominates among weedy, opportunistic species (Table 4.2). Brooding in weedy corals may reflect the need for asexual reproduction by isolated colonies following disturbance, but may also entail a trade-off between reproductive output and genetic heterozygosity in environments where competition is low. Conversely, broadcast spawning in competitive, stress-tolerant and generalist species may increase genetic heterozygosity where competition is high, but might also result in a limited ability to recover from small population sizes following disturbance (e.g., Allee effects, Knowlton 2001). Consequently, the reproductive mode of corals may be a response to the trade-off between colonization ability and competition, thus giving rise to intermediate strategies and seemingly unusual trait combinations that attempt to optimize these trade-offs.

Corals do not occupy all of the trait space of the hypothetical triangle framework (Fig. 4.3b). This may be because most reef corals are good competitors, compared to other benthic components of coral reefs (Lang and Chornesky 1990), moving species towards the competitive side of the triangle. We hypothesize that other components of the coral reef benthic community, such as sponges, soft corals, and algae, might primarily occupy trait space within the weedy and stress-tolerant zones to further complete the life-history triangle. Future efforts to quantify life history strategies for the entire benthic community would also be more comparable to larger groups of taxa (i.e., plants, Grime 1977, fishes, Winemiller and Rose 1992, see also Grime and Pierce 2012) for which life-history theories were originally developed. Understanding the life-history strategies of the entire coral reef benthic community might also reveal whether ongoing shifts towards non-coral assemblages (Norström et al. 2009) are associated with different life-history strategies. Overall, this highlights the need for more trait information within coral species and other benthic groups.

Biogeographic and phylogenetic patterns

The life-history strategies we have identified appear largely independent of biogeography as Atlantic and Indo-Pacific species occur within each cluster (Fig. 4.1). For example, two lower-level clusters of weedy taxa are apparent in the PCoA ordination and each sub-cluster includes Atlantic and Indo-Pacific species (Fig. 4.1, Fig. 4.3b). One sub-cluster includes shallow, fast-growing, branching taxa, such as *Pocillopora damicornis*, *Seriatopora hystrix*, *Stylophora pistillata* and species of digitate *Porites* from the Indo-Pacific (*P. cylindrica*, *P. rus*) and two Atlantic taxa (*P. furcata* and *P. porites*), while a slower-growing, domed and plating sub-cluster includes species of *Agaricia*, *Porites astreoides*, *Siderastrea radians* in the Atlantic, and several faviid species from the Indo-Pacific (*Cyphastrea ocellina*, *Goniastrea aspera*, *Leptastrea purpurea*). However, different traits nevertheless separated regional taxa within the four clusters. Random forests identified growth rate and colony growth form as the most important traits differentiating clusters of Indo-Pacific species, while reproductive mode and colony size were the most important traits differentiating Atlantic species (Fig. 4.2, Appendix B).

One of the more remarkable differences observed between the regions was the larger proportion of weedy taxa in the Atlantic (15 weedy species out of 32 total species, ~47%) than the Indo-Pacific (8 out of 111, ~7%). This pattern likely reflects the overabundance of brooders (a trait of weedy corals) in the Atlantic, which has been hypothesized to be associated with colonization history: more brooding species may have been able to colonize Atlantic reefs from the eastern Pacific because brooded autotrophic larvae can be effective long-distance dispersers (Baird et al. 2009). The overabundance of brooders could also reflect the higher survival of brooding taxa following regional patterns of extinction over longer time scales (Edinger and Risk 1995, van Woesik et al. 2012).

Many life-history traits are phylogenetically conserved and our classifications may in part reflect evolutionary relationships. For example, most life history classifications are consistent within genera. Of the 22 genera with more than two species included in our analysis, only seven genera (*Cyphastrea*, *Goniastrea*, *Montipora*, *Pocillopora*, *Porites*, *Siderastrea* and *Turbinaria*) have species in different life history groups. This suggests that for most taxa (15 out of 22, or 68%), genus-level identification may be sufficient to

classify coral life histories. There was more variability within families. Of the 15 families (based on Fukami et al. 2008) with more than one species, 10 had multiple life-history classifications. This suggests that scleractinian families often include species with diverse life histories, although continued reconstruction of reef coral phylogenies may also resolve some of this variability.

Forecasting the future of coral communities and the usefulness of a trait-based approach

A key question arising from our results is whether we can predict shifts in coral communities on the basis of life-history strategies. We hypothesize that while competitive species can dominate less impacted reefs, increasing stress and disturbance from human impacts (fishing, pollution, sedimentation) or environmental conditions (thermal stress and ocean acidification) can lead to the loss of these sensitive competitive corals and their replacement with stress-tolerant, weedy, and generalist species, which may be better able to persist in unproductive conditions and recolonize disturbed reefs.

There is some evidence that shifts from competitive to stress-tolerant, weedy, and generalist life histories have occurred on contemporary coral reefs. Following the precipitous loss of competitive acroporid corals from Caribbean reefs in the 1970s, stress-tolerant and generalist *Montastraea* corals dominated communities until disease, bleaching and other disturbances led to high mortality of *Montastraea* and other stress-tolerant species (Alvarez-Filip et al. 2011). Currently, reefs are often dominated by weedy *Agaricia* and *Porites* corals (Aronson et al. 2004, Green et al. 2008), although even these species have experienced population declines, likely associated with recruitment failure (Hughes and Tanner 2000). Furthermore, weedy and generalist species went regionally extinct from the Caribbean during large-scale climate disturbances of the Plio-Pleistocene (van Woesik et al. 2012), suggesting even more 'hardy' life histories may be vulnerable to population losses. Such shifts away from architecturally-complex competitive species towards the simpler morphologies of stress-tolerant, weedy, and generalist life histories may underlie the 'flattening' of Caribbean coral reefs observed in the past decades (Alvarez-Filip et al. 2009, 2011) and may also be associated with region-wide declines in Caribbean reef fish populations linked to

habitat degradation (Paddack et al. 2009). Comparable community shifts have been reported on Indo-Pacific reefs (McClanahan et al. 2007b,c, Rachello-Dolmen and Cleary 2007, Hughes et al. 2012), although further studies are needed to fully evaluate hypotheses of life-history replacement within coral assemblages.

Conclusions

Species traits are implicit in life-history theory, yet the lack of quantitative, trait-based methods to classify life-history strategies has impeded the evaluation and adoption of life-history frameworks (Westoby 1998). There are advantages to identifying such frameworks. Trait-based life-history strategies may contribute to the generality of community ecology through a more mechanistic understanding of community assembly and species coexistence (e.g., McGill et al. 2006). Furthermore, objectively quantifying life-history strategies directly from species traits may be a pragmatic approach to predict the increasing impacts of environmental and anthropogenic stressors on diverse species assemblages. Here, we have provided an objective, statistical approach to identify life-history strategies from species traits that can be applied to any ecological community. Our findings in relation to corals are consistent with findings for communities of plants, insects and fishes, which suggests that there may be a limited number of life-history strategies available to organisms (Stearns 1977, Grime and Pierce 2012). The next step may be to simplify the assignment of species to conceptual strategies described by multiple traits by defining the axes of life-history variation using single traits (e.g., the leaf-height-seed strategy, Westoby 1998), which can allow even more direct global comparisons across species. Establishing simple and universal frameworks of species life histories can be used to understand fundamental axes of life-history variation and identify general patterns in community ecology.

Chapter 5.

The role of life histories and co-tolerance for long-term coral community dynamics⁴

Abstract

Climate change is reshaping biological communities against a background of existing human impacts. Evaluating the impacts of multiple stressors on community dynamics can be particularly challenging in species-rich ecosystems, such as coral reefs. Here, we investigate whether life-history strategies and species-specific co-tolerances can predict community responses to fishing and temperature-driven bleaching using a 20-year time series of coral assemblages in Kenya. We found that the initial life-history composition of competitive, stress-tolerant and weedy taxa largely determined the impacts of bleaching and coral loss on coral communities. Prior to the 1998 bleaching event, coral assemblages protected from fishing were composed of all three life histories, including competitive branching and plating species, and exhibited strong declines following bleaching and limited recovery. Fished reefs had lower live coral cover and fewer genera, but were composed of stress-tolerant and weedy corals that were less affected by bleaching over the long-term. However, we found limited evidence for consistent co-tolerance responses of these life histories, as coral genera were extremely variable in their sensitivities to fishing and bleaching. Regardless, only one-quarter of Kenyan coral genera were identified as 'survivors', which is consistent with expectations that multiple stressors will negatively affect coral diversity and critical reef habitat.

⁴ T.R. McClanahan and I.M Côté are co-authors on this chapter, which is currently in preparation for submission.

Introduction

Our ability to predict the impacts of climate change on ecological communities is often limited by our incomplete understanding of interactions among multiple stressors. Global climate change is fundamentally altering the world's ecosystems (Parmesan and Yohe 2003) and reshuffling species into historically unprecedented assemblages (Graham and Grimm 1990, Williams and Jackson 2007). However, the impacts of climate change are not occurring in isolation, but against a background of existing anthropogenic stressors, including overexploitation, pollution, land-use changes and habitat loss (Chapin et al. 2000, Jackson et al. 2001, Halpern et al. 2008a). The impacts of multiple stressors are expected to reshuffle ecological communities into novel assemblages of species that can tolerate the impacts of both climate change and human pressures (e.g., Vinebrooke et al. 2004, Yakob and Mumby 2011). A key challenge is identifying species that may be 'winners' and 'losers' to evaluate expected changes to ecosystem processes and services (Graham et al. 2011c).

Life-history strategies and stressor co-tolerances are two ecological characteristics that may determine a species' response to multiple stressors (Vinebrooke et al. 2004, Grime and Pierce 2012). In terms of life histories, competitively dominant species, which effectively use resources in stable or ideal environments, are often more sensitive to chronic environmental stress or acute disturbances than species with 'slower' life histories, which can persist in unfavourable conditions, or opportunistic 'weedy' species, which can quickly recolonize after disturbances (Grime and Pierce 2012). Given trade-offs among traits underpinning primary life-history strategies, species may display similar responses to different stressors, for example, if traits that allow tolerance to one stressor are the same traits that provide tolerance to another stressor. This relationship between species tolerances (or sensitivities) to different stressors describes co-tolerance, a concept that can be used to identify vulnerable species and predict trajectories of community disassembly in response to multiple stressors (Vinebrooke et al. 2004). Species that are tolerant to multiple stressors are expected to remain in the community as 'winners' or 'survivors', while species that are sensitive to one or both stressors will likely be 'losers' (e.g., Loya et al. 2001, van Woesik et al. 2011).

Here, we investigate the influence of species life histories and co-tolerance on long-term coral reef dynamics. Coral reefs are one of the most vulnerable ecosystems to climate change and human impacts associated with overexploitation, pollution and sedimentation (McClanahan et al. 2002, Hughes et al. 2003, Newton et al. 2007, Hoegh-Guldberg et al. 2007, Halpern et al. 2008a). Global, long-term declines of coral cover and habitat complexity (Gardner et al. 2003, Bruno and Selig 2007, Alvarez-Filip et al. 2009) make it urgent to understand and predict the impacts of multiple stressors on coral reef ecosystem functions and services (Darling et al. 2010, Graham et al. 2011c; Chapter 3). Scleractinian corals are one of the foundation species of coral reef ecosystems and can provide critical habitat for the diverse assemblages of reef fishes and invertebrates on coral reefs (Bellwood et al. 2004, Graham et al. 2006, Pratchett et al. 2008). Up to four primary life-history strategies based on species traits have recently been classified for scleractinian corals: (1) 'competitive' fast-growing branching and plating species, (2) 'stress-tolerant' slow-growing, long-lived massive, submassive and encrusting species, (3) 'weedy' corals, which are small and brood their larvae, and (4) a 'generalist' group of species that display characteristics of the other three strategies (Chapter 4; Darling et al. 2012). However, a key question is whether the relative prevalence of these life-history strategies within coral assemblages can predict the impacts of different disturbances. Our objectives were first, to evaluate the impacts of two common stressors, fishing and climate-change associated thermal stress, on reef coral life-history assemblages, and second, to identify specific taxa that might be 'winners' or 'losers' based on their life-history strategies and stressor co-tolerances. We addressed these objectives using a 20-year time-series of data on coral composition on Kenyan reefs.

Coral reefs in Kenya experienced a mass bleaching and mortality event in 1998 as a result of sustained thermal stress, which led to widespread coral mortality throughout the western Indian Ocean (McClanahan et al. 2001, Ateweberhan et al. 2011). For many reefs, thermal stress and coral bleaching occurred against a background of fishing pressure from a small-scale coral reef fishery. However, some reefs had been protected for > 10 years within enforced, no-take marine protected areas (MPAs) (McClanahan et al. 2005a, Wells et al. 2007). In a previous study focusing on total coral cover, we found that corals on fished reefs were disproportionately less vulnerable to temperature-driven

coral loss than corals within marine reserves (Chapter 3; Darling et al. 2010). We therefore now hypothesize that differences in life history composition and patterns of co-tolerance within coral assemblages could explain the unequal effects of bleaching on fished and unfished reefs. Specifically, we test two predictions: (1) Before the mass coral bleaching event in 1998, reefs exposed to the chronic impacts of fishing were composed of stress-tolerant, weedy, and generalist life histories that were less vulnerable to coral bleaching and mortality, while unfished reefs had a higher abundance of competitive corals that were more sensitive to bleaching and mortality; (2) Corals display positive co-tolerance to the combined impacts of fishing and bleaching, such that corals on fished reefs are less sensitive to both fishing and bleaching impacts, while corals on unfished reefs are more sensitive to both stressors. Finally, we examined how life history and species co-tolerance have affected the recovery rate of coral assemblages following coral bleaching.

Methods

Coral reef communities were surveyed annually between 1991 and 2011 at 12 sites (five unfished and seven fished) along the Kenyan coast. Unfished sites were located within three enforced, no-take Marine National Parks (Malindi, two sites; Watamu, one site; Mombasa, one site) while fished sites were located on four heavily exploited reefs (Diani, two sites; Kanamai, two sites; Ras Iwatine, one site; and Vipingo, two sites). All sites are in shallow back-reef lagoons typical of Kenya's fringing reef system, and fished and unfished reefs are interspersed along the coast (for maps, see McClanahan and Graham 2005a, Wells et al. 2007; O'Leary et al. 2012). Other common anthropogenic stressors, such as sedimentation and eutrophication, are limited at these sites due to strong currents and tidal flushing (McClanahan and Obura 1997, Obura 2001a). In a previous study of the same sites, we found no evidence for spatial autocorrelation of coral cover across sites or an initial bias in the selection of unfished reefs (Chapter 3; Darling et al. 2010). The 12 sites do vary in reef height and water retention during low tides, which can affect water flow, temperature variability, and subsequently the impacts of thermal anomalies; however, there are no systematic differences in these features between fished and unfished reefs (McClanahan and Maina 2003, McClanahan et al. 2009).

At each site, coral communities were quantified using 10 m line intercept transects ($n = 9$ to 12 transects per site). On each transect, we measured the length of all coral colonies > 3 cm and identified hard corals to genus. The genus *Porites* was subdivided into three distinct morphological groups: massive *Porites*, branching *Porites* and the subgenus *Synaraea* (*Porites rus*). At each site, we calculated the mean percent cover for each genus from the average of transect-level estimates of absolute percent cover. We also calculated the richness of coral genera at each site as a measure of community diversity. Thirty-six coral genera were recorded; three of these were non-scleractinians (*Millepora*, *Tubipora* and *Tubastrea*) that were not major components of coral communities over the time series ($0.76 \pm 1.0\%$ absolute cover, mean \pm standard deviation, $N = 216$ site-year replicates) and thus removed from further analysis.

Coral life-history classification

Scleractinian corals have recently been classified into four major life-history strategies (competitive, stress-tolerant, weedy, and generalist) based on species traits (Chapter 4; Darling et al. 2012). We applied the method used in Chapter 4 (see also Darling et al. 2012) to derive a life-history classification for the 33 scleractinian coral genera observed on Kenyan reefs between 1991 and 2011 (Appendix C). We did not simply classify our coral genera according to the previous life-history classification of 143 global scleractinian corals for two reasons. First, three genera (*Coscinarea*, *Goniopora*, *Herpolitha*) that are present in Kenya were not included in the previous analysis because they did not meet the data coverage criteria. Life history categorization was needed for these new taxa. Second, geographic variability in life-history strategies may be expected if the selective pressures that shape life histories vary spatially. We therefore wanted to produce a life-history categorization that was strictly relevant to Kenyan corals. Consequently, we repeated the hierarchical clustering with non-parametric multivariate analyses of variance (MANOVAs) visualized by Principal Coordinates ordination and random forests analyses (for details see Chapter 4, Darling et al. 2012) only for coral species that occur in Kenya, which was determined based on global species distributions maps (Veron 2000). We limited our analysis to the 135 species (out of 300 species known to occur in Kenya) that had published information for six out of the 11 life history traits used in the global evaluation. The data cut-off of six traits was chosen

because it allowed us to include species of all genera observed in the coral community surveys.

The re-analysis of life histories for Kenyan scleractinian corals largely upheld the results of the global analysis (Appendix C). Of the 89 species included in both the Kenya and global analyses, 76 (or 85.4%) were assigned to the same life-history strategy. The species that changed life-history groups were generalist species from the global analysis that were now classified as stress-tolerant in the Kenya analysis, with the exception of one species, *Alveopora fenestrata*, that was formerly assigned to the stress-tolerant group and now classified as weedy in the Kenya analysis. However, we found statistical support for only two or three life-history strategies in Kenya instead of up to four strategies in the global analysis (Appendix C). Selective pressures in Kenya thus do not appear have favoured a generalist life history. Species in the three genera (*Coscinarea*, *Goniopora*, *Herpolitha*) that were absent from the global analysis were all classified as having a stress-tolerant life-history strategy.

We used the species life-history classifications for Kenyan corals to generate life-history classifications for each genus, in order to match the genus-level resolution of the survey data. We then summed the cover of genera within each life-history group to estimate the absolute coral cover of each life history at each site. Most genera (25 out of 33, 75.8%) had consistent life-history classifications across species and were easily assigned to one life-history strategy (Appendix C). However, eight genera (*Goniastrea*, *Hydnophora*, *Leptastrea*, *Montipora*, *Pavona*, *Psammocora*, *Pocillopora*, and *Turbinaria*) included species classified to different life histories. For these genera, we distributed coral cover to each of the represented life histories in proportion to the number of species within each life history. For example, for the three species of *Pocillopora* that occur in Kenya, two (*P. eydouxi* and *P. verrucosa*) have a competitive life history and one (*P. damicornis*) has a weedy life history. Thus, of the total *Pocillopora* cover, 2/3 contributed to the total coral cover of the competitive group and 1/3 to the weedy group. Arguably, it might have been better to weight the contribution of different species by their abundance (i.e., cover) but our survey data, like many other coral monitoring efforts, were not collected at the species level.

Time-series trends in coral communities

We evaluated the effects of year, fishing (fished / unfished), the 1998 mass coral bleaching event (before / after), life-history strategy (competitive / stress-tolerant / weedy), and their interactions on coral cover. We used multivariate linear models with correlated error to account for the temporal correlation in the data; spatial correlation in coral cover between sites was not significant (see Methods above, Chapter 3; Darling et al. 2010). We modeled the trend in each life-history group at each site between 1991 and 2011 and included an autoregressive (AR-1) correlation structure between residuals of time points to account for temporal auto-correlation of time series data. Incorporating a one-year time lag to the model residuals improved model fit (Akaike's Information Criteria, AIC: 1964.5) compared to models without an auto-correlation structure (AIC: 2216.3). Auto-correlation plots indicated additional auto-correlation at three- and five-year time lags. However, similar correlation structures only marginally affect F-statistics and p-values (Schabenberger and Pierce 2002, Zuur et al. 2009) so we chose a one-year auto-correlation of error as the optimal structure in order to model the temporal nature of the data in a reasonable, if not perfect, manner. Model selection was performed using a backwards elimination process of non-significant interactions and main effects, confirmed by likelihood ratio tests and AIC scores. Model diagnostics were performed visually and the final model met assumptions of normality and homogeneity of residuals. We used R (R Core Development Team 2012) for all analyses.

Responses of coral life histories to fishing and bleaching

We calculated effect sizes for fishing and bleaching for each of the three coral life histories following Chapter 3 and Darling et al. (2010). The effect size of fishing was calculated as:

$$Fishing = \left(\bar{\chi}_{Fished1991-1997} - \bar{\chi}_{Unfished1991-1997} \right) / \bar{\chi}_{Unfished1991-1997} \quad (\text{eqn. 1})$$

where $\bar{\chi}_{Fished1991-1997}$ is the mean cover of each life history on fished reefs between 1991 and 1997, i.e. before the 1998 mass coral bleaching event, and $\bar{\chi}_{Unfished1991-1997}$ is the

mean cover on unfished reefs for the same time period. We applied the delta method (Oehlert 1992, Casella and Berger 2001) to estimate the variance of the fishing effect size, $\text{var}_{\text{Fishing}}$, from the variances of the coral cover estimates on fished ($s_{\text{Fished}1991-1997}^2$) and unfished reefs ($s_{\text{Unfished}1991-1997}^2$):

$$\text{var}_{\text{Fishing}} = s_{\text{Fished}1991-1997}^2 * \left(\frac{1}{\bar{\chi}_{\text{Unfished}1991-1997}} \right)^2 + s_{\text{Unfished}1991-1997}^2 * \left(\frac{-\bar{\chi}_{\text{Fished}1991-1997}}{\left(\bar{\chi}_{\text{Unfished}1991-1997} \right)^2} \right)^2 \quad (\text{eqn. 2})$$

We calculated the 95% confidence interval of the fishing effect size from the t-distribution of the variance, which is more appropriate for small samples (Zar 1999).

We calculated two effect sizes for bleaching: (1) the immediate effect of bleaching mortality between 1997 and 1999, and (2) recovery after bleaching between 1999 and 2011. For each effect size, we calculated a geometric rate of change (CRg) to estimate annual rates of change in coral cover (Côté et al. 2005). The CRg effect size accounts for variation in the initial amount of coral cover across sites and can estimate change across non-linear time series; this metric also preserves proportionality (e.g., a 10% to 1% change in cover yields the same effect size as a 50% to 5% decline) and is symmetrical with respect to declines or increases in coral cover (Côté et al. 2005). The effect size of bleaching mortality between 1997 and 1999 was calculated for each site as:

$$\text{Bleaching}_{1997-1999} = \left[\left(\frac{C_{1999,i}}{C_{1997,i}} \right)^{\frac{1}{2}} - 1 \right] \quad (\text{eqn. 3})$$

where $C_{1999,i}$ is coral cover at site i immediately after bleaching in 1999 and $C_{1997,i}$ is coral cover at site i before bleaching in 1997. The rate of bleaching recovery from between 1999 and 2011 was calculated as:

$$Bleaching_{1999-2011} = \left[\left(\frac{C_{2011,i}}{C_{1999,i}} \right)^{\frac{1}{12}} - 1 \right] \quad (\text{eqn. 4})$$

where $C_{2011,i}$ is the coral cover at site i in 2011 and $C_{1999,i}$ is the coral cover at site i in 1999. We estimated mean effect sizes for each life history on fished and unfished reefs. For one effect size, bleaching mortality, two sites (Diani 2 and Vipingo 1) displayed very large increases (~300% and ~1200%, respectively) in the abundance of stress-tolerant species between 1997 and 1999. We did not include these two sites in the estimate of mean bleaching mortality for stress-tolerant taxa on fished reefs because we assumed that these unrealistically large increases were associated with sampling error. We estimated 95% confidence intervals using bias-corrected and accelerated bootstraps using the package 'boot' (Canty and Ripley 2010) for all bleaching effect sizes.

Co-tolerance

We evaluated the patterns of co-tolerance to fishing and thermal stress for scleractinian coral genera by plotting the relationship between the sensitivity to fishing against sensitivity to bleaching. For each genus, we calculated a fishing sensitivity index from the effect size of fishing (eqn. 1). The index was log-transformed and rescaled around zero to normalize the mean and variance of the index (Kaiser et al. 2006, Graham et al. 2008). Values above zero indicate genera that are sensitive to fishing (i.e., abundance is lower on fished reefs compared to unfished reefs), and values below zero indicate the genera are less sensitive to fishing (i.e., abundance is higher on fished reefs compared to unfished reefs). We could not calculate a fishing effect size for four rare genera (*Echinophyllia*, *Gardineroseris*, *Herpolitha* and *Seriatopora*) that did not occur on our studied reefs during the pre-bleaching time period (1991 to 1997); these genera were removed from the analysis of co-tolerance. To estimate the sensitivity of each genus to thermal stress and bleaching, we used a published index of bleaching response that assesses the frequency and severity of bleaching for coral genera in the Western Indian Ocean (McClanahan 2004; McClanahan et al. 2007b). Bleaching responses for the 29 Kenyan genera included in this analysis ranged from 5.6 (*Psammocora*) to 30.8

(*Alveopora*); taxa with lower bleaching responses were observed to bleach less frequently and severely than taxa with a higher bleaching response (Appendix C). However, while this metric is an indicator of the sensitivity of taxa to bleaching, it may not always indicate mortality following with bleaching or recovery after bleaching (McClanahan 2004), which require future investigations. We used linear models to evaluate the relationship between the sensitivity of corals to fishing bleaching for the entire coral community and each coral life history separately.

Results

Before 1998, coral communities on fished and unfished reefs had different life-history assemblages, which influenced the subsequent effects of the temperature-driven bleaching and coral decline (life history x management x bleaching interaction, $P = 0.035$; Table 5.1; Fig. 5.1a). Prior to bleaching, unfished reefs had twice as many coral taxa as fished reefs (t-test, $t_{df, 70} = 10.3$, $P < 0.001$; mean genera richness \pm SD, unfished: 14.8 ± 2.4 ; fished: 7.7 ± 3.3) and were composed of all three life histories (stress-tolerant, $19.4 \pm 6.7\%$ mean \pm SD absolute cover; competitive, $9.3 \pm 7.8\%$, and weedy, $6.9 \pm 6.9\%$). Immediately following the 1998 bleaching event, coral assemblages changed more on unfished reefs than those on fished reefs (management x bleaching, $P = 0.0017$; Table 5.1, Fig. 5.1a). In particular, unfished reefs experienced a substantial loss of competitive and weedy corals between 1997 and 1999; the abundance of stress-tolerant corals on unfished reefs was less affected by the 1998 bleaching event (Fig. 5.2). By 2011, competitive corals on unfished reefs had recovered to just 22.5% of their pre-bleaching abundance (Figs. 5.1a, 5.2). Weedy corals also exhibited moderate post-bleaching recovery and had attained 43.4% of their pre-bleaching cover by 2011 (Figs. 5.1a, 5.2). Stress-tolerant corals on unfished reefs slowly increased in abundance between 1999 and 2011 and had fully recovered to their pre-bleaching cover by 2011 (105.3%; Figs. 5.1a, 5.2). However, despite substantial changes in life-history composition, unfished reefs continued to have more coral genera than fished reefs following bleaching (average genera richness between 1999 and 2011 on unfished reefs: 13.9 ± 2.9 vs. fished reefs: 9.3 ± 3.3 , $t_{df, 142} = 8.7$, $P < 0.001$).

Table 5.1. Best-fit model of a multivariate time-series general linear regression analysis used to evaluate the effects of year, life history (competitive, stress-tolerant, weedy), fisheries management (fished, unfished) and a mass bleaching event (before, after 1998) on coral abundance on Kenyan reefs.

Parameter	df	F	P
(Intercept)	1	193.46	<0.0001
Year	1	14.67	0.0002
Life history	2	36.69	<0.0001
Management	1	7.47	0.0066
Bleaching	1	18.74	<0.0001
Life history x Management	2	15.5	<0.0001
Life history x Bleaching	2	10.03	0.067
Management x Bleaching	1	2.72	0.0017
Life history x Management x Bleaching	2	3.38	0.035

Coral life-history assemblages on fished reefs over the 20-year period were less affected by bleaching (Fig. 5.1b). Before 1998, fished reefs were composed of primarily weedy ($12.5 \pm 2.7\%$ mean \pm SD absolute cover) and stress-tolerant corals ($6.0 \pm 3.8\%$); corals with a competitive life history were extremely rare ($0.7 \pm 0.7\%$). After bleaching, weedy corals experienced significant bleaching mortality on fished reefs, but recovered to 97% of their pre-bleaching cover within four years after bleaching, although this recovery was punctuated over the following nine years by another decline, recovery, and decline (Fig. 5.1b, 5.2). Stress-tolerant corals on fished reefs exhibited moderate declines following bleaching but had doubled in absolute cover by 2011 relative to their pre-bleaching abundance (199.8%, Fig. 5.1b, 5.2). In 2011, fished reefs remained composed of stress-tolerant ($12.0 \pm 6.1\%$) and weedy ($8.1 \pm 5.9\%$) corals, although the relative prevalence of these two life histories was reversed compared to pre-bleaching years. Competitive corals remained uncommon ($0.4 \pm 0.4\%$) on fished reefs in 2011 (Fig. 5.1b).

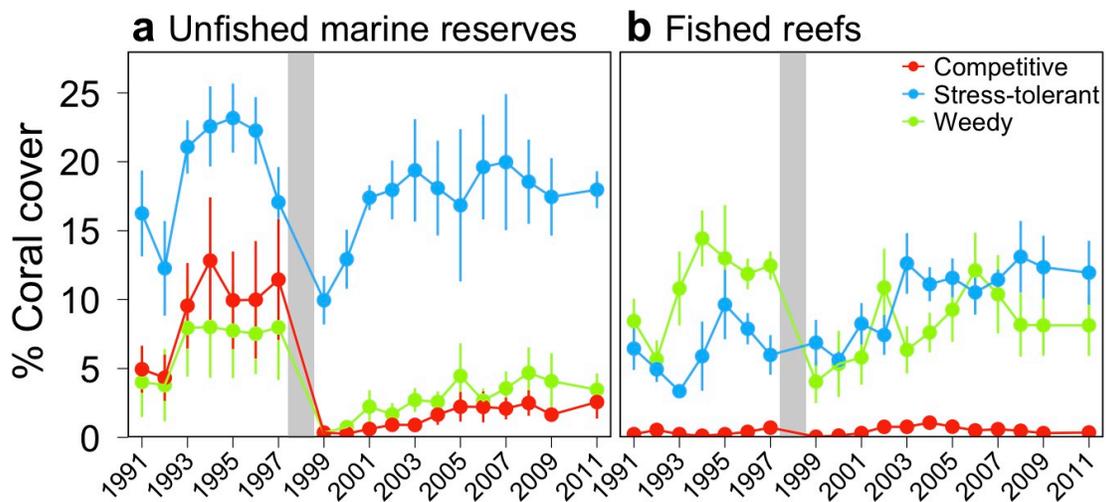


Figure 5.1. Time-series of Kenyan coral communities between 1991 and 2011 on (a) unfished no-take marine reserves and (b) fished reefs in Kenya. The three major life-history strategies of scleractinian corals are indicated by colour (red: competitive, blue: stress-tolerant, green: weedy). The y-axis shows absolute percent coral cover. The 1998 El Niño Southern Oscillation and Indian Ocean Dipole resulted in a temperature anomaly that caused mass coral bleaching, as indicated by the grey bar.

The three coral life histories had different responses to fishing and bleaching (Table 5.1; Fig. 5.2). Fishing nearly eliminated the cover of competitive taxa and reduced stress-tolerant taxa to less than half of their cover on unfished reefs; weedy taxa increased in abundance on fished reefs. Competitive and weedy corals exhibited similar responses to bleaching, with high immediate mortality followed by moderate recovery; stress-tolerant taxa were less affected by bleaching, yet still experienced some mortality, and also moderate recovery across most sites (Fig. 5.2).

At the overall community level, we found no relationship between the sensitivity of coral genera to fishing and bleaching ($P = 0.90$, Fig. 5.3a), nor did we see evidence for co-tolerance in any life history group (Figs. 5.3b-d). Competitive taxa were the most vulnerable to the combined effects of fishing and climate change -- all competitive taxa were sensitive to fishing disturbances and 3 out of the 5 taxa (*Acropora*, *Montipora* and *Pocillopora*) were also highly sensitive to bleaching (Fig. 5.3b). In comparison, stress-tolerant and weedy taxa displayed more variable responses to fishing and bleaching, with taxa falling in all four quadrants of the co-tolerance plots (Figs. 5.3c-d). Seven coral genera (out of 29, 24%; *Astreopora*, *Cyphastrea*, *Fungia*, *Lobophyllia*, *Pavona*, *Psammocora* and *Turbinaria*) occurred in the bottom-left quadrant of the plot with low

sensitivity to both stressors; these genera could be labeled as ‘survivors’ (Fig. 5.3a). These species are mostly taxa with stress-tolerant life histories, although one genus, *Psammocora*, has a weedy life history, and one genus (*Turbinaria*) has a competitive life history. The remaining taxa (22 out of 29, 75.8%) displayed sensitivity to fishing, bleaching, or both stressors and can be labeled as ‘losers’ (Fig. 5.3a). These taxa include competitive, stress-tolerant and weed life histories.

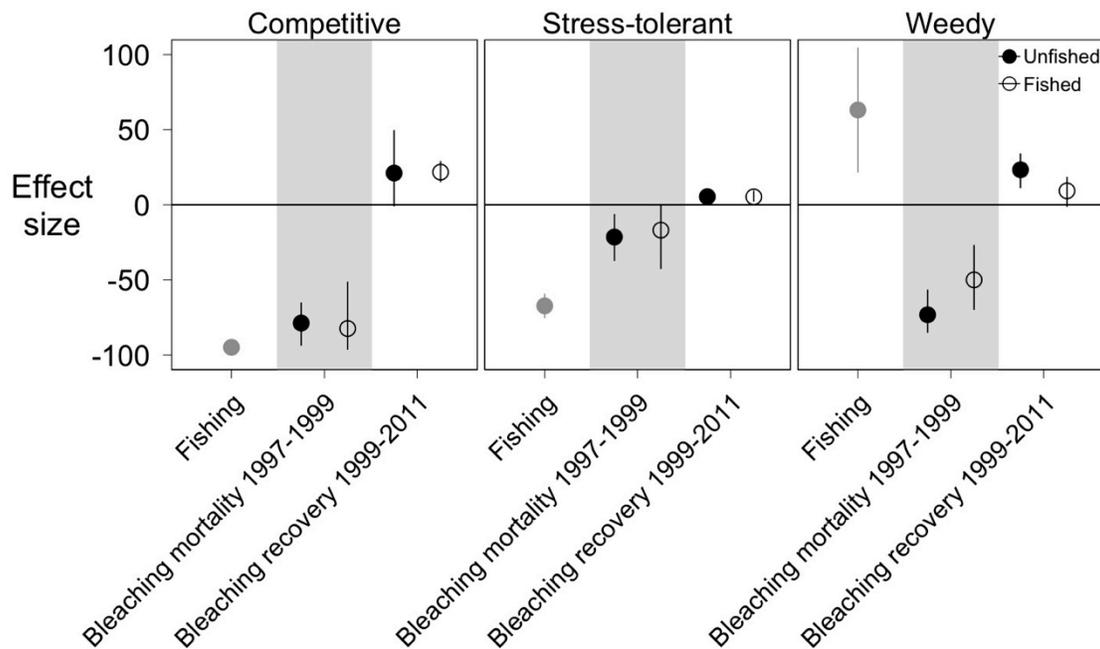


Figure 5.2. Coral life histories have different responses to fishing and bleaching stressors. Effect sizes \pm 95% confidence intervals are given. The grey bar indicates the immediate effects of the 1998 mass coral-bleaching event (i.e., change in coral cover occurring from the year before to the year after the event). The horizontal line at zero indicates no change in coral cover; values below zero indicate a decline in coral cover and values above zero indicate an increase in coral cover. For the bleaching effect sizes, filled circles are the responses of corals within no-take marine reserves (unfished) and unfilled circles indicate fished reefs.

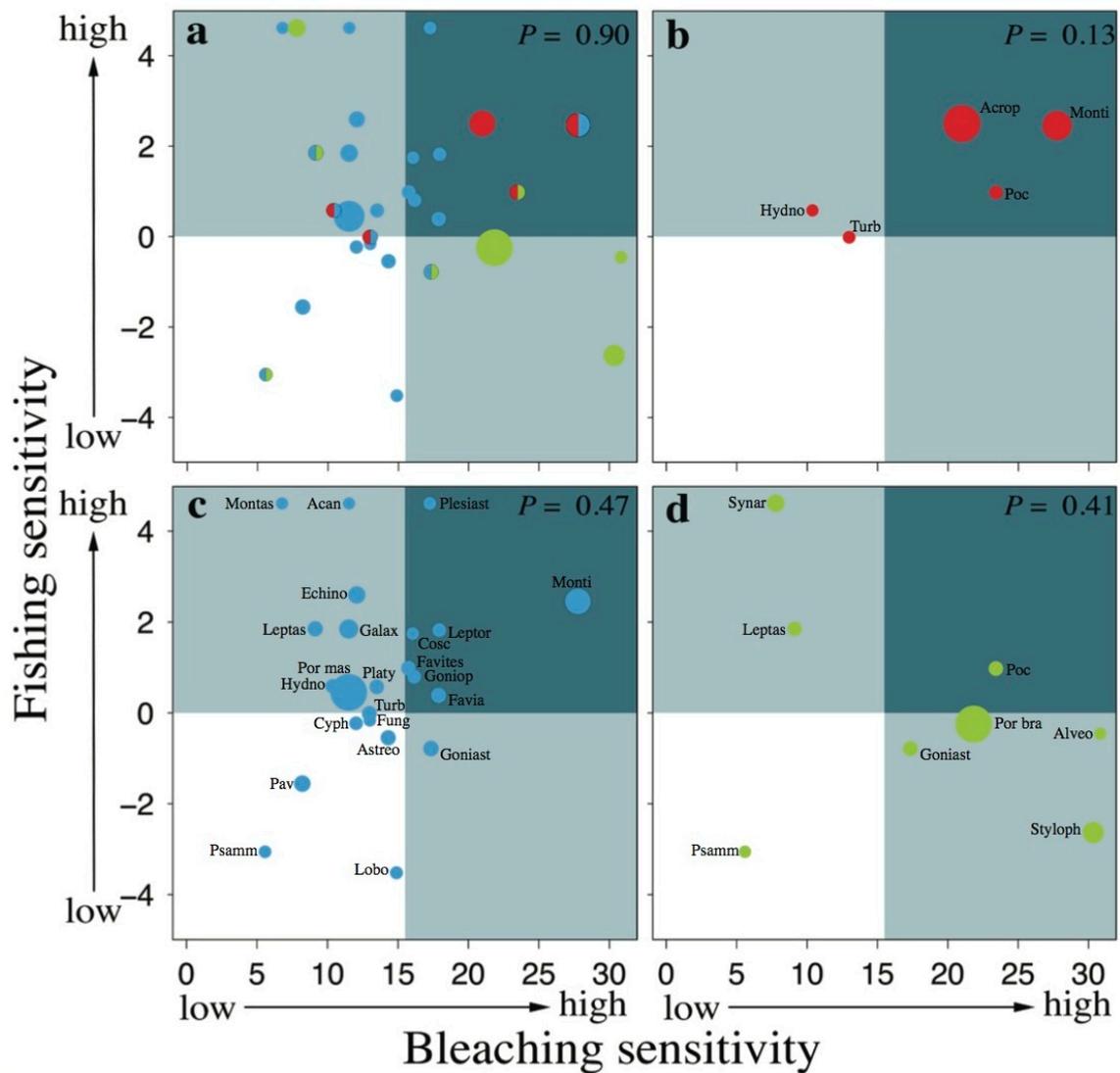


Figure 5.3. Relationship between sensitivities of 29 Kenyan coral genera to the impacts of fishing and coral bleaching for a) the whole coral community, b) competitive, c) stress-tolerant, and d) weedy taxa. Shading represents the impacts of fishing, bleaching and their cumulative effects. The size of the points is proportional to averaged coral cover on fished and unfished sites prior to bleaching. Colour indicates life history (red: competitive; blue: stress-tolerant, green: weedy); multi-coloured points indicates that the genus includes species in more than one life-history group. Labels are abbreviated genus names (see also Appendix C).

Discussion

The interaction between fishing and a temperature-driven bleaching event influenced the life-history composition of coral communities and the relative abundance of different taxa. As predicted, there were different coral assemblages on fished and unfished reefs prior to the major bleaching event of 1998. Differences in taxonomic composition can be broadly summarized in terms of coral life histories and the interaction between fishing and coral bleaching: coral communities subjected to intensive fishing pressure were composed of stress-tolerant and weedy taxa, while unfished coral communities before 1998 were more diverse and included corals with a competitive life history. We found that distinguishing coral assemblages by competitive, stress-tolerant and weedy life histories provided a pragmatic and general approach to evaluate the long-term dynamics of diverse scleractinian coral communities, as opposed to focusing solely on total coral cover, a composite metric that can overlook important shifts in community composition (Hughes et al. 2010). This may in part explain why coral cover is not always a good predictor of coral reef dynamics or state (Tanner et al. 2009, McClanahan et al. 2011).

Impacts of fishing on coral life histories

The most obvious impact of fishing on Kenyan coral assemblages was the near-complete loss of competitive species (Fig. 5.1a). A number of direct and indirect mechanisms may explain the community-level impacts of fishing on the structure of coral assemblages (e.g., Roberts 1995, Jennings and Kaiser 1998). In Kenya, fishing activities can directly damage corals by anchoring and grounding boats on the reef, using weighted nets that are dragged along the reef and traps that are dropped on corals, and from direct trampling by fishers (Cros and McClanahan 2004, Mangi and Roberts 2006). Competitive corals are commonly species of *Acropora* and *Montipora* that form delicate branching and plating colonies that are easily broken (e.g., Marshall 2000). While some acroporids can reproduce asexually by fragmentation and the re-establishment of broken colonies (Highsmith 1982), this does not appear to have prevented the functional extirpation of competitive corals from fished reefs in Kenya. Predators, competitors, and disease may further exacerbate damaged colonies of branching and plating corals (Cumming 2002, McClanahan et al. 2009).

In addition to direct damage, fishing might indirectly affect juvenile competitive corals by altering coral predators and grazers (e.g., Dulvy et al. 2004, Mumby et al. 2007b, O’Leary et al. 2012). On Kenyan reefs, fishing commonly results in a shift from fishes to sea urchins as dominant grazers and predators (McClanahan 1997). Overgrazing on crustose coralline algae by sea urchins can have indirect repercussions on coral communities, by reducing the availability of settlement substrate for coral recruits (O’Leary and McClanahan 2010; O’Leary et al. 2012). Sea urchins can also ‘bulldoze’ small juvenile corals by crawling over them (Hughes & Connell 1999; Cover 2011; E. Darling, pers. obs.). The removal of grazing herbivorous parrotfishes and surgeonfishes by the fishery can result in more macroalgae on fished reefs, which has been shown to reduce the recruitment, the survival, and growth of coral recruits and juveniles (reviewed in McCook et al. 2000; Mumby 2009). However, future studies are needed assess the resulting impacts of altered grazers and predators on the structure of coral communities, particularly in relation to life-history composition. Given the observation that competitive corals are less abundant on fished reefs, we would hypothesize that juvenile acroporids are sensitive to the loss of settlement substrates, damage by sea urchins and competition with macroalgae.

Traits of stress-tolerant and weedy taxa may reduce the vulnerability of these life histories to the direct and indirect effects of fishing (Fig. 5.1b). Stress-tolerant and weedy species can have massive, submassive or encrusting colony morphologies that are less likely to be damaged by fishing disturbances (e.g., Marshall 2000) and also more likely to recover from partial colony mortality (Soong et al. 1993). Juveniles with ‘domed’ hemispherical colonies may also be more tolerant of sea urchin ‘bulldozing’ (E. Darling, pers. obs.). However, even damaged colonies may be able to persist - some stress-tolerant and weedy corals can reproduce by asexual fragmentation and re-attachment of broken colonies (e.g., branching and massive *Porites*, *Pocillopora damicornis*, encrusting *Goniastrea* and *Leptastrea*; Highsmith 1982, van Woesik et al. 2011). Weedy corals in Kenya are typically small species that reproduce by brooding – a type of coral reproduction that can produce locally-dispersed larvae (Ayre and Miller 2004) with less stringent requirements for settlement substrate (O’Leary et al. 2012; A. Baird, pers. comm.). However, further tests of the mechanisms underpinning the persistence of stress-tolerant and weedy species on fished reefs are needed.

Impacts of bleaching on coral life histories

Corals in all three life histories declined in response to the 1998 temperature anomaly and coral bleaching event. Competitive and weedy corals exhibited larger declines than stress-tolerant corals following bleaching, and these declines were fairly consistent across fished and unfished reefs (Fig. 5.2). However, competitive and weedy life histories recovered at a faster rate than stress-tolerant corals (Fig. 5.2), likely because competitive and weedy corals grow faster than stress-tolerant species (Chapter 4; Darling et al. 2012). While both competitive and weedy corals gradually increased in abundance after bleaching, this recovery occurred in different patterns. On fished reefs, weedy corals recovered quickly within the first four years and then experienced another decline, recovery and decline (Fig. 5.1). Competitive corals, on the other hand, exhibited a 'slow and steady' recovery over the entire 12-year recovery period – the rate of recovery of competitive corals was, on average, similar across fished and unfished reefs, although more variable on unfished reefs (Fig. 5.2) suggesting that site-specific influences of environment, habitat, recruitment supply, and predators may be important determinants of recovery (McClanahan et al. 2005b). However, despite similar annual rates of recovery on fished and unfished reefs (Fig. 5.2), competitive corals only reached any meaningful abundance on unfished reefs (~7% absolute cover) and remained functionally extirpated (<1% absolute cover) from fished reefs throughout the entire 20-year time series (Fig. 5.1a,b).

Previous studies have also noted variable patterns of bleaching mortality and recovery across coral taxa. For example, a decade-long study following the 1998 bleaching event in Japan found that thermally-tolerant massive and encrusting species often survived as 'short-term' winners while 'long-term' winners included faster-growing branching and plating acroporids due to rapid regrowth of surviving colonies, as well as strong recruitment from regionally persistent populations (Loya et al. 2001, van Woesik et al. 2011). This suggests that competitive corals can recover from bleaching when given enough time and connectivity to other populations; in Kenya, however, we only observed recovery on unfished reefs. If reefs protected from fishing harbour a higher abundance of bleaching-sensitive, competitive acroporids than fished reefs, this may further explain the results of a global meta-analysis that found marine reserves have not mitigated temperature-driven declines in coral cover (Selig and Bruno 2010, Selig et al. 2012).

Co-tolerance to multiple stressors – identifying ‘survivors’ and ‘losers’

We did not find evidence to support the hypothesis that coral communities displayed positive co-tolerance to fishing and bleaching stressors in Kenya (Fig. 5.3a). Species in all three life histories displayed high variability in their sensitivities to fishing and bleaching, and we found no support for community co-tolerance of Kenyan corals to fishing and bleaching (Fig. 5.3b-d). Most taxa (22 out of 29, or 76%) were highly sensitive to the independent effects of fishing and bleaching, or both stressors. Community co-tolerance may be more likely occur when stressors have weaker impacts, for example on reefs with less intensive fishing and weaker impacts of coral bleaching. Kenyan coral reefs experience heavy fishing pressure as well as thermal stress, which makes these reefs fairly unique throughout the western Indian Ocean region (McClanahan et al. 2007b, Maina et al. 2008). We are planning future investigations at less disturbed sites in the western Indian Ocean to evaluate whether the type of stressor, or severity of impact, influences co-tolerance. Nevertheless, the absence of a community pattern of co-tolerance within Kenyan coral assemblages suggests that fishing and bleaching may have fairly independent effects (i.e., an additive interaction, Vinebrooke et al. 2004). This may in part explain why we previously found evidence for an additive or antagonistic relationship, and not a synergy, between fishing and bleaching on Kenyan coral reefs (Chapter 3; Darling et al. 2010).

The variation in co-tolerance responses with coral life histories may at first appear contradictory to the clearer impacts of fishing and bleaching on coral life histories over the 20-year time series. However, the co-tolerance analysis includes all coral genera, whether they were common and rare within Kenyan coral assemblages (indicated by dot size in Fig. 5.3). The time-series of community dynamics are instead driven by the responses of common taxa (e.g., Gaston and Fuller 2008, Hillebrand et al. 2008). Common corals on Kenyan reefs include competitive *Acropora* and *Montipora*, which are sensitive to both fishing and bleaching stress (top right quadrant, Fig. 5.3b), stress-tolerant massive *Porites*, which are moderately sensitive to fishing and less sensitive to bleaching (top left, Fig. 5.3c), and weedy branching *Porites* and *Stylophora*, which are sensitive to bleaching and less sensitive to fishing (bottom right, Fig. 3d). However, even considering only a subset of more abundant and common corals, there is still no statistical support ($P > 0.05$) for co-tolerance with Kenyan coral communities.

Overall, we suggest that identifying potential ‘survivors’ and ‘losers’ based on life-history strategies and species-specific co-tolerances may help scientists and managers predict community-level responses to multiple stressors. Most corals were ‘losers’ and sensitive to the independent and combined impacts of fishing and coral bleaching on Kenyan reefs (Fig. 5.3, all quadrants except bottom left). Taxa identified as ‘survivors’ (Fig. 5.3, bottom left quadrant) were predominantly stress-tolerant taxa, hence some traits of these slow-growing massive, submassive and encrusting taxa may allow species to persist on disturbed reefs.

Conclusions

Scleractinian corals will not disappear entirely owing to the ongoing impacts of human activities and climate change. However, coral assemblages are expected to shift towards less diverse and more homogenous assemblages of species that can tolerate these disturbances (Hoegh-Guldberg et al. 2007, Hughes et al. 2012, Riegl et al. 2012). If coral reefs are on a ‘slippery slope to slime’ (Pandolfi et al. 2005), there will likely be pit stops at assemblages of stress-tolerant ‘survivor’ corals, as well as other alternative states dominated by macroalgae, sponges and soft corals (McClanahan et al. 2002; Norström et al. 2009). Shifts towards stress-tolerant corals might result in lower-relief assemblages with reduced structural complexity, especially if there are concurrently shifts towards smaller colonies (e.g., McClanahan et al. 2008b, Reigl et al. 2012). A critical question is whether these altered benthic assemblages will be able to support the diverse and productive communities of fishes and invertebrates currently associated with coral reefs (Graham et al. 2006, Pratchett et al. 2008, Chong-Seng et al. 2012). Slowing the degradation of coral communities by protecting and recovering important reef architects – such as branching and plating competitive species and large colonies of stress-tolerant corals – should be an urgent focus for coral reef conservation and management.

Chapter 6.

General Discussion: Rethinking the resilience of coral reefs in the face of multiple stressors⁵

Coral reefs are among the most biodiverse ecosystems on the planet and provide immense ecological and economic benefits that contribute to the welfare of millions of people (Moberg and Folke 1999). However, coral reefs are also one of the most vulnerable ecosystems to climate change and anthropogenic stressors (Roberts 1995, Hughes et al. 2003, Hoegh-Guldberg et al. 2007, Halpern et al. 2008). This may seem puzzling because modern scleractinian (reef-building) corals have experienced, and survived, extreme variation in environmental conditions (including multiple mass extinction events) since their appearance in the Middle Triassic, some 240 million years ago (Stanley 2003). However, the current 'coral reef crisis' is unique for two reasons. First, the rates of increase in atmospheric carbon dioxide concentrations, and associated changes in carbonate availability and seawater acidity, are simply unprecedented (Knoll et al. 2007). Second, these rapid environmental changes are occurring against a background of widespread human-induced disturbances, such as fishing, coastal run-off, pollution and invasive species, which have placed one-third of reef-building corals at an elevated risk of extinction (Carpenter et al. 2008).

⁵ Versions of this chapter appear as, Darling E.S. and I.M. Côté (In press) Vulnerability of coral reefs to climate change and multiple stressors. In *Climate Vulnerability* (Ed. R. Pielke Sr) *Volume 4: Ecosystem Function* (Eds. K. Suding and T. Seastedt), and Côté I.M. and E.S. Darling (2010) Rethinking ecosystem resilience in the face of climate change. *PLoS Biology*, 8, e1000438.

Understanding the cumulative impacts of stress on ecosystems and rethinking our management philosophies to explicitly incorporate multiple, interacting stressors is a critical challenge for 21st century conservation (Paine et al. 1998). In this respect, coral reefs are unfortunately a model ecosystem to evaluate the cumulative impacts of multiple stressors and how to manage for them. In this final chapter, we consider how the interaction between climate change and local, human-caused stressors can affect coral reef management. Central to current thinking about the management of coral reefs is the concept of resilience. We outline the conventional view of coral reef resilience to climate change, and offer an alternative that considers how changes in coral community structure resulting from local stressors can affect resilience. Finally, we consider the implications of these two resilience frameworks for coral reef management and the role that no-take Marine Protected Areas (MPAs) can play in a rapidly changing climate. We conclude that there is hope for the survival of coral reefs. However, the cumulative impacts of climate change and local human impacts may motivate a new agenda for coral reef conservation.

Climate change and human impacts on coral reefs

Increasing atmospheric CO₂ and climate change are warming and acidifying the world's oceans. This future "hot and sour soup" (Palumbi 2010) will have widespread consequences for scleractinian corals (Hoegh-Guldberg et al. 2007, Wild et al. 2011; Frieler et al. 2012). Over the past century, average global sea surface temperatures (SSTs) have risen by 0.6°C and temperature anomalies, i.e. deviations from long-term temperature averages, are occurring more frequently (Hoegh-Guldberg 1999, Hoegh-Guldberg and Bruno 2010). Warmer than normal SSTs can result in coral bleaching, caused by a breakdown in the relationship between corals and the endosymbiotic unicellular algae (zooxanthellae) that provide corals with most of their metabolic requirements. Thermal stress can trigger the expulsion of the colourful zooxanthellae from their coral hosts, which can cause the coral to turn white, or 'bleach' (Hoegh-Guldberg 1999). Corals can recover from short-term bleaching, by adopting new zooxanthellae which are sometimes more thermally resistant than the ejected strain (Baker 2001, Baker et al. 2004, Berkelmans and Van Oppen 2006), but the physiological stress of bleaching interrupts growth and reproduction and may make recovering corals

more susceptible to diseases (Harvell et al. 2002, Bruno et al. 2007). Sustained SSTs 1°C above average can lead to mass bleaching, which can affect hundreds to thousands of kilometers of reef area and result in widespread coral mortality (Hoegh-Guldberg 2005). The loss of live coral cover and architectural complexity on bleached reefs can have substantial ecological and economic consequences, affecting a broad range of coral reef fish and invertebrates and the fisheries they support (Pratchett et al. 2008).

Climate change is also increasing the acidity of seawater. More than one-third of atmospheric CO₂ emissions are absorbed by the oceans and dissolve to fundamentally alter ocean chemistry (Pelejero et al. 2010). Over the past 150 years, sea surface pH has dropped by 0.1 units and sea surface acidity has increased by ~26% (Doney et al. 2012). Increased ocean acidity reduces the ability of corals to build their calcium carbonate skeletons and can also disrupt critical metabolic processes, such as gas exchange, and reproduction (Kleypas and Yates 2009, Pelejero et al. 2010). Ocean acidification can also reduce the availability of the preferred settlement substrate for juvenile corals, crustose coralline algae (Anthony et al. 2008), and can disrupt important cues for coral recruitment (Doropolous et al. 2012). Ocean acidification may profoundly affect the structure and function of coral reef benthic communities. A glimpse of such impacts is provided by 'champagne reefs', such as those found in Papua New Guinea. These reefs persist in naturally acidic waters caused by the bubbling of carbon dioxide released from volcanic seeps in the substrate, the pH at acidic sites – around 7.8 – is consistent with some scenarios of predicted ocean acidity by the end of this century (Fabricius et al. 2011). The naturally acidic reef communities are depauperate in coral diversity and have fewer structurally complex framework-building corals, less crustose coralline algae, fewer juvenile coral recruits, and a higher cover of fleshy macroalgae and seaweeds compared to adjacent reefs in 'normal' 8.1 pH (Fabricius et al. 2011). Other potential influences of climate change include sea level rise, which is expected at a rate of 0.2 – 0.8 cm year⁻¹, and changes in storm regimes caused by warmer SSTs (Hoegh-Guldberg 2005, Doney et al. 2012). However, these effects are expected to be more benign than the fundamental threats to coral survival posed by a warmer and more acidic ocean. Nevertheless, while climate change is an unprecedented threat, it is one of many threats that jeopardize coral reefs.

In addition to climate change, coral reefs are impacted by a multiplicity of local stressors. These include fishing, which removes species with important ecological functions, sedimentation from coastal and watershed development, eutrophication from agricultural and urban runoff, and invasive species, which can outcompete or prey upon native species. Many of world's coral reefs are faced with high and unsustainable levels of human activities (Newton et al. 2007; Halpern et al. 2008). The cumulative impacts of local and global stressors have resulted in widespread losses of live coral cover (Gardner et al. 2003, Bruno and Selig 2007) and an elevated risk of extinction of one-third of all reef-building corals (Carpenter et al. 2008). Shifts have been observed in the structure and diversity of coral reef communities (McClanahan et al. 2007b,c, Knowlton and Jackson 2008, Sandin et al. 2008), such as the flattening of coral reef habitats when architecturally complex coral species are gradually replaced by smaller, simpler taxa (Alvarez-Filip et al. 2009, 2011). Such fundamental changes in the reef framework can have cascading consequences for reef fish and invertebrate abundance and diversity, which depend on reef habitat for food and shelter (Graham et al. 2008, Pratchett et al. 2008, Messmer et al. 2011). The cumulative impacts of multiple stressors are undoubtedly already affecting the ecosystem functions and services of coral reefs, which are estimated to be worth more than \$30 billion annually (Cesar et al. 2003). The impacts on tourism, coastal protection, and fisheries will be most obvious. For example, the 1998 mass coral bleaching event in the Indian Ocean resulted in an estimated \$706 million to \$8.2 billion in economic damages (Wilkinson et al. 1999). Intact coral reefs have high vertical relief, which effectively dissipates the wave energy reaching the coastline, protecting beaches and buildings from storm surges and tsunamis (Sheppard et al. 2005). The loss of healthy reefs may therefore limit the protection they can provide to coastal communities (Barbier et al. 2011). Declining coral reef fish and invertebrate populations stemming from declines in the quality or availability of reef habitat will have economic consequences for coral reef fisheries and the millions of people in developing countries that depend on coral reef resources for subsistence and livelihoods (Pratchett et al. 2008, Barbier et al. 2011). There are therefore very convincing ecological and economic reasons to understand how multiple stressors interact to produce such drastic effects, and whether there might be ways to manage stressors to mitigate these interactions.

Cumulative impacts of multiple stressors

There is increasing concern that the decline of coral reefs (and other ecosystems impacted by multiple stressors) has been driven by synergies, a type of non-additive interaction between two or more stressors characterized by a combined impact that is greater than the simple sum of the individual impacts (Folt et al. 1999, Breitburg and Riedel 2005) (Figure 6.1). In effect, synergies occur when the result is more than the sum of the parts. Synergies are one type of unpredictable 'ecological surprise' that can accelerate biodiversity loss (Brook et al. 2008) and impair the functioning of marine ecosystems (Paine et al. 1994, Hoegh-Guldberg and Bruno 2010). However, the presence of multiple stressors does not necessarily imply that synergies should be expected. For example, the impacts of multiple stressors can be mitigated by antagonisms, which are interactions where the combined impact is less than the sum of the individual impacts; the cumulative effect of multiple stressors can also be simply equal to the sum of the impacts of individual stressors, resulting in a straightforward additive effect (Folt et al. 1999, Breitburg and Riedel 2005) (Figure 6.1). Two recent meta-analyses of dozens of published studies evaluated the combined impacts of multiple stressors in terrestrial and aquatic ecosystems; the findings suggest that synergies, antagonisms and additive effects may be equally common when two stressors are acting (Chapter 2; Darling and Côté 2008, Crain et al. 2008). However, the addition of a third stressor can often, though still not always, result in a synergistic outcome (Crain et al. 2008).

Evaluating the cumulative impacts of multiple stressors is critical to forecast future ecological change on coral reefs and effectively manage the combined impacts of multiple stressors. One of the greatest scientific uncertainties concerning the decline of coral reefs is how local human impacts (e.g., fishing, pollution) will interact with global climate change (Knowlton and Jackson 2008). It is generally assumed that local human impacts will erode the ability of coral reefs to resist the impacts of climate change and that coral reefs already exposed to human disturbances will be less resilient to climate change and 'tip' into a degraded and less desirable, coral-poor state sooner than more pristine reefs. Thus enhancing resilience by reducing the impacts of local stressors is deemed by many to be crucial for conserving coral reefs in the face of global climate change.

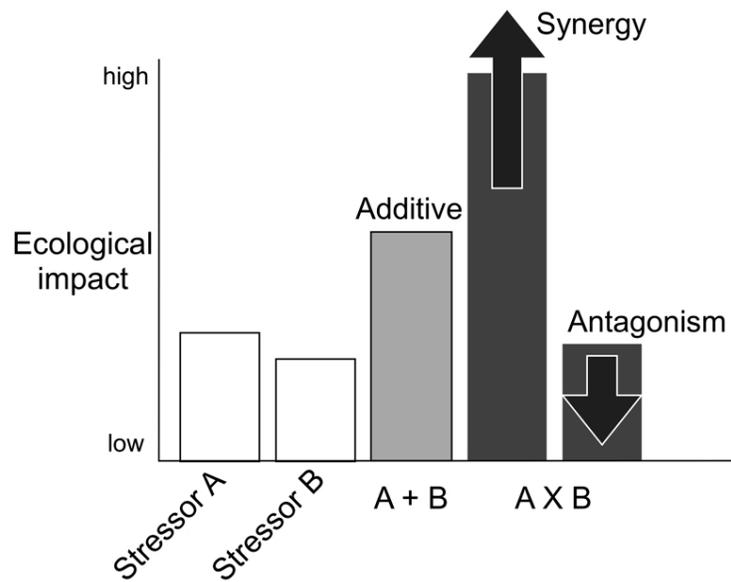


Figure 6.1. The cumulative ecological impact of two stressors can result in simple additive effects, synergies or antagonisms. Synergies and antagonisms are examples of ‘ecological surprises’, where the combined impact of two or more stressors is greater than (synergy) or less than (antagonism) the simple additive sum of the two individual stressors.

What is resilience?

The concept of resilience now underpins much of the thinking about the management of coral reefs. It was first proposed by Holling (1973), who defined resilience as “a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables.” Holling explicitly recognised that ecosystems are dynamic, spatially and temporally heterogeneous, and can exist in multiple alternative states depending on environmental conditions. For example, temperate lakes in North America and Europe can persist in a state of clear water or in an alternative state of high turbidity depending on the input of nutrients and the presence of predatory fishes, similarly, savannas and grasslands may either be grass-dominated or shrub-dominated, depending on the intensity of grazing (Folke et al. 2004). Coral reefs are no different. Under certain conditions, coral reefs are ‘coral-rich’, with a high cover of coral and a low cover of macroalgae, but in altered environments, they can transform, sometimes quickly, into coral-poor reefs with extensive stands of fleshy algae (Bellwood et al. 2004). Other

alternative states are also possible for coral reefs, such as domination by sponges and soft corals (Norström et al. 2009). Resilience may therefore be functionally defined as the capacity of an ecosystem to absorb and adapt to shocks and disturbances without fundamentally shifting into an alternative state (Scheffer et al. 2001, Hughes et al. 2010).

An ecosystem may be resilient for two reasons. On the one hand, an ecosystem may be resistant to a given perturbation. Carpenter et al. (2001) defined *resistance* as the amount of external pressure needed to bring about a given amount of disturbance in a system. Differences in intrinsic resistance between ecosystems may be conveyed, for example, through differing species compositions, with some assemblages made up of species that can withstand greater magnitudes of the perturbation of interest than other assemblages. On the other hand, two ecosystems may have similar resistance to a given perturbation, but may differ in their potential for *recovery*, that is their ability and/or swiftness to return to a state that is functionally similar to the pre-disturbance state. Functional similarity is the operative term here: recovery does not mean returning to a state identical to the original one, but to a state that responds to the same drivers and feedbacks. Resistance and recovery are therefore two sides of the resilience coin, and it is not clear how they co-vary, if at all.

The dual nature of resilience, developed in the general ecological literature, has for some reason not always been fully embraced by coral reef scientists. In the coral reef world, the term resilience has become interchangeable with recovery. For example, Hoegh-Guldberg et al. (2007) defined resilience as “the rate at which an ecosystem returns to a particular state after a perturbation or disturbance”. Similarly, Hughes et al. (2007) equate resilience with “the ability of coral reefs to absorb recurrent disturbances and rebuild coral-dominated systems”. Several authors have recognised the importance of both resistance and recovery but called the latter ‘resilience’ (West and Salm 2003, Knowlton and Jackson 2008). Here, we use the terminology that resilience is a two-part process of ‘resistance’, the ability of a system to withstand disturbance, and ‘recovery’, the capacity of a system to bounce back to the original, pre-disturbance state.

Two important general issues surrounding resilience remain. The first is that resilience is not always a good thing. Resilience can be desirable or undesirable (Carpenter et al. 2001), depending on whether it characterises ecosystem states that are or are not

favoured by society. Some ecosystem states, such as grasslands converted to desert because of overgrazing, are undesirable because they provide reduced services, but they can be highly resilient. The second, related to the first, is that resilience needs to be defined not only in terms of the ecosystem state (e.g., resilience of grassland or of desert, resilience of coral-rich reefs vs coral-poor reefs), but also in terms of the perturbation of interest. A particular ecosystem state may be highly resilient to one type of disturbance, but less so to another. In this final chapter, we consider the resilience of coral-rich reefs to cumulative impacts and, in particular, climate change.

The conventional view of coral reef resilience

For most coral reef scientists, the conventional view of resilience is that pristine, unstressed coral communities are highly resilient to climate change, and that human impacts reduce the ability of coral reefs to withstand climate change (Hughes et al. 2003, Hoegh-Guldberg et al. 2007, Hughes et al. 2010). This conventional view of cumulative impacts and resilience on coral reefs is illustrated in the simple conceptual model shown in Figure 6.2A, which shows the relationship between ecosystem state and climate disturbance. Ecosystem state can be thought of in terms of coral cover or coral species diversity, with the implicit notion that a coral-rich state is more desirable, while climate disturbance can incorporate both changes in mean and increased variability of various climatically driven conditions, such as temperature. The general trajectory of coral reef ecosystems under climate stress is expected to be sigmoidal (Figure 6.2), with relatively little change in ecosystem state over low levels of climate disturbance, and a precipitous shift to an alternative state once a climate threshold, commonly referred to as the tipping point, is exceeded (Hughes et al. 2010). The magnitude of the threshold can be used as a proxy for the resistance aspect of resilience.

This model can easily be adapted to reflect the additional impact of non-climatic, local stressors on coral reef state, and how this modifies the response of coral reefs to climate disturbances. According to the conventional view of resilience, more pristine coral reefs (i.e. with a higher coral cover and species diversity) have a high resistance to climate change and will only cross the tipping point and shift into an alternative ecosystem state at high levels of climate disturbance (Figure 6.2A). However, as non-climatic, local

impacts (e.g., fishing, pollution) degrade the original ecosystem, moving the state of the ecosystem down the y-axis, the coral community moves from a pristine to a disturbed to a very disturbed assemblage (see photos, Figure 6.2). In response, the tipping point shifts to the left, making the ecosystem less resistant to climate disturbances.

The mechanisms underscoring the conventional view of resilience often implicate overfishing and nutrient pollution in the loss of coral resilience (or, really, resistance) to thermal stress and subsequent bleaching (Bellwood et al. 2004, Knowlton and Jackson 2008). Overfishing of herbivorous grazing reef fishes and nutrient pollution from coastal runoff can lead to the proliferation of macroalgae, which can harbor harmful microbes and pathogens that can increase coral disease (Nugues et al. 2004, Dinsdale et al. 2008). Fishing can also damage and break corals (Mangi and Roberts 2006) and reduce the types of suitable coralline algae substrate available for the settlement and growth of juvenile corals (O’Leary et al. 2012). Impacted colonies have to spend energy on tissue and skeleton repair, which can limit their ability to withstand and recover from climate-related stresses, such as coral bleaching and ocean acidification (Knowlton and Jackson 2008, Anthony et al. 2009, 2011, Carilli et al. 2009).

If coral reef state varies in relation to climate disturbance as depicted in Figure 6.2A, then two predictions arise. First, coral communities exposed to local or chronic disturbance should be more susceptible to climate change than less degraded, ‘pristine’ communities, and second, the combined impacts of local disturbances and global climate change should be either additive or synergistic, but definitely not antagonistic. We now briefly evaluate the empirical evidence for each prediction.

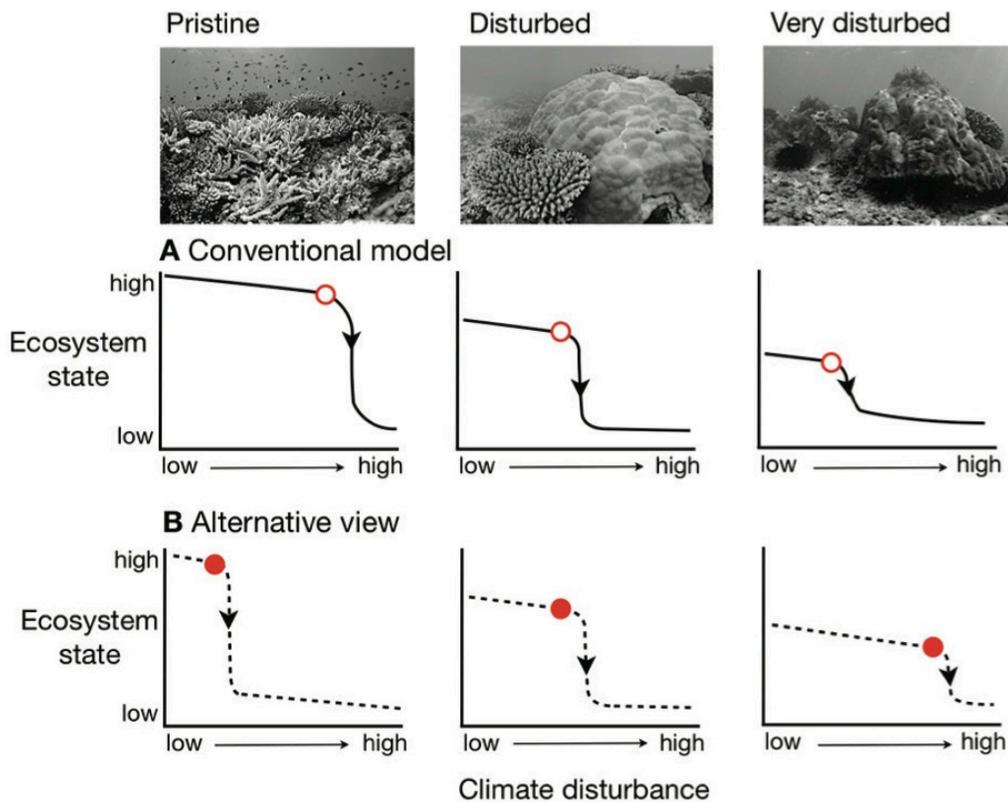


Figure 6.2. The relationship between ecosystem state and climate disturbance under conventional and alternative views of resilience. With the conventional view of resilience (A, solid lines), pristine, coral-rich reefs (left panel) are expected to tip into an alternative coral-poor state only at very high levels of climate disturbance. As coral reefs are increasingly degraded by chronic anthropogenic impacts (e.g., fishing, pollution, middle and right panels) the tipping points (open circles) are expected to shift to the left, such that disturbed reefs are less resistant to climate disturbance than pristine reefs. In an alternative view of resilience (B, dashed lines), pristine coral reefs (left panel) are dominated by sensitive species, which have a limited resistance to climate disturbance, which allows these reefs to tip very easily into an alternative coral-poor state. As human impacts remove these sensitive species from reefs (middle and left panels), the tipping points (solid circles) shift to the right, such that disturbed reefs are more resistant to climate change.

Prediction 1: Disturbed coral reefs are more susceptible to climate change

The conventional view of resilience assumes that disturbed coral communities are more susceptible to climate change than ‘pristine’ and undisturbed coral communities. The observation that thermally induced coral bleaching events are increasing in frequency and extent (McWilliams et al. 2005, Hoegh-Guldberg et al. 2007) on reefs that are globally degraded (Gardner et al. 2003, Bruno and Selig 2007) could be taken as

supporting evidence for the assumption that degraded reefs are more susceptible to climate change. However, this signal is confounded by increasing sea surface temperature anomalies over time (Hoegh-Guldberg et al. 2007, Hoegh-Guldberg and Bruno 2010). Thus, even in the absence of degradation caused by local stressors, more widespread and/or intense bleaching would be expected if the response of corals is directly related to temperature.

There are arguably no pristine coral reefs left in the world. However, reefs around remote, uninhabited islands, such as the northern Line Islands in the Central Pacific, may be as close to pristine as any reefs on Earth (Knowlton and Jackson 2008). These reefs boast extraordinary densities of sharks and other large predatory fishes and high coral abundance (Sandin et al. 2008), which reflect the lack of local anthropogenic pressures which are pervasive elsewhere. These reefs should be highly resistant to high-temperature events. Yet, the corals of Palmyra, the best studied of the northern Line Islands, can bleach as severely as more impacted reefs (e.g., in American Samoa, Fiji, and the Philippines), despite the fact that they experience similar temperature regimes (Oliver and Palumbi 2009). We agree with Knowlton and Jackson (2008) who state, “there are no data to suggest that corals become less vulnerable to bleaching with reduced local impacts”.

Prediction 2: Multiple stressors interact additively or synergistically on coral reefs

The second assumption of the conventional view of resilience is that global climate change will reinforce the negative impacts of existing local stressors through additive or synergistic interactions. There have been few empirical studies of how multiple stressors interact on coral reefs. Until recently, most were small-scale experiments carried out in the laboratory, they involved only two stressors, and most did not use the appropriate statistical techniques to reveal the interaction type unambiguously (Dunne 2010).

In one of the very few attempts at unraveling the nature of interactions between local and climate stressors on natural reefs, here in Chapter 3 and published as Darling et al. (2010), we evaluated the interaction between fishing and coral bleaching on coral cover using a long-term time series on Kenyan coral reefs. We found that both stressors influenced coral cover. A comparison of fished and unfished reefs prior to the 1998

mass bleaching event revealed that fishing on its own reduced coral cover by 51%, while a comparison of unfished reefs before and after the mass bleaching event suggested that the effect of bleaching was much larger, reducing coral cover by 74%. However, on reefs subjected to both stressors (i.e. post-bleaching, fished reefs), coral cover had declined by 72% on average, which was consistent with an antagonistic interaction, or a very weakly additive effect. This is not what the conventional view of coral reef resilience to climate change would have predicted.

An alternative view of resilience in a disturbed world

There is an alternative view of ecological resilience to multiple stressors, which suggests that degraded reefs may, in fact, be *more* rather than less resistant to climate disturbances (Côté and Darling 2010). This alternative outlook is predicated on the fact that disturbance-sensitive taxa are lost first following the impacts of local stressors, which can explain why more intact reef communities do not appear to be more resilient to climate disturbance. Local stressors can actually increase the relative abundance of disturbance-tolerant species within a community (Rachello-Dolmen and Cleary 2007, McClanahan et al. 2007, Cleary et al. 2008), and thus, the ability of an ecosystem to resist the impacts of climate disturbance.

Species are not lost randomly following disturbances (Srivastava and Velland 2005, Ives and Carpenter 2007, Bracken et al. 2008, Zavaleta et al. 2009). Instead, disturbed ecological communities tend to first lose species with stress-sensitive life histories. Community composition shifts as these stress-sensitive species are lost, leaving assemblages composed of stress-tolerant and opportunistic species that can rapidly colonize following a disturbance. Thus, the remaining community can be composed of 'survivor' stress-tolerant and weedy species, which can be expected to be as resistant, or even more resistant, to subsequent climate disturbances.

There is much evidence that such community shifts are occurring on coral reefs. Changes in the structure and composition of coral communities have been observed in the aftermath of diverse natural and anthropogenic disturbances, such as hurricanes and storms (Hughes and Connell 1999, Bak et al. 2005, Madin et al. 2008), pollution

(Rachello-Dolmen and Cleary 2007), sedimentation (McClanahan and Obura 1997, Aronson et al. 2004, Dikou and van Woesik 2006, Cleary et al. 2008, Jupiter et al. 2008), fishing (McClanahan 2008, Darling et al. 2010; Chapters 3 and 5), disease (Aronson et al. 2004) and outbreaks of coral predators (e.g., crown-of-thorns sea stars, Pratchett et al. 2009). In the Indo-Pacific region, disturbances have generally shifted coral communities from assemblages of stress-sensitive branching and plating corals, such as species of *Acropora* and *Montipora*, towards altered assemblages of stress-tolerant massive corals such as species of massive *Porites*, and faviids (e.g., *Cyphastrea*, *Favia*) (Loya et al. 2001, McClanahan et al. 2007, Rachello-Dolmen and Cleary 2007, Cleary et al. 2008). In the Caribbean, the primary reef-building corals *Acropora* and *Montastraea* species have been replaced by ‘weedy’ coral species that form small colonies, grow quickly and are short-lived (Knowlton 2001, Precht and Miller 2006). For example, the relative abundance of ‘weedy’ *Porites astreoides* has increased significantly over the past four decades (Green et al. 2008) as coral cover has declined – a sign of reef degradation – across the region (Gardner et al. 2003). Disturbed Caribbean reefs have also been shown to converge to communities dominated by *Agaricia*, whose opportunistic life history and high environmental tolerance have been suggested to explain its persistence on degraded reef habitats (Aronson et al. 2004).

The shift from stress-sensitive to stress-tolerant corals may make communities on disturbed reefs actually *more* resistant to bleaching and climate change. This alternative view of reef resilience is depicted in Figure 6.2B. Pristine or undisturbed communities are often dominated by disturbance-sensitive species that have limited resistance to climate stress and can tip into an alternative state at low levels of climate disturbance. When pristine reefs are exposed to the impacts of local stressors, their coral communities are altered towards a higher relative abundance of disturbance-tolerant species. Thus degradation can shift the tipping point in response to climate change to the right, resulting in disturbed ecosystems having a higher resistance to climate disturbance than pristine, unstressed reefs. This alternative view of resilience may, in part, depend on whether a species’ tolerance to a non-climatic disturbance is correlated with its tolerance to climatic impacts (e.g., positive co-tolerance, Vinebrooke et al. 2004). In Chapter 5, we show that while some species are co-tolerant to the impacts of two stressors, fishing and climate change, we did not find evidence for a general pattern of

community co-tolerance within Kenyan coral assemblages. Anecdotal evidence for patterns of species replacement on other reefs suggests future evaluations of the co-tolerance hypothesis are required (e.g., Côté and Darling 2010, Chapter 5).

The resistance of coral communities to climate change will likely be a dynamic process as coral species adapt and acclimatize to thermal stress. Such adaptation can occur if corals acquire heat-tolerant symbiotic zooxanthellae (Berkelmans and Van Oppen 2006) or through the adaptation of host coral populations. For example, coral communities in South East Asia that bleached severely during the 1998 mass bleaching event, were less impacted by a second bleaching event in 2010, both bleaching events were triggered by comparable temperature anomalies (Guest et al. 2012). What is remarkable is that some bleaching-sensitive corals, such as species of *Acropora* and *Pocillopora*, displayed more resistance to the successive bleaching event in 2010, possibly because of adaptation through natural – the loss of bleaching-susceptible individuals from the population in 1998 resulted in the survival and reproduction of bleaching-tolerant individuals that then increased the mean bleaching tolerance within the population in 2012 (Guest et al. 2012). It is unclear how generalizable these results are to other reefs and other coral species. Nonetheless it provides some hope that even some of the most vulnerable corals will be able to increase their resistance to future thermal stress and coral bleaching events.

The alternative view of resilience focuses on some of the earliest changes in coral communities, the replacement of stress-sensitive corals with stress-tolerant and weedy corals. Such initial changes in ecological communities may increase the resistance of coral communities to climate change. However, species losses and declines and patterns of community disassembly are not a single event, but a series of successive events that can reflect progressive and cascading losses in community and ecosystem function (Zavaleta et al. 2009). Even thermally-tolerant species will have limits which may be exceeded by future ocean warming and acidification (Hoegh-Guldberg et al. 2007). Overwhelming anthropogenic stressors may also precipitate the loss of even these hardy coral species and cause the replacement of coral communities with macroalgae, soft corals, seagrasses and/or sponges (McClanahan et al. 2002; Norström et al. 2008). Furthermore, disturbed coral communities and alternative non-coral systems may be unable to support the immense biodiversity and economic benefits

provided by intact coral reef ecosystems. A critical goal for coral reef conservation is therefore preserving coral populations and the reef architecture that supports reef-associated organisms and services, but how to do this will depend on reef resilience to the cumulative impacts of local stressors and climate change.

Implications for conservation and management

Increasing the resilience of coral reefs to climate change is a critical challenge for conservation and management. Local stressors are expected to erode the ability of coral reefs to withstand climate change (Hughes et al. 2003, 2010, Knowlton and Jackson 2008). It is perhaps not surprising then that removing local stressors to increase resilience to climate change has emerged as a strong focus of coral reef management, perhaps more so than for any other ecosystem.

The conventional view of resilience suggests that removing local stressors and reducing human impacts should increase the ability of coral reefs to withstand climate change (e.g., Hughes et al. 2010). As ecosystems are degraded by anthropogenic stressors and transition from pristine to disturbed to very disturbed states, management that seeks to control local stressors and reverse degradation is therefore expected to increase resistance by shifting the tipping point back to the right and keeping reefs further away from such tipping points (Figure 6.2A). One of the most popular ways that has been suggested to increase resilience to climate change is through the use of marine reserves, or Marine Protected Areas (MPAs) (Hughes et al. 2003, 2010, Bellwood et al. 2004, Mora et al. 2006, Hoegh-Guldberg et al. 2007). Marine protected areas are a form of spatial management that seeks to control local stressors, primarily fishing. Integrated land and sea conservation efforts that target terrestrial activities adjacent to MPAs may also reduce coastal runoff and the amount of nutrient and sediment pollution that reaches coral reefs (Álvarez-Romero et al. 2011), but these are still relatively uncommon.

MPAs have been shown to have positive effects on the abundance and diversity of a variety of fish and invertebrates within their boundaries (Halpern 2003; Graham et al. 2011a). Many reserves, but not all, have increased coral cover (McClanahan 2008,

Selig and Bruno 2010, Darling et al. 2010; Chapter 3), coral species diversity (McClanahan 2008; Chapter 5) and coral recruitment (Mumby et al. 2007b), with concomitant declines in macroalgae and seaweeds (Mumby et al. 2007b, McClanahan 2008; Mumby and Harborne 2010). Such benefits provided to coral reef communities are an indirect result of protecting fish populations from fisheries. In particular, the protection and recovery of populations of herbivorous fishes (e.g., parrotfishes and surgeonfishes) can maintain a variety of critical ecosystem functions, such as bioerosion which exposes the reef matrix for coralline algae and juvenile corals, and scraping and grazing, which removes algae, leading to higher coral cover and coral recruitment (Elmqvist et al. 2003, Bellwood et al. 2004, Mumby et al. 2007a,b; O'Leary & McClanahan 2010; O'Leary et al. 2012). Healthy populations of herbivorous reef fishes can reinforce positive feedbacks that promote coral recruitment and healthy coral cover within MPAs, while the loss of herbivores can keep reefs in a coral-poor and unhealthy state (Mumby and Steneck 2008). The higher species and functional diversity on protected reefs can provide ecological insurance and functional redundancy, both of which are expected to increase resilience to large-scale disturbances, such as climate change (Loreau et al. 2003, Nyström et al. 2008).

However, any positive effects of MPAs on the resilience of corals to climate change may be unintentional. MPAs were designed to target local-scale impacts of anthropogenic stressors and not the global-scale impacts of climate change (Mumby and Steneck 2008; Hughes et al. 2010). There is no evidence that marine reserves are located in areas that are less likely to get hot according to current predictions of climate change (Maina et al. 2008), nor is there any expectation that marine reserves will alleviate the impacts of ocean acidification on corals (Mumby and Steneck 2008). Thus it is probably not surprising that marine reserves do not reduce the frequency or intensity of thermally induced coral bleaching (Hughes et al. 2003, Coelho and Manfrino 2007, Mumby and Steneck 2008) or bleaching-induced coral mortality (Chapter 3; Graham et al. 2008, Darling et al. 2010, Selig et al. 2012). It is even more sobering that the impacts of climate change can, in a single bleaching event, override years of coral recovery within MPAs (Chapter 3; Darling et al. 2010, Selig and Bruno 2010).

Why are corals within MPAs not protected from coral bleaching? Why do they in fact often experience greater mortality following bleaching than corals on unprotected reefs

(Chapter 3; Graham et al. 2008, Darling et al. 2010)? The vulnerability of protected corals to thermal stress and bleaching could reflect the higher initial coral cover within MPAs: when disturbance strikes, there is simply more coral to lose (Graham et al. 2008, 2011). However, this is unlikely to be the whole story. The types of corals fostered by MPAs are often very sensitive to disturbance and thus it may not be only about how *much* coral can be lost, but how *easily* it can be lost (Chapters 3 and 5; Darling et al. 2010). Notably, there is often a higher abundance of thermally sensitive corals, such as species of *Acropora* and *Montipora*, within marine reserves, leading to increased susceptibility of protected coral assemblages to climate disturbances (Chapters 5, McClanahan et al. 2007b,c, McClanahan 2008). These differences in the types of corals and composition of coral assemblages between protected and unprotected reefs could be due to an initial bias in site selection, whereby less degraded coral reefs with higher diversity of coral species are favoured as sites where MPAs are established. There are few old and effectively enforced MPAs with pre-protection baseline data to evaluate the potential effects of site bias. However, in Kenya where data do exist for one MPA prior to protection, we found that there were no differences in coral cover between the incipient MPA and fished reefs surveyed in the same year, suggesting that the effects of protection on resilience, at least in some MPAs, can be independent of bias associated with habitat selection (Chapters 3 and 5, see also Selig and Bruno 2010). At such sites, protection itself, by eliminating destructive fishing and restoring fish populations, may also favour the ecological succession of competitively dominant branching and plating corals that may be extremely sensitive to climate disturbances (Chapter 5).

In Chapters 3 and 5, we make the observation that coral assemblages within MPAs are disproportionately vulnerable to coral bleaching and climate change. This is consistent with the alternative view of resilience, which holds that managing local stressors in order to return ecosystems to a more pristine state may actually *increase* their vulnerability to climate disturbances. Thus, the effect of management action that seeks to control local anthropogenic disturbances and move communities back from a disturbed to a pristine state may inadvertently shift the tipping point back to the left by recovering pristine assemblages of disturbance-sensitive species (Figure 6.2B). The ultimate result may be to compromise the resistance of protected reefs to climate disturbances.

The cynical interpretation of the alternative view of resilience is that, if degraded reefs are likely to weather the impacts of climate change, then we should allow degradation by local stressors to proceed. This would be extremely short sighted and our alternative view of resilience certainly does not advocate against the value of MPAs. Marine Protected Areas provide diverse and unparalleled benefits to biodiversity and ecosystem function on coral reefs (Halpern 2003; reviewed in Graham et al. 2011a). The alternative view of resilience is instead a call to action for local management that is climate smart.

Three ways to manage coral reefs in the face of climate change

What are the options for managing coral reefs in the face of climate change if the alternative view of resilience applies? In other words, how can management foster increased resistance of coral reefs to climate change if the conventional approach of controlling local stressors is not effective? One explanation for why MPAs have not buffered coral reefs from climate change is because of the current way they are designed (Selig et al. 2012). We can suggest three strategic ways that might help management to mitigate the effects of ocean warming and subsequent bleaching on coral reefs.

First, the placement of MPAs should be strategic with respect to predictions of future warming and thermal stress. The location of MPAs is too often the result of socio-political compromise and too seldom based on scientific advice. Spatial planning must take into account the fact that warming is predicted to occur heterogeneously across the seascape. Not all areas of the world's oceans will warm equally (Maina et al. 2008, 2011) and yet few MPAs are designed to take advantage of naturally cool conditions that can avoid the worst impacts of coral bleaching. For example, only two out of 61 managed coral reefs in the Western Indian Ocean are located in areas of low climate susceptibility (Maina et al. 2008). Finding and predicting 'cold spots' where MPAs will experience less thermal stress will be critical for the survival of coral biodiversity. Some areas, such as the northwest Caribbean and northern Madagascar and southern Tanzania in the western Indian Ocean, are expected to be exposed to low levels of climate stress (McClanahan et al. 2007b,c, Maina et al. 2011). It is therefore imperative to target these climate 'cold spots' for protection (West and Salm 2003, Mumby and

Steneck 2008). This will be difficult because it means that MPA planning at the national scale may no longer be relevant. Instead, regional, trans-boundary coordination will be needed to identify priority areas and effectively protect them. Moreover, countries near climate 'cold spots' may have to bear the opportunity costs associated with MPA establishment, such as the loss of fishing grounds, to generate conservation benefits at the regional scale. These inequalities may call for a reassessment in the way MPAs are funded in order to shift the financial burden from national to regional pockets (e.g., Balmford et al. 2004).

Second, MPA design must become adaptive. By this, we mean that the size, shape and location of MPAs can be changed in response to new information. Flexible boundaries would allow MPAs to track the changing regimes and impacts of thermal stress and climate change (Maina et al. 2011). Corals have one of the fastest rates of poleward range expansion in response to climate change and range shifts have been observed to be as fast as 14 km/year (Yamano et al. 2011). Moving-target MPAs could therefore be used to protect novel coral assemblages as their range limits expand or contract with climate change (Hobday 2011). MPA networks may also facilitate the maintenance of connectivity even with the impacts of climate change (Mumby et al. 2010, McLeod et al. 2011). It is widely held that MPAs work best when embedded in a web of protected areas, which are interconnected to various degrees by the exchange of nutrients, eggs, juvenile and adult organisms that disperse with currents or actively migrate (WCPA/IUCN 2007). Patterns of connectivity are very likely to be altered by climate change, which will alter currents and accelerate temperature-dependent processes such as larval development (O'Connor et al. 2007). However, actually implementing climate-tracking MPAs would require a major overhaul of the legislative process leading to MPA designation, which in most places moves at glacial speeds.

Third, bigger may be better when it comes to MPAs. There is strong enthusiasm for the establishment of 'mega-MPAs' (e.g., Knowlton and Jackson 2008, Sheppard et al. 2012). Some recently established MPAs in the Pacific and Indian Oceans are very large indeed. The Chagos Archipelago, for example, is the world's largest MPA and covers more than 550,000 km², which is larger than France or the state of California (Sheppard et al. 2012). Large MPAs can provide important baselines for what nearly intact coral reef systems look like and how they function (Knowlton and Jackson 2008). However, it

is unclear whether such 'pristine' baselines will be informative for understanding the dynamics of degraded reefs or if it is even possible to return severely degraded reefs to a state approaching these gold standards. Nevertheless, the main potential advantage of very large MPAs in terms of bolstering resistance to climate change is that not all reefs within them may be affected by acute climatic disturbances. Owing to their sheer size, mega-MPAs may well encompass climatic 'cold spots' provided by upwelling and other local oceanographic conditions (e.g., West and Salm 2003). Also, given the average size of most thermal anomalies, it is more likely that some areas within very large MPAs will escape thermal stress and bleaching anomalies (Selig et al. 2012). If large MPAs can provide a bleaching refuge to coral populations, this may give corals a chance to adapt through the natural selection of thermally-tolerant symbionts and coral hosts (Berkelmans and Van Oppen 2006, Guest et al. 2012). Finally, large MPAs will also hold, in absolute terms, larger populations of stress-resistant corals than smaller MPAs.

Managing for resistance versus recovery

Even if protection does not usually enhance reef resistance to climate change, protection may provide substantial benefits for other facet of resilience: recovery. Many ecosystems have the capacity to recover from catastrophic disturbances. Large and infrequent pulse disturbances are the 'usual state of affairs' and in the past, they did not override the eventual recovery of ecosystems (Paine et al. 1998). For example, historical cyclones occur every decade or so on reef crests of the Great Barrier Reef and are considered 'normal' events that, until recently, did not provoke shifts to an alternative and undesirable macroalgal-dominated state (Hughes et al. 2010). This is likely because historical reefs were in a more pristine condition and able to bounce back following even large-scale natural disturbances. However, there is grave concern (and some empirical evidence) that the increasing scale of anthropogenic stressors is limiting the ability of ecosystems to recover from natural cycles of disturbance. For example, coral reefs along the Mesoamerican Barrier Reef in Belize and Honduras that had experienced more anthropogenic stress recovered more slowly, in terms of coral growth rates, from the 1998 bleaching event than less impacted reefs (Carilli et al. 2009). Similarly, the pristine and isolated reefs of Kingman and Palmyra in the Line Islands had higher rates of recovery following warm water and coral bleaching events than the more disturbed

coral reefs of nearby Kiritimati and Tabuaeran, which are inhabited by people (Sandin et al. 2008).

MPAs are expected to increase coral recovery by maintaining the diversity of reef fish species and functional groups, particularly herbivorous fishes that can graze algae and facilitate the recruitment of juveniles corals (Bellwood et al. 2004, Mumby et al. 2007, Hughes et al. 2010). The evidence for better recovery following bleaching events within MPAs is still equivocal, but hopeful. Studies of reefs in the Bahamas (Mumby and Harborne 2010) and Indian Ocean (Ateweberhan et al. 2011) have found greater rates of recovery of live coral cover within MPAs than on unprotected reefs. However, studies of MPAs from around the world (Selig and Bruno 2010) and MPAs within Kenya (Chapter 3) and the western Indian Ocean (Graham et al. 2008) have found no evidence of higher recovery rates of coral cover within MPAs, and in some cases, coral recovery can be significantly slower in MPAs than on unprotected reefs (Graham et al. 2011a,b). MPAs, especially older ones, can nevertheless be effective at preventing further coral losses that are occurring on more disturbed reefs, although any benefit of this protection can be wiped out following bleaching (Chapter 5; Selig and Bruno 2010, Selig et al. 2012). Overall, the effects of MPAs on coral recovery are strongly context-dependent and differ across regions, the type of disturbance and the amount of post-disturbance coral cover (Graham et al. 2011a,b). The species composition of the remaining coral community can also affect recovery as fast-growing, opportunistic genotypes or species will recover more quickly than slower-growing corals (Chapter 5; Selig and Bruno 2010). It would be interesting in this context to see whether the fast-growing taxa that promote reef recovery are robust or sensitive to climate disturbances. In Chapter 5, we identified fast-growing corals on fished reefs as having a 'weedy' life history on Kenyan coral reefs, which were sensitive to climate disturbances with a 'boom and bust' population dynamic. Stress-tolerant taxa were generally less sensitive to coral bleaching than the other three life histories, but still declined after bleaching. Thus without substantial adaptation and acclimation (e.g. Guest et al. 2012), the impacts of climate change may exceed the physiological limits of scleractinian corals (Hoegh-Guldberg et al. 2007).

When considering the increasingly stressful future for most ecosystems, it is imperative to clearly define and distinguish 'resistance' and 'recovery' as two processes of the more general term, 'resilience'. While the main focus of management has been on recovery,

finding ways to bolster resistance may be as important, if not more important, than facilitating recovery in the years ahead. For example, future projections of climate change predict that bleaching-inducing thermal anomalies will become more frequent (Hoegh-Guldberg et al. 2007, Donner et al. 2009), which will shrink the available window of coral recovery in between bleaching events. Perhaps this window is already too small, as many coral reefs have failed to recover even after more than a decade following the 1998 worldwide mass coral bleaching event (Graham et al. 2011a,b). Furthermore, it is unclear if there will be any potential for recovery to chronic climate stressors, such as globally increasing average sea surface temperatures and the rising acidity of the world's oceans.

Conclusions

The cumulative impacts of climate change and local human impacts of overfishing, pollution threaten the diversity, ecological function and ecosystem services provided by coral reefs to millions of people around the world. Such ongoing and unprecedented changes, particularly the two faces of climate change – ocean warming and acidification – are creating a 'brave new ocean' with wide-reaching ecological consequences (Jackson 2008). Finding workable solutions is not easy and it is important to remember that any successful conservation initiative will require the support of local communities. The best opportunities for success may be to try many different tactics of conservation and management in order to hedge our bets as we identify a portfolio of actions that will have the most success at maintaining the ecological and socio-economic services of marine ecosystems.

Strategic local conservation and management actions will hopefully buy us some time for globally supported initiatives to control the drivers of climate change. Marine Protected Areas, and other forms of local land and sea management, are important tools to manage coral reefs, but they will need to be climate-ready and climate-smart. If MPAs can protect large areas of critical habitat and are placed in areas of the ocean that are the most likely to escape the full force of climate change, coral reefs may stand a fighting chance. Identifying climate-resistant 'survivor' species (e.g., Chapter 5) and reefs that are able to survive climate change will be equally important as we expand our focus of

resilience-based management to include both resistance and recovery. However, local conservation and management actions will likely never be the silver bullet that can single-handedly protect ecosystems against the onslaught of current and future climate change, particularly the unparalleled threat of ocean acidification.

The continuing degradation of coral reefs from climate change and other human impacts is an invaluable warning for other ecosystems around the world. Coral reefs are likely to be one of the first ecosystems to reach a tipping point of cumulative impacts.

Understanding, quantifying and managing for multiple stressors on coral reefs can provide a benchmark for other ecosystems. Ecosystem-based management actions and policies that explicitly consider, evaluate and adapt for interactions between stressors are immediately needed. We believe there is hope for the future of coral reef ecosystems and the millions of people who depend on the resources provided by coral reefs every day. However, in addition to managing local impacts, it is critical that we tackle the root cause of planetary change, global carbon dioxide emissions, to guarantee that future generations can benefit from the “surpassing beauty...and wonders of a coral sea” (Wallace 1869).

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Appendices

Appendix A.

Supporting material for Chapter 2

Information on the studies included in the meta-analysis. Part A: The 57 experiments within the dataset that reported information about standard deviation that were able to be classified as synergistic, additive or antagonistic. Experiments are ordered from strongest effect to weakest effect within each interaction group by the difference between observed combined-stressor log ratio and the predicted additive log ratio. Part B: The remaining 55 experiments did not report standard deviation and were unable to be classified by interaction. Experiments are sorted alphabetically by lead author.

A. Reference	No. experiments	Organism	Species	Stressors	Interaction
Peachey 2005	9	Crab	<i>Libinia dubia</i>	UV x Pollutant	Synergy
Peachey 2005	9	Crab	<i>Libinia dubia</i>	UV x Pollutant	Synergy
Peachey 2005	9	Crab	<i>Callinectes sapidus</i>	UV x Pollutant	Synergy
Peachey 2005	9	Crab	<i>Callinectes sapidus</i>	UV x Pollutant	Synergy
Long et al. 1995	1	Amphibian	<i>Rana pipens</i>	pH x UV	Synergy
Peachey 2005	9	Crab	<i>Panopeus herbstii</i>	UV x Pollutant	Synergy
Bonsdorff et al. 1995	2	Clam	<i>Macoma balthica</i>	Predation x Sedimentation	Synergy
Peachey 2005	9	Crab	<i>Panopeus herbstii</i>	UV x Pollutant	Synergy
Peachey 2005	9	Crab	<i>Callinectes sapidus</i>	UV x Pollutant	Synergy
Peachey 2005	9	Crab	<i>Callinectes sapidus</i>	UV x Pollutant	Synergy
Boone et al. 2007	3	Amphibian	<i>Ambystoma maculatum</i>	Pollutant x Competition	Synergy
Peachey 2005	9	Crab	<i>Menippe adina</i>	UV x Pollutant	Synergy
Bonsdorff et al. 1995	2	Clam	<i>Macoma balthica</i>	Predation x Sedimentation	Synergy
Przeslawski et al. 2005	24	Gastropod	<i>Bembicium nanum</i>	UV x Salinity	Synergy
Pahkala et al. 2002	2	Amphibian	<i>Rana temporaria</i>	pH x UV	Synergy
Przeslawski et al. 2005	24	Gastropod	<i>Bembicium nanum</i>	UV x Salinity	Synergy
Przeslawski et al. 2005	24	Gastropod	<i>Siphonaria denticulata</i>	Thermal stress x Salinity	Synergy
Przeslawski et al. 2005	24	Gastropod	<i>Bembicium nanum</i>	Thermal stress x Salinity	Synergy
Przeslawski et al. 2005	24	Gastropod	<i>Siphonaria denticulata</i>	Thermal stress x Salinity	Synergy
Przeslawski et al. 2005	24	Gastropod	<i>Siphonaria denticulata</i>	UV x Salinity	Synergy
Kawai & Tokeshi 2007	6	Mussel	<i>Septifer virgatus</i>	Thermal stress x Wave action	Additive
Hojer et al. 2001	1	Collembolan	<i>Folsomia candida</i>	Pollutant x Drought	Additive
Kawai & Tokeshi 2007	6	Mussel	<i>Septifer virgatus</i>	Thermal stress x Wave action	Additive
Relyea 2003	6	Amphibian	<i>Rana clamitans</i>	Pollutant x Predation	Additive
Relyea 2003	6	Amphibian	<i>Hyla versicolor</i>	Pollutant x Predation	Additive
Relyea 2003	6	Amphibian	<i>Rana pipens</i>	Pollutant x Predation	Additive
Relyea 2003	6	Amphibian	<i>Rana catesbeiana</i>	Pollutant x Predation	Additive
Kawai & Tokeshi 2007	6	Mussel	<i>Septifer virgatus</i>	Thermal stress x Wave action	Additive
Boone et al. 2007	3	Amphibian	<i>Ambystoma maculatum</i>	Pollutant x Competition	Additive
Relyea 2003	6	Amphibian	<i>Bufo americanus</i>	Pollutant x Predation	Additive
Relyea 2006	3	Amphibian	<i>Rana catesbeiana</i> & <i>R. clamitans</i>	pH x Predation	Additive
Relyea 2006	3	Amphibian	<i>Rana catesbeiana</i> & <i>R. clamitans</i>	Pollutant x Predation	Additive
Relyea 2006	3	Amphibian	<i>Rana catesbeiana</i> & <i>R. clamitans</i>	Pollutant x Predation	Additive
Przeslawski et al. 2005	24	Gastropod	<i>Dolabrifera brazieri</i>	UV x Salinity	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Siphonaria denticulata</i>	UV x Salinity	Antagonism
Boone & Semitsch 2003	1	Amphibian	<i>Rana catesbeiana</i>	Pollutant x Predation	Antagonism
Boone et al. 2007	3	Amphibian	<i>Ambystoma maculatum</i>	Pollutant x Pollutant	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Dolabrifera brazieri</i>	Thermal stress x Salinity	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Dolabrifera brazieri</i>	Thermal stress x UV	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Bembicium nanum</i>	Thermal stress x Salinity	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Siphonaria denticulata</i>	Thermal stress x UV	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Dolabrifera brazieri</i>	Thermal stress x Salinity	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Dolabrifera brazieri</i>	UV x Salinity	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Dolabrifera brazieri</i>	Thermal stress x Salinity	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Bembicium nanum</i>	Thermal stress x UV	Antagonism
Pahkala et al. 2002	2	Amphibian	<i>Rana temporaria</i>	pH x UV	Antagonism
Boone & Bridges-Bitton 2006	3	Amphibian	<i>Hyla versicolor</i>	Pollutant x Pollutant	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Siphonaria denticulata</i>	Thermal stress x Salinity	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Bembicium nanum</i>	Thermal stress x UV	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Dolabrifera brazieri</i>	Thermal stress x Salinity	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Siphonaria denticulata</i>	Thermal stress x Salinity	Antagonism
Boone & Bridges-Bitton 2006	3	Amphibian	<i>Hyla versicolor</i>	Pollutant x Pollutant	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Bembicium nanum</i>	Thermal stress x Salinity	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Dolabrifera brazieri</i>	Thermal stress x UV	Antagonism
Boone & Bridges-Bitton 2006	3	Amphibian	<i>Hyla versicolor</i>	Pollutant x Pollutant	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Siphonaria denticulata</i>	Thermal stress x UV	Antagonism
Przeslawski et al. 2005	24	Gastropod	<i>Bembicium nanum</i>	Thermal stress x Salinity	Antagonism

B. Reference	No. experiments	Organism	Species	Stressors
Baud & Beck 2005	1	Amphibian	<i>Pseudacris crucifer</i>	UV x Pollutant
Boone & James 2003	1	Amphibian	<i>Rana sphenoccephala</i>	Pollutant x Competition
Boone et al. 2005	1	Amphibian	<i>Rana clamitans</i>	Pollutant x Pollutant
Chen et al. 2004	4	Zooplankton	<i>Simocephalus vetulus</i>	Pollutant x Food stress
Chen et al. 2004	4	Zooplankton	<i>Simocephalus vetulus</i>	pH x Pollutant
Chen et al. 2004	4	Amphibian	<i>Rana pipiens</i>	Pollutant x Food stress
Chen et al. 2004	4	Amphibian	<i>Rana pipiens</i>	pH x Pollutant
Chu & Chow 2002	3	Nematode	<i>Caenorhabditis elegans</i>	Pollutant x Pollutant
Chu & Chow 2002	3	Nematode	<i>Caenorhabditis elegans</i>	Pollutant x Pollutant
Chu & Chow 2002	3	Nematode	<i>Caenorhabditis elegans</i>	Pollutant x Pollutant
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulex</i>	Thermal stress x Pollutant
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulex</i>	Thermal stress x Food stress
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulex</i>	Pollutant x Food stress
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulicaria</i>	Thermal stress x Pollutant
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulicaria</i>	Thermal stress x Food stress
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulicaria</i>	Pollutant x Food stress
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulex</i>	Thermal stress x Pollutant
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulex</i>	Thermal stress x Food stress
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulex</i>	Pollutant x Food stress
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulicaria</i>	Thermal stress x Pollutant
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulicaria</i>	Thermal stress x Food stress
Folt et al. 1999	12	Zooplankton	<i>Daphnia pulicaria</i>	Pollutant x Food stress
Kawai & Takeshi 2007	6	Mussel	<i>Septifer virgatus</i>	Thermal stress x Wave action
Kawai & Takeshi 2007	6	Mussel	<i>Septifer virgatus</i>	Thermal stress x Wave action
Kawai & Takeshi 2007	6	Mussel	<i>Septifer virgatus</i>	Thermal stress x Wave action
Macias et al. 2007	3	Amphibian	<i>Rana perezii</i>	UV x Pollutant
Macias et al. 2007	3	Amphibian	<i>Rana perezii</i>	UV x Pollutant
Macias et al. 2007	3	Amphibian	<i>Bufo bufo</i>	UV x Pollutant
Metts et al. 2005	1	Amphibian	<i>Ambystoma maculatum, A. opacum</i>	Pollutant x Competition
Relyea 2003	6	Amphibian	<i>Rana sylvatica</i>	Pollutant x Predation
Relyea 2005	4	Amphibian	<i>Hyla versicolor, Rana pipiens, Bufo americanus</i>	Pollutant x Competition
Relyea 2005	4	Amphibian	<i>Hyla versicolor, Rana pipiens, Bufo americanus</i>	Pollutant x Pollutant
Relyea 2005	4	Amphibian	<i>Hyla versicolor, Rana pipiens, Bufo americanus</i>	Pollutant x Predation
Relyea 2005	4	Amphibian	<i>Hyla versicolor, Rana pipiens, Bufo americanus</i>	Pollutant x Predation
Roe et al. 2006	1	Amphibian	<i>Ambystoma talpoideum</i>	Pollutant x Competition
Shaw et al. 2006	20	Zooplankton	<i>Daphnia ambigua</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia ambigua</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia ambigua</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia ambigua</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia ambigua</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Ceriodaphnia dubia</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Ceriodaphnia dubia</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Ceriodaphnia dubia</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Ceriodaphnia dubia</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Ceriodaphnia dubia</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia pulex</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia pulex</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia pulex</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia pulex</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia magna</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia magna</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia magna</i>	Pollutant x Pollutant
Shaw et al. 2006	20	Zooplankton	<i>Daphnia magna</i>	Pollutant x Pollutant

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Appendix B.

Supporting material for Chapter 4

B.1. Description of reef coral life-history traits and literature searches

We collected trait information for 847 scleractinian corals, comprising 101 western Atlantic and Caribbean species and 746 Indo-Pacific species. This information came from 236 sources, including taxonomic monographs, regional identification guides, published literature, secondary sources and online databases (see Table B.1). To search the published literature, we used *Scopus* and *ISI Web of Science* online databases and checked the reference lists of identified studies in an attempt to find all relevant literature. Search terms used for each trait are detailed below. While coral species in the Atlantic and Indo-Pacific regions have unique taxonomic compositions resulting from distinct geological and ecological histories, we combined them in a single analysis since our goal was to evaluate global patterns in reef coral life histories

Regional and depth distribution

The **regional distribution** of species (Atlantic or Indo-Pacific) was derived from taxonomic monographs (Veron and Pichon 1976, Veron et al. 1977, Veron and Pichon 1980, Veron and Pichon 1982, Veron and Wallace 1984) and identification guides (Veron 1993, Veron 2000, Humann and Deloach 2001). We defined the **depth distribution** as the median depth range reported for each species in the IUCN Red List assessment for global reef-building corals (Carpenter et al. 2008). We hypothesized that species with deeper median depth ranges would be more adapted to chronically stressful conditions (e.g., low light) than corals with shallower depth distributions.

Morphology

Colony growth form was assessed following descriptions, drawings and photographs from taxonomic monographs (Veron and Pichon 1976, Veron et al. 1977, Veron and Pichon 1980, 1982, Veron and Wallace 1984) and identification guides (Veron 1993, Veron 2000, Humann and Deloach 2001). Growth forms were classified as branching, plating and/or domed. Domed morphology includes encrusting, submassive and massive colony growth forms. We hypothesized that branching species are good competitors for space and light on coral reefs, while plating and domed taxa are subdominant competitors more adapted to environments subject to stress and/or disturbance. Each of the three growth forms coded separated as a binary characteristic, where '0' indicates the species does not show the morphology and '1' indicates the species displays the morphology. Classifying colony growth form as three separate binary traits allowed us to assign more than one growth form to each species, since many species display more than one growth form (e.g., species that show both branching and plating morphologies). When calculating the Gower dissimilarity index across all the species traits, the three binary traits of colony morphology were 'down-weighted' such that each column was weighted by 0.33 to avoid biasing the dissimilarity matrix (Laliberté and Legendre 2010).

Corallite size was described by the widest diameter of a corallite (cm) and derived from taxonomic monographs (Veron and Pichon 1976, Veron et al. 1977, Veron and Pichon 1980, 1982, Veron and Wallace 1984), identification guides (Veron 1993, Veron 2000, Humann and Deloach 2001) and surveys of the literature (see Table S1). For online literature searches in *Web of Science* and *Scopus*, we used the search terms [corallite* and (diameter or size)]. Corallite size is an indicator of energy storage of individual coral polyps and we hypothesized that species with

larger corallites can store more energy to persist in more harsh environments than species with smaller corallites.

Colony size was evaluated as the maximum reported colony size from taxonomic monographs (Veron and Pichon 1976, Veron et al. 1977, Veron and Pichon 1980, Veron and Pichon 1982, Veron and Wallace 1984) and identification guides (Veron 1993, Veron 2000, Humann and Deloach 2001). Maximum colony size was determined as the maximum diameter (cm) of living tissue reported for each species. When maximum colony size was not reported in taxonomic monographs or identification guides, we obtained maximum colony sizes from the literature (see Table S1). Our search terms were [coral* and colon* and size*]. We only included studies that had randomly surveyed colonies and reported size distributions by species, we recorded the largest observed individual of each species as an estimate of maximum colony size. We hypothesized that species with larger maximum colony sizes would have more available energy (i.e., more coral polyps) to persist in non-ideal conditions, and that larger colonies would be more likely to experience partial mortality associated with stress and/or disturbance as compared to total colony mortality that may be experienced by species with smaller colonies.

Reproduction

We classified the **reproductive mode** of species as brooders or broadcast spawners based on a global review (Baird et al. 2009). We hypothesized that broadcast spawners could be limited by low population sizes (i.e., Allee effects, Knowlton et al. 2001) following mortality and disturbance, while brooders have the potential to self-fertilize (Baird et al. 2009), which may promote recovery on disturbed reefs. Brooding and broadcast spawning were coded as two binary traits (0 indicates species does not display trait, 1 indicates species displays trait). Thus a handful of species with mixed reproduction (e.g., *Pocillopora damicornis*, *Goniastrea aspera*, *Porites cylindrica*) were classified as having a '1' in both the brooding and broadcast spawning columns. When calculating the Gower dissimilarity index, each of the two binary states were weighted by 0.5 to avoid biasing the dissimilarity matrix (Laliberté and Legendre 2010).

Reproductive output (fecundity) was measured as the number of eggs per polyp and based on an extensive survey of the literature (see Table B.1). For massive colonies where mesenteries can hold several polyps, fecundity was assessed as the number of eggs per mesentery. Our search terms were [coral* and (fecund* or egg* or polyp*)]. Species with high fecundity were hypothesized to be better able to persist and/or recover from conditions of stress and disturbance than species with less fecundity.

Generation length (years) was defined as the average age of parents or mature individuals and used as a timeframe to assess the reproductive capacity and life span of coral species, data on generation length for coral species were taken from an IUCN Red List expert assessment for reef-building corals (Carpenter et al. 2008). We hypothesized that longer-lived species can tolerate more stressful environments than shorter-lived species that may have a 'boom and bust' opportunistic life-history strategy adapted to recovery following disturbances.

Growth rates

Growth rate and **skeletal density** were evaluated based on an extensive survey of the literature (see Table B.1). **Growth rate** was defined as the annual rate of linear extension (mm year^{-1}), which was the most common growth rate metric reported in the literature. Our search terms were [coral* and growth or extension]. We hypothesized that faster growing species are better competitors and could also recover from disturbances faster than slower-growing species, which might be better able to persist under stressful conditions. **Skeletal density** was defined in weight of calcium carbonate per unit colony volume ($\text{g CaCO}_3 \text{ cm}^{-3}$), which was the most commonly reported metric of skeletal density. Our search terms were [coral* and (skeletal* or densit*)]. We hypothesized that species with denser skeletons would be less vulnerable to damage from

disturbances, such as storms, while species with less dense skeletons would be more vulnerable to breakage and colony damage.

As growth rate and skeletal density have been recorded to change with environmental conditions, we recorded the year for which these metrics were measured (1790-2007 for growth rate, 1350-2008 for skeletal density). For studies that reported data from multiple years, we used the midpoint year of the study and we used the year of publication for studies that did not report the year(s) of data collection. For each study, we calculated the mean growth rate or skeletal density for each species and fit a general linear model between time (year) and growth rate or skeletal density. We found no effect of survey year on growth form ($t_{df=274} = -1.20$, $P = 0.23$) or skeletal density ($t_{df=104} = 1.31$, $P = 0.19$), indicating that the data included in our study were not biased by sampling date.

Symbiont diversity

Coral growth and survival depend on an endosymbiotic relationship between the coral host and photosynthetic dinoflagellate algae (*Symbiodinium* spp.) (Muscatine et al. 1981). The diversity and identity of symbionts can affect the resilience of reef corals to thermal stress (Rowan 2004, Berkelmans and Van Oppen 2006, Jones et al. 2008). Nine divergent *Symbiodinium* clades have been described, although sub-clade diversity is generally recognized as more accurate than clade diversity to describe the flexibility of the coral–*Symbiodinium* association (Stat et al. 2011). In the present study, **symbiont diversity** was evaluated from a global database of sub-clade *Symbiodinium* 18s, 28s, cp23s, Internal Transcribed Spacer-1 (ITS-1) and Internal Transcribed Spacer-2 (ITS-2) genotypes associated with 357 reef coral species (48 Atlantic taxa, 309 Indo-Pacific taxa, T. Oliver, unpublished data, for references see Table B.1).

We used genotypic richness as an indicator of the number of *Symbiodinium* ‘types’ (or ‘species’) associated with each reef coral species. We hypothesized that ‘flexible’ coral species that associate with more genotypes of *Symbiodinium* would be able to persist in a wider variety of environments than ‘specialist’ reef corals associated with fewer *Symbiodinium* genotypes. However, estimates of *Symbiodinium* richness strongly depend on sampling effort, thus we simulated a semi-log rarefaction curve between the number of samples and subclade richness for each coral species. We report the average slope (m) of this curve for each species based on 100 bootstraps as an estimate of *Symbiodinium* richness given the effort of sampling. Larger m -values indicate that the coral species can associate with more diverse symbiont communities than species with smaller m -values.

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Table B.1. Source references (N = 225) for species trait information of 143 global coral species. Numbers refer to the reference list below. Information on solitary colony formation is included within growth form. Region indicates Atlantic (Atl) or Indo-Pacific (IP) distributions. (Rep. mode: Reproductive mode; Fecund.: Fecundity; Gen. length: Generation length).

Species	Region	Life history	Growth form	Rep. mode	Colony size	Corallite diameter	Depth range	Fecund.	Gen. length	Growth rate	Skeletal density	Symbiont diversity
<i>Acanthastrea echinata</i>	IP	4 - Stress-tolerant	206	10	205	206	33	172	33			116, 120
<i>Acropora aspera</i>	IP	1 - Competitive	206	10		206	33	213	33	25	28	116, 120, 200
<i>Acropora cerealis</i>	IP	1 - Competitive	206	10		206	33	109	33			50, 62, 114, 116, 120, 200
<i>Acropora cervicornis</i>	Atl	1 - Competitive	103	10	103	132	33	176, 185, 203	33	47, 48, 104, 192	102, 192	14, 15, 16, 42, 113, 162, 189
<i>Acropora cytherea</i>	IP	1 - Competitive	206	10	206	206	33	109	33	39, 91		62, 114, 116, 120, 148, 178, 179, 181
<i>Acropora divaricata</i>	IP	1 - Competitive	206	10	206	206	33		33	39		116, 120, 125, 200
<i>Acropora elseyi</i>	IP	1 - Competitive	206	10		206	33	109	33	8, 91		120
<i>Acropora florida</i>	IP	1 - Competitive	206	10	205	206	33	172, 210	33	91		116, 120, 200
<i>Acropora formosa</i>	IP	1 - Competitive	206	10		206	33		33	37, 91, 184	28, 102, 133	54, 95, 99, 114, 116, 120, 137
<i>Acropora gemmifera</i>	IP	1 - Competitive	206	10		206	33	89, 109	33			38, 114, 116, 120, 200
<i>Acropora glauca</i>	IP	1 - Competitive	206	10		206	33		33		28	120, 221
<i>Acropora grandis</i>	IP	1 - Competitive	206	10	205, 206	206	33		33			116, 120
<i>Acropora granulosa</i>	IP	1 - Competitive	206	10	206	206	33	172, 210	33			120
<i>Acropora hemprichii</i>	IP	1 - Competitive		10	88		33	172	33	64		17
<i>Acropora horrida</i>	IP	1 - Competitive	206	10		206	33		33		28	62, 120
<i>Acropora humilis</i>	IP	1 - Competitive	206	10		206	33	109, 172	33	39, 170	53, 133, 170	38, 114, 116, 120, 125, 200, 211
<i>Acropora hyacinthus</i>	IP	1 - Competitive	206	10	11	206	33	89, 109, 172, 186, 210	33	39	133	38, 114, 116, 120, 148, 200, 208
<i>Acropora longicyathus</i>	IP	1 - Competitive	206	10		206	33	172, 210, 213	33		28	83, 114, 118, 125, 126, 200
<i>Acropora loripes</i>	IP	1 - Competitive	206	10		206	33	172, 210	33			116, 120, 200
<i>Acropora lutkeni</i>	IP	1 - Competitive	206	10	206	206	33		33			120
<i>Acropora microclados</i>	IP	1 - Competitive	206	10	205, 206	206	33		33			114
<i>Acropora microphthalma</i>	IP	1 - Competitive		10	205	206	33		33	104		116, 120
<i>Acropora millepora</i>	IP	1 - Competitive	206	10	11	206	33	89	33			19, 20, 50, 62, 98, 99, 107, 114, 116, 120, 141, 180, 182, 200, 202
<i>Acropora nobilis</i>	IP	1 - Competitive	206	10		206	33	109, 172, 210	33	91		98, 114, 116, 120
<i>Acropora palmata</i>	Atl	1 - Competitive	103	10	103	132	33	176	33	12, 47, 48, 104	4, 102	14, 16, 42, 55, 113, 162, 189
<i>Acropora polystoma</i>	IP	1 - Competitive	206	10		206	33	109	33			114
<i>Acropora pulchra</i>	IP	1 - Competitive	206	10		206	33		33	8, 91, 104, 225	28	38, 120, 125, 149, 200
<i>Acropora robusta</i>	IP	1 - Competitive	206	10		206	33		33	91, 170	170	120
<i>Acropora samoensis</i>	IP	1 - Competitive	206	10		206	33	109	33			120
<i>Acropora sarmentosa</i>	IP	1 - Competitive	206	10		206	33	172, 210	33			62, 116, 200
<i>Acropora secale</i>	IP	1 - Competitive	206	10	206	206	33		33			114, 116, 120
<i>Acropora solitaryensis</i>	IP	1 - Competitive	206	10	205	206	33		33	91	28	120
<i>Acropora subulata</i>	IP	1 - Competitive	206	10	206	206	33		33			114, 120

Species	Region	Life history	Growth form	Rep. mode	Colony size	Corallite diameter	Depth range	Fecund.	Gen. length	Growth rate	Skeletal density	Symbiont diversity
<i>Acropora tenuis</i>	IP	1 - Competitive	206	10		206	33	109	33			38, 50, 114, 116, 120, 141, 194, 200, 202
<i>Acropora valenciennesi</i>	IP	1 - Competitive	206	10	206	206	33		33	49		
<i>Acropora valida</i>	IP	1 - Competitive	206	10	205	206	33	109, 172, 210	33	91	28	38, 98, 114, 116, 120, 125, 194, 196, 197, 200, 208
<i>Acropora verweyi</i>	IP	1 - Competitive	206	10		206	33	109	33			116
<i>Acropora yongei</i>	IP	1 - Competitive	206	10	205	206	33		33	91		38, 116, 211
<i>Agaricia agaricites</i>	Atl	2 - Weedy	103	10	103, 138	2, 5	33	199	33	47, 104	102	16, 42, 113, 188
<i>Agaricia fragilis</i>	Atl	2 - Weedy	103	10	103	5, 132				47	102	113, 223
<i>Agaricia humilis</i>	Atl	2 - Weedy	103	10	103, 138		33	199	33	47		16, 113
<i>Agaricia lamarcki</i>	Atl	2 - Weedy	103		103	132	33		33	47	102	215
<i>Agaricia tenuifolia</i>	Atl	2 - Weedy	103	10	103		33		33	47		16, 113
<i>Alveopora fenestrata</i>	IP	4 - Stress-tolerant	206			206	33		33	170	170	
<i>Astreopora myriophthalma</i>	IP	4 - Stress-tolerant	206	10	136	206	33	172	33	29, 93		38, 69, 114, 116, 120, 168
<i>Caulastrea furcata</i>	IP	4 - Stress-tolerant		10	205	206	33		33			116
<i>Colpophyllia natans</i>	Atl	4 - Stress-tolerant	103	10	24, 103, 138	147	33		33	47, 104	102	15, 16, 41, 42, 113
<i>Cyphastrea chalcidicum</i>	IP	4 - Stress-tolerant	206	10	206	206	33		33			69, 174
<i>Cyphastrea microphthalma</i>	IP	4 - Stress-tolerant	206	10	68	206	33	18, 172	33			116, 145
<i>Cyphastrea ocellina</i>	IP	2 - Weedy	206	10			33	172	33	160		115, 162
<i>Cyphastrea serailia</i>	IP	4 - Stress-tolerant	206	10	68	206	33		33	91		62, 69, 98, 114, 116, 120, 221
<i>Dendrogyra cylindrus</i>	Atl	1 - Competitive	103	10	103	2	33	185	33	101		16, 113
<i>Dichocoenia stokesi</i>	Atl	4 - Stress-tolerant	103	10	103, 138, 153	2	33		33		102	16, 41, 113, 167
<i>Diploastrea heliopora</i>	IP	4 - Stress-tolerant	206	10	205	216	33		33	31		62, 116, 120
<i>Diploria clivosa</i>	Atl	4 - Stress-tolerant	103	10	103, 177	2, 147, 193	33	218	33	104		16, 113
<i>Diploria labyrinthiformis</i>	Atl	4 - Stress-tolerant	103	10	103, 138	2, 147	33	3, 218	33	47, 63, 124	63, 102	15, 16, 41, 113, 167
<i>Diploria strigosa</i>	Atl	4 - Stress-tolerant	103	10	24, 66, 103, 138, 177	2, 147	33	185, 218, 224	33	104		15, 16, 41, 113, 167
<i>Echinophyllia orpheensis</i>	IP	4 - Stress-tolerant	206	10	205, 206	206	33		33			38, 116
<i>Echinopora gemmacea</i>	IP	3 - Intermediate	206	10	136	206	33	130	33	170	170	116, 120
<i>Eusmilia fastigiata</i>	Atl	4 - Stress-tolerant	103	10	103, 138	2, 103	33		33		102	16, 113
<i>Favia fávus</i>	IP	4 - Stress-tolerant	206	10	68	206	33	90, 172	33			38, 62, 108, 114, 120
<i>Favia fragum</i>	Atl	4 - Stress-tolerant	103, 206	10	60, 103, 177	2, 193	33	176, 185, 218	33			16, 113, 162, 167
<i>Favia mathaii</i>	IP	4 - Stress-tolerant	206	10	68	206	33		33			116
<i>Favia pallida</i>	IP	4 - Stress-tolerant	206	10	68		33		33	91, 93, 96, 104	93, 96	116, 120, 145
<i>Favia stelligera</i>	IP	4 - Stress-tolerant	206	10	68, 206	206	33		33	29, 91, 104		69, 116, 120
<i>Favites abdita</i>	IP	4 - Stress-tolerant	206	10	68, 205	206	33		33	121		38, 95, 116, 120, 174, 180, 182, 221
<i>Favites chinensis</i>	IP	4 - Stress-tolerant	206	10	68	206	33		33			120
<i>Favites halicora</i>	IP	4 - Stress-tolerant	206	10	68	206	33		33			116, 120
<i>Favites pentagona</i>	IP	4 - Stress-tolerant	206	10	68, 205	206	33	172	33			120

Species	Region	Life history	Growth form	Rep. mode	Colony size	Corallite diameter	Depth range	Fecund.	Gen. length	Growth rate	Skeletal density	Symbiont diversity
<i>Fungia fungites</i>	IP	4 - Stress-tolerant	206	10	79		33		33	29, 104		99, 116, 120
<i>Fungia granulosa</i>	IP	4 - Stress-tolerant	206	10	206		33		33	36		116, 120
<i>Galaxea astreated</i>	IP	4 - Stress-tolerant	206	10	205, 206	206	33		33			116, 120
<i>Galaxea fascicularis</i>	IP	4 - Stress-tolerant	206	10	136, 205, 206		33	172	33	170	170	38, 62, 99, 100, 116, 120, 137, 168, 174, 208, 211
<i>Gardineroseris planulata</i>	IP	4 - Stress-tolerant	206	10		206	33	81, 172	33	85, 131	131	116, 120
<i>Goniastrea aspera</i>	IP	2 - Weedy	206	10	68, 205	206	33	9	33	91		26, 69, 95, 99, 120, 174
<i>Goniastrea australensis</i>	IP	4 - Stress-tolerant	206	10	68		33		33	91		69, 98, 116, 174
<i>Goniastrea edwardsi</i>	IP	4 - Stress-tolerant	206	10	205	206	33		33			69, 116, 120
<i>Goniastrea favulus</i>	IP	4 - Stress-tolerant	206	10	68		33	9	33	91		120, 180, 182, 221
<i>Goniastrea retiformis</i>	IP	4 - Stress-tolerant	206	10	68, 205, 206	206	33	89, 172	33	29, 91, 93, 96, 104	93, 96	38, 69, 116, 120
<i>Heliofungia actiniformis</i>	IP	4 - Stress-tolerant	206	10	111		33		33	111		69, 116, 125
<i>Hydnophora exesa</i>	IP	3 - Intermediate	206	10	136	206	33		33		170	38, 62, 116, 120
<i>Hydnophora microconos</i>	IP	4 - Stress-tolerant	206	10	68, 136	206	33		33	29, 93		120
<i>Isophyllia sinuosa</i>	Atl	2 - Weedy	103	10	103	2, 132, 193	33		33			16, 113, 167
<i>Leptastrea purpurea</i>	IP	2 - Weedy	206	10	206	206	33		33			115, 116, 120, 125
<i>Leptoria phrygia</i>	IP	4 - Stress-tolerant	206	10	68	152	33	130	33		133, 170	38, 116, 120
<i>Lobophyllia corymbosa</i>	IP	4 - Stress-tolerant	206	10	205		33	90, 172	33			69, 180, 182
<i>Lobophyllia pachysepta</i>	IP	4 - Stress-tolerant	206	10	68	206	33		33			69
<i>Madracis decactis</i>	Atl	2 - Weedy	103	10	103, 204	5, 146	33		33			42, 57, 58, 74, 76, 113, 167
<i>Madracis formosa</i>	Atl	2 - Weedy	103	10	103, 204	132	33		33			57, 58, 74, 75, 76, 113
<i>Madracis pharensis</i>	Atl	2 - Weedy	103	10	103, 204	146	33		33			57, 58, 74, 75, 76
<i>Manicina areolata</i>	Atl	2 - Weedy	103	10	103	2	33		33			16, 113
<i>Meandrina meandrites</i>	Atl	4 - Stress-tolerant	103	10	103, 138	2, 132	33		33	47		16, 41, 71, 113, 167
<i>Merulina ampliata</i>	IP	3 - Intermediate	206	10	70	92	33	70	33	59		38, 116, 120
<i>Montastraea annularis</i>	Atl	4 - Stress-tolerant	103	10	60, 103, 138	2, 103, 219	33	176, 185, 218	33	13, 34, 47, 51, 104, 139, 140, 165, 191	13, 34, 102	16, 41, 57, 71, 77, 113, 163, 164, 189, 190, 215
<i>Montastraea cavernosa</i>	Atl	4 - Stress-tolerant	103	10	24, 103, 138, 177	5, 103, 132	33	176	33	47, 104, 165	102	15, 16, 41, 42, 71, 113, 167, 215
<i>Montastraea faveolata</i>	Atl	3 - Intermediate	103	10	24, 138	219	33	23, 207, 217, 218	33	32, 51, 94, 165	94	16, 41, 56, 71, 113, 163, 164, 189, 190, 215
<i>Montastraea franksi</i>	Atl	3 - Intermediate	103	10	27	219	33	218	33	47, 165		41, 71, 77, 167, 189, 190
<i>Montastrea curta</i>	IP	4 - Stress-tolerant	206	10	68	206	33		33	91		38, 54, 116, 120, 221
<i>Montastrea valenciennesi</i>	IP	4 - Stress-tolerant	206	10	68	206	33		33			38, 116, 120
<i>Montipora capitata</i>	IP	1 - Competitive		10			33	45, 46	33	157		115, 151, 181, 183, 201

Species	Region	Life history	Growth form	Rep. mode	Colony size	Corallite diameter	Depth range	Fecund.	Gen. length	Growth rate	Skeletal density	Symbiont diversity
<i>Montipora danae</i>	IP	3 - Intermediate	206	10	136	206	33		33			116, 201
<i>Montipora digitata</i>	IP	1 - Competitive	206	10		206	33		33	170, 171	170	38, 98, 114, 120, 180, 182, 201, 211
<i>Montipora monasteriata</i>	IP	3 - Intermediate	206	10	136	206	33		33			114, 116, 120, 211
<i>Montipora venosa</i>	IP	4 - Stress-tolerant	206	10	136	206	33		33			116
<i>Montipora verrucosa</i>	IP	3 - Intermediate	206	10		206	33		33	44, 84	93	116, 120, 162, 201
<i>Mycetidium elephantotus</i>	IP	3 - Intermediate	206	10	206	206	33		33			38, 116, 120
<i>Mycetophyllia ferox</i>	Atl	2 - Weedy	103	10	103	193	33	185	33			71
<i>Oulophyllia crispa</i>	IP	4 - Stress-tolerant	206	10	205	206	33		33			116, 120
<i>Pachyseris rugosa</i>	IP	3 - Intermediate	206	10	206	206	33		33			62, 116, 120
<i>Pachyseris speciosa</i>	IP	3 - Intermediate	206	10	205	206	33		33			40, 62, 116, 120
<i>Pavona clavus</i>	IP	4 - Stress-tolerant	206	10	206	206	33		33	78, 85, 104, 106, 131, 170, 220	93, 102, 131, 170	119
<i>Pavona decussata</i>	IP	3 - Intermediate	206		136	206	33		33	170	170	38, 62, 98, 120, 125, 137, 145
<i>Pavona gigantea</i>	IP	4 - Stress-tolerant	206	10			33	81, 172	33	85, 104, 131, 220	131	105, 119
<i>Pavona varians</i>	IP	4 - Stress-tolerant	206	10	136	206	33	172	33	85, 131	131	38, 69, 82, 114, 115, 116, 120, 137, 181
<i>Physogyra lichtensteini</i>	IP	4 - Stress-tolerant	206	10	206	206	33		33			120
<i>Platygyra daedalea</i>	IP	4 - Stress-tolerant	206	10	11, 68, 136	142	33	18, 129	33		170	116, 120, 145
<i>Platygyra lamellina</i>	IP	4 - Stress-tolerant	206	10	136	142	33	172	33	29, 91, 93, 104		116, 120
<i>Platygyra sinensis</i>	IP	4 - Stress-tolerant	206	10	68, 136	142	33	9	33	91, 121		62, 120, 149
<i>Plerogyra sinuosa</i>	IP	4 - Stress-tolerant		10	206	206	33		33			62, 116, 120
<i>Plesiastrea versipora</i>	IP	4 - Stress-tolerant	206	10	205	206	33		33	30		38, 120, 125, 158, 159, 174
<i>Pocillopora damicornis</i>	IP	2 - Weedy	206	10	136	206	33	172	33	81, 85, 91, 93, 104, 106, 131, 134, 155, 160, 170, 212, 214	93, 131, 133, 170	38, 62, 69, 98, 108, 114, 115, 116, 117, 119, 120, 125, 128, 137, 149, 150, 151, 162, 166, 174, 180, 181, 182, 195, 197, 198, 208, 211, 221, 222
<i>Pocillopora elegans</i>	IP	1 - Competitive	206	10			33		33	85, 106, 131	131	120, 150
<i>Pocillopora eydouxi</i>	IP	1 - Competitive	206	10			33		33	29, 104, 106, 170	170	115, 116, 120, 128, 149, 150, 181
<i>Pocillopora meandrina</i>	IP	1 - Competitive	206	10	1, 205		33		33	106		115, 116, 117, 119, 120, 128, 150, 181
<i>Pocillopora verrucosa</i>	IP	1 - Competitive	206	10			33	112, 169, 172, 173	33	39, 135		54, 99, 105, 116, 117, 119, 120, 128, 137, 149, 150, 154

Species	Region	Life history	Growth form	Rep. mode	Colony size	Corallite diameter	Depth range	Fecund.	Gen. length	Growth rate	Skeletal density	Symbiont diversity
<i>Porites annae</i>	IP	4 - Stress-tolerant	206	10		206	33		33		133	114, 116, 120
<i>Porites astreoides</i>	Atl	2 - Weedy	103	10	24, 66, 103, 138, 177	2, 5	33	176, 185	33	34, 47, 48, 67, 91, 104, 124	67, 102	15, 16, 71, 113, 167, 188, 215
<i>Porites australiensis</i>	IP	4 - Stress-tolerant	206	10		206	33	90, 172	33	143	143	69
<i>Porites compressa</i>	IP	1 - Competitive	206	10			33	172	33	44, 61, 84, 104, 157		62, 115, 145, 151, 162
<i>Porites cylindrica</i>	IP	2 - Weedy	206	10	136, 206	206	33		33	91, 170	133, 170	38, 69, 72, 95, 98, 114, 116, 120, 151, 180, 182, 208, 209
<i>Porites furcata</i>	Atl	2 - Weedy	103	10		132	33		33	104	102	16, 113
<i>Porites lobata</i>	IP	4 - Stress-tolerant	206	10		206	33	80, 172	33	29, 39, 65, 81, 84, 85, 104, 110, 157, 175	175	6, 95, 115, 120, 125, 181
<i>Porites lutea</i>	IP	4 - Stress-tolerant	206	10	136	206	33	90, 172	33	29, 39, 49, 93, 96, 104, 161, 170, 187	93, 97, 170	6, 7, 38, 62, 95, 116, 120, 211
<i>Porites porites</i>	Atl	2 - Weedy	103	10	24, 103	2	33	176	33	104	102	71, 113, 167
<i>Porites rus</i>	IP	2 - Weedy	206	10	136	73, 206	33		33	170	170	69, 114, 115, 116, 120
<i>Psammocora superficialis</i>	IP	3 - Intermediate	206	10	206		33		33	85		119
<i>Seriatopora hystrix</i>	IP	2 - Weedy	206	10		52	33		33	91	133	21, 40, 108, 114, 116, 120, 125, 126, 166, 180, 182, 221
<i>Siderastrea radians</i>	Atl	2 - Weedy	103	10	103, 177	2	33	176	33	104	102	16, 71, 113, 167, 188, 215
<i>Siderastrea siderea</i>	Atl	4 - Stress-tolerant	103	10	24, 103, 138, 177	2	33	86, 176, 185	33	34, 35, 47, 87, 104	102	15, 41, 43, 71, 113, 189, 215
<i>Stephanocoenia intersepta</i>	Atl	4 - Stress-tolerant	103	10	103	2	33		33	144		15, 71, 113, 167
<i>Stylophora pistillata</i>	IP	2 - Weedy	206	10	136	206	33	89, 156, 172	33	22, 64, 123	53, 123, 133	17, 38, 72, 98, 108, 114, 116, 120, 122, 125, 127, 141, 166, 168, 174, 180, 182, 202, 211, 221
<i>Turbinaria frondens</i>	IP	3 - Intermediate	206	10	206	206	33		33	91		116, 120, 221
<i>Turbinaria mesenterina</i>	IP	1 - Competitive	206	10	205	206	33		33			38, 168, 174

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Figure B.1. Best-fit models of life-history clusters from hierarchical cluster analysis. We compared model fit (R^2) between two and ten cluster groups. Models with two, three and four clusters received the highest support.

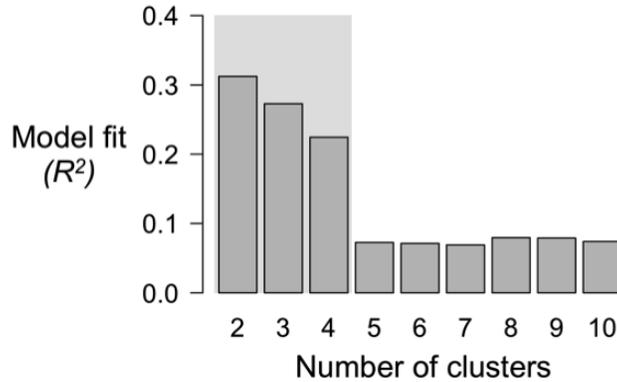
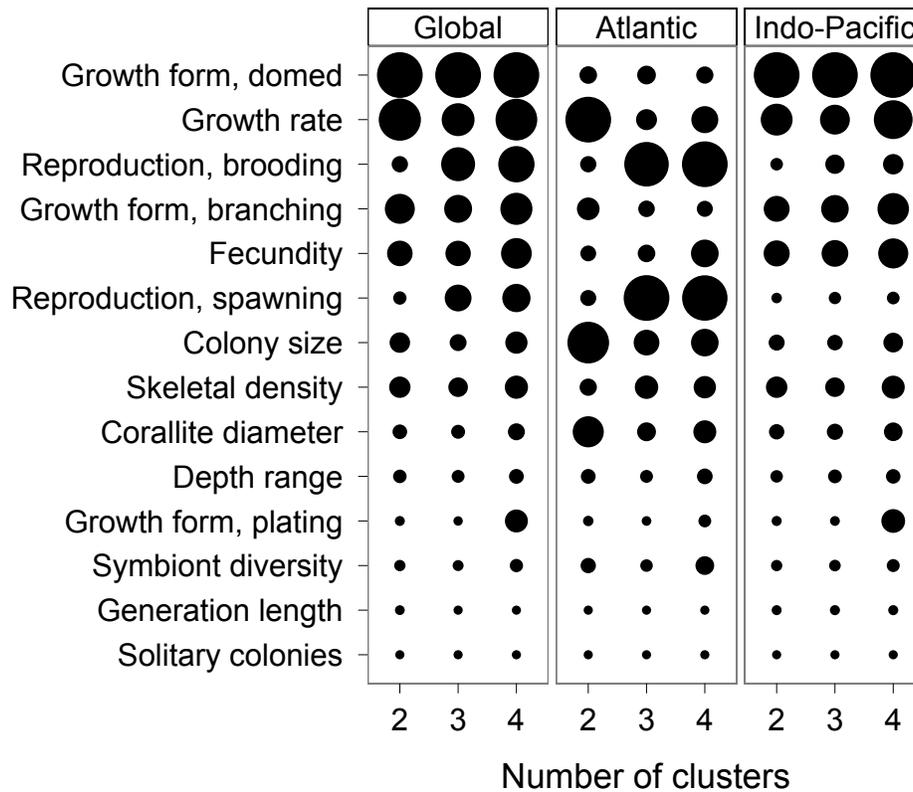


Figure B.2. Importance of individual life-history traits across two, three and four life-history clusters from random forests analyses. Circle size indicates trait importance, where larger circles represent more important traits than smaller circles



Appendix C.

Supporting material for Chapter 5

Table C.1. Summary of species traits across three life histories of Kenyan reef corals (N = 135 species). For categorical traits of colony growth form, solitary colony formation and reproductive mode, the percent of species with each trait characteristic is presented. For continuous traits, mean (standard deviation) are reported

Life history	No. spp	% Branch	% Domed	% Plating	% Solitary	% Brood	% Spawn	Colony size (cm)	Coralite diameter (cm)	Depth range (m)	Fecundity (eggs polyp ⁻¹)	Gen. length (years)	Growth rate (mm year ⁻¹)	Skeletal density (g cm ⁻³)	Symbiont diversity (m-value)
Competitive	41	95.1	0	48.8	0	0	100	274.96 (388.68)	2.60 (1.28)	12.38 (5.35)	13.61 (16.68)	9.88 (0.78)	43.21 (36.99)	1.55 (0.35)	1.93 (1.26)
Stress-tolerant	82	6.1	100	22	9.8	1.2	100	179.37 (305.95)	6.48 (7.67)	16.07 (5.14)	568.06 (889.38)	10.06 (1.36)	11.37 (9.34)	1.64 (0.22)	1.34 (0.86)
Weedy	12	58.3	50	8.3	0	100	36.4	176.36 (201.04)	2.61 (2.88)	11.96 (4.92)	8.09 (8.21)	8.50 (2.28)	19.22 (10.08)	1.67 (0.29)	2.40 (2.17)

Table C.2. Life history classifications for 32 genera of scleractinian reef corals observed on Kenyan reefs during annual surveys on unfished and fished reefs between 1991 and 2011. Average absolute percent cover is reported as mean (standard deviation). Fishing sensitivity is on a log-scale from -4.6 (more abundant on fished reefs) to 0 (no change) to 4.6 (extirpated on fished reefs compared to unfished reefs). Bleaching sensitivity is based on observations of the bleaching frequency and severity of taxa during thermal stress events. Genera with 'mixed' life histories where species were assigned to more than one life history are identified.

Genus	Life history group	Unfished % cover 1991-1997	Fished % cover 1991-1997	Fishing sensitivity	Bleaching sensitivity	Species classifications for mixed life-histories
<i>Acanthastrea</i>	Stress-tolerant	0.12 (0.07)	0 (0)	4.62	11.52	
<i>Acropora</i>	Competitive	7.1 (6.81)	0.52 (0.25)	2.50	20.98	
<i>Alveopora</i>	Weedy	0.1 (0)	0.16 (0.13)	-0.46	30.83	
<i>Astreopora</i>	Stress-tolerant	0.49 (0.66)	0.85 (0.69)	-0.55	14.31	
<i>Coscinarea</i>	Stress-tolerant	0.09 (0)	0.02 (0.01)	1.74	16.04	
<i>Cyphastrea</i>	Stress-tolerant	0.3 (0.12)	0.38 (0.37)	-0.23	12.03	
<i>Echinopora</i>	Stress-tolerant	2.14 (2.65)	0.14 (0)	2.60	12.06	
<i>Echinophyllia</i>	Stress-tolerant	0 (0)	0 (0)	NA	6.47	
<i>Favia</i>	Stress-tolerant	0.73 (0.38)	0.49 (0.28)	0.39	17.89	
<i>Favites</i>	Stress-tolerant	0.77 (0.46)	0.28 (0.14)	0.98	15.73	
<i>Fungia</i>	Stress-tolerant	0.1 (0.04)	0.12 (0.08)	-0.16	13.01	
<i>Galaxea</i>	Stress-tolerant	2.71 (2.03)	0.41 (0.26)	1.84	11.50	
<i>Gardineroseris</i>	Stress-tolerant	0 (0)	0 (0)	NA	9.64	
<i>Goniastrea</i>	Stress-tolerant/Weedy	0.5 (0.36)	1.11 (0)	-0.78	17.34	4 Stress-tolerant (<i>G. australensis</i> , <i>G. edwardsi</i> , <i>G. pectinata</i> , <i>G. retiformis</i>) 1 Weedy (<i>G. aspera</i>)
<i>Goniopora</i>	Stress-tolerant	0.5 (0.3)	0.22 (0.17)	0.80	16.15	
<i>Herpolitha</i>	Stress-tolerant	0 (0)	0 (0)	NA	4.42	
<i>Hydnophora</i>	Competitive/Stress-tolerant	0.76 (0.56)	0.42 (0.18)	0.58	10.37	1 Competitive (<i>H. rigida</i>) 2 Stress-tolerant (<i>H. exesa</i> , <i>H. microconos</i>)
<i>Leptastrea</i>	Stress-tolerant/Weedy	1.21 (1.11)	0.18 (0.22)	1.85	9.12	2 Stress-tolerant (<i>L. bottae</i> , <i>L. transversa</i>) 1 Weedy (<i>L. purpurea</i>)
<i>Leptoria</i>	Stress-tolerant	0.52 (0.16)	0.08 (0)	1.82	17.95	
<i>Lobophyllia</i>	Stress-tolerant	0 (0)	0.34 (0)	-3.52	14.89	
<i>Montastrea</i>	Stress-tolerant	0.09 (0)	0 (0)	4.62	6.79	
<i>Montipora</i>	Competitive/Stress-tolerant	5.24 (6.22)	0.4 (0.36)	2.46	27.76	3 Competitive (<i>M. aequituberculata</i> , <i>M. digitata</i> , <i>M. mollis</i>) 9 Stress-tolerant (<i>M. danae</i> , <i>M. efflorescens</i> , <i>M. foliosa</i> , <i>M. grisea</i> , <i>M. monasteriata</i> , <i>M. peltiformis</i> , <i>M. tuberculosa</i> , <i>M. venosa</i> , <i>M. verrucosa</i>)
<i>Pavona</i>	Competitive/Stress-tolerant	0.33 (0.1)	1.56 (0.94)	-1.56	8.21	1 Competitive (<i>P. clavus</i>) 2 Stress-tolerant (<i>P. decussata</i> , <i>P. varians</i>)
<i>Platygyra</i>	Stress-tolerant	0.72 (0.26)	0.41 (0.35)	0.57	13.48	
<i>Plesiastrea</i>	Stress-tolerant	0.3 (0.16)	0 (0)	4.62	17.26	
<i>Pocillopora</i>	Competitive/Weedy	1.08 (0.37)	0.4 (0.22)	0.98	23.43	2 Competitive (<i>P. eydouxi</i> , <i>P. verrucosa</i>) 1 Weedy (<i>P. damicornis</i>)
<i>Porites</i> branching	Weedy	6.16 (6.4)	7.87 (3.25)	-0.24	21.85	
<i>Porites</i> massive	Stress-tolerant	6.58 (4.05)	4.17 (2.67)	0.45	11.50	
<i>Psammocora</i>	Stress-tolerant/Weedy	0 (0)	0.22 (0.07)	-3.06	5.58	1 Stress-tolerant (<i>P. superficialis</i>) 1 Weedy (<i>P. contigua</i>)
<i>Seriatopora</i>	Weedy	0 (0)	0 (0)	NA	16.71	
<i>Stylophora</i>	Weedy	0.35 (0.25)	4.92 (1.99)	-2.63	30.34	
<i>Synaraea</i>	Weedy	3.22 (1.2)	0 (0)	4.62	7.78	
<i>Turbinaria</i>	Competitive/Stress-tolerant	0.65 (0.17)	0.66 (0)	-0.02	12.97	1 Competitive (<i>T. mesenterina</i>) 2 Stress-tolerant (<i>T. frondens</i> , <i>T. reniformis</i>)

Figure C.1. Kenyan scleractinian corals classified to life-history strategies from species traits. (a) Hierarchical cluster analysis of 135 Kenyan scleractinian coral species. (b) Clustering scenarios with two and three cluster received the most model support from non-parametric MANOVAs. (c) Importance of individual traits as determined by random forests analysis; larger circles indicate more influential traits than smaller circles.

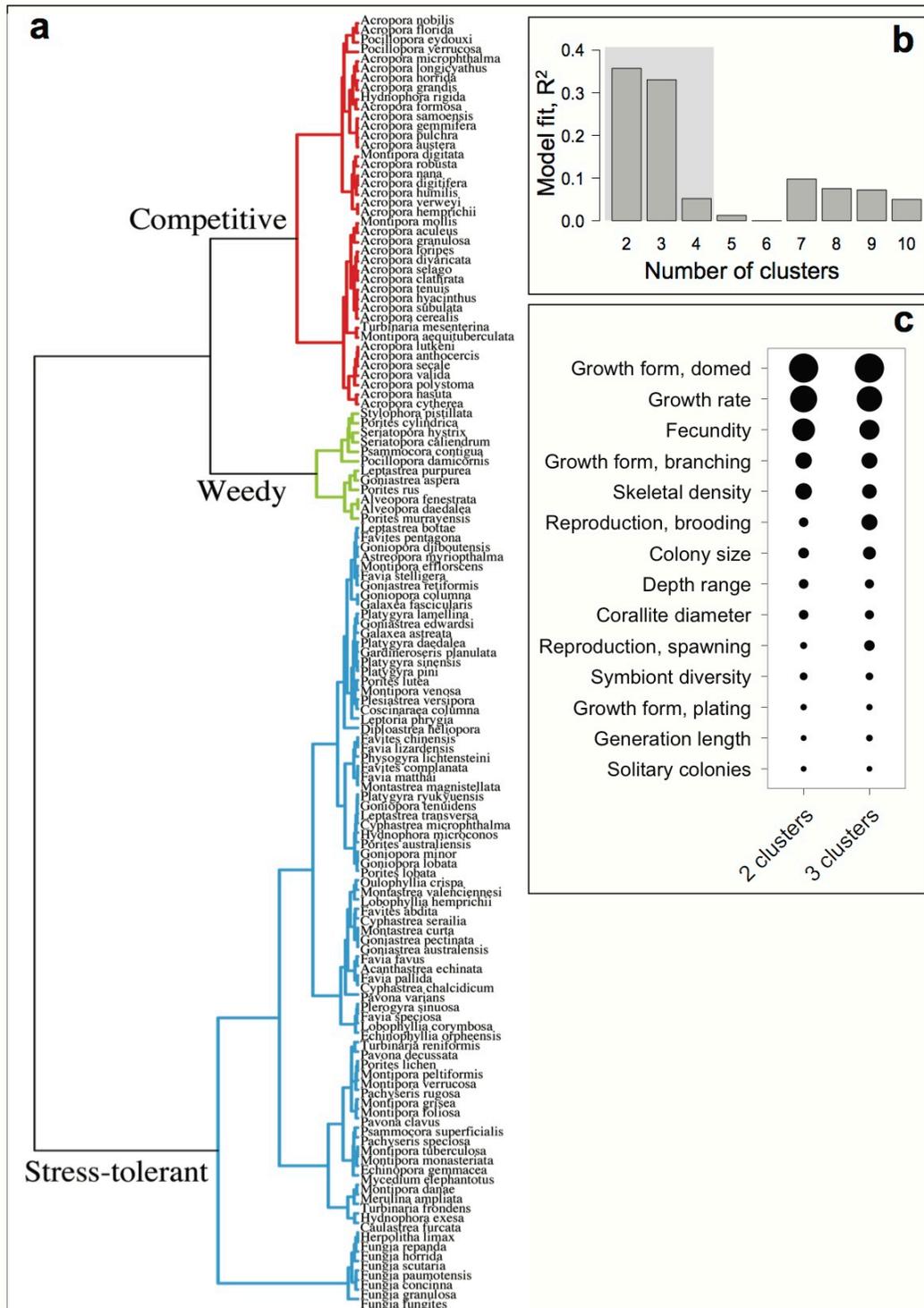


Figure C.2. Principal Coordinates ordination based on a Gower dissimilarity matrix of 11 species traits of 135 Kenya species with three life-history strategies (red: competitive, green: weedy, blue: stress-tolerant). Traits are numbered from most to least important from the random forests analysis (Fig. S1c): (1) domed growth form, (2) growth rate, (3) fecundity, (4) branching growth form, (5) skeletal density, (6) brooding reproduction, (7) colony size, (8) depth range, (9) corallite diameter, (10) broadcast spawning reproduction, (11) symbiont diversity, (12) plating growth form, (13) generation length, (14) solitary colony formation.

